A review of estimation methods for natural mortality and their performance in the context of fishery stock assessment

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Abstract

Natural mortality (M) is one of the most influential parameters in fisheries stock assessment and management. It relates directly to stock productivity and reference points used for fisheries management advice. Unfortunately, M is also very difficult to estimate, and hence very uncertain. Representing the uncertainty in M and how this influences estimates of management quantities is therefore an important component of conducting stock assessments. This paper outlines the range of methods available to estimate M for use in stock assessment. The methods include those based on maximum age, life history theory, relationships between "well-known" values for M (those found in the literature and based on data for the stock being assessed) and covariates, use of tagging data and catch curve analysis, and estimation within a single- or multi-species stock assessment model. All methods are likely subject to bias and imprecision due to incorrect assumptions and incomplete data. Furthermore, M is generally assumed to be constant over time, age, and sex - assumptions that are unlikely to be true for any stock. Based on our review, there is an obvious benefit to directly estimating M using data and within a stock assessment while assigning a prior based on empirical methods. This approach effectively uses all the available information while also representing the uncertainty. Carefully examining diagnostics and checking for model misspecification is required to ensure that the available data and stock assessment model assumptions are appropriately informative about M when it is estimated during the model fitting process. For situations where direct estimation is not possible (a condition found in data-limited to data-rich stock assessments), the use of multiple methods with robust sensitivity exploration is recommended. Even when direct data are integrated into a stock assessment, we recommend using other methods to estimate M and analysing the direct data outside the stock assessment model as diagnostic tools.

Keywords: fisheries management; natural mortality; parameter estimation; population dynamics, stock assessment

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1. Introduction

Natural mortality (*M*) is a fundamental part of modelling structured (e.g., age, length, or stage) population dynamics. There are many ways to define natural mortality, ranging from annual survival rates to instantaneous rates. We define *M* as it is commonly used in fishery stock assessments as the instantaneous rate of natural mortality defined on an annual basis such that the survival over a year in the absence of fishing is exp[-*M*], and it acts continuously and simultaneously with fishing mortality such that the survival over a year in the presence of fishing mortality is exp[-(*M*+*F*)]. Seasonal or other time-step models can lead to modifications of this general form. In general, *M* represents all mortality not attributed to the fishery (e.g., predation, starvation, disease, senescence) and may include some forms of human-induced mortality not due to fishing. In some cases, estimates of *M* may also account for unreported catch or movement of fish out of the assessed area. In applications, the definition of natural mortality may change depending on the stock assessment model used.

The fact that *M* directly affects estimates of stock productivity and reference points makes it one of the most influential parameters in fisheries stock assessment and management. Management quantities (e.g., MSY, the maximum sustainable yield), and reference points (e.g., B_{MSY}, the biomass corresponding to MSY, and F_{MSY}, the fishing mortality rate corresponding to MSY) form the central basis of most successful management systems (Hilborn and Ovando, 2014). While *M* is central to these quantities, it is also very difficult to estimate (due to lack of informative and unbiased data, such as tagging data or age-composition in the absence of fishing, and confounding with other stock-assessment model parameters, such as catchability and selectivity (particularly when dome-shaped)) and the assumptions underlying its estimation (e.g., time invariance and constancy over age and sex) are likely to be violated. Hence both *M* and those reference points can be highly uncertain. Representing the uncertainty in *M* and how this influences estimates of management quantities is therefore an important component of conducting stock assessments. Typically, estimates arise from rationalized assumptions made by experts (often informed by information for other stocks or species), calculated from general empirical relationships, and/or are based on life history theory. *M* is also usually assumed to be constant over time, age, and (somewhat less often) sex to simplify model complexity— assumptions that are unlikely to be true for any stock. In some stock assessments, the value of *M* has been unchanged for decades at values based on little, if any, support from actual data. Many of these issues were identified by Vetter (1988) over three decades ago, and they have yet to be fully addressed.

Several methods have been developed to estimate *M* outside the stock assessment model, including those based on mark-recapture data (e.g., Chapman, 1961; Seber, 1982), catch-at-age data (e.g., Chapman and Robson, 1960; Paloheimo, 1980), maximum observed age (Hoenig, 1983, Then et al. 2015, Hamel and Cope, this issue), life history theory (Roff, 1984; Charnov, 1993; Jensen, 1996; Alverson and Carney, 1975), and empirical relationships between *M* and covariates (Pauly, 1980; Gunderson, 1997; Hoenig, 1983). Each of these methods has its strengths and weaknesses, and accepted approaches for specifying values for *M* for use in stock assessments vary widely as summarized in a review by Brodziak et al. (2011).

The information used in the methods to estimate *M* outside of a stock assessment (e.g., catch-at-age/length and tagging data) can be integrated within the stock assessment model (e.g., Methot and Wetzel, 2013; Punt et al., 2013; Maunder and Punt, 2013); the process for achieving this is the focus of this review. Theoretically, if data provide reliable information about M using traditional direct methods (e.g., tagging or catch-curve analysis), the same data should also provide reliable information about M inside an assessment. However, there has been general pessimism regarding this approach (e.g., Deriso et al., 1985; Gudmundsson, 1998) because estimates of M are often highly correlated with estimates of other model parameters (e.g., catchability, selectivity (particularly when dome-shaped), steepness, and the primary focus of the assessment – fishing mortality) (MacDonald and Butler, 1982; Schnute and Richards, 1995; Clark, 1999; Wang, 1999; Fu and Quinn, 2000) or there is no information about M in the data available for estimation purposes. However, some studies have shown that it is possible to estimate M within a stock assessment model (e.g., Fournier et al., 1998; Maunder and Wong, 2011; Lee et al., 2011) if the assessment is suitably constrained to effectively behave like a multi-cohort catch curve analysis. Misspecification of complex assessment models can bias the estimates of M (Piner et al., 2011).

This paper reviews the methods for estimating M for use in fishery stock assessments and highlights the strengths and weaknesses of each. Evaluating the alternative methods to estimate M is important for recommending good practices. We consequently provide a summary of how well each method performs given what is known about them. We do not explicitly test the approaches, but rely on the information available in the literature. The evaluation is mostly qualitative, but we provide quantitative measures of performance when available. The true value of M, insofar as it exists, is unknown, so there is no direct test of estimation performance based on the results of actual assessments.

Two main approaches have been used in the literature to evaluate the alternative methods (see Hoenig et al., 2016, for a discussion). These approaches are not necessarily applicable to all methods, making the comparison of the performance of the methods difficult. The first approach is to simulate the performance of estimators under known conditions where the true natural mortality rate or rates are known (e.g., Lee et al. 2011), although this approach depends on acceptable simulation specification and assumptions (Francis, 2012). The second approach is to evaluate which estimators predicted the values of M found in the literature (the reliability of these estimates of M is of course unknown) and use cross validation when the estimators are created based on the same values (e.g., Then et al. 2015; Hoenig et al. 2016).

We first separate methods that estimate M independently from the stock assessment model (and may be used to construct an informative prior distribution for use in an assessment; Section 2) from those that estimate M within the assessment (Section 3). Following Hoenig et al. (2016), we then separate methods that estimate M independently of the stock assessment into those based on directly informative data (e.g., catch curve analysis and tagging analysis) and those based on indirect information such as theory and empirical relationships. Data used in the direct approaches can also be used within stock assessment models to provide information to estimate M, whereas "data" providing indirect information are better suited for developing Bayesian priors.

2. Methods used to estimate M independently from a stock assessment

The methods traditionally used to estimate M for input into stock assessments can be divided into four groups: 1) methods based on life history theory; 2) empirical relationships; 3) analysis of tagging data; and 4) analysis of catch-at-age data. We argue that estimators based on theory are generally more susceptible to violation of the underlying assumptions of each method and consequently discuss them as a stepping stone to determine the relationships to use as empirical estimators. This section is therefore separated into empirical relationships (subsection 2.1), tagging analysis (subsection 2.2), and catch-curve analysis (subsection 2.3).

2.1 Empirical estimators

Empirical estimators, or those dependent on predictive relationships, are some of the most commonly applied ways to determine *M* for assessment of commercially managed fisheries within the U.S. and Australia. Table 1 lists the equations on which the methods of this section are based. We summarize the main types and groups of estimators, but there are often many variants within each type of estimator (Kenchington, 2014; Then et al., 2015), only some of which are listed here. Table 1 shows a subset of the "revised" variants of some of the most popular relationships based on different data sets and/or assumptions about the error between the "well-known" values for *M* (those found in the literature and based on data for the stock under consideration) and the model predictions.

Given that uncertainty and estimation error in *M* scales with *M*, and therefore untransformed data demonstrate substantial heteroscedasticity, many analysts have taken the appropriate step of log-transforming both *M* and associated life-history covariates (e.g., Pauly, 1980; Hoenig 1983; Hamel, 2015), while others have not, or have not done so for a subset of analyses (e.g., Jensen, 1996; Then et al., 2015). Analyses based on untransformed data likely give too much weight to data points with high *M* estimates, and therefore skew the results and are likely to provide poor estimates, particularly for species with low *M* values, i.e., long-lived species.

Observed variability in the relationship between covariates and *M* represents a combination of the actual variability in the relationship among taxa combined with error in the estimated values of *M* and covariates used (e.g., Gunderson et al., 2003; Hamel and Cope, this issue) and inconsistencies in assumed functional forms (e.g., von Bertalanffy growth, constant *M* across age). Data acquisition, including sampling issues and ageing error can affect estimates across the range of life-history parameters, and can affect each of the methods discussed below.

2.1.1 *M* estimators based upon maximum age

Conceptually, estimators based on maximum age should be preferred because maximum age, or longevity, relates more directly to, or arises from, *M* (or more accurately total mortality, but see below). Methods used to estimate *M* using the maximum observed age (t_{max}) are based on models of the probability of a fish living to a given age under a given level of total mortality. These, and in particular the inverse relationship of *M* to t_{max}, are theoretically appealing, as a population with a well-defined population maximum age follows the logic of a life table (Caswell 2001). The total mortality rate can be calculated from the standard exponential decay model of population dynamics, $N_t = N_0 \exp(-Z_t)$. This decay model is rearranged so that the proportion *p* living to at least a given age *t* is $p = N_t / N_0 = \exp(-Z_t)$. This equation can then be used to determine the probability of observing a given aged fish in a sample from the population (while ignoring ageing error). A rule of thumb used in the past to estimate *M* was $M = 3/t_{max}$ (Eqn T1.2.1a; e.g., Rugolo et al., 1998) that derives from the formula $M = -ln(p)/t_{max}$ (Eqn T1.2.1), where $p = 0.05$ is the proportion of fish that survive to age of t_{max} or older assuming constant *M* with age. Intuitively, t_{max} (and p) should represent an age at which senescence leads to high M and therefore relatively few older individuals. However, $p = 0.05$ is an arbitrary value. The appropriate value for p will depend on several factors including the sampling design, sample size, and the relative timing of the onset of senescence.

Hoenig (1983) developed a non-linear empirical t_{max}-based estimator by using log-space regression of M on maximum age for 84 unexploited or lightly exploited stocks (Eqn T2.2.2a). Then et al. (2015) revisited this non-linear approach (Eqn T2.2.2.b) and another using non-linear least squares (Eqn T2.2.2c) with an updated and larger data set. Hewitt and Hoenig (2005) found an inverse relationship for M that was 40-50% higher than the $M = 3/t_{max}$ rule of thumb (Eqn T2.2.1a), which suggests that the corresponding value of p is much lower (Hewitt and Hoenig, 2005). Hamel (2015) revisited Hoenig's (1983) data and found an inverse relationship (Eqn T2.2.1b) close to that of Hewitt and Hoenig (2005). Then et al (2015) evaluated an inverse relationship using their data set (Eqn T2.2.1c), but failed to transform the data. Hamel and Cope (this issue) evaluated Then et al.'s (2015) data under a more appropriate transformation (Eqn T3.2.1).

