Studies of Mortality Estimation

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By

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To my parents, who believed in the importance of education and supported the pursuit of my dreams, and to my lifelong mentors, Denis Lu and Hai Eng, who saw something more in me than I did in myself.
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ABSTRACT

Instantaneous total mortality rate $Z$ can be partitioned into two components: fishing, $F$, and natural mortality, $M$. A number of data-poor methods have been developed to estimate $Z$, $F$, and $M$, and these methods tend to rely on fairly restrictive assumptions as well as on data types that are easy to obtain, e.g., length or other life history information. The overarching goal of this dissertation is to contribute to the advancement of methods for estimating these important and influential stock parameters. The relevant issues and the gaps in knowledge pertaining to these data-poor methods are outlined in the Introduction chapter (Chapter 1). The research papers presented in this dissertation fall into two main categories, namely, the evaluation of existing methods and the improvement of existing methods to estimate mortality rates. In Chapter 2, Monte Carlo simulation is utilized to compare the performance of two length-based methods developed by Beverton and Holt (1957) and Ehrhardt and Ault (1992), for estimating $Z$. I examine the impact of (1) variability in size at age and (2) the method of handling length truncation on the performance of the estimators. Results show that the Ehrhardt-Ault method exhibits complex patterns of bias and is not unequivocally better than the Beverton-Holt method. In Chapter 3, an existing non-equilibrium, mean length-based estimator of $Z$ is modified to use additional information on fishing effort. The $Z$ parameters are replaced with $Z = qf_t + M$ where $q$ is the catchability coefficient and $f_t$ is the fishing effort in year $t$. Thus, only $q$, $M$, and the residual error need be estimated. This methodology appears promising for estimating $F (= qf)$ and $M$, based on simulation studies. Furthermore, even if the estimates of $F$ and $M$ are imprecise and highly correlated, the resultant estimates of $Z$ are year-specific and may be quite precise. The method may serve to bridge the gap between data-poor and data-rich methods to estimate $Z$. Chapter 4 addresses a long-standing gap in knowledge with respect to the ranking and predictive performance of existing empirical estimators of natural mortality of fish stocks. To address this question, a dataset of over 200 direct $M$ estimates and corresponding life history parameters from unique fish species was compiled. Using this dataset, we were able to definitively quantify the predictive ability and update the equations of four widely used empirical estimators and their variants. Estimators based on maximum age perform substantially better than those based on growth parameters, either with or without consideration of water temperature. Results from this research will provide useful tools and guidelines for stock assessment scientists who need to estimate $M$ and $Z$ for both data-poor and data-rich stocks.
AUTHOR’S NOTE

The chapters that comprise this dissertation were written in manuscript format for a scientific publication. Thus, the formatting of each chapter follows the guidelines of the publication to which the manuscript was or will be submitted. At the time of writing, citations for individual chapters are as follows:

CHAPTER 2

CHAPTER 3

CHAPTER 4
Studies of Mortality Estimation
CHAPTER 1

General introduction
INTRODUCTION

Instantaneous total mortality rate, $Z$, can be partitioned into two components: fishing, $F$, and natural mortality, $M$. Mortality rates, particularly $M$, are keystone parameters in stock assessments as they represent loss terms in a surplus production model and are measures of stock productivity as well as exploitation rates, which are of great interest to stock assessment scientists (Clark, 1999; Lee et al., 2011). However, mortality rates are difficult to estimate directly and reliably. Sampling and aging demands for the mortality parameters are also highly resource-intensive and costly.

Several methods have been developed to estimate $Z$ and the reliability of these methods depends on specific assumptions being met in the data analyzed. An extensive review of this subject has been given by Beverton and Holt (1956). The general principles outlined in that review include (1) assumptions of theoretical methods in estimating $Z$ must be tested by observations or experiments before acceptance of the derived $Z$ estimates, and (2) variability and bias in sampled data can affect accuracy of $Z$ estimates in non-intuitive ways – these are still relevant in present day fisheries. An important point to note is that the estimation of $Z$ is easier than the estimation of the individual components $F$ and $M$. 
Reviews that specifically address methods and current issues in the estimation of \( M \) in fish stocks have been conducted by Vetter (1988), Siegfried and Sansó (2009), and Brodziak et al. (2011). A common thread among these reviews is the concern that \( M \) is often assumed to be a constant in many stock assessments, at least for the post-juvenile stages, even though a large body of evidence indicates that \( M \) may vary spatially, temporally, seasonally, by age, by stocks within species, and by sex. Another concern pertains to the degree of reliability of existing methods that are used to estimate \( M \) (and \( Z \)). Some of the other important issues raised in the reviews that are relevant to this dissertation will be highlighted in the individual chapters.

Depending on the data used, the methods for estimation of mortality rates can be loosely categorized as data-rich or data-poor. This dissertation will focus on the latter category of methods for estimating mortality rates. The development and reliability of data-poor methods are of primary interest given that (1) targeted stocks need to be assessed regardless of whether sufficient or reliable data are available, (2) mortality rates, especially \( M \), are important and influential stock assessment parameters but options to estimate these for data-poor stocks are very restricted, (3) existing methods that are widely used may not have been evaluated with respect to robustness and bias, and (4) incorporation of additional information may help address certain restrictive assumptions in simpler models and improve estimation of mortality components.

The discussion in this chapter will focus primarily on description of data-poor methods to estimate mortality rates as well as critical knowledge gaps
associated with these methods. Discussion of data-rich methods is made briefly when the methods are relevant to this dissertation. Excluding this general introduction and a conclusion chapter, the dissertation consists of three manuscripts, written in journal format, that broadly fall into two categories, i.e., (1) evaluation of existing methods, and 2) development of new methodology. Briefly, the first part of the dissertation will compare the performance of two mean length-based estimators of total mortality rates, followed by development of an extended non-equilibrium method to estimate year-specific $Z$ from time series data of mean length and fishing effort. The final portion of the dissertation comprises an evaluation study of existing empirical estimators of natural mortality.

**Data-rich methods**

Data-rich methods, as the name suggests, require substantial amounts of data to account for the complexities modeled and the number of parameters to be estimated. Hence application of these methods tends to be restricted to commercially important stocks. Commonly used data-rich methods to estimate mortality rates include cross-sectional and longitudinal age-based catch curve analyses (e.g., Ricker, 1975; Chapman and Robson, 1960), effort-based catch analyses (e.g., Paloheimo, 1980), mark-recapture models (e.g., Seber, 1973; Hoenig et al. 1998a, b), estimation of predation rates from food webs (e.g., Tsou and Collie, 2001), and statistical catch-at-age models (e.g., Stock Synthesis (see
Methot and Wetzel, 2013)). For the purpose of this dissertation, only the catch methods will be discussed below.

Catch curve analyses, by determining the best fitted regression to the descending limb of log-transformed age frequency data, yield $Z$ estimates that approximate $M$ when it is possible to assume that the stock is unexploited or lightly fished, i.e., $F \approx 0$. Some of the common assumptions associated with catch curves are constant selectivity and recruitment over time (when using cross-sectional analyses that track multiple cohorts), density-independent and constant post-recruit $M$ over age and time, and no errors in aged samples. These restrictive assumptions are often not met in the data collected, but problems can be detected visually from a curvilinear catch curve.

Despite the disadvantages of age-based catch curves, this method is commonly applied to obtain direct estimates of $Z$ or $M$. When age composition data are available by sex or areas, one can obtain sex-specific and stock-specific estimates of $Z$ and $M$. Catch curve methods that are robust to violations of assumptions, such as those proposed by Chapman and Robson (1961) and evaluated by Dunn et al. (2002) and Smith et al. (2012), may yield more useful estimates of $Z$ or $M$ than other methods such as non-weighted regression.

\[1\text{In the dataset of } M \text{ for over 200 fish stocks compiled for Chapter 4 of this dissertation, about 70\% of the } M \text{ estimates had been derived from age-based catch curve methods.}\]

\[2\text{The robust Chapman and Robson method is used to revise } M \text{ estimates for select fish stocks in the dataset compiled for Chapter 4.}\]
Simple methods involving joint analyses of several catch curves and fishing effort data to estimate $M$ involve determining the relationship between $Z$ and effort via regression or manipulation of various ratios to estimate the $Z$ value at zero effort ($F \approx 0$). Issues arising with such analyses include (1) the need for large contrast in effort data across a number of years in order to obtain a reasonable estimate of $M$, (2) the assumption of representative age composition data and constant catchability over time may not be met, (3) varying selectivity and non-standardized fishing effort when multiple fishing gears and vessels are deployed, and (4) estimation of $M$ can be confounded with other correlated parameters such as catchability. Some of these issues are examined further in Chapter 3 using simulation to study a newly developed method that may bridge the gap between data-rich and data-poor stocks. Specifically, year-specific effort, $f_i$, is incorporated in the non-equilibrium mean-length-based estimator of Gedamke and Hoenig (2006) to obtain estimates of $M$, catchability $q$ and year-specific $Z (= qf_i + M)$.

Data-poor methods

Data-poor methods to estimate $Z$ and $M$ can be loosely categorized as direct or indirect methods. The former rely on the use of information that pertains strictly to the stock of interest, such as length information. Length is a convenient surrogate for age, either due to lack of resources for aging or due to age determination not being possible such as in crustaceans. Length-based methods to estimate $Z$ and $M$ are often based on, and therefore share assumptions similar to,
their age counterparts (e.g., length-converted catch curve by Pauly (1990) and mean length-based estimator by Beverton and Holt (1956)). Gulland and Rosenberg (1992) provided a thorough review of length-based stock assessments, including methods to estimate $Z$ and $M$.

While length frequency data are relatively easier and cheaper to obtain than age data, they are also highly variable such that a single age can correspond to a large range of lengths for many fish species. Assumptions of no individual variability in growth in length-based methods are not tenable, and the robustness of these methods in the face of growth variability should be evaluated carefully. Characterizing growth rates and variability is an important aspect of applying many length-based methods to estimate $Z$.

Indirect methods, on the other hand, ‘borrow’ data from multiple stocks or species, typically data-rich ones, to inform estimation of the parameter of interest, in this case, $M$. (Punt et al., 2005). Indirect approaches generally utilize meta-

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$^1$The mean length-based methods of Beverton and Holt (1956) and Ehrhardt and Ault (1992) were evaluated for bias and precision when applied to simulated length samples that were subject to varying degree of upper truncation under reasonable scenarios of growth variability (Chapter 2).

$^2$Estimates of standard deviation in length at age, based on literature values as well as fitted growth curves, were used to parameterize simulations of growth variability for Chapter 2. Effects of growth variability were also examined for the non-equilibrium mean length method in Chapter 3.
analyses, possibly in conjunction with theoretical considerations, to develop an empirical relationship between $M$ and predictive parameters, such as the von Bertalanffy growth coefficients, longevity, and water temperature (e.g., Pauly, 1980; Hoenig, 1983). The reliability of the developed predictive equation hinges, in part, on (1) quality of the data, (2) universality of the relationship across broad taxonomic or ecological groups, and (3) amount of variability accounted for in the derived empirical equation.

The ease of application of these methods to estimate $M$ has given rise to the development of many different indirect estimators; they are now routinely used to obtain estimates of $M$, or to cross-check direct estimates. However, the use of these methods yield highly variable $M$ estimates for a given stock, calling into question their general reliability. Pascual and Iribarne (1993) suggested that these empirical estimators be evaluated on the basis of their predictive power rather than merely on goodness of model fit but did not provide conclusive guidelines on how this should be done or which estimators are preferred. A comprehensive evaluation of these methods is necessary, particularly of their predictive performance, but it is an arduous task given that (1) we do not know true $M$ for any fish and (2) these estimators rely on different predictor variables.

Another strong contention to the use of these indirect estimators of $M$ is the usefulness of a point estimate for a parameter that potentially varies considerably over time and space. Do methods that account for the spatio-temporal variability render these indirect estimators obsolete? Some recent research suggests that the assumption of a constant $M$ in more complex models
has merit, even when the underlying $M$ is age and time-varying (e.g. Deroba and Schueller, 2013; Johnson et al., (in press)). Chapter 4 examines the question of which empirical estimator(s) is (or are) preferred on the basis of reproducibility of direct $M$ estimates; updated versions of the preferred estimators are provided as well.
REFERENCES


CHAPTER 2

Comparison of two length-based estimators of total mortality:

a simulation approach
Length-based methods for estimating the total mortality rate, $Z$, are appealing due to their potential application in data-poor situations, particularly when assessing tropical and invertebrate fisheries where age composition data are lacking. We evaluate two length-based estimators due to Beverton and Holt (1956) and to Ehrhardt and Ault (1992) for precision and accuracy when applied to simulated length data generated under varying combinations of $Z$ rates, growth rates, variability in length at age, degree of actual truncation of the age distribution on the right, and the degree of length truncation imposed by the data analyst. The Beverton-Holt method generally overestimates $Z$, with bias ranging from -5% to +40%, when the abundance of the oldest age groups is less than that associated with a constant mortality rate; the bias in the Ehrhardt-Ault method ranged from –80% to +140%, depending on the $Z$ and $K$ combinations, the degree of imposed length truncation, and the method for mean length calculation. In general, the Ehrhardt-Ault estimator exhibited complex behavior which made it difficult to summarize the direction and magnitude of the bias and mean squared error. The best length truncation to impose on the length samples to apply the Ehrhardt-Ault method often did not coincide with the ‘true’ length of truncation especially with more realistic scenarios of variability in length-at-age. Additional simulations parameterized with the life history of two tropical species did not provide concrete support for the Ehrhardt-Ault estimator as being superior to the Beverton-Holt method when applied in tropical fisheries settings. The Beverton-Holt method has the advantage of having known directional biases and predictable behavior. We recommend a case-by-case evaluation when considering the usage of the Ehrhardt-Ault method.
INTRODUCTION

Length-based methods for assessing stock status have gained widespread use for data-poor stocks where age-based methods are typically not applicable. The idea behind these methods is to use length information as a proxy for age. One of the earliest of such methods to estimate total instantaneous mortality rate, \( Z \), from length distribution was developed by Beverton and Holt (1956). The Beverton-Holt (BH) estimator of \( Z \) is based on the mean length of a sample of fully recruited fish as well as knowledge of the von Bertalanffy growth parameters. The estimator is applied under the assumption of equilibrium conditions, i.e., the observed mean length reflects the current \( Z \) rate experienced by the stock (Gedamke and Hoenig 2006). In addition, the estimator is based on the assumptions of \( Z \) operating independently of size, no individual variability in growth and continuous and constant recruitment into the fishery.

Despite these restrictive assumptions, the BH estimator remains appealing due to its simplicity and minimal data requirement. The behavior of the estimator with respect to the violations of assumptions has been explored: Wetherall et al. (1987) examined the effects of sample size, actual \( Z \) magnitude and unknown von Bertalanffy parameters; Ralston (1989) looked at the effects of seasonal recruitment; Chih (2011) explored impacts of cluster sampling on sample mean lengths; Hufnagl et al. (2013) examined seasonally varying growth, mortality and
recruitment. In addition, various improvements to the BH method have been proposed: Powell (1979) suggested various ways of estimating the parameters in the BH method; Ebert (1981) substituted the Richards function for the von Bertalanffy growth equation and allowed for periodic recruitment; Ehrhardt and Ault (1992) adjusted the BH estimator to account for upper truncation in the length distribution (discussed in further detail below); Gedamke and Hoenig (2006) derived a non-equilibrium version of the BH method which estimates period-specific mortality rates from a time series of mean length; Gedamke et al. (2008) extended the non-equilibrium approach to allow for variable recruitment by incorporating a year-specific index of recruits in the model; Then (this dissertation) incorporated the use of fishing effort data in addition to mean length observations to estimate year-specific Z rates.

Ehrhardt and Ault (1992) questioned the use of the BH estimator for tropical fisheries. Their first argument is that these fish stocks display high growth and mortality rates and typically have finite exploitable life spans. They modeled a knife-edge upper limit to the life span which corresponded to a knife-edge maximum length in the length-frequency distribution. Second, the use of multiple, highly selective, artisanal fishing gears in many tropical fisheries results in not only lower but upper truncations in the length frequency distributions. Upper truncation is not accounted for in the derivation of the BH method. Ehrhardt and Ault (1992) incorporated an upper age parameter \( t_\lambda \) in their model and then substituted a function of length for \( t_\lambda \) in order to derive an estimator that uses length data. Thus, the data analyst must specify an age – and the corresponding
length – below which fish are subject to a constant natural mortality rate and are fully vulnerable to the fishing gear.

The Ehrhardt-Ault (EA) estimator has similar assumptions as the BH estimator. Ehrhardt and Ault showed that their estimator was unbiased under the conditions in their simulations, but did not account for varying size at age. The EA estimator requires numerical methods to solve for $Z$ and requires the specification of an $L_\lambda$ input value which reflects the upper length and corresponding age truncation that is presumably occurring in the length frequency data. Clear guidelines are lacking as to how one might detect this upper truncation or determine the appropriate value to apply for $L_\lambda$ when analyzing length frequency data.

This paper seeks to examine both the BH and EA estimators with respect to directional biases and variances in $Z$ estimates when applied to simulated fish populations with known parameters, realistic variability in length-at-age, and varying degrees of age-length truncation existing in the population and assumed by the data analyst. It is of interest to examine the performance of the EA method on length frequency data with no underlying age truncation. We present simulations based on a factorial design as well as species-specific scenarios with parameterizations based on two tropical species.
THE ESTIMATORS

Beverton and Holt (1956) derived an expression for the mean length in a population, $\bar{L}$, as

$$\bar{L} = \frac{\int_{t_c}^{\infty} N_t L_t \, dt}{\int_{t_c}^{\infty} N_t \, dt} \quad (1)$$

where length at age $t$, $L_t$, is given by the von Bertalanffy growth equation

$$L_t = L_\infty (1 - e^{-K(t-t_o)}) \quad (2)$$

and $K$ is the von Bertalanffy growth coefficient yr$^{-1}$, $L_\infty$ is the von Bertalanffy asymptotic length, $t_o$ is the age-axis intercept, $t_c$ is the age at first capture, and $N_t$ is the fraction surviving to age $t$ given by $N_t = e^{-Zt}$.

After substituting a function of length for age, simplifying, and solving for the mortality rate they obtained the well-known $BH(\hat{Z})$ estimator,

$$BH(\hat{Z}) = \frac{K\left(L_\infty - \bar{L}\right)}{\bar{L} - L_c}, \quad (3)$$

where $\bar{L}$ is the mean of all lengths $> L_c$ in a sample of lengths and $L_c$ is the length at first capture, corresponding to age $t_c$ via equation (2).

Details on the derivation of the above estimator have been described elsewhere (e.g., Ehrhardt and Ault 1992; Gedamke and Hoenig 2006). Major assumptions of the estimator are (1) known and constant von Bertalanffy parameters, (2) no individual variability in growth, (3) constant and continuous
recruitment over time, (4) constant mortality over age and time, (5) knife edge selectivity of lengths > \(L_c\), such that population mean length reflects current mortality rate. Note that, in practice, the analyst would specify \(L_c\) as the minimum length used in the analysis such that all lengths < \(L_c\) in the catch data would be discarded prior to computing \(\bar{L}\). Henceforth \(\bar{L}_{BH}\) will be used to denote computation of mean length based on lengths > \(L_c\).

The Ehrhardt and Ault (1992) estimator \(\hat{E}A(\hat{Z})\) is derived the same way as the Beverton and Holt estimator except that the integrals in equation (1) extend from age \(t_c\) to an upper age limit \(t_\lambda\). The estimated mortality rate is then obtained from the resulting equation by iteratively solving the following for \(Z\):

\[
\left[ \frac{L_u - L_\lambda}{L_\infty - L_c} \right] \frac{Z}{K} = \frac{Z(L_c - \bar{L}) + K(L_u - \bar{L})}{Z(L_\lambda - \bar{L}) + K(L_\infty - \bar{L})}
\]

where \(L_\lambda\) is the upper length of truncation (corresponding deterministically to the upper age of truncation \(t_\lambda\) via equation (2) and \(L_\lambda \leq L_\infty\)) and all other symbols except \(\bar{L}\) are as before (see below). Equation (4) always has zero as a solution and generally, but not always, has a positive, real-valued solution (see Appendix 1a).

There could be more than one way to compute \(\bar{L}\). The natural approach would be to discard all lengths < \(L_c\) and all lengths > \(L_\lambda\) and compute the mean from the remaining observations. However, it could be argued that, because of variability in size-at-age, lengths > \(L_\lambda\) should be included in the calculation of the
sample mean. We computed \( \bar{L} \) for the EA estimator using both methods, i.e.,
using \( \bar{L}_{BH} \) and using lengths in the interval \([L_c, L_\lambda]\) which we will refer to as \( \bar{L}_{EA} \).

Determining the input value of \( L_\lambda \) for the EA estimator requires some thought. Ehrhardt and Ault (1992) considered two situations to be equivalent in terms of the data generated. These situations are: 1) absence of old fish in tropical species due to increasing mortality rate with age, and 2) absence of old fish due to low gear selectivity for the largest and oldest animals. They accounted for these phenomena in their derivation by truncating the theoretical age distribution at an upper age \( t_\lambda \). To use the resulting estimator, it is necessary to specify an upper length \( L_\lambda \) corresponding to the upper age \( t_\lambda \). One practical choice for \( L_\lambda \) is the maximum size \( L_{\text{max}} < L_\infty \) observed in the sample but this may not be satisfactory if the truncation with age is gradual rather than abrupt. Thus, in general, one would try to identify from the length sample a size that is a) small enough that all fish less than the size are fully selected and not subject to the increased mortality associated with old age, and b) large enough that a significant portion of the size distribution is not needlessly discarded. Note that \( L_\lambda \) must be \( < L_{\text{max}} \) to solve equation (4); hence, if any fish are observed to be greater than \( L_\infty \) they must be discarded when determining the sample \( L_{\text{max}} \) if \( L_{\text{max}} \) is to be used as \( L_\lambda \) in equation (4).
SIMULATIONS

Our simulation goals were three-fold. First, we wished to determine how the degree of age and length truncation, and the values of $Z$ and $K$, affect the performance of the two estimators. Second, we wished to evaluate the effect of the choice of $\bar{L}_{EA}$ versus $\bar{L}_{BH}$ on $EA(\hat{Z})$. Third, we were interested in how variability in size at age affects the performance of the estimators.

In performing the simulations it is important to recognize that two processes are at work. First, the population age and size structure is shaped by the pattern of mortality with age, the growth rates, and the variability in size at age. We simulate populations with a constant mortality rate and then truncate the age structure at a specified value of $t_λ$ (if the underlying goal involves introduction of age truncation) to match the derivation in Ehrhardt and Ault (1992). We refer to the simulated age of truncation as the actual $t_λ$. The expected length at the actual $t_λ$ is referred to as the actual $L_λ$ (but note that, because of individual variability in size at age, there can still be fish in the population larger than $L_λ$). Second, the data analyst receives a sample of lengths and makes two decisions when using the EA estimator. One decision is the choice of $L_λ$ to use in equation (4), the value of the actual $L_λ$ generally not being known perfectly to the data analyst. The value of $L_λ$ selected by the data analyst is referred to as the imposed $L_λ$. The other decision
is how to compute the mean length in the sample. As described earlier, we evaluated the use of both $\bar{L}_{EA}$ and $\bar{L}_{BH}$.

To address our goals, we focus on three scenarios: (1) simulated age distribution was generated with truncation and then samples were analyzed with six different values for imposed $L_\lambda$ in equation (4) and the mean length for the EA estimator was computed as $\bar{L}_{EA}$ and $\bar{L}_{BH}$; (2) simulated age distribution was generated with truncation, as in (1), imposed $L_\lambda$ was set at the minimum of $(L_{max}, L_\infty)$ where $L_{max}$ is the largest sized fish in the sample, and $\bar{L}_{EA}$ was used as the mean length for the EA estimator; (3) simulated age distribution was generated with no age truncation, imposed $L_\lambda$ was set at the minimum of $(L_{max}, L_\infty)$, and mean length for the EA estimator was $\bar{L}_{EA}$. Figure 1 summarizes the data generation (left) and the subsequent data analysis (right) processes. Note that there are two decisions to be made when using the Ehrhardt-Ault estimator: what value of $L_\lambda$ to specify in the estimator and what method to use for calculating mean length.

For the first scenario, we applied a 5 x 4 factorial design with five levels of $Z$ (0.1, 0.25, 0.5, 1.0, 2.0 yr$^{-1}$) and four levels of $K$ (0.1, 0.4, 0.7, 1.0 yr$^{-1}$). We used the Pauly (1980) dataset truncated at $M < 2.5$ yr$^{-1}$ to assess the plausibility of the $Z$ and $K$ combinations and found that two of the combinations were highly improbable in nature ($Z = 0.1, K = 0.7$ and $Z = 0.1, K = 1.0$); these combinations were thus not presented in the results. In these scenarios, the $L_\infty$ parameter
(scaling factor) was fixed. We arbitrarily used $L_c = 400$ mm (the approximate average size of fish in the Pauly (1980) dataset).

For the second and third scenarios, we parameterized our simulations based on the life history of tropical species. Since the EA estimator was intended for application to tropical stocks, we expected that the EA estimator would perform well in this set of species-specific simulations. We surveyed the literature for plausible ranges of Z as well as growth parameters for tropical fish species. Based on 54 species, the $K$ rates ranged from 0.08 to 2.5 yr$^{-1}$ and $Z$ values ranged from 0.05 to 5.0 yr$^{-1}$; many of these estimates came from relatively lightly or moderately exploited fish stocks (Then, unpublished data). This suggests that plausible $K$ and $Z$ estimates for various tropical fish stocks vary widely.

We selected two tropical species, *Lutjanus vitta*, the brownstripe red snapper and *Chrysoblephus cristiceps*, the daggerhead seabream, which represented the two end spectrums of growth (see Table 1 for actual parameter values used). Since these stocks were fairly lightly exploited, we conducted these sets of simulation under two fishing scenarios (fishing mortality $F = 0$ and $F = 0.3$) and four $\sigma$ levels (0, 3, 6, and 9 % of $L_c$).

For all simulations, we assume that a population experiences constant and continuous recruitment and is subject to constant mortality rate across time (up to age $t_\lambda$). Body growth is assumed to follow a von Bertalanffy growth model with constant parameters. These assumptions conform to those of the BH and EA estimators.
For all simulations, samples of ages were drawn repeatedly from an exponential distribution with decay parameter \( Z \). These samples of ages were then left-truncated to mimic knife-edge selectivity such that the minimum age was \( t_c \). For scenarios (1) and (2) with life span truncation, the generated age samples were right-truncated at an upper age \( t_\lambda \). All ages were then converted to lengths via equation (2).

To simulate variability in length-at-age, we used two approaches. First, we assumed that the magnitude of variability in length-at-age is constant across all ages. Normally distributed errors in length (\( \varepsilