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

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ABSTRACT

Natural morality (*M*) is a notoriously difficult population parameter to estimate, yet it is also one of the most important measures of life history that sets, as Beverton and Holt called it, "the course of events". Stock assessments that include this parameter often show great sensitivity to its value, reflecting the need to characterize the uncertainty inherent in its estimation. Direct measurement of natural mortality is often limited to resource intensive tag-recapture studies. Indirect measures are more often used, and are built on life history theory, relating natural mortality to traits such as age, size, maturity and reproductive condition (or just assuming 0.2). The Natural Mortality Tool attempts to accumulate several empirical estimators of *M* into one application. Users simply input life history values to obtain estimates of natural mortality. These estimates can be taken individually or can be combined into a weighted density function that can be used to develop an *M* prior that integrates uncertainty across several estimates. Comparing estimators can also reveal inconsistencies in life history values that may lead to further refining of basic biological understanding. Two examples are used to demonstrate tool functionality and highlight general recommendations on implementation. Making these estimators and the development of uncertainty in estimating natural mortality more widely available hopefully supports transparent and defensible decision-making on the treatment of this important population parameter.

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., 2019), disease (Cigler et al., 2020; Stenkat et al., 2013), predation (Hill et al., 2019), 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 when in a time step 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 1998). 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). While there are advanced treatments to remove other predation sources from *M* (often called M2 (Pope et al., 2021)), we define *M* here to include all sources of mortality excluding fishing mortality.
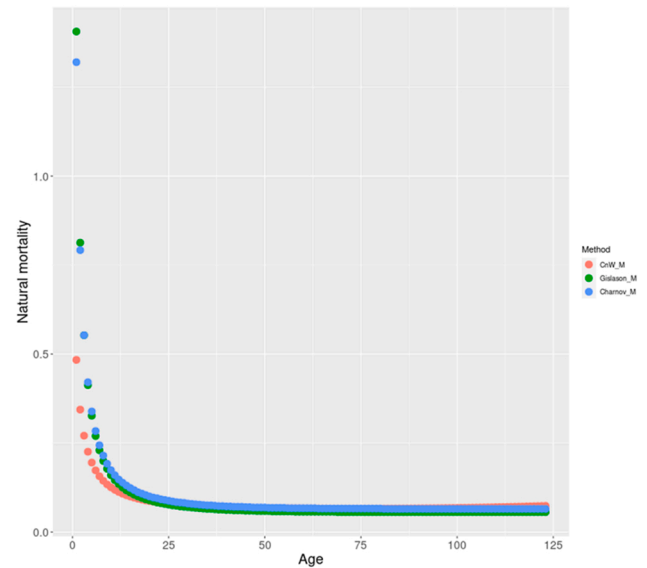
A) Yelloweye rockfish
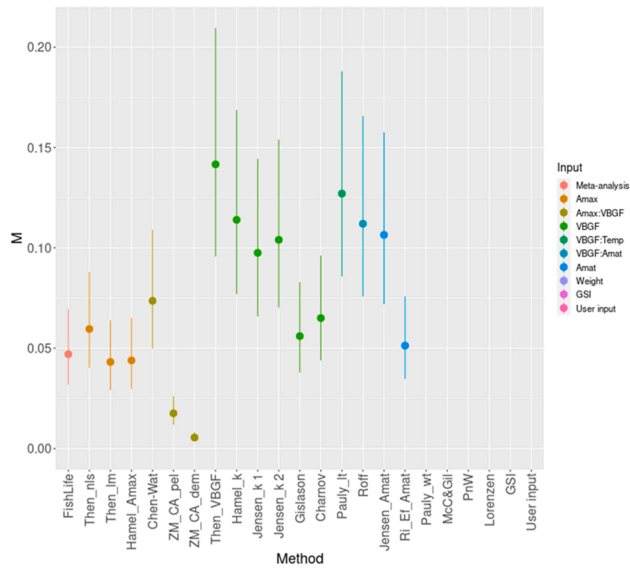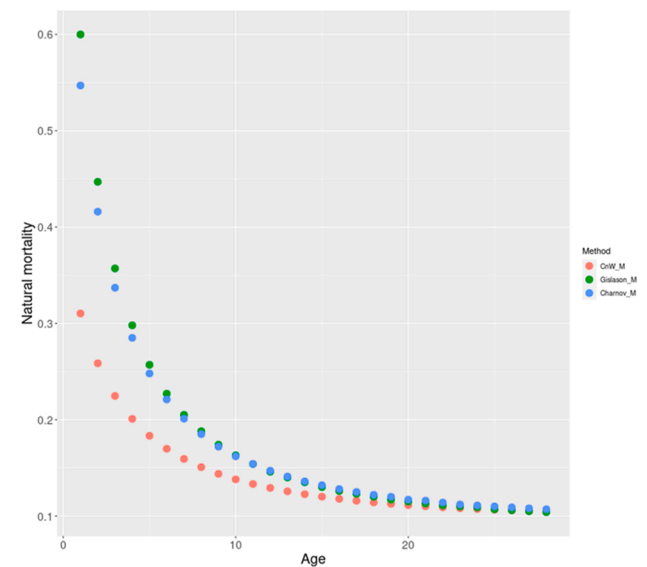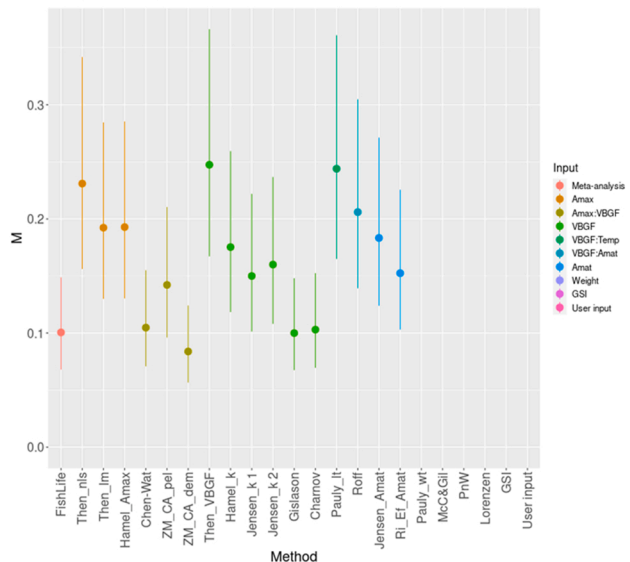

B) Gopher rockfish

Fig. 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.

In many of the analytical approaches used to estimate population status and other important fisheries management metrics under conditions of varying data and resource availability (Cope et al. in prep), *M* is an essential input parameter. In those models, *M* is widely recognized as both a highly influential parameter in population modelling and in defining population productivity and subsequent fishery reference points, but is difficult to directly measure in marine organisms (Maunder et al., this issue; Punt et al., 2021). This is particularly true for populations with individuals that move around, do not stay in the sampling area and/or are in habitats that make routine monitoring a challenge. Direct estimation of *M* in age-structured models is possible, but requires adequate biological composition data and an understanding of the functional form of fishery selectivity (Lee et al., 2011). Mark-recapture studies (Chapman, 1961; Seber, 1982) or age-based sampling of cohorts through time (Chapman and Robson, 1960; Schnute and Haigh, 2007; Thorson and Prager, 2011) are other direct ways to measure mortality. In some instances, *M* can be directly estimated separate from Z (Hoenig et al., 1998; Jiang, 2005; Jiang et al., 2007), though it is

common that *Z* rather than *M* is estimated, thus *F* would be required to derive *M* from *Z* (i.e., *M*= *Z-F*).

In one of the most famous and cheeky derivations of *M*, John Pope in 1975 showed the evolution of a question mark into an often assumed value of *M* = 0.2 (Fig. 1 of Anderson, 2015 and Pope et al., 2021). Sadly, 0.2 was indeed a commonly used default value when no other *M* value was available. Since then, a host of empirical approaches have been developed to allow the indirect estimation of *M*. These approaches have been well described and evaluated elsewhere (Kenchington, 2014; Maunder et al., in this issue; Then et al., 2015; Vetter, 1988). While there are some approaches that are favored over others (Hamel and Cope, in this issue), having ready access to the many empirical estimators of *M* allows for more examination and comparison of these estimators under a variety of situations. This paper describes the Natural Mortality Tool, a free software application with a graphical user interface (GUI) designed to be a practical, user-friendly way to explore a wide variety of empirical *M* estimators. Available methods, tool features, and recommendations for use are provided herein to demonstrate the range of tool

Table 1

List of empirical M estimators and the inputs needed to apply the method. A link 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_∞, k
Hamel_k	k
Jensen_k 1	k
Jensen_k 2	k
Gislason	L_∞, k, length
Charnov	L_∞, k, length
Pauly_lt	L_∞, k, Temp
Roff	k, age at maturity
Jensen_Amat	age at maturity
Ri_Ef_Amat	age at maturity
Pauly_wt	W_∞, k_w, Temp
McC&Gil	dry weight, Temp
PnW	dry weight
Lorenzen	wet weight
GSI	GSI

functionality and how it can support both point estimation and uncertainty analysis in this critical model parameter.

2. The natural mortality tool (NMT)

The NMT[1] is written in the Shiny (Chang et al., 2021) package for R (R Core Team, 2021), which allows for the creation of interactive graphical user interface (GUI) web-based applications. The GUI is a key feature of this tool, as it allows for user interaction and real-time response based on user input. It also allows for saving output objects and images. It does not require the user to know how to formally use R. The code can also be downloaded from the GitHub repository[2] for running the tool offline, where user installation instructions are found. The NMT currently has 23 different estimators of M based on 14 possible inputs (all of which can be expanded as new methods develop), with an additional input available for unlimited user supplied M values (e.g., 0.2). This provides a plaform to compare M values generated from each estimator and/or user supplied value. Not all inputs need to be entered, only those that are available to the user, and thus outputs will only be provided for those methods fully specified by those inputs. The NMT has links that open windows to show associated references and a table (Table 1) of the inputs needed for each method. Of the 23 estimators (22 provide a constant M across ages and 3 (including two that also provide a constant M value) provide age-specific M estimates), one is based on the R library FishLife (Thorson et al., 2017; Thorson, 2019), six are based on the fishmethods R library (using the function $M.empirical$(); Nelson, 2021), and the remaining are coded within the NMT. The latest version of each of these estimators are used, with updates and additions to the M estimators an ongoing point of tool maintenance. The authors welcome further recommendations of additional M estimators to include, as well as comments on the usefulness of those estimators currently available, via issues reporting on the GitHub repository.

2.1. Empirical Estimators in the NMT

Empirical estimation of M is generally based on relationships between other, easier to measure life history parameters. Beverton and

Holt (1959) were early investigators on building relationships between M and growth parameters, maximum age, and reproductive biology (Beverton, 1992; Prince et al., 2015). Subsequent work has built on those relationships and developed multi-parameter relationships to estimate M (Charnov et al., 2013; Chen and Watanabe, 1989). By entering just the scientific name of the species, one can access the estimate of M from the FishLife library that applies a taxonomically-structured multivariate model to information found in the FishBase database to build life history parameter relationships (Thorson et al., 2017; Anon, 2021).

Maximum age is one of the most commonly used values to build relationships to M, as it makes intuitive sense that higher life expectancies must mean a lower population mortality rate (Hamel and Cope, this issue; Maunder et al., this issue; Then et al., 2015). While using maximum age tends to be preferred, establishing the maximum age (not necessarily the maximum age ever recorded) of a population is not always straightforward or available (Hamel and Cope, in this issue; Maunder et al., in this issue). Maximum age can be affected by ageing error, sample size, and/or sampling age-truncated populations (Hamel and Cope, in this issue; Hoenig, 2017). Thus, while possibly easier to measure than M, maximum age– and the meta-analytical estimators based on them– still suffers from uncertainty that needs careful consideration. There are currently six methods in the NMT that can use longevity in the estimation of M (the Chen and Watanabe, 1989 method can take any age, as it provides age-specific M estimates, but longevity is recommended when using one age value), with three combining maximum age with other parameters in the estimator (Table 1).

Parameters of the Beverton and Holt (1959) version of the von Bertalanffy growth function (L_∞, k and t_0) are also commonly used in empirical M estimators. The process of accounting for metabolism and its allocation to maintenance, growth, reproduction, and mortality links these processes and are foundational to life history theory (Boukal et al., 2014; Enberg et al., 2012; Essington, 2001). The individual growth coefficient k is most directly related to M (even forming what is considered a dimensionless ratio within or across taxa, M/k; Beverton and Holt, 1959; Charnov et al., 1993; Jennings and Dulvy, 2008; Prince et al., 2015), though several methods (Table 1) also require either the theoretical age at size 0 (t_0) and/or average maximum size (L_∞) in the population. While less directly related to M than maximum age, the von Bertalanffy growth parameters tend to be easier to estimate than maximum age (though issues of ageing error, fishery selectivity and sampling, along with the correlation among the three parameters, can also make this difficult, especially for k and t_0), thus providing, in some cases, a more accessible method when maximum age is poorly understood. There are currently 11 methods in the NMT that use von Bertalanffy growth parameters, three of which use only k, three of which use both k and L_∞ on their own or with length information, and five that use other parameters, including three of which combine with age (Table 1). One of the growth-based methods also includes water temperature as it may affect metabolism and behavior thus indirectly influencing M (Pauly, 1980).

The original von Bertalanffy growth function was derived using weight (W) (von Bertalanffy, 1938; Essington, 2001), but is converted to length using the common power weight-length relationship of $W=aL^b$. Thus, weight (either wet or dry) can also be related to M carrying over the logic used in those relationships derived from length (Pauly, 1980). The NMT contains four weight-based M estimators, two of which use weight only, two of which include temperature, and one that uses the weight-based von Bertalanffy equation (W_∞, k_w; Table 1).

Reproduction is also part of the energy allocation equation, and the onset of reproductive years usually dictates when growth begins to slow (Enberg et al., 2012). This interplay between growth and reproduction also makes the length or age at maturity another candidate as an estimator of M (Jensen, 1996). There are three estimators that use age at maturity as an input, with only one of them adding an additional parameter (k) in the equation (Table 1).

A) Yelloweye rockfish
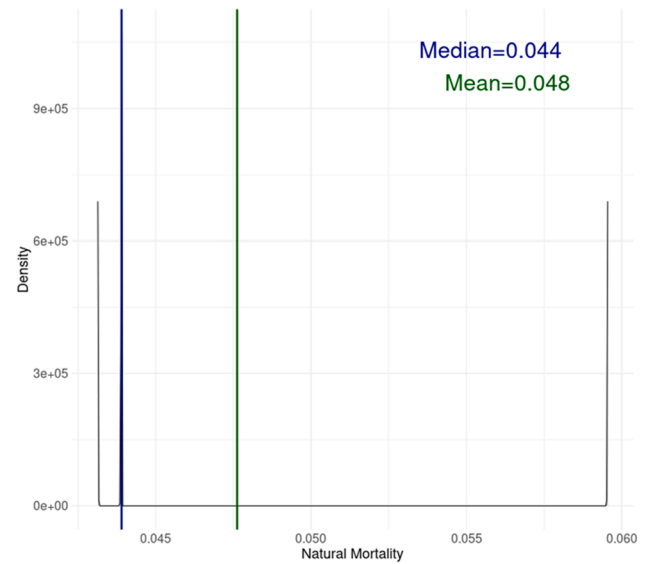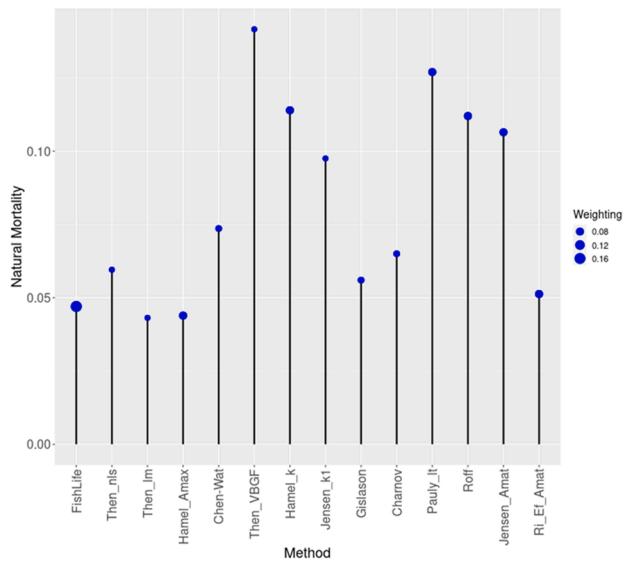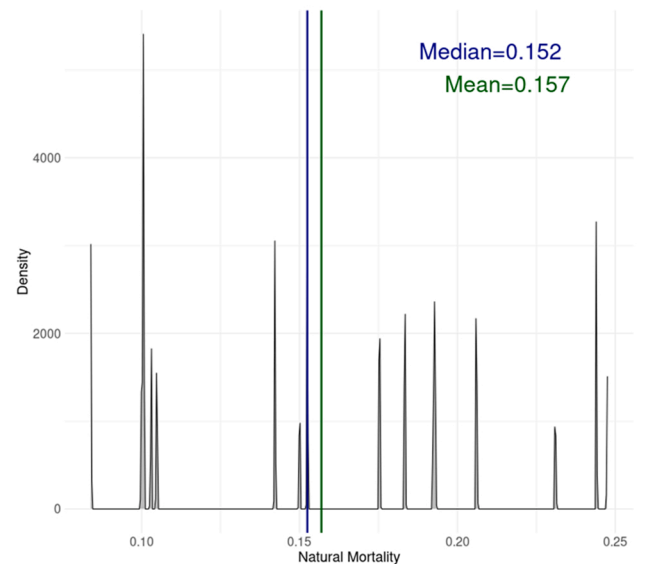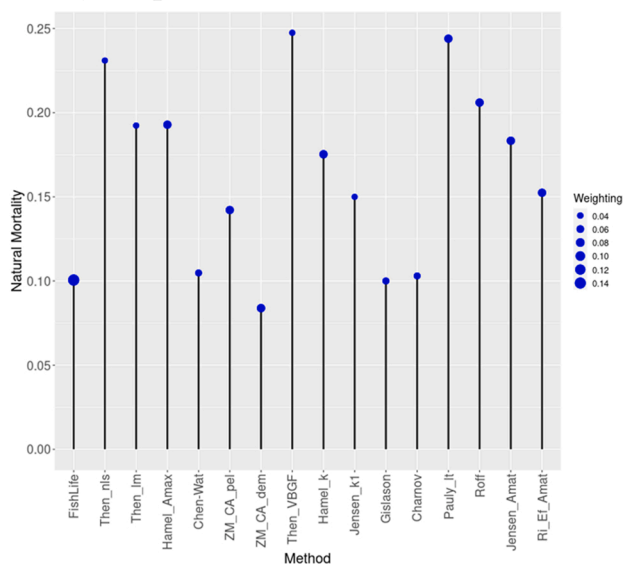

B) Gopher rockfish

Fig. 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.

The remaining method uses the allometric concept of growth and reproduction as related to mortality and interprets the *M* relationship through the ratio of reproduction (measured by the gonad weight) and fish weight to express reproductive effort (Gunderson, 1997; Hamel, 2015). The gonadosomatic index (GSI) is a metric not often sampled, thus represents a unique, often unavailable, but relatively easy to measure value as an option to estimate *M*.

The tool responds to user inputs as they are included, producing both a figure of outputs across the different methods and a simple table to see the actual quantities illustrated in the plot. Both the table (as a .csv file) and the figure are downloadable with a click of the button, as is an R object that contains all user inputs and the resulting *M* values. This object is especially notable as it preserves a record of the exact inputs used to produce the *M* values, in addition to an object that can be imported into R.

2.2. Accounting for M uncertainty using the NMT

Sources of uncertainty in *M* can be expressed in at least two main ways: among estimators and within estimators. The default is to assume each estimator produces a point estimate, though there is an option to include either lognormally or normally distributed error with a user-specified amount of error. Lognormally distributed error is more appropriate for most estimators, as *M* itself is a rate parameter that occurs in the exponent when relating to population size. Estimated uncertainty is only empirically available for some methods and requires the initial dataset for calculation (Hamel, 2015; Hamel and Cope, in this issue). Instead, an option for user input uncertainty is included and assumed the same for each estimate for tool simplicity. Future modifications to the tool could consider method-specific uncertainty, but may also overly complicate the tool. One could also go back and attempt to calculate uncertainty from the original data set used to create a given empirical relationship and input that value into the NMT. Further
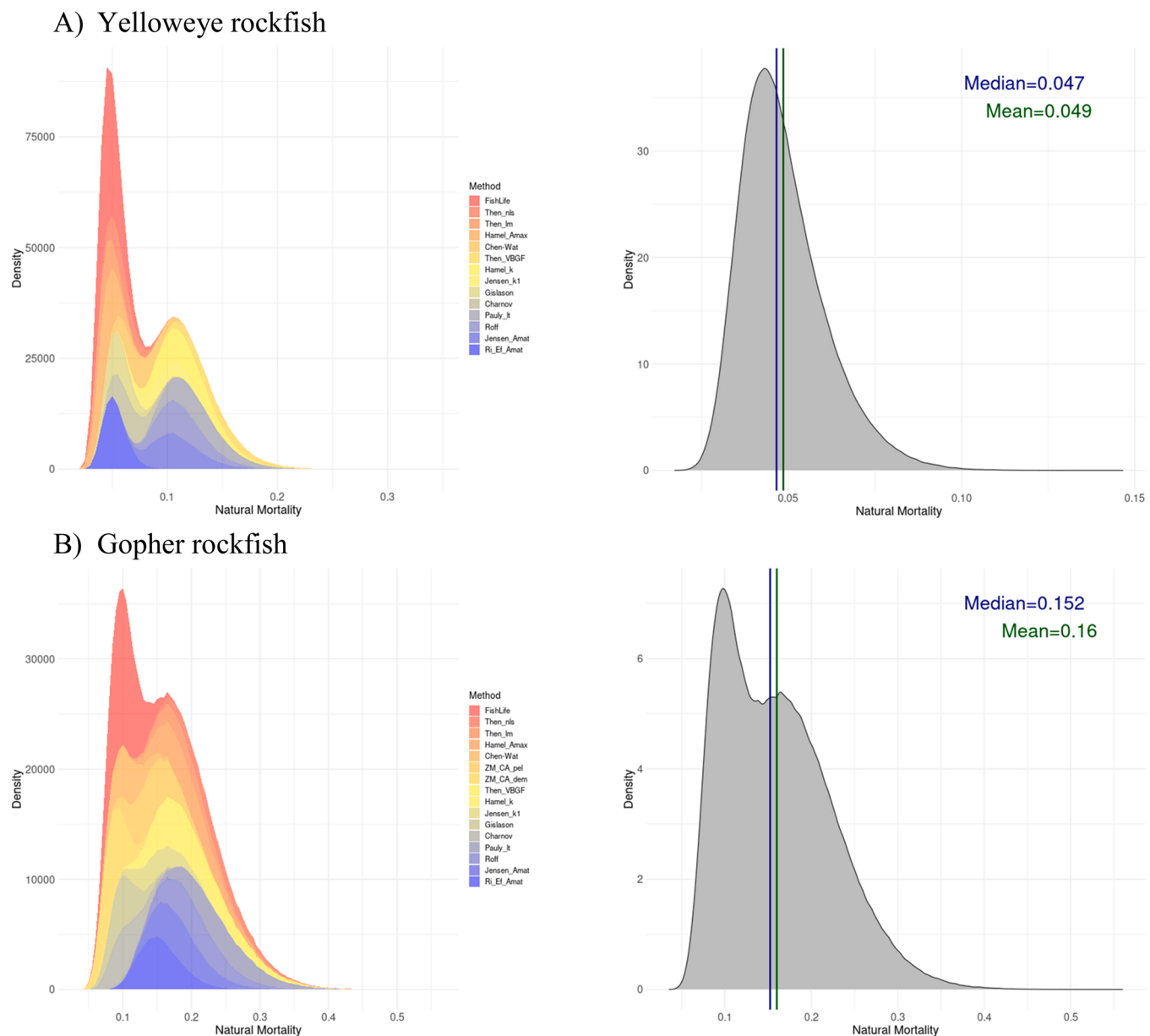
A) Yelloweye rockfish

B) Gopher rockfish

Fig. 3. Weighted empirical *M* estimators with additional variance (CV = 0.2) 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.

uncertainty can also be explored through changing input values (e.g., what if longevity is 60 years instead of 50 years?).

Once the estimators are activated via parameter inputs and additional variance included, the user can navigate to the second tab ("Composite M: User weighted") to create a custom distribution of *M* that combines all *M* estimators and associated uncertainty into a composite distribution (Figs. 2 and 3). A user-specified method-weighted (i. e., percent contribution) approach is used to construct the composite distribution of *M*. This composite can then be used in a Monte Carlo approach for resampling or used to specify a prior on *M*. Allowing for user-based weighting of each method addresses multiple issues:

1. Input influence: Multiple methods may use the same input (e.g., longevity), thus causing unequal input influence when comparing *M* estimates across methods if all methods are equally weighted. For instance, if there are three methods that use only longevity and one that uses GSI, weighting each method equally upweights the

influence of the longevity input purely based on the number of estimators used. One solution is to downweight each longevity-based estimator by two-thirds so the overall weighting of each adds up to one. The user gets to determine the combination of weightings based on their preferences. The default weightings in the NMT are a mix of applying the above rational to avoid outsized input influence and starting some estimators at a weight of 0 as they often produce outliers (see issue 2).

2. Method removal: Included in the user decision of how to weight each method is whether to include each method at all. There are many reasons why some methods may produce highly questionable values (e.g., extreme outliers) when applied in certain situations. The user may decide to ignore that method by setting the weighting to 0. Recommendations of using some estimators over others (e.g., longevity-based estimators are preferred over growth-based estimators when longevity is well estimated; Then et al., 2015) may also be a reason to omit certain estimators.

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_{∞} (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°)	7	10
Wet wt. (g)	5000	500

3. Custom priors: The custom combination of weightings across all M estimators and any additional uncertainty the user may have included creates the composite M distribution. The construction of the composite is first done by setting X number of total composite samples (user defined, but the default is one million). The individual method weightings are then turned into standardized weights (individual method weight/sum of all method weightings) to give the Y_i number of samples from the total number of X samples for each estimator, where i is the estimator (e.g., 200000 out of 1000000 samples for estimator 1) and $X = \Sigma Y_i$. If there is no additional uncertainty added to the methods, then the point estimate is replicated Y_i times for each method i. If there is a specified error distribution (either lognormal or normal), then a Y_i random sample is taken for each distribution. A final option to tune the bandwidth, which when > 1 can smooth out the density distribution and allow the user to make more diffuse priors if they so choose, is offered for further M distribution customization.

Once the user specifies the composite weightings, number of samples, and choice of density bandwidth, a plot of both the component points (left column plots in Fig. 2) or distributions (left column plots in Fig. 3) and the overall density distribution (right column plots in Figs. 2 and 3) are provided for download and examination. R objects that contain the details of the sampling of each method and the final composite M values by methods are also provided for download.

A second approach to characterizing uncertainty (third tab: "Composite M: Inverse variance") that develops a lognormal Bayesian prior distribution from multiple methods is also available (Hamel, 2015). This approach essentially multiplies the individual distributions together, and thus weights the alternative methods based upon the inverse of the variance (or 1 divided by the square of the input standard deviation). Additional user-specified weights, as presented previously, can also be included. Where individual distributions are bimodal, this approach will provide a single central mode, in contrast to the treatment of biomodal results for the first approach. Thus the two approaches to characterizing uncertainty represent distinct views of the information each distribution provides relative to the other distributions included. The tool offers users their choice of either or both.

Overall, the point estimates (from the first tab) and/or the composite distributions and priors (from the second and third tabs) offer different ways of processing the estimates from each method. Each can then be used to parameterize the variety of stock assessment methods that require natural mortality as an input, specify operating models used in simulation testing, or any other application that needs a value or distribution of M values.

3. Benefits of and best practices when using the NMT

The intent of the NMT goes beyond just easy access to the numerous M estimators. When considering the vagaries of inputs available for any given method, and the life history theory that underpins these methods, it is advantageous to be able to look across multiple M estimators and consider how they can be applied collectively to reflect uncertainty in M

for a given population. To demonstrate and highlight some of the recommended uses of the tool, applications are presented using two rockfish (genus *Sebastes*) species, yelloweye (*Sebastes ruberrimus*) and gopher (*S. carnatus*) rockfishes (Table 2).

Comparing life history inputs across methods often results in a variety of possible M values, including the potential for large discrepancies in estimates (Fig. 1). But which should be used? Considering the yelloweye rockfish example (Fig. 1A), the method-specific estimates group roughly by those using longevity and those using either growth or maturity, with the latter group estimating higher M values. These groups result in a bimodal composite distribution of M under default method weightings (Fig. 3A).

Given the previously stated difficulties in defining a representative longevity estimate, uncertainties in growth parameters, and potential variability in parameter relationships across taxa, seeing such discrepancies offers an avenue to explore these differences. One could ask the question "how much do I need to change the longevity input to achieve M values near the estimators using growth and maturity?" In this example, longevity needs to be lowered to a value of ~50 years to match the growth and maturity estimates of M. This is well outside the uncertainty envelope of longevity for yelloweye rockfish. One could do a similar exploration with the von Bertalanffy values, which would take a 50% reduction in the k value to achieve M values as low as the longevity estimators. The differences in the estimators may be due to departures in the generalized life history relationships for a given taxa or species. For example, some *Sebastes* species tend to grow to near maximum size (L_{∞}) quickly relative to their lifespans, and therefore, as noted in Beverton (1992), the standard cross-taxa relationship between k and M may be expected to be biased high for species, like some *Sebastes*, that grow quickly to asymptotic size (thus lower relative M/k). In contrast to the yelloweye rockfish results, there is less difference among the estimates of M for gopher rockfish among estimator groups, but still notable variability among individual methods that results in a bimodal distribution (Fig. 3B).

The treatment of the resultant bimodal distributions should depend on the source of the bimodality. For the yelloweye example, there are two modes comprised of different estimators: one from longevity estimators and the other from growth and maturity (left plot of Fig. 3A). Given neither could be resolved through initial confirmation of poor estimations of any of the inputs, one perspective is the two modes represent distinct distributions of M that represent alternative hypotheses. The expression of alternative hypotheses in life history parameters is a standard approach to characterize uncertainty in population modelling and defining "states of nature" for decision analysis (Punt and Hilborn, 1997). In this approach, there is no requirement to assume equal probability of these alternative hypotheses, and requires separating out methods into each hypothesis to construct each distribution. For the case of yelloweye rockfish, the higher M mode consists of growth and maturity-based estimators, but as previously stated, clearly incompatible with realistic longevity expectations. Fig. 3A (right plot) shows a treatment that uses the methods weighting approach (second tab in the NMT) to downweight to zero all estimators except the longevity-based estimators, isolating the lower M mode. For the gopher rockfish example, there is no grouping distinction or obvious reasoning to exclude certain estimators, so one may choose to use the overall bimodal composite distribution (Fig. 3B, right plot), or either downweight the growth based estimators (as done with yelloweye rockfish) or the longevity based estimators (if there is concern with the maximum age estimate) to use a single mode.

Some general recommendations on estimating natural mortality emerge from using the NMT:

1. Enter all available inputs (including other available estimates of M entered as user input) into the NMT. Critical evaluation of inputs should occur both before inclusion in the tool and once M values are generated (as it may become clearer some inputs are questionable

upon seeing the estimated M) to gain some sense of potential reliability in methods based on that input. This exercise may also indicate the need to revist available life history parameters to improve those values.

2. Consider adding uncertainty to the M estimates rather than just using point estimates. A lognormal distribution is typically assumed. For example, Hamel and Cope (in this issue) recommend standard deviations of 0.31 when using longevity estimators and 0.85 for growth-based estimators.

3. Initially consider the longevity (if available) estimators of M as most informative (Then et al., 2015), but compare them to the other estimators. If there is low overlap between longevity and other estimators (or between estimators in general), consider again the quality of the life history inputs and observe deviations in well-known life history correlations (e.g., fast growing and quick to mature, but long-lived) at the species or other taxonomic level. If the major differences are by groups of estimators, investigate what it takes to change input values to achieve the estimates of M from other estimators (e.g., changing longevity for yelloweye rockfish to match M estimates from the growth- and/or maturity-based M estimators), and determine whether these input changes are realistic (e.g., yelloweye rockfish longevity needed to change to unreasonably low values to obtain M estimates similar to growth-based methods)

4. If multiple modes are present and there are no obvious errors in the life history inputs or notable bias in estimators for the particular taxon, but uncertainty remains in the reliability of the longevity estimate,

   a. Consider the multiple modes as different hypotheses of M and create separate distributions. Altering the weighting of methods (e.g., downweighting certain estimators to isolate others) to create hypothisis-specific M distributions is one way to do this. These alternative hypotheses of M do not need to be treated equally, and in some cases, some modes may be deemed unrealistic (e.g., M values that seem much too high; see M values from growth and maturity estimators in yelloweye rockfish) and can be ignored (Fig. 3A, right panel). Prior distributions should consider intra-input weighting (e.g. if two estimators use longevity, weight each by 0.5 so they are not unintentionally upweighted) to avoid unintentional overweighting the influence of certain inputs.

   b. If there are no evident natural groupings of the M estimates based on methods, but still multiple modes, one can either use a distribution inclusive of all methods (e.g., Fig. 3B, right panel) or choose to break them out into multiple distributions as in (3a).

5. The resultant prior distributions is downloadable as a vector of M values by method with a user-specified number of random draws (with the default being 1 million draws). This object can then be used as a prior distribution or used to calculate summary statistics.

Additionally, it may also be appropriate to consider the age-specific estimates that also are provided by the NMT, if the required inputs are available.

The ultimate formulation of a value or distribution of M is up to the user, but the *in situ* ability to compare across methods offers the potential for building an ongoing understanding of how these methods relate to one another under a variety of data conditions and life history configurations. These types of comparisons may eventually reveal inherent patterns and sensitivities in certain methods under different life history types. For instance, the revised versions of the Alverson and Carney (1975) method (Zhang and Megrey, 2006) often result in extremely low estimates of natural mortality (Fig. 1A, left panel, ZM_AC_dem and ZM_AC_pel; see Zhang and Megrey, 2006 results that also show this tendency), but in some cases can show more reasonable values (Fig. 1B, left value, ZM_CA_dem and ZM_CA_pel). Understanding such individual vagaries on top of the already complicated evaluation of input value quality and life history types on M estimators benefits from extensive
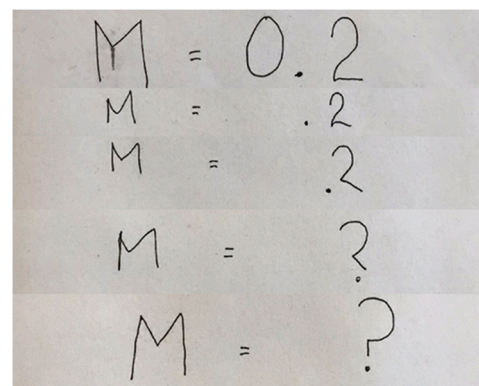

Fig. 4. The reversion of M that invites inquiry. Using a tool like the NMT can turn the question mark into a species-specific estimate of M.

applications and comparisons. The Natural Mortality Tool, while making these methods accessible, provides the space to grow intuition on applying M estimators. The tool is also open to further estimator inclusion and additional diagnostics and functionality improvements, offering an adaptable interface and utility as options change and grow.

We are well beyond the default days of $M = 0.2$. May we now instead turn 0.2 back into a question mark (Fig. 4) and use the power of empirical analysis and accessible, transparent tools to promote investigation and construction of M values that embrace uncertainty and are situation-specific.

CRediT authorship contribution statement

Jason Cope: Conceptualization, Methodology, Software, Formal Analysis, Primary writing. **Owen Hamel:** Conceptualization of table 3 in the NMT. Writing – review & editing.

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 will be made available on request.

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References

Alverson, D.L., Carney, M.J., 1975. A graphic review of the growth and decay of population cohorts. J. du Cons. Int. pour l'Exploration De. la Mer. 36, 133–143.

Anderson, E.D., 2015. Lessons from a career in fisheries science. ICES J. Mar. Sci. 72, 2169–2179. https://doi.org/10.1093/icesjms/fsv098.

Anderson, S.C., Branch, T.A., Cooper, A.B., Dulvy, N.K., 2017. Black-swan events in animal populations. Proc. Natl. Acad. Sci. 201611525. https://doi.org/10.1073/pnas.1611525114.

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., 1959. A Review of the Lifespans and Mortality Rates of Fish in Nature, and their Relation to Growth and Other Physiological Characteristics. In: Ciba Foundation Symposium - The Lifespan of Animals (Colloquia on Ageing). John Wiley & Sons, Ltd, pp. 142–180. https://doi.org/10.1002/9780470715253.ch10.

Boukal, D.S., Dieckmann, U., Enberg, K., Heino, M., Jørgensen, C., 2014. Life-history implications of the allometric scaling of growth. J. Theor. Biol. 359, 199–207. https://doi.org/10.1016/j.jtbi.2014.05.022.

Chang, W., Joe Cheng, J.J. Allaire, Carson Sievert, Barret Schloerke, Yihui Xie, Jeff Allen, Jonathan Mc.Pherson, Alan Dipert and Barbara Borges. 2021. shiny: Web Application Framework for R. R package version 1.7.1. https://CRAN.R-project.org/package=shiny.

Chapman, D.G., 1961. Statistical problems in dynamics of exploited fisheries populations. In: Jerzy Neyman (Ed.), Berkeley Symp. . Math. Stat. Probab. 153–168.

Chapman, D.G., Robson, D.S., 1960. The analysis of a catch curve. Biometrics 16, 354–368. https://doi.org/10.2307/2527687.

Charnov, E.L., Berrigan, D., Shine, R., 1993. The M/k ratio is the same for fish and reptiles. Am. Nat. 142, 707–711.

Charnov, E.L., Gislason, H., Pope, J.G., 2013. Evolutionary assembly rules for fish life histories. Fish Fish 14, 213–224. https://doi.org/10.1111/j.1467-2979.2012.00467.x.

Chen, S., Watanabe, S., 1989. Age dependence of natural mortality coefficient in fish population dynamics. Nippon Suisan Gakkaishi 55, 205–208. https://doi.org/10.2331/suisan.55.205.

Cigler, P., Kvapil, P., Kastelic, M., Gombač, M., Švara, T., Vobr, J., Račnik, J., Bartova, E., 2020. Retrospective study of causes of animal mortality in Ljubljana Zoo 2005–2015. zamd 51, 571–577. https://doi.org/10.1638/2019-0206.

Cordue, P.L., 2012. Fishing intensity metrics for use in overfishing determination. ICES J. Mar. Sci. 69, 615–623. https://doi.org/10.1093/icesjms/fss036.

R. Core Team 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Du, C., Jia, D., Jin, L., Shi, L., 2018. The impact of neutral reward on cooperation in public good game. Eur. Phys. J. B 91, 234. https://doi.org/10.1140/epjb/e2018-90052-6.

Ebert, T.A., 1999. Plant and Animal Populations: Methods in Demography. Academic Press, San Diego, p. 312.

Enberg, K., Jørgensen, C., Dunlop, E.S., Varpe, Ø., Boukal, D.S., Baulier, L., Eliassen, S., Heino, M., 2012. Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence. Mar. Ecol. 33, 1–25. https://doi.org/10.1111/j.1439-0485.2011.00460.x.

Essington, T.E., Kitchell, J.F., Walters, C.J., 2001. The von Bertalanffy growth function, bioenergetics, and the consumption rates of fish. Can. J. Fish. Aquat. Sci. 58, 2129–2138.

Fey, S.B., Siepielski, A.M., Nusslé, S., Cervantes-Yoshida, K., Hwan, J.L., Huber, E.R., Fey, M.J., Catenazzi, A., Carlson, S.M., 2015. Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events. PNAS 112, 1083–1088. https://doi.org/10.1073/pnas.1414894112.

Froese, R. and D. Pauly. Editors. 2021. FishBase. World Wide Web electronic publication. www.fishbase.org, (08/2021).

Gertseva, V. and Cope, J.M., 2017. Stock assessment of the yelloweye rockfish (Sebastes ruberrimus) in state and federal waters off California, Oregon and Washington. Pacific Fishery Management Council. 293 pages. https://www.pcouncil.org/documents/2017/12/stock-assessment-of-the-yelloweye-rockfish-sebastes-ruberrimus-in-state-and-federal-waters-off-california-oregon-and-washington.pdf/.

Gunderson, 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. https://doi.org/10.1093/icesjms/fsu131.

Hamel, O.S., J.M. Cope in this issue. Development and considerations for application of a longevity-based prior for the natural mortality rate. Fisheries Research.

Hill, J.E., DeVault, T.L., Belant, J.L., 2019. Cause-specific mortality of the world's terrestrial vertebrates. Glob. Ecol. Biogeogr. 28, 680–689. https://doi.org/10.1111/geb.12881.

Hoag, H., 2003. Atlantic cod meet icy death. Nature 422, 792. https://doi.org/10.1038/422792b.

Hoenig, J.M., 2017. Should natural mortality estimators based on maximum age also consider sample size? Trans. Am. Fish. Soc. 146 (1), 136–146.

Hoenig, J.M., Barrowman, N.J., Hearn, W.S., Pollock, K.H., 1998. Multiyear tagging studies incorporating fishing effort data. Can. J. Fish. Aquat. Sci. 55, 1466–1476.

Jennings, S., Dulvy, N.K., 2008. Beverton and Holt's Insights into Life History Theory: Influence, Application and Future Use. In: Advances in Fisheries Science. John Wiley & Sons Ltd, pp. 434–450. https://doi.org/10.1002/9781444302653.ch18.

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.

Jiang, H. 2005. Age-dependent tag return models for estimating fishing mortality, natural mortality and selectivity. Doctoral dissertation. North Carolina State University, Raleigh.

Jiang, H., Pollock, K.H., Brownie, C., Hoenig, J.M., Latour, R.J., Wells, B.K., Hightower, J.E., 2007. Tag return models allowing for harvest and catch and release: evidence of environmental and management impacts on striped bass fishing and natural mortality rates. North Am. J. Fish. Manag. 27, 387–396.

Kenchington, T.J., 2014. Natural mortality estimators for information-limited fisheries. Fish and Fisheries 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. https://doi.org/10.1016/j.fishres.2011.01.021.

Lendrem, B.A.D., Lendrem, D.W., Gray, A., Isaacs, J.D., 2014. The Darwin Awards: sex differences in idiotic behaviour. BMJ 349, g7094. https://doi.org/10.1136/bmj.g7094.

Lenting, B., Gartrell, B., Kokosinska, A., Duignan, P.J., Michael, S., Hunter, S., Roe, W.D., 2019. Causes of adult mortality in two populations of New Zealand sea lions (Phocarctos hookeri). Vet. Anim. Sci. 7, 100057 https://doi.org/10.1016/j.vas.2019.100057.

Maunder, M.N., Hamel, O.S., Lee, H.-H., Piner, K.R., Cope, J.M., Punt, A.E., Ianelli, J.N., Methot, R.D. in this issue. A review of estimation methods for natural mortality and their performance in the context of fishery stock assessment. Fisheries Research.

Monk, M.H., and He, X., 2019. The combined status of gopher (Sebastes carnatus) and black-and-yellow rockfishes (Sebastes chysomelas) in U.S. waters off California in 2019. Pacific Fishery Management Council. 229 pages. https://www.pcouncil.org/documents/2019/10/gopher-black-and-yellow-assessment-2019.pdf/.

Nelson, G.A., 2021. fishmethods: Fishery Science Methods and Models. R. Package Version 1, 11–12. https://CRAN.R-project.org/package=fishmethods.

Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. ICES J. Mar. Sci. 39, 175–192.

Pope, J.G., Gislason, H., Rice, J.C., Daan, N., 2021. Scrabbling around for understanding of natural mortality. Fish. Res. 240, 105952 https://doi.org/10.1016/j.fishres.2021.105952.

Prince, J., Hordyk, A., Valencia, S.R., Loneragan, N., Sainsbury, K., 2015. Revisiting the concept of Beverton -Holt life-history invariants with the aim of informing data-poor fisheries assessment. ICES J. Mar. Sci. 72, 194–203. https://doi.org/10.1093/icesjms/fsu011.

Punt, A.E., Hilborn, R., 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. Rev. Fish. Biol. Fish. 7, 35–63.

Reznick, D., Ghalambor, C., Nunney, L., 2002. The evolution of senescence in fish. Mech. Ageing Dev. 123, 773–789. https://doi.org/10.1016/s0047-6374(01)00423-7.

Schnute, J.T., Haigh, R., 2007. Compositional analysis of catch curve data, with an application to Sebastes maliger. ICES J. Mar. Sci.: J. du Cons. 64, 218–233.

Seber, G.A.F., 1982. The Estimation of Animal Abundance and Related Parameters. Griffin, London, p. 654.

Sparre, P. and S.C. Venema. 1998. Introduction to tropical fish stock assessment. Part 1: Manual. FAO Fisheries Technical Paper No. 306.1, Rev. 2. Rome FAO 407p.

Stenkat, J., Krautwald-Junghanns, M.-E., Schmidt, V., 2013. Causes of morbidity and mortality in free-living birds in an urban environment in Germany. EcoHealth 10, 352–365. https://doi.org/10.1007/s10393-013-0868-9.

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 over 200 fish species. ICES J. Mar. Sci. 72, 82–92. https://doi.org/10.1093/icesjms/fsu136.

Thorson, J. 2019. FishLife: Predict Life History Parameters For Any Fish. R package version 2.0.0. http://github.com/James-Thorson/FishLife.

Thorson, J.T., Prager, M.H., 2011. Better catch curves: incorporating age-specific natural mortality and logistic selectivity. Trans. Am. Fish. Soc. 140, 356–366. https://doi.org/10.1080/00028487.2011.557016.

Thorson, J.T., Munch, S.B., Cope, J.M., Gao, J., 2017. Predicting life history parameters for all fishes worldwide. Ecol. Appl. 27, 2262–2276. https://doi.org/10.1002/eap.1606.

Vetter, E.F., 1988. ESTIMATION OF NATURAL MORTALITY IN FISH STOCKS. undefined.

von Bertalanffy, L., 1938. A quantitative theory of organic growth (inquiries on growth laws II). Hum. Biol. 10, 181–213.

Zhang, C.-I., Megrey, B.A., 2006. A revised Alverson and Carney model for estimating the instantaneous rate of natural mortality. Trans. Am. Fish. Soc. 135, 620–633.