A lingering concern with estimating M from maximum age is that the estimate is based on the maximum age observed and not the maximum age in the population. Holt (1965) provided a closed form solution to the expected maximum age for a sample size of n: $E(t_{max}) \cong \ln(2n+1)/Z + t_1$, where t_1 is the age-at-first capture, from which total mortality (Z) can be computed (Hoenig, 2017). Hoenig (1983) argued that the maximum age tends to increase slowly with increasing sample size after about 200 individuals have been examined (although this will depend on selectivity of the gears used to collect the samples and Z). However, there is some debate over the possible magnitude of the effective sample size and its influence (Maunder and Wong, 2011; Kenchington, 2014; Hoenig 2017; Hamel and Cope, this issue). Nevertheless, since the proportion, p, is arbitrary and the effective sample size is usually unknown, we recommend using the empirical relationships rather than theory, finding that defining methods that include the sample size is not useful. Instead, it is assumed that the stock for which M is being estimated is a random sample from the population of stocks from which the stocks used to generate the relationship were also sampled randomly. This helps with other issues that affect the estimate of maximum age, such as ageing error.

2.1.2 M estimators based on growth and reproduction

Life history theory has been used to develop a multitude of relationships to estimate M (e.g., Roff, 1984; Charnov, 1993; Jensen, 1996; Alverson and Carney, 1975; Gislason et al., 2010), based upon the idea that a species' life history has evolved to maximize lifetime reproductive fitness or the population growth rate r through tradeoffs among reproduction, growth, and natural mortality (Roff, 1984). While a step removed from using longevity, information and/or assumptions about growth and reproduction can be used to infer M.

In order to maximize lifetime reproductive fitness, maturity should occur when fecundity exactly matches, or exceeds, for the first time, the expected future fecundity losses from increased mortality and reduced growth due to the costs of reproduction. Since we do not generally know the exact impact of maturity on growth and mortality, various reasonable assumptions have been made. The first Beverton and Holt life history invariant (Charnov, 1993): $Mt_m = C_1$ (Eqn T1.1.1) indicates that the age of maturity (t_m) occurs when some particular proportion of a cohort remains, and thus is closely linked to longevity. Others have assumed that maturity should occur when at peak cohort reproductive output (t_{mb} or t_c; Alverson and Carney, 1975; Roff, 1984; Zhang and Megrey, 2006), or at the inflection point of the von Bertalanffy growth equation (Jensen, 1996). In situations where both t_m and von Bertalanffy K are known, Roff's (1984) original equation would apply (Eqn T1.1.3). Alverson and Carney (1975) approximate t_{mb} as a constant fraction of maximum observed age (t_{max}) based on regressions with empirical data, and do not account for variation in the relative age of maturity. Zhang and Megrey (2006) generalized Eqn T1.1.3 to include population-specific values for t_0 and β (a difficult proposition; Eqn T1.1.4) and recommend using data to calculate t_{mb} based on regression with t_{max} from specific ecological groups.

The second Beverton and Holt life history variant (Charnov, 1993): $M/K = \mathrm{C}_2$ (Eqn T1.1.2) suggest that M is proportional to K, and hence that an increased rate of growth towards maximum size is correlated with increased mortality rate. Jensen (1996) calculated the constants of the Beverton and Holt invariants (Eqns T 1.1.1 and T1.1.2) by assuming that the age at maturity equalled the age at the inflection in the von Bertalanffy growth equation in weight and assuming Roff's equation (Eqn T1.1.3).

More complicated approaches have been used to estimate M based on life history. Beverton (1992) derived a relationship among length-at-maturity (L_m), asymptotic length (L_∞), von Bertalanffy K, and M (Eqn T1.1.5). Chen and Watanabe (1989) provided a function for age-specific M, with higher rates at young and old ages based on the von Bertalanffy growth parameters using the assumption that mortality is inversely proportional to growth (Eqn T1.1.6).

Empirical relationships have been developed via regressions using "well known" estimates of M against life-history covariates. Pauly (1980) conducted one of the earliest comprehensive analyses by regressing M on von Bertalanffy growth rate (K) and asymptotic size (either weight or length), and water temperature (T) using data for 175 marine and freshwater fish stocks (Eqn T2.3.3; converted to natural logarithms; Quinn and Deriso, 1999). Using data for the 175 stocks in Pauly (1980), Jensen (1996) estimated $M/K = 1.60$ (Eqn T2.3.4a). However, this analysis was conducted without log transformation of the data, and therefore is subject to impacts of heteroscedasticity. Then et al. (2015) made the same assumption in analysing their data (Eq. T2.3.4c). Hamel (2015) analysed data from Pauly under log transformation and estimated $M = 1.75K$ (Eq. T2.3.4b). Conducting the same analysis using the updated data set from Then et al. (2015) leads to the relationship $M = 1.55K$ (Eqn T3.3.4). Beverton (1992) suggested that M/K would vary among taxa, ranging between 0.2 and 2.5 across species, questioning the invariant nature of this ratio (Nee et al., 2005). Ralston (1987) provided M/K relationships for snappers and groupers (Eqn T2.3.5). Using a similar approach, Charnov and Berrigan (1990) found that $Mt_m \sim 2$ (Eqn T2.3.6). Beverton (1963) estimated Mt_m at 1.54 for cod, 1.54 for flatfish, and 3.33 for brown trout. These results provide a wide range of values but are somewhat consistent with relationships using life history theory. Finally, Thorson et al. (2017) present a taxonomically based hierarchical model and tool (FishLife) that constructs species-specific M/K (as well as M by itself) using the FishBase database.

Body length and weight (or mass) have also been used as predictors of M. Lorenzen (1996) analysed the relationship between body weight and M in juvenile and adult fish for six aquatic ecosystems types (lakes, rivers, ocean, pond, cage, and tank aquaculture systems) using a power function. The parameters were estimated for fish in the six ecosystems, as well as within selected populations, species and families. At the ecosystem level, no significant differences in parameters were found between lakes, rivers and the ocean, and a joint relationship was estimated for all natural ecosystems (Eqn T3.3.10). Eqn T3.3.10 allows for size-specific *M*, although it can also be used to obtain an overall *M*. McGurk (1987) fitted a similar model to Lorenzen (1996) but obtained a different exponent (Eqn T2.3.8). Gulland (1987) responded to the work of McGurk (1986), providing estimates of *M* based on weight or length (Eqns T1.3.1 and T1.3.2), and Peterson and Wroblewski (1984) provided an equation for *M* as a function of size formulated on Silvert and Platt's (1980) work related to the theory on the distribution of biomass as a function of size (Eqn T2.3.9). All of these relationships, as with many others discussed here, display wide variability, and therefore the relationship is uncertain and likely variable among taxa and stocks.

Based on the r-K selection theory, *M* is expected to be positively correlated with reproductive effort (Gunderson, 1980; Gunderson and Dygert, 1988). Gunderson and Dygert (1988) provided a linear relationship between *M* and the gonadosomatic index (GSI = ovary weight/ somatic body weight) and Gunderson (1997) updated the relationship using 28 stocks of fish to yield $M = 1.79GSI$ (Eqn T2.3.7). This analysis was undertaken on untransformed data. Hamel (2015) analysed these data after log-transformation and found a similar relationship of $M = 1.82GSI$ (Eqn T3.3.7). There are several issues with providing accurate values for *GSI*, including annual variability due to feeding conditions (Gunderson and Dygert, 1988), reproductive stage, and the timing within spawning season.

Each of the above methods use differing degrees of relatedness to *M* (maximum age the strongest, size or weight much less strong) to form predictors with a range of values, and are only as good as the inputs. Given the various degrees of separation to *M* and the reliability of life history value estimates, there is no one superior approach. Applying multiple empirical estimators is recommended when determining either a fixed value to use within a stock assessment, or a prior to aid estimation of *M* internal to a stock assessment (Cope and Hamel, this issue).

2.1.3 Performance

The 'performance' of each method is the difference between the true value and the value from the prediction equation. However, in practice the true value is never known. Instead, we evaluate the prediction based on its uncertainty. The error associated with estimates of *M* based on empirical methods reflect error in creating the relationship and error in the covariates for the specific stock being analysed. Error in creating the relationship includes model error (i.e., the equation used for prediction is wrong) and estimation error which encompasses error associated with measurements of the covariates for the species used to create the relationship and to which it is applied, error in the values of *M* used to create the relationship, and variation in the relationship among species or stocks.

Empirical methods offer insight into the relationship between *M* and other life history parameters. However, accurate estimates of *M* based on life history theory require accurate estimates of associated life history parameters. Any error or bias in these quantities will impact the predictions of *M* (Quinn and Deriso, 1999), although those errors exist in the data used to create the relationships, and so those actually represent the relationship between estimated, rather than true values of life history covariates and *M*.

Estimates of K are often confounded with estimates of L_∞ (e.g., Fig. 1), and there may be considerable uncertainty in the estimate of K for the same species across regions. For example, estimates of M based on Jensen's empirical relationship, $M = 1.6K$, for 42 data sets for dorado (*Coryphaena hippurus*) stocks presented in Chang and Maunder (2012), which include different data types and aging methods, range over an order of magnitude (Fig. 1). K may also change over time. Similarly, estimates of M based on t_m will be somewhat uncertain, because maturity may occur over a range of ages and may vary across years and with environmental conditions, the method used to estimate maturity may be inaccurate, or there may be ageing or sampling errors leading to uncertainty in the estimate of t_m. The relationship between M and the life history parameters may differ from the theory for individual species, leading to additional uncertainty in the estimates of M. Trade-offs between reproductive effort and adult growth or survival have been reported in many field studies and manipulation experiments (e.g., Roff, 1992; Stearns, 1992), indicating that the life-history parameters and/or the relationships may vary over time. For example, estimates of M based on K vary substantially over time for English sole (*Parophrys vetulus*) off the US West Coast (Table 2). Finally, since M is likely to vary with age, a single estimate from life history will be incorrect to some degree for some ages even if it is correct on average. However, attempting to account for variation in M with age does not guarantee a more accurate result.

The observed or estimated maximum age will be affected by the recruitment and exploitation history of a stock. For example, if there are infrequent large spikes in recruitment, the maximum aged fish is more likely to come from the cohort represented by a large recruitment event, particularly for species with shorter lifespans. Where fishing mortality has been significant, selectivity, refugia and sampling approach are all important factors. There are other issues related to applying methods based on maximum age, including ageing error and age-dependence in M. Consequently, some analysts ignore the oldest recorded age if it is perceived to be an outlier (and perhaps an age-reading error) and use the second oldest age, the oldest age that has a few observations, or a percentile. For example, Monk et al. (2018) conducted an analysis for California scorpionfish (*Scorpaena guttata*) where M was determined by averaging the three oldest estimated ages of each sex, and Wetzel et al. (2017) used an age less than the maximum age to account for possible aging error based on the range of other ages available with multiple observations. However, these assumptions are *ad hoc*. Maximum age relationships can also be used to evaluate whether the other relationships make sense (Cope and Hamel, this issue).

Evaluating the prediction error of M for empirical approaches is complicated due to the multiple sources of uncertainty, which are usually unknown (Hoenig et al., 2016; Hamel, 2015). Hamel (2015) highlighted the importance of the difference between prediction intervals and confidence intervals when considering methods for predicting M using covariates such as maximum observed age, growth parameters, and GSI, noting the considerable difference between the two (Fig. 2), with the latter encompassing the expected range of a new observation. The sources of error include error in the values of M used in the regression, error in the measurement of the covariates (e.g., K, A_max), individual variability in M given the covariates, error in the model used to represent the relationship, and error due to finite sample size. Without information on these components of the uncertainty, completely unbiased estimates of the uncertainty in the value of *M* are not possible. Confidence intervals for the regression will underestimate the uncertainty, providing uncertainty around the mean *M* given observed covariates, while prediction intervals, which represent variability in the estimated value of *M* (i.e., what was used in the regression), will overestimate the uncertainty in the true value of *M* due to incorporating both true variation in the relationship between estimated covariates and *M* and estimation error in the *M* values used for the regression (Hamel and Cope, this issue). When using these empirical relationships as the basis for priors for *M* in stock assessment, Hamel and Cope (this issue) recommend reducing the width of the prediction intervals, and priors, based on reasonable assumptions.

Attempts to quantify the error associated with empirical methods for estimating *M* have been based on cross-validation and regression diagnostics. For example, Pascual and Iribane (1993) computed the prediction errors associated with estimators of *M* based on growth parameters and temperature (Pauly, 1980), gonad weight (Gunderson, 1980; Gunderson and Dygert, 1988), and body length (Oshumi, 1979) and found median prediction errors from 10-36%. Prince et al. (2015) fitted the model of Beverton (1992) to 123 marine species data sets and found considerable variation in the Beverton-Holt life history invariants among species, concluding that there is *"predictable natural variation in the BH-LHI ratios and the relationships between size, age, and reproductive potential that they determine*". Kenchington (2014) concluded that none of the 30 estimators he examined provided accurate estimates for every species, and none appeared sufficiently precise for use in analytical stock assessments, while several performed so poorly as to have no practical utility. This conclusion likely applies to most empirical methods, but in many cases, empirical estimates of *M* are the only options. Thorson et al. (2017) conducted an extensive investigation of life history ratios and found that the ratio *M*/*K* varies systematically based on the timing of maturation, which is correlated with species taxonomy, following similar conclusions by Beverton (1992).

Attempts to quantify the uncertainty associated with estimating *M* using empirical methods lead to levels of error from 50 to 200% of the estimate based on Kenchington (2014), whereas MacCall (2009) found a CV of 50% based on the methods he reviewed. The two methods developed and preferred by Then et al. (2015) had prediction errors of 32% and 60% (based on that which used t_{max} and another based on growth parameters).

Hamel (2015) developed an approach for combining priors for *M* based on multiple methods, weighting each prior by the inverse of its prediction variance, and accounting for the overlap in the data used in the construction of the equations on which the methods are based. Hamel and Cope (this issue) expand on this work and that of Then et al. (2015) to develop a new age-based prior. Cope and Hamel (this issue) present a tool (The Natural Mortality Tool) that offers ways of developing priors based on maximum age and other relationships while incorporating intra- and inter-method variability. The CVs of the distributions for *M* based on the method of Hamel (2015) depend on the number of empirical methods that can be applied. In practice, this method led to estimates of *M* with CVs ranging from 28% to 58% for US West Coast groundfish stocks. In recent years, assessments for these stocks set *M* based on maximum age alone, using the updated Then et al. (2015) data along with the method from Hamel (2015), which results in a CV of 46%. In some applications the predicted value has been used as a fixed value for *M* while in others the information is used to create a log-normal prior (median = $5.4/t_{\mathrm{max}}$ and log-space sd = 0.438). For example, Haltuch et al. (2017) conducted two analyses in which the first fixed female M at the median of the prior based on a maximum age of 21 and the male M was estimated and the second estimated male and female M (with priors). Hamel and Cope (this issue) take the same analysis, but account for error in M values in the meta-analysis to arrive at a log-space prediction error = 0.31 (or CV = 32%).

Table 1 provides estimation equations based on theory or "rules of thumb" (Table 1a), equations based on empirical analysis methods that are not or no longer recommended (Table 1b) and equations for methods that are recommended (Table 1c). Recommended methods are based on more recent and well-vetted data sets and use more appropriate transformations for analysis.

2.2 Mark recapture methods

2.2.1 Overview

Mark-recapture data can be the basis for reliable ways to estimate M (Vetter, 1988; Fonteneau and Pallares, 2005). The methodology has been well studied, and the properties of the commonly used estimators are well understood (e.g., Seber, 1982; Brownie et al., 1985; Lebreton et al., 1992). The basis for estimating survival rates in most tagging methods is the 'Brownie model' (originally summarized by Brownie et al. [1985]). Given an estimate of the reporting rate, this method allows the estimation of natural and fishing mortality. Latour et al. (2003) discuss tagging lobsters just below and just above the legal size limit, which allows separating F from M without having to know the tag reporting rate. Pollock et al. (1991) expressed total mortality in the Brownie model in the form of continuous natural mortality and fishing mortality rates. The basic methods for estimating M (and other quantities) using tag-recapture data have been extended in numerous ways given the particular concerns for specific cases. For example, Hoenig et al. (1998a) extended the basic approach so that fishing effort can be used as an index of fishing mortality, and Hoenig et al. (1998b) illustrated how to allow for non-mixing of tagged animals. Jiang et al. (2007a) extended the approach to allow fishing and natural mortality to depend on age while Jiang et al. (2007b) showed how it is possible to allow for animals that are caught and released and subsequently harvested. Bacheler et al. (2008) extended the latter model by allowing for differential selectivity between fish that are harvested and those caught and released. Rudd et al. (2014) developed a spatially explicit tag-based model that permitted estimation of M among spatial strata and fitted it to acoustic telemetry data for Gulf sturgeon (*Acipenser oxyrinchus desotoi).*

Integrating the tagging data into the stock assessment model has several advantages (Maunder 1998; 2001). Sibert (1984) and Hilborn (1990) developed a multi-area stock assessment framework in which tagging data are used to estimate movement. This framework can make use of tagging data as well as other conventional stock assessment data. Hampton (1991) applied this framework to data for southern bluefin tuna (*Thunnus maccoyii*) and tested it using simulations. While estimates of M were obtained, they were highly imprecise (CV > 100% for some cases). Better precision is expected with improved sample designs and higher sample sizes.

Non-mixing of tags can be accounted for by estimating a parameter to represent the difference in fishing mortality in the first few periods while the tagged fish are mixing with the untagged fish. In applications where tagged fish never fully mix with untagged fish or fishing effort is unavailable, cohort analysis can be applied to the tagging data. For example, the Murphy-Tomlinson method (Bayliff, 1971) is based on applying a virtual population analysis to tagging data (e.g., Maunder et al., 2009). This method has the advantage that knowledge of the fishing effort or the numbers of non-tagged fish is not required. However, either all the tagged fish have to be dead after some time or a terminal fishing mortality has to be assumed. It also requires that the total number of tagged fish removed is known, which implies that the reporting rate is 100% or known. The more general approach is that of Ishii (1979) and Hilborn (1990), which simulates the dynamics of the tagged population, accounts for fish removed from the population due to fishing and is more consistent with contemporary integrated fisheries stock assessment models (e.g., Maunder and Punt, 2013). Maunder (1998, 2001) and Hampton and Fournier (2001) have extended tagging analysis into the integrated fisheries stock assessment modelling framework (see Goethel et al., 2011) and it is now commonly found in integrated packages used for assessments (e.g., Methot and Wetzel, 2013).

2.2.2 Performance

Extensive evaluation of tag-based approaches for estimating mortality has been undertaken to evaluate the reliability of the estimates of the parameters of tag-based models, particularly in "self tests" in which the model used to generate artificial data sets is the same as that on which the estimator is based. However, there are notable exceptions. For example, Lauretta and Goethel (2017) examined the performance of a tag-based estimator of movement and mortality focused on Atlantic bluefin tuna *Thunnus thynnus* using an operating model based on a continuous time model and generated artificial conventional and gene-based tagging data.

Common issues with tagging analysis include non-reporting of tags, tag shedding, and tag-induced mortality (either initial or long-term) (Pollock, 1991). Underestimates of the magnitude of these alternative explanations for tag loss results in positively biased estimates of *M*, and it is therefore important to either minimize these factors through well-designed tagging studies or to have reliable estimates of them. Non-mixing of tagged fish with the untagged population is also a common issue and may bias estimates of *M*. Tagging may also modify fish behaviour, changing their vulnerability to capture. Estimates of *M* may also be biased by migration if it is not appropriately accounted for.

If sample sizes are adequate and the appropriate information collected, estimates of *M* can be obtained for different components of the population (e.g., by size [Hampton, 2000] or sex). While tagging-based methods provide, in principle, unbiased estimates of *M*, the estimates for particular cases can be quite poor, making it near impossible to provide generic bounds on how precise estimates of *M* based on tagging are likely to be, as precision is directly related to the number of tag-recaptures. For example, Frusher and Hoenig (2001) estimated *M* for southern rock lobster (*Jasus edwardsii*) to be 0-0.018 yr^{-1}, with 95% confidence intervals that included 0.3 yr^{-1} and larger. The low estimate of *M* was attributed to confounding with the tag-reporting rate and the relatively low sample size. A more realistic (and precise) estimate of 0.12 yr^{-1} (SE 0.14) was obtained by Frusher and Hoenig (2003) when they related fishing mortality to effort, assuming constant catchability over years but unequal catchability within periods of the year. Estimates of *M* by age/stage have rarely been obtained. However, Hampton (2000) estimated size group-specific *M* for skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*), and bigeye tuna (*Thunnus obesus*) in the western tropical Pacific Ocean, with CV ~ 25%.

Close-kin mark-recapture (CKMR) is an approach that integrates genetic methods of population estimation and population dynamics models to estimate abundance and potentially a range of demographic parameters including natural mortality-at-age. The approach uses genetic markers to identify animals that are related (e.g., parent-offspring pairs; half sibling pairs, and perhaps other relationships; Skaug, 2001; Bravington et al., 2016a). The data are analysed within the general framework of mark-recapture data, but the analysis is not subject to many of the problems typically associated with conventional tagging data such as tag-loss, tag mortality, and tag reporting. The method requires an assumption that the spawning component of the population is discrete and sampled proportionally. The estimates of absolute abundance from CKMR can be more precise than those from typical stock assessments (CV = ~0.17 for southern bluefin tuna; Bravington et al., 2016b) and even the estimates of survival are remarkably precise (CV = ~0.03 for southern bluefin tuna; Bravington et al., 2016b).

2.3 Catch curve type methods

2.3.1 Overview

Catch-at-age data are commonly collected for commercially exploited species, and the age-structure of the population provides information on total mortality. Catch-curve analysis is based on the decline in cohort abundance through time [i.e., $N_t = N_0 e^{-Zt}$]. If the absolute numbers in a cohort are known for two time periods (e.g., at ages t and t + 1), then the difference is the total number of individuals that die during that time period. However, it is typical that only relative numbers are known, so only the rate of total mortality can be determined. There are two types of catch-curve analysis and they both assume there is no trend in fishing mortality over time. The first, cross-sectional catch curve analysis, creates a “synthetic” cohort (Quinn and Deriso, 1999) from a single year of data, and assumes that all ages have the same selectivity (catchability) and that recruitment shows no trend over time (Tuckey et al., 2007). Multiple years of data may be averaged to reduce the influence of variation in recruitment. The second, longitudinal catch curve analysis likewise typically assumes that that all ages have the same selectivity (catchability), but also assumes catchability remains the same from year to year and requires a reliable measure of relative abundance (e.g., CPUE) (Tuckey et al., 2007). The benefit of longitudinal catch curve analysis is that it does not make any assumptions about recruitment. Tuckey et al. (2007) outline diagnostics applied to multiple catch curves (i.e., several years of catch-at-age data) to evaluate whether the assumptions have been violated and the possible causes.

Catch curve methods (e.g., regression of log-numbers on age, i.e., $\ln(N_t) = \ln(N_0) - Z_t$, or the Chapman and Robson (1960) method) can be applied to estimate M directly in cases where fishing mortality is known to be negligible (e.g., the samples are taken from an MPA, assuming that M in areas open and closed to fishing are the same) (e.g., Beverton and Holt, 1957). More generally, catch-at-age data include the effects of both fishing and natural mortality. If total mortality (Z) has been estimated, for example, based on catch curve methods, it can be regressed on effort E to estimate M (Beverton and Holt, 1956):

$$Z = M + qE + \varepsilon \tag{2}$$

where q is the catchability coefficient and the intercept (effort = 0) is an estimate of the M (Quinn and Deriso, 1999). This assumes that the relationship between fishing mortality and effort is linear and measured accurately. The estimates of M will be biased if the relationship is nonlinear, as is often the case (Harley et al., 2001; Rose and Kulka, 1999), and potentially more so if the relationship between biomass and catchability is nonlinear. In addition, since catch curves assume stationary mortality over age and time for enough years to use a linear regression to reliable estimate Z, this approach is probably not practical in most situations. Therefore, catch curve analysis that does not use data from an unexploited population or does not have other data to estimate F (e.g., when integrated into a stock assessment model), is unlikely to provide reliable estimates of M.

Catch curve methods can be made more sophisticated by integrating them into population models along with the relationship $Z = M + qE$. Paloheimo (1980) developed the first cohort-based regression model using catch-at-age and effort data to estimate catchability (q), M, and recruitment using multiple regression. Paloheimo and Chen (1996) improved the method by developing a more appropriate error structure. Correlation between estimates of M and q is usually high, but separation may be possible if fishing effort varies substantially among years (Paloheimo and Chen, 1996). This approach can be considered a modification of catch-curve analysis that analyses multiple cohorts simultaneously and is a stepping stone towards contemporary integrated fisheries stock assessment methods.

Catch-at-age data are sparse for some poorly sampled or difficult to age stocks. In such cases, length-frequency data can be converted into age-frequencies using an age-length key, although the estimates of catch-at-age might be biased if the age-length key is borrowed from another year (or years). Beverton and Holt (1957) developed a simple catch curve-based estimator for mortality using length-frequency data and the von Bertalanffy growth parameters (L_∞ and K), i.e.:

$$Z = K \frac{L_\infty - \bar{L}}{\bar{L} - L_c} \tag{2}$$

where L_c is the length at first capture, selectivity is knife-edged, and $\bar{L}$ is the average length of those animals longer than L_c. This approach does not require age data for every year, but generally does require some age data to estimate the parameters of the von Bertalanffy growth curve. These methods have been extended into a family of stock assessment methods designed to estimate mortality with a series of diagnostic tests of the assumptions of these methods (e.g., a test for dome-shaped selectivity) (Then et al., 2018).

Authors	Data	Assumptions/details
Beverton and Holt (1956)	mean length	Equilibrium
Gedamke and Hoenig (2006)	mean length, several years	time-varying Z
Gedamke et al. (2008)	mean length, index of recruits	time-varying Z and recruitment
Huynh et al. (2017)	mean length, overall catch rate	time-varying Z and recruitment
Then et al. (2018)	mean length, effort	Estimates q and M (thus annual F and Z)

2.3.2 Performance

The accuracy of catch curve analysis is influenced by several factors such as whether the method is applied to data for a true cohort or to a synthetic cohort, and whether selectivity is known. In addition, any error in the age data will influence the results of a catch-curve analysis. Estimates of mortality will also be confounded with migration. There are also concerns with double use of the catch-at-age data if estimates of *M* based on catch curves are then introduced into assessments that fit to the same data as part of the overall likelihood.

Wilderbuer and Turnock (2009) applied the standard catch curve and Chapman-Robson methods, along with the empirical method of Hoenig (1983) to data for arrowtooth flounder *Atheresthes stomias* in Alaska, which is lightly fished, with the estimates of *M* differing among methods and years (0.11 – 0.51yr^{-1}). Estimates of *M* based on an integrated analysis assessment fell within the range of estimates from the other methods. The major problem with regressing Z on effort (and methods based on more sophisticated approaches) is that estimates of *M* and *q* are highly correlated as they both contribute to total mortality, and the method fails to account for transient behaviour when estimating Z, resulting in bias (Punt et al., 2021). Changes in *M* will also be confounded with changes in the catchability of survey index age-patterns as illustrated mathematically by Zhang et al. (2020).

The selectivity of the gear used to collect the catch-at-age data influences relative abundance-at-age. Typically, the data used to develop a catch curve show an initial increase in the abundance of subsequent age classes of young fish in the catch. This is typically interpreted as increasing selection to the gear, which normally is followed by a decrease that is due to mortality (Quinn and Deriso, 1999). It is therefore common to ignore the first few ages that are not fully selected by the gear. Unfortunately, it is often difficult to determine which age is fully selected and the selectivity may decline with age for older fish. Domed-shaped selectivity patterns are confounded with mortality (Thompson, 1994), and assuming a misspecified asymptotic selectivity curve will result in positively biased estimates of mortality. The choice of ages is generally done in an *ad hoc* fashion by choosing the ages that show a linear decline (Quinn and Deriso, 1999). Smith et al. (2012) review and evaluate which ages to use.

Zhou et al. (2011) estimated *M* for grooved tiger prawns (*Penaeus semisulcatus*) based on a state-space weekly delay-difference model fitted using the Bayesian framework to periods during the year when there is little recruitment, thus approximating the $Z = M + qE$ approach. The estimate of *M* was 0.053 wk^{-1} (95% credibility interval 0.028-0.078 wk^{-1}). Kienzle et al. (2016) estimated *M* for brown tiger prawns (*Penaeus esculentus*) based on a similar model fitted to catch data by week. Two of the scenarios considered by Kienzle et al. (2016) estimated *M*, leading to a very precise estimate of *M* (best model 0.032 wk^{-1}, SE 0.002). Simulation self-tests for this estimator confirmed that it was able to reproduce the true parameter values, given assumptions were not violated. Then et al. (2018) extended the estimator of *Z* developed by Gedamke and Hoenig (2006) by adding a time-series of fishing effort, and year-specific estimates of *Z*. While this method may provide reliable information on changes in *Z* over time, the correlation between *M* and *q* is high (-0.999 for Norway lobster *Nephrops norvegicus* off Portugal), resulting in poor precision in those parameters when *M* and *q* were estimated simultaneously, and thus poor ability to estimate *M*.

2.4. Estimating M within integrated population models

2.4.1 Fitting population models without consumption information

All of the major packages used to conduct stock assessments based on the ‘integrated’ paradigm include the option for estimating *M*, generally as a constant, but also optionally as a function of age, sex and time (Punt et al., 2021, see also the summary of assessment packages by Dichmont et al., 2016). In the past, there has been skepticism about estimating *M* within an assessment. For example, Schnute and Richards (1995) argued that *M* is only estimable when catch-at-age data are available back to the start of the fishery, when the population was unexploited and, in addition, constraints on the pattern of recruitment are needed. However, an increasing number of assessments conducted in jurisdictions such as the USA, Australia, New Zealand and South Africa at least consider treating *M* was an estimable parameter (Punt et al., 2021).

Intuitively, estimating *M* within an assessment is equivalent to integrating a catch-curve-type analysis into the assessment and Butterworth and Punt (1990) show that *M* is estimable (in principle) within an integrated assessment when *M* is independent of age, time, and sex, catch-at-age data are available, fishery selectivity is constant over time and asymptotic, and an index that is linearly proportional to abundance is available. Unfortunately, it is seldom the case that all of these assumptions are valid (or can be shown to be valid). Consequently, whether the estimate of *M* from an integrated assessment is reliable (in the sense of being unbiased and fairly precise) will be case-specific. The ability to estimate *M* reliably depends on the data that are available, the other parameters estimated in the assessment, and whether *M* is assumed to be time-varying (as might be expected given climate change) or age- or sex-specific. The best case is when age data at the start of a fishery provides information on *M*, while later age data provide information on total mortality, allowing the separation of fishing and natural mortality (e.g., for blue grenadier *Macruronus novaezelandiae*; Punt et al., 2001). However, it is seldom the case that age data are available from the start of exploitation. Another possibility is when the stock has collapsed and there is a fishing moratorium and catches are very low for several years. However, this situation provides information on *M* at low stock sizes and density-dependent effects could be a concern.

Fournier et al. (1998) were able to obtain fairly precise estimates of age-specific natural mortality for albacore tuna *Thunnus alalunga* using catch-at-length data, perhaps because of integrating several types of data from multiple gears, and the method of parameterizing selectivity and *M*. Several studies involving simulating data sets from known populations have explored the extent to which *M* is estimable (see Table 1 of Punt et al., 2021, for a summary), and Sippel et al. (2017) identified the age-structured production model diagnostic as a means of assessing when *M* can be estimated.

Particular concerns when estimating *M* within an assessment include that its estimate maybe highly confounded with other parameters (e.g., catchability of the index of abundance, the growth rate; trends in recruitment, and the declining slope of a dome-shared (and to a lesser extent, the entirety of any) selectivity pattern) (Butterworth and Punt, 1990) and the consequences of model misspecification. Thompson (1994) showed that estimating selectivity and *M* simultaneously is particularly problematic when the selectivity pattern is dome-shaped. Hamel (2007) estimated $M = 0.07\text{yr}^{-1}$ for darkblotched rockfish when the steepness of the Beverton-Holt stock-recruitment curve was fixed, but $= 0.10\text{yr}^{-1}$ when that parameter was estimated along with *M*. However, the overall scale of the stock and the catch advice was similar between the two models. Estimates of *M* from any catch curve approach, including integrated analysis, are vulnerable to trends in recruitment which are in turn affected by steepness.

Model misspecification is common in stock assessments and the estimate of *M* can be biased if the assessment model is misspecified (Szuwalski et al., 2018). Misspecification can arise for many reasons, including a failure to correctly represent the true spatial and stock structure in the population dynamics, use of incorrect assumptions regarding functional relationships, in particular selectivity, and whether catchability is time-varying. Szuwalski et al. (2018) show that estimating time-varying *M* when it is actually time-invariant can “address” retrospective patterns caused by other parameters being time-invariant but assumed to be time-dependent. Data weighting remains a key challenge for ‘integrated’ assessment methods with multiple data types (and complex models with many parameters), although some guidance is available (Maunder et al., 2017). Incorrect assumptions regarding data weighting will lead to incorrect estimates of the precision of estimates of management quantities, including *M*. Perhaps more seriously, assumptions related to data weighting exacerbate the problems that arise from model misspecification.

2.4.2 Fitting population models to multiple sources of information

An advantage of integrated assessment methods is that multiple data types and sources of information can be analysed simultaneously (e.g., Maunder and Punt, 2013), potentially allowing the assessment to more realistically capture the underlying population dynamics (e.g., by using spatially structured population dynamics models with several time-varying parameters). However, complex assessments involve many assumptions, which can lead to model misspecification. Each of the major stock assessment packages have different features, and hence advantages and disadvantages. It is beyond the scope of the current paper to contrast these packages and when they are the appropriate information, but this information is available in summary form in Punt et al. (2020) and at the web-site (http://toolbox.frdc.com.au/; Dichmont et al., 2021).

An advantage of integrated methods is that it is possible to include the methods outlined above into an analysis with multiple data types. Integration of multiple data sources (e.g., tagging data) into the stock assessment model allows information other than those data (e.g., catch-at-age data) to provide information on *M*. Alternatively, as with other approaches, priors can be used to transfer information on *M* from, say, an external tagging analysis or life-history covariates into the stock assessment model. Care is needed to ensure consistency between the external analyses and the stock assessment (e.g., assumptions about selectivity) and to prevent the loss of information, potentially on other model parameters, when data are used in the external analysis rather than being integrated into the stock assessment (Maunder, 2001). For example, tagging data have been integrated into stock assessment models that estimate *M* (e.g., Maunder, 1998; Hampton and Fournier, 2001) and are now included in the likelihood component of three commonly used general stock assessment models, MULTIFAN-CL (Hampton and Fournier, 2001), CASAL (Bull et al., 2012), and Stock Synthesis (Methot and Wetzel, 2013).

2.4.3 Performance

As is the case for the other methods, it is hard to evaluate the ability of assessment methods to estimate *M* within an assessment because the true value is not known for actual cases. Two generic approaches have been used. The first is to report the precision (or perceived precision) of estimates of *M* for actual stocks, and the second is to use simulation studies to determine when it possible to reliably estimate *M*.

2.4.3.1 Perceived precision of *M*

The perceived precision of the estimates of *M* depends on how the assessment is specified, with lower (perceived) variance when more parameters are pre-specified, and there is considerable variation in how precise estimates of *M* from assessments can appear to be.

For example, Cappo et al. (2000) estimated *M* for Australian "salmon" *Arripis truttaceus* using a multi-area age-structured model fitted to tag recapture data by age. Best estimates of annual survival rates were precise (0.54 ± 0.043 for mature fish and 0.74 ± 0.024 for juveniles). Candy et al. (2011) estimated *M* (independent of age and time) for Patagonian toothfish (*Dissostichus eleginoides*) using an age-structured population model for tagged animals, along with a likelihood for the catch-at-age and number of recaptures by age over time (the CCODE method of Candy [2011]). Unlike Cappo et al. (2000), the estimate of *M*, while plausible (0.155 yr^{-1}), was very imprecise (95% confidence interval 0.055-0.250 yr^{-1}). Given the variation in how assessments are specified, and which parameters are estimated or fixed, the level of precision coming out of an assessment does not directly indicate the quality of the estimate.

2.4.3.2 Simulation studies

Many simulation studies have been undertaken (see Table 1 of Punt et al., 2021). Unfortunately, there is still little generic understanding of the likely quality of estimates of *M* from integrated assessments, except that performance tends to be better when the assessment is not misspecified and with higher quality and more informative data. Of the many simulation studies, the following provide an illustration of the types of results obtained to date.

- Aanes et al. (2007) found that estimates of *M* tend to be overestimated when the true value is low and vice versa using simulations based on Northeast Arctic cod (*Gadus morhua*).
- Fu and Quinn (2000) explored whether data for pink shrimp were able to estimate time-variation in *M*, the length-at-50% selectivity (L_{50}), and catchability within the context of a size-structured population model fitted to survey biomass, length-frequency, and catch data. They found that inter-annual variation in *M* and L_{50} could be estimated reliably, but only if catchability was assumed time-invariant and known. This result is surprising and may be a consequence of growth also being assumed to be known with selectivity assumed to be asymptotic.
- Lee et al. (2011) explored whether it is possible to estimate *M* when the assessment model is correctly specified based on data for 12 US West Coast groundfish stocks. The estimates of *M* were in most cases quite accurate (bias < 5%). However, in some cases, the estimates were very biased, despite the model mimicking the assumptions in the simulation. For example, the "true" value of *M* used for sablefish (*Anoplopoma fimbria*) was 0.07yr^{-1} but the median estimated value was 0.051 yr^{-1}, i.e., a negative bias of 30%.

Lee et al. (2011) noted that the simulated data were conditioned on the original value of *M* and had no patterns in the residuals (as is common with most simulation studies). They concluded that if a simulation analysis shows that *M* can be estimated with reasonable precision and accuracy, unrealistic estimates of *M* are a good indication of severe model misspecification (e.g., use of asymptotic selectivity when selectivity is actually dome-shaped, misspecification of growth parameter values and the extent of variation in recruitment). This concept was formalized by Piner et al. (2011).

- Maunder and Wong (2011) used simulation to evaluate whether it is possible to estimate *M* (by sex) for US mid-Atlantic summer flounder (*Paralichthys dentatus*). They found that if correctly specified, the stock assessment model was able to estimate both female and male *M* with reasonable precisions but with a positive bias when true *M* was low, and a negative bias when true *M* was high. When applied to the actual data for US mid-Atlantic summer flounder, Maunder and Wong (2011) found that the estimates of *M* were quite sensitive to other assumptions of the model.
- Murphy et al. (2018) estimated *M* by sex, maturity state and time for eastern Bering Sea snow crab (*Chionoecetes opilio*) using a size-structured population dynamics model within the context of a random effects estimation framework. The estimates of time-varying *M* were surprisingly precise, and the fits to the data were almost perfect, suggesting that overfitting may have occurred.

2.4.4 Fitting population models using consumption information

Predation is a major component of *M*, particularly for juvenile fish. Predation estimates can be used to estimate *M*, or at least that component of *M* that can be attributed to predation. Several approaches have been developed to include predation into assessment models. The simplest approach is to include a covariate for *M* into the stock assessment based on predation information. For example, Methot (1989) modelled anchovy *M* as time-varying given time-series for the biomass of Pacific mackerel and Livingston and Methot (1998) incorporated predation into a population assessment model of eastern Bering Sea walleye pollock. Hollowed et al. (2000) allowed for more complex predator-prey relationships and uncertainty in predation mortality for Gulf of Alaska walleye pollock.

Predation sources based on diet information is one way to drive improved estimation of natural mortality. Another, less commonly addressed issue is mortality on predators due to *the lack of prey*. This may be particularly important for juvenile fish. Hoenig et al. (2017) note that lack of suitable prey may result in greater vulnerability to disease and may play a role in affecting natural mortality. Trochta et al. (2021) tested methods for detecting disease and sudden mortality events in Pacific herring. They found that time-varying mortality from disease could be estimated reliably.

2.4.4.1 Extended single-species assessment methods

Perhaps the simplest way to jointly model multiple stocks, and hence the interaction among them, is the approach of using correlated processes among stocks (Albertsen et al., 2017). However, most multispecies models are based on an explicit component for predation (and perhaps competition). The most common way to allow for multi-species effects in stock assessments is to treat *M* as the sum of a residual (or basal) rate of natural mortality and to add predation mortality to it, i.e.:

$$M^{i}_{y,a} = M^{i,residual}_{a} + \sum_{j} M^{i,j}_{y,a} \qquad (3)$$

where $M^{i}_{y,a}$ is the rate of natural mortality for animals of species i (the stock being assessed) and age a during year y, $M^{i,residual}_{a}$ is the residual natural mortality (i.e., mortality to due causes other than predation by the species included in the model such due to starvation and disease, and predation due to predators not included in the model) for animals of species i and age a, and $M^{i,j}_{y,a}$ is the rate of natural mortality for animals of species i and age a during year y due to predator j. Livingston and Methot (1998) modelled $M^{i,j}_{y,a}$ as the product of the number of predators of species j during year y, E^{j}_{y}, and a "catchability' coefficient, $q^{i,j}_{a}$, i.e. $M^{i,j}_{y,a} = q^{i,j}_{a} E^{j}_{y}$. Hollowed et al. (2000) extended this basic approach by scaling the predation mortality for a predator by the ratio of its consumption rate in year y to its consumption saturation point. The model developed by Hollowed et al. (2000) allowed for uncertainty in predator numbers and was fitted to conventional data sources such as survey index data as well as fishery and survey catch proportion-at-age data, but also to data on predation per unit of predator effort and predator diet data. Hollowed et al. (2000) also estimated the residual natural mortality rates for ages 1 and 3+, with that for age 2 set to the average of that for ages 1 and 3.

2.5 Multi-species assessment methods

The first stock assessment method that explicitly modelled the dynamics of multiple species was multispecies Virtual Population Analysis (MSVPA; Gislason and Hegason, 1985; Sparre, 1991; Magnusson, 1995). This approach uses diet data to estimate predator suitabilities and hence predation mortality. The process of calculating the numbers-at-age matrix involves applying the standard VPA backcalculation process based on the predation mortalities from a predation model, updating the predation mortalities based on the results of the VPA backcalculation process, and iterating these steps until convergence. In common with standard single-species VPA, this approach requires estimates of catch-at-age for all years (and species) and assumes that the catch-at-age (and diet) data are measured with negligible error.

Several integrated multispecies stock assessment methods have been developed based on the predation model on which MSVPA is based (e.g., Jurado-Molina et al., 2005, 2006; Kinzey and Punt, 2009; Van Kirk et al., 2010; Curti et al., 2013; Ross-Gillespie, 2016; Holsman et al., 2016; Trijoulet et al., 2019). These methods make use of the stomach content data for parameter estimation and differ in terms of how predation mortality is modelled and parameterized. In general, the inclusion of predation mortality in population dynamics models increases the rate of natural mortality for younger animals, with the result that estimates of recruitment from multi-species models are usually markedly higher than from single-species models.

Multispecies assessment methods are very data-intensive compared to traditional single-species methods owing to their need for data on predator rations, and depending on the model, data on the proportion of prey by age in the diets of predators by age. This limits the jurisdictions in which these types of models can be applied to data-rich stocks with surveys that permit the collection of diet data. The aim of a multispecies assessment is that the residual mortality rate ($M^{i,residual}_{a}$ in Eq. 3) is as small as possible. For example, the multispecies model developed by Punt and Butterworth (1995) to examine the impact of predation by Cape fur seals (*Arctocephalus pusillus pusillus*) on catches of the Cape hakes (*Merluccius capensis* and *M. paradoxus*) aimed to capture 95% of the mortality on large hake. This was possible in that case owing to the high levels of cannibalism and inter-species predation among the two species of Cape hake. However, it is seldom straightforward to determine how many species to include in a multispecies model given that including more species increases realism but also the complexity of the model and associated parameter estimation scheme, as well as the data requirements. Models of Intermediate Complexity for Ecosystem Assessment (MICE) (Plaganyi et al., 2014) attempt to achieve an appropriate balance between complexity and realism given the objectives of the model, and represent a way to more fully integrate multispecies models in tactical management applications.

2.6. Other approaches

2.6.1 Direct estimation

It is possible to estimate *M* for sedentary species by direct observation. For example, McShane and Naylor (1997) estimated *M* for New Zealand abalone (*Haliotis iris*) by monitoring enclosed populations and counting shells. Macpherson et al. (2000) estimated *M* for five fish species based on direct measurements at a Marine Reserve off eastern Spain.

Natural mortality can also be estimated from electronic tags using arrays of detectors (e.g., in salmon) or archival tags that can detect mortality events. (Starr et al., 2005; Patterson and Pillans, 2019; Topping and Szedlmayer, 2013). This method is not applicable to most species owing to the need to be able to track individual animals and assign changes in population numbers to natural mortality, rather than say, migration. However, acoustic telemetry tagging is seeing increased usage (e.g., Peterson et al., 2021; Lees et al., 2021) and can provide good information about *M* if enough receivers are deployed. Acoustic tagging does not suffer from the human reporting issues of conventional tagging, but incomplete detection is an issue but that has been addressed by Pollock et al. (2004). The potential for estimating *M* for more stocks will increase as the availability of large-scale receiver arrays increases.

2.6.2. Inferences from rates of increase

Smart et al. (2018) estimated natural survival for juvenile grey reef shark (*Carcharhinus amblyrhynchos*) to be 0.72 (95% credibility intervals, 0.66-0.79; Great Barrier Reef) and 0.78 (95% credibility interval, 0.70-0.85) based fitting a demographic model to data on increase rates within a Bayesian estimation framework.

3. Variation by age, sex, time, and other factors

Vetter (1988) concluded that *M* is not constant for many fish stocks and that this variability is extensive enough that it should not be ignored. *M* is not a single constant across time, age, and gender. At a minimum, *M* should be considered to be higher for young individuals, increase for old individuals, and differ between genders. Although there have been few studies that have reliably estimated age and/or sex-specific *M*, such a general practice is advisable.

3.1. Age-specific natural mortality

Vetter (1988) suggested that assessments should use age-specific M to avoid bias, a view supported by Beverton and Holt (1959) based on age-based catch curves. It is well known that fish, with their high fecundity, are among the types of animals that exhibit Type III survivorship curves. M is highest for young individuals due to predation and physiological processes (Hjort, 1914; Cushing, 1975a). Based on the observation that the exponents in Eqns T2.3.7 and T3.3.20 are approximately equal to -1/3, Lorenzen (2000) suggested that M is inversely proportional to length. The results from stocked fished studies (Lorenzen, 2000) indicate that the coefficient may vary among populations, and therefore it may need to be estimated for each population. Direct measurement of age-specific M is generally not feasible in marine systems, except where young fish have been tagged. Hampton (2000) demonstrates estimation of age-specific M for tropical tunas using mark-recapture data.

Fortunately, it is often (but not always, Rindorf et al., 2020; 2022) not critical for estimation of fishery management quantities to model M for young individuals that have low selectivity to the fishery. This is because it is only the survival of fish into the first fished ages that must be quantified. However, some situations require accurate estimates of M for young ages, such as Pacific bluefin tuna (*Thunnus orientalis*), which are caught at substantial numbers as young of the year (Ichinokawa et al., 2010) and red snapper in the Gulf of Mexico where the impact of substantial bycatch of juveniles is highly confounded with age-specific (Gallaway et al., 2017) and density-dependent M (Gazey et al, 2008; Forrest et al., 2013).

Brodziak et al. (2011) advocate for the modelling of age-specific M being a good practice for fish stock assessments. This option is available in Stock Synthesis (Methot and Wetzel, 2013) and other assessment frameworks. Age-specific M has been modelled using a piecewise linear function in assessments for Antarctic minke whales *Balaenoptera bonaerensis* (Punt et al., 2014) and bigeye (*Thunnus obesus*) and yellowfin (*Thunnus albacares*) tuna in the Pacific Ocean (e.g., Xu et al., 2020; Minte-Vera et al., 2020). Stock Synthesis' implementation of Lorenzen M is commonly employed in assessments in the U.S. Southeast region. Tagging data can be used to directly inform estimation of age-specific M by including age-specific M and mark-recapture analysis in an integrated assessment model such as Stock Synthesis. Such integrated analyses also aid in the disentanglement of age-specific M from age-specific fishery selectivity.

Relationships such as Lorenzen (1996) and McGurk (1987) do not allow for an increased M for older individuals. Senescent mortality may occur due to the declining ability to respond to stress, increasing homeostatic imbalance, increased risk of disease and parasitism, and decreasing ability to repair biological damage in older individuals (Fonteneau and Pallares, 2005). Chen and Watanabe (1989) propose an equation for age-specific natural mortality that represents three phases: initial death rate, stable death rate, and death due to senescence, which correspond to three phases of growth. By relating M to growth, they use the parameters of the von Bertalanffy equation to estimate age-specific M. Similarly, Siler (1979) provided a flexible model of survival that can be used to model high M for both young and old individuals. Siler's (1979) function includes components for immature individuals, mature individuals, and senescence:

$$M_t = a_1 \exp[-b_1 t] + a_2 + a_3 \exp[b_3 t] \tag{4}$$

The values for the five parameters are not provided and need to be assumed or estimated (e.g., Punt et al., 2014). The first term in Eqn 4 could be replaced with, for example, Lorenzen's (1996) or Gulland's (1987) models if they are considered more appropriate representations of immature mortality. Lehodey et al. (2008) used the same term for mortality of immature animals (predation) but combined it with a logistic function for senescence:

$$M_t = a_1 \exp[-b_1 t] + \frac{a_2}{1+\exp[b_2(t-a_{50})]} \tag{5}$$

where a_{50} is the age at which 50% of the senescence mortality occurs. Eqn 5 differs from Eqn 4 in that the *M* levels off at old ages, which is consistent with *M* increasing for mature individuals since the proportion mature is often modelled using a logistic curve. However, Eqn 5 does not account for senescence at old ages.

Maunder (2011) developed a model for age- and sex-specific *M* based on five assumptions: 1) *M* for younger fish is due mainly to processes (e.g., predation) that are functions of the size of the individuals; 2) *M* increases after individuals become reproductively mature; 3) maturity follows the logistic curve (refined in Appendix A); 4) *M* due to reproduction may differ by gender, but juvenile *M* is independent of gender; and 5) *M* due to senescence over and above that caused by reproduction is either small or occurs at an age for which there are few fish alive, so it is not influential. The model is based on combining Lorenzen's (2000) observation that *M* is inversely proportional to the length for young fish and Lehodey et al.'s (2008) logistic model for older fish (see Appendix A for a revised version of the model). This model has been applied recently to the stock assessment of albacore tuna (*Thunnus alalunga*) in the South Pacific Ocean (south of the equator), incorporating the Convention areas of the Western and Central Pacific Fisheries Commission (WCPFC) and the Inter American Tropical Tuna Commission (IATTC) (Castillo-Jordan et al., 2021).

3.2 Sex-specific natural mortality

There is ample evidence from sex ratios-at-age that *M* differs between males and females for many stocks (e.g., Maunder and Wong, 2011), with males often having the higher rates (Beverton and Holt, 1959). Some tuna species are notable exceptions in that female *M* appears to increase after they become mature (Cushing, 1975b), a fact Watters and Maunder (2001) associate with the higher physiological costs of reproduction (also see Appendix A). Hoenig and Hewitt (2005) present several models for analysing sex ratio data showing that sex ratio information can provide sex-specific estimates of mortality in some cases and in others can allow estimation of the difference in mortality rates between the sexes (though we note that either differential fishing mortality or differential natural mortality may be the cause). There are many examples of stock assessments where different values are pre-specified (e.g., Hamel et al., 2013; Lee et al., 2014) or estimated (e.g., Cope et al., 2016; Thorson and Wetzel, 2016; Haltuch et al. 2017) for males and females. Note that sex-specific *M* is confounded with selectivity-at-age, and differentiating between the two phenomena is challenging (e.g., Cope et al., 2016).

3.3 Time-varying natural mortality

Most models that estimate *M* assume it to be a constant over time, perhaps with some age-dependency. Exceptions to this include assessments that account explicitly for predation mortality. Time-varying *M* has been included in stock assessments using covariates (e.g., Marty et al., 2003; Deriso et al., 2008) and as random effects. Increasingly, time-variation in *M* is being included in state-space stock assessment models either directly (e.g., Swain and Benoît, 2015; Cadigan, 2016; Stock and Miller, 2021) or indirectly (Gudmundsson and Gunnlaugsson, 2012; Nielsen and Berg, 2014; Berg and Nielsen, 2016; Perreault et al., 2020; but see Aldrin et al., 2019), including in the Bayesian methods developed by Millar and Meyer (2000), Lewy and Nielson (2003) and Aanes et al. (2007). The extent of time-variation in *M* is constrained by a regularization or distribution-based penalty in these methods.

Aanes et al. (2007) and Aldrin et al. (2021) found that trends in *M* tend to be estimated better than the absolute value for *M*. Information on temporal variability in *M* can be identified when there are changes in the slopes of cohort-catch curves that cannot be accounted for by reported catches (e.g., Wiedenmann and Legault, 2022). This is consistent with how time-varying *M* (constant over size) is estimated for Bristol Bay red king crab (*Paralithodes camtschaticus*) and St Matthew Island blue king crab (*Paralithodes platypus*) where the baseline value for *M* is pre-specified rather than being estimated (e.g., Palof et al., 2019; Zheng and Siddeek, 2019). Allen et al. (2017) explored the performance of a cohort reconstruction model for salmon populations including some in which *M* was separable into age and time components and others in which *M* by age and time was estimated.

The assessment of walleye (*Sander vitreus*) in Saginaw Bay has traditionally been based on analysis of tag returns. Fielder and Bence (2014) developed an assessment method that integrated multiple sources of data, including tagging data and explored three treatments of *M*: (a) constant, (b) age-specific, and (c) time-varying. The tagging data were found to be inconsistent with the fishery data, likely due to the dynamics of the tagged population differing from that of the entire population. Model selection was accomplished using the Deviance Information Criterion (DIC), with age-varying *M* selected.

Jiao et al. (2012) developed an age-structured statistical catch-at-age model that allows for a variety of formulations for age- and time-variation in *M*. The model was fitted using Bayesian methods and DIC was used for model selection. Jiao et al. (2012) also tested whether model fits were improved by linking time-varying *M* to environmental covariates. Their results suggested that temporal variation in natural mortality was more important than age-specific natural mortality.

Recently, condition information has been used to provide estimates of a component of *M* (Casini et al., 2016; Björnsson et al., 2022; Regular et al., 2022), or provide an index of *M* (Varkey et al., 2022; Cadigan et al., 2022). This is a data type that is easy and often routinely collected, although determining critical condition values when starvation occurs may be a challenge if starvation experiments are not practical. Density-dependence may also lead to temporal variation in *M*. Density dependence may involve the effects of cannibalism and dilution of predation mortality by large year classes or recruits (e.g., Rindorf et al., 2020; Rindorf et al., 2022).

4. Discussion

The value of *M* is generally highly influential on quantities that are important for providing management advice (see Punt et al., 2021). Therefore, given the uncertainty surrounding the estimation of *M*, many stock assessments include sensitivity analyses to the (assumed) value for *M*. For example, assessments often bracket uncertainty by providing results for different levels of *M* (e.g., Hamel, 2007; Hamel et al., 2013; Haltuch et al., 2013). However, sensitivity analysis requires some notion of relative plausibility of the different levels of *M*. A sensitivity analysis using a value for *M* that is unrealistic is unhelpful for management purposes. For example, Hamel et al. (2013) profiled over values from 0.01 to 0.10yr^{-1} for aurora rockfish (*Sebastes aurora*), which includes both unrealistically low and high values for this species, and therefore may be misleading or uninformative at the extremes. The relative probability of a series of values for *M* can be calculated based on the fit to the data, although this is essentially the same as estimating *M* within the assessment, while providing a credibility interval. Bayesian analysis can be used to evaluate the relative probability of different values of *M* by combining prior information (e.g., from indirect or direct estimates of *M*) with the data used to fit the stock assessment model. This would require uncertainty estimates for the indirect estimates of *M* so that the appropriate priors could be developed (e.g., Hamel, 2015; Hamel and Cope, this issue).

Management of some species is very sensitive to the value of *M* because the management rules are based on both fishing mortality rates and stock status determinations. For example, many groundfish stocks are managed based on rules that decrease the target fishing mortality rate when the biomass is below a target level (e.g., Punt et al., 2008; Anon, 2019). Since both the estimated target biomass and fishing mortality depend on *M*, lower levels of assumed or estimated *M* often mean that the estimated target fishing mortality is lower and the target biomass is higher, leading to a 'doubling' effect on allowable catches.

Analysis of tagging data, particularly genetic (close kin) tagging (Bravington et al. 2016a), is probably the most promising direct method to estimate *M* for stocks for which adequate funding is available to conduct a well-designed study. However, it is difficult and expensive to design and implement a traditional tagging study that addresses all the issues that can bias the results. Even in data-rich cases there is debate whether the estimates of *M* are reliable (Cadigan, 2016; Rose and Walters, 2019; Regular et al., 2022).

4.1 Good practices for M in assessments

Although many new methods for estimating *M* have been developed since Vetter (1988) outlined the main concerns over three decades ago, many of these concerns remain. The same traditional methods based on violated assumptions and unreliable data are still used even though Vetter (1988) concluded that all methods have limitations or disadvantages. Attempts to estimate *M* inside stock assessment models, although much more common than in the past, are often unsuccessful. Consequently, *M* and its variability are still very poorly known for even the most studied fish stocks that have been subject to continuous exploitation for decades. *M* is frequently assumed to be constant over age, gender, or time even though this is unlikely. Unfortunately, the values of *M* often become institutionalized mainly from customary use (Zhang and Megrey, 2006). This section offers some suggestions for “good practices”, recognizing that the field is not yet really in a position to establish “best practices”.

Many values for *M* used in assessments remain based on life history theory, maximum age, and regression (LHMR) approaches. There will be cases when LHMR methods are more reliable than direct estimates and the results of stock assessments. However, LHMR methods should be used only if more direct estimates or stock assessment internal estimates are unavailable or unreliable (which, admittedly, is most of the time). If they are to be used, they should be accompanied by measures of uncertainty (e.g., Cope and Hamel, this issue; Hamel and Cope, this issue), which should be propagated into the results of the assessment either directly through Bayesian or related approaches, or through sensitivity analyses and profiles. Catch curve analyses, while crude and dependent on many assumptions that are likely to be violated, should be considered and compared to LHMR methods, especially when multiple years of catch-at-age data are available from the start of fishing or from unfished populations. However, it is preferable to integrate the catch-at-age data into the assessment and estimate *M*. This ensures that the assumptions used to estimate *M* are consistent with those used in the assessment, so that all data sources inform *M,* and that uncertainty is effectively represented. As noted in section 2.4, integrating multiple data sources within a single framework is not a panacea and it is easy to envisage situations when the estimate of *M* from a single maximum age-based approach will be less biased that the estimate of *M* from a misspecified integrated assessment.

Estimating *M* inside the assessment model may allow estimation of a wider range of sampling processes (e.g., selectivity) that may improve bias and precision of estimated quantities. Data conflicts can be evaluated within an integrated stock assessment model by using likelihood component profiling (Beyer-Rogers et al., 1997; Maunder and Starr, 2001; see Perreault and Cadigan (2021) for cases with random effects) on *M* and other approaches (Carvalho et al., 2017, 2021). This method can be more appropriate than independent analyses because it is conducted within the same framework and is therefore not dependent on the assumptions of the independent analyses. Nevertheless, it remains useful to analyse the data sets independent of the integrated model to obtain additional insights into the data and assumptions, and to evaluate the possibility that the integrated model is misspecified and the estimates of *M* biased.

Careful repeated tagging/marking experiments probably hold the most promise for determining *M* with any reasonable degree of accuracy. However, it is difficult and expensive to design and implement a tagging study that addresses all the issues that can bias the results. The development of integrated analyses (Fournier and Archibald, 1982; Methot, 2009; Maunder and Punt, 2013; Punt et al., 2013) that allow the inclusion of multiple types of data into the stock assessment, including tagging data (e.g., Maunder, 1998, 2001, 2004; Hampton and Fournier, 2001; Goethel et al., 2011) along with more recent tagging-based methods (e.g. Hoenig et al. 1998a, b, Myers and Hoenig 1997, Jiang et al. 2007a,b) may allow relaxation of some of the violated assumptions required for historical methods for analyzing tagging data. Integrated analysis also allows other information (e.g., catch-at-age data) to provide information about *M* in addition to the information in the tagging data, which may lead to lead to improved estimates. This suggests that integrated analysis with tagging data should be the gold standard for fisheries stock assessment of exploited fish stocks. However, care should be taken to check for model misspecification, which can lead to an artificial perceived ability to estimate *M*, and to apply appropriate weights to each data type. Conducting a tagging-only analysis using a more recent tagging-based method is one way to potentially identify model misspecification in a complex integrated assessment. Finally, close-kin tagging is a promising method that may provide the best estimates of *M*. This is mainly because the approach avoids some of the common assumptions required in traditional tagging studies.

We see the value for using multi-species models to estimate *M* (and its variation with age and time), but recognize that the age-classes subject to predation by monitored species are often those that have yet to recruit to the fishery such that estimates of quantities of management importance such as spawning stock biomass are often very similar between conventional assessment methods and those that account for predation mortality (e.g., Kinzey and Punt, 2009; Holsman et al., 2016; Adams et al., 2022). Yet we note that the parameter controlling the degree of density-dependence in spawner-recruitment is equally difficult to estimate (Lee et al., 2012; Thorson et al., 2019), and with multiple fished species of predators preying on juveniles, perhaps more insight on spawner-recruitment curvature can come from multi-species models through, for example, explaining temporal variation in recruitment (Rossberg et al., 2013).

The success of estimating *M* within a stock assessment model varies among stocks and depends on the amount and type of data that are available, the assumptions that are made in the assessment, and how *M* is modelled. Data used in other approaches to estimate *M* can be included in stock assessments, and the stock assessment approach more appropriately identifies and deals with model assumptions, improves consistency, and propagates error. This automatically allows total mortality to be split into fishing and natural mortality since catch is also integrated into the assessment. Information from indirect methods or other species can be included in the assessment model using priors. This requires estimating the uncertainty in the estimates of *M* (Hamel and Cope, this issue; Cope and Hamel, this issue) and is probably the best way to force analysts to think about how reliable their indirect estimates of *M* really are. The assessment model will then update the estimates of *M* based on the information available in the data used in the assessment model.

Variability in *M* with age, gender, time, and other factors may be influential on management advice and has yet to be dealt with as a generally accepted approach. In particular, it is important to include age-specific *M* in an assessment model when some fisheries catch much younger fish than other fisheries (Gallaway et al., 2017). Collection of sex composition data has identified that sex-specific differences in *M* are common and can be used as the basis to estimate sex-specific *M* (e.g., Maunder and Wong, 2011), highlighting the importance of collecting sex-composition data.

It is advisable to use a variety of approaches to estimate *M* (Quinn and Deriso, 1999; Cope and Hamel, this issue; Höffle and Planque, this issue). We suggest that for each species assessed, a comprehensive evaluation of *M* should be undertaken (e.g., Maunder and Wong, 2011). For example, Hewitt et al. (2007) provided an extensive evaluation of *M* for Chesapeake Bay blue crab *Callinectes sapidus*. They compared estimated survival rates from tagging data using a Brownie model and separated out *M* by estimating exploitation rates from catch and survey estimates of abundance. These were compared with indirect methods based on empirical relationships and life history theory. The estimates from tagging data, indirect methods, and from an assessment model (Miller et al., 2005) were higher than previous estimates that were based on conservative assumptions about maximum age.

Unfortunately, irrespective of how estimation of *M* is addressed in the assessment and how much data are available for estimation purposes, some uncertainty in *M* will remain. Best practices for addressing this uncertainty include (a) capturing estimation uncertainty to maximum extent possible, e.g. by estimating *M* with a prior and hence representing uncertainty in *M* in the posteriors for model outputs or including *M* as an axis of uncertainty in ensembles (Maunder et al., 2020), (b) accounting for uncertainty in *M* when setting scientific uncertainty buffers (e.g. within the US deciding on the size of the buffer between the overfishing level and the acceptable biological catch, e.g. Monk et al., 2018), (c) providing decision makers with ‘decision tables’ that show the sensitivity of assessment outcomes to uncertainty in *M* (e.g. Monk et al. 2018), and (d) using management strategy evaluation (Punt et al., 2016) to identify harvest strategies that are as insensitive to uncertainty in *M* as possible.

4.1 Future research

Despite some progress in improving methods to represent and estimate *M* either inside or outside the stock assessments, there is substantial work to be done. The ultimate goal is to provide management advice for exploited fisheries. Therefore, evaluation of the reliability of methods for estimating *M* should be viewed in this context. Several studies have reviewed the current literature and evaluated the performance of a particular approach or group of approaches, and proposed an improved approach (e.g., Then et al. 2018). Other studies have tackled issues with a particular estimator (e.g., Hoenig, 2017), and others that have evaluated the consequences of estimation error in terms of management advice (e.g., Punt et al., 2021). However, there has not been a comprehensive evaluation of the alternative approaches and their appropriateness for providing management advice. Here we have attempted to review the literature and provide guidance on the potential of different approaches when applied for stock assessment purposes.

Further research is needed to determine the appropriateness of using the alternative approaches for the provision of management advice, particularly the representation of uncertainty and how this is taken into consideration in the advice provided to managers. The type of management advice differs depending on the characteristic of the population, fishery, and management objectives. In addition, data availability will constrain the approaches that can be applied. Therefore, it is difficult to provide thorough advice that covers all situations. However, integrated stock assessment models that provide stock status evaluations or evaluate harvest control rules are commonly applied and is an area that allows focused research. Only limited simulation studies to evaluate the performance of estimating *M* in integrated models have been conducted (e.g., Maunder and Wong, 2011; Lee et al. 2011; Aldrin et al. 2021; Cronin-Fine and Punt, 2022). Some have evaluated more complicated forms of natural mortality such as age- or sex-specific formulation (e.g., Lee et al., 2011) and time-varying natural mortality (Aanes et al., 2007; Jiao et al. 2012). A more thorough simulation analysis is needed. This may require using a more complex operating model that includes multiple interacting species and environmental drivers.

The sensitivity of data-limited stock assessments to uncertainty in *M* remains an area for exploration, though it is not uncommon to incorporate wide priors and Monte Carlo simulation to incorporate uncertainty in *M* (Dick and MacCall 2011, Cope 2013). This research should evaluate not only framework-specific data-limited approaches (e.g., LBSPR, DB-SRA), but also equivalently specified approaches in an integrated model (e.g., Cope 2013; Rudd et al., 2021) and more fully specified integrated models that better represent the uncertainty.

In conclusion, the fisheries science community should spend more effort on understanding and estimating fundamental population dynamic process parameters, such as *M*, that are highly influential on management advice. We recommend using approaches that use all the available information and appropriately represent uncertainty. This essentially means estimating *M* in the assessment, using priors from indirect information (e.g., relationships with maximum age), and integrating direct information into the stock assessment.

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Table 1. Equations for representing or estimating natural mortality. M is the instantaneous rate of natural mortality, K is the growth rate, L_∞ is the asymptotic length, W_∞ is the asymptotic weight, t_0 is the theoretical age at which the fish would have length zero, t_m is the age at maturity, t_{m*} is the age at the end of reproductive span (where senescence starts; Chen and Wantanabe, 1989), L_m is the length at which 50% of a year-class reaches maturity, t_{max} is the maximum age, p is the proportion surviving to the maximum age, T is water temperature, GSI is the gonadosomatic index, L is length, W is body weight, M^* is the limiting value of M approached by the largest fish, β is the exponent of the weight-length relationship, t_c is the critical age (the time that the cohort achieves its maximum biomass, Zhang and Megrey, 2006).

Table 1a. Theoretical approaches.

Approach	**Reference**	**Notes**	**Equation**	**Eqn No**
Life history approaches				
Jensen t_m	Jensen (1996)		$M = 1.65/t_m$	T1.1.1
Jensen K	Jensen (1996)		$M = 1.5K$	T1.1.2
Roff	Roff (1984)		$M = 3K/(\exp(t_m K)-1)$	T1.1.3
Zhang and Megrey	Zhang and Megrey (2006)	t_c could be t_m or a fraction of t_{max}	$M = \beta K/(exp(K(t_c - t_0)) - 1)$	T1.1.4
Beverton	Beverton (1992)	$L_m / L_\infty = 3/(3+M/K)$	$M = K\left(\frac{3L_\infty}{L_m} - 3\right)$	T1.1.5
Chen and Watanabe	Chen and Watanabe (1989)	$t_{m*} = -\frac{1}{K} ln[1 - e^{Kt_0}] + t_0$ $a_0 = 1 - e^{-K(t_{m*}-t_0)}$ $a_1 = Ke^{-K(t_{m*}-t_0)}$ $a_2 = -\frac{1}{2}K^2 e^{-K(t_{m*}-t_0)}$	$M = \begin{cases} \frac{K}{1 - e^{-K(t-t_0)}}, & t \le t_{m*} \\ \frac{K}{a_0 + a_1(t - t_{m*}) + a_2(t - t_{m*})^2} & t \ge t_{m*} \end{cases}$	T1.1.6
Maximum age				
Proportion surviving to maximum age		p = proportion remaining	$M = -ln(p)/t_{max}$	T1.2.1
Rule of thumb		$p = 5\%$	$M = 3/t_{max}$	T1.2.1a
M correlations				
Gulland-W	Gulland (1987)		$M = M(L/L_\infty)^{-1.5}$	T1.3.1
Gulland-L	Gulland (1987)		$M = M(W/W_\infty)^{-0.5}$	T1.3.2

Table 1b. Non-recommended empirical estimates. * = old data set ^ = questionable substitution # = no transformation ‘ = overly complex

Approach	Reference	Notes	Equation	Eqn No
Maximum age				
Inverse relationship-1	Hewitt and Hoenig (2005)		$M = 4.22/t_{max}$	T2.2.1a*^
Inverse relationship-2	Hamel (2015)		$M = 4.374/t_{\max}$	T2.2.1b*
Inverse relationship-3	Then et al. (2015)		$M = 5.109/t_{\max}$	T2.2.1c#
Hoenig	Hoenig (1983)	Fish, converted from $\ln(M) = 1.46 - 1.01\ln(t_{max})$ Mollusks, fish, and cetaceans, Converted from $\ln(M) = 1.44 - 0.982\ln(t_{max})$	$M = 4.3060 t_{max}^{-1.01}$ $M = 4.2207 t_{max}^{-0.982}$	T2.2.2a*’
Hoenig-revised-1	Then et al. (2015)	Converted from $\ln(M) = 1.717 - 1.01\ln(t_{max})$	$M = 5.5678 t_{max}^{-1.01}$	T2.2.2b’
Hoenig-revised-2	Then et al. (2015)	Nonlinear least squares	$M = 4.899 t_{max}^{-0.916}$	T2.2.2c#
M correlations				
Pauly	Pauly (1980)	Converted from $\log_{10}(M) = -0.0066 - 0.279\log_{10}(L_\infty) + 0.6543\log_{10}(K) + 0.4634\log_{10}(T)$	$M = 0.9849 K^{0.6543} L_\infty^{-0.279} T^{0.4634}$	T.2.3.3*
Empirical K	Jensen (1996)		$M = 1.60K$	T2.3.4a*#
Empirical K-revised-1	Hamel (2015)		$M = 1.753K$	T2.3.4b*
Empirical K-revised-2	Then et al. (2015)		$M = 1.692K$	T2.3.4c#
Ralston	Ralston (1987)		$M = -0.0666 + 2.52K$	T2.3.5*
Empirical t_m	Charnov and Berrigan (1990)		$M = 2/t_m$	T2.3.6*
Gunderson	Gunderson (1997)		$M = 1.79GSI$	T2.3.7#
McGurk	McGurk (1987)	Converted from $\ln(M) = -4.778 - 0.397\ln(W)$ for daily mortality	$M = 3.07W^{-0.397}$	T2.3.8*

Peterson - Wroblewski	Peterson and Wroblewski (1984)		$M = 1.92W^{-0.25}$	T2.3.9*

Table 1c. Equations for representing or estimating natural mortality. Only the recommended estimator of each class is provided, other estimators are given above.

Approach	**Reference**	**Notes**	**Equation**	**Eqn No**
Maximum age				
Inverse Relationship	Hamel and Cope (this issue)	*Uses Then et al. (2015) data* *SD in log space = 0.31*	$M = 5.4/t_{\max}$	T3.2.1
M correlations				
Pauly-revised	Then et al. (2015)		$M = 4.1181K^{0.73}L_{\infty}^{-0.33}$	T3.3.3
Empirical K	Hamel and Cope (this issue)	*Uses Then et al. (2015) data* *SD in log space = 0.85*	$M = 1.55K$	T3.3.4
Gunderson-revised	Hamel (2015)		$M = 1.817GSI$	T3.3.7
Lorenzen	Lorenzen (1996)		$M = 3W^{-0.288}$	T3.3.10

Table 2. Estimates of M (yr^{-1}) from K (yr^{-1}) using Jensen’s (1996) theoretical relationship $M = 1.5K$ for the values of K estimated in the English sole stock assessment (Stewart, 2007).

	K		*M*	
Year	Female	Male	Female	Male
1876-1960	0.36	0.48	0.54	0.72
1961-1970	0.34	0.45	0.51	0.68
1971-1980	0.24	0.33	0.36	0.49
1981-1990	0.22	0.29	0.32	0.43
1991-2006	0.22	0.29	0.33	0.44

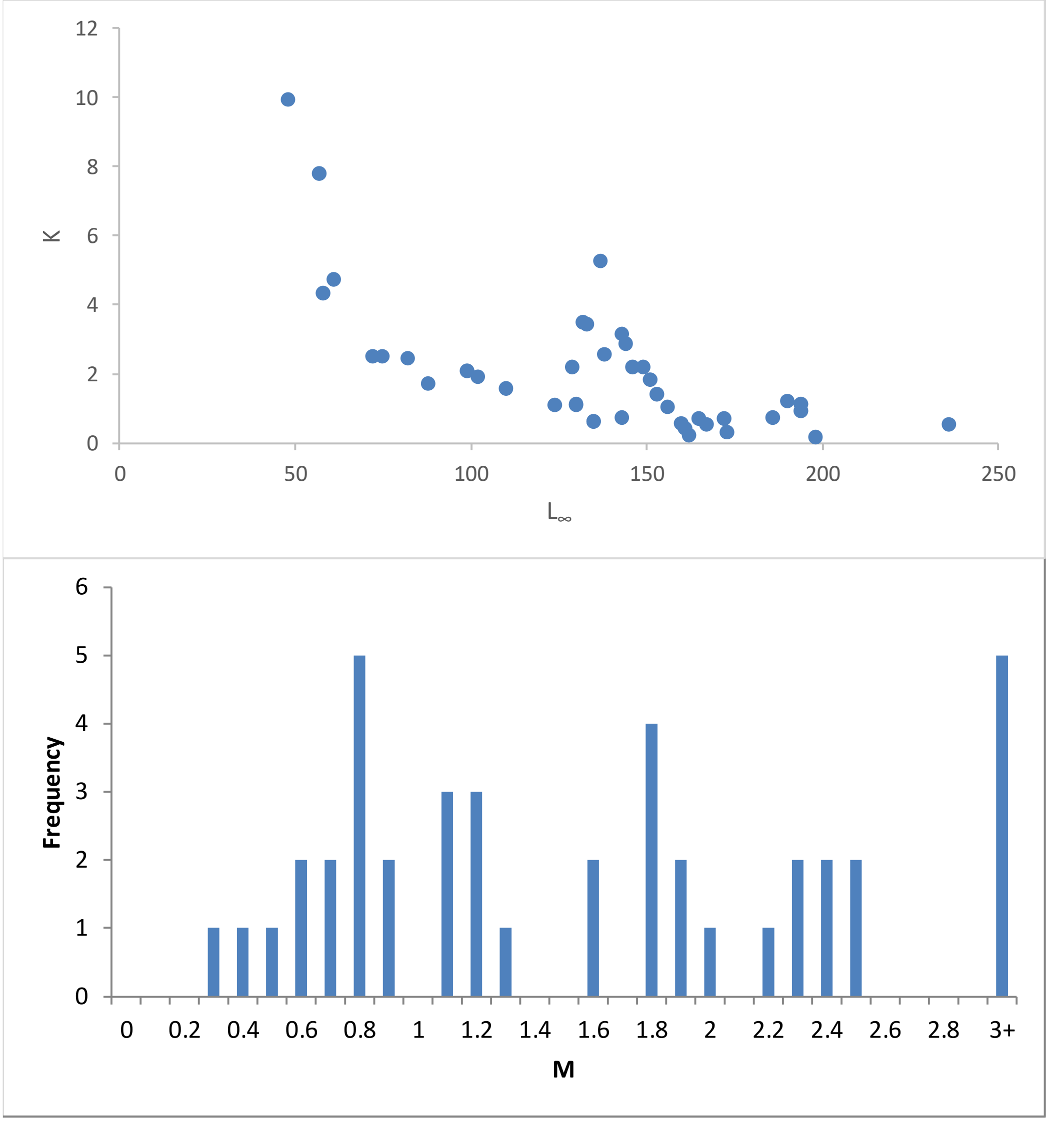

Figure 1. Correlation between von Bertalanffy growth rate and asymptotic length parameters K (y^{-1}) and L_∞ (cm) (top) and estimates of natural mortality, M (y^{-1}) (bottom) based on Jensen's empirical relationship, $M = 1.6K$ for the 42 estimates of the von Bertalanffy K for dorado (*Coryphaena hippurus*) from different data and stocks presented in Chang and Maunder (2012).

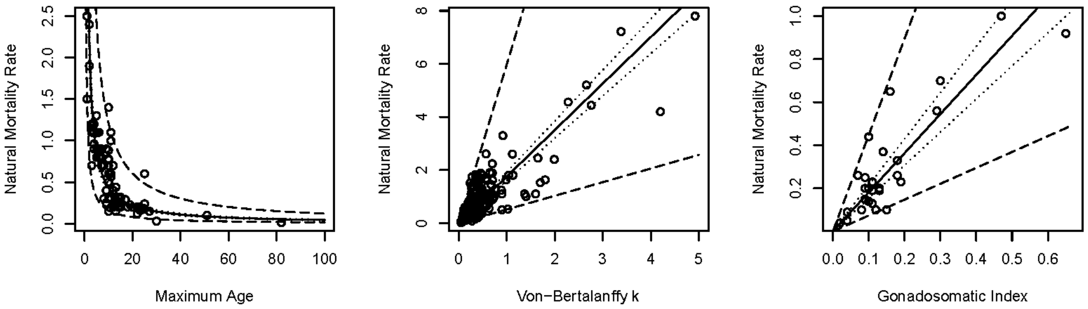

Figure 2. Relationships between maximum age (left), von-Bertalanffy K (middle), and gonadosomatic index (right) and natural mortality with 95% confidence intervals (dotted lines) and prediction envelopes (dash lines) from Hamel (2015).

Appendix A: A suggested model for natural mortality

A general model for age- and sex-specific natural mortality that expands that developed by Maunder et al. (2009) and Maunder (2011), and is based on the assumptions outlined in the main text:

$$M_{s,a} = M_{juv}\left(\frac{L_{s,a}}{L_{mat*}}\right)^{\lambda} + \frac{M_{mat,s} - M_{juv}\left(\frac{L_{s,a}}{L_{mat*}}\right)^{\lambda}}{1 + exp\left[\beta_s\left(L_{s,a} - L_{50,s}\right)\right]}$$

with the defaults $\lambda = -1.5$ from Gulland(1987), β_s and $L_{50,s}$ from the maturity curve, $M_{mat,s} = 5.4/t_{max,s}$ (Hamel and Cope, this issue) if t_{max} is available otherwise $M_{mat,s} = 4.118K_s^{0.73}Linf_s^{-0.33}$ (Then et al. 2015) and $M_{juv} = 3W_{mat*}^{-0.288}$ from Lorenzen (1996), L_{mat*} and W_{mat*} are the length and weight of a fish when they first become mature for either sex (could be set at the minimum length over both sexes when 5% of the fish are mature) or some other convenient corresponding length and weight of a fish before it becomes mature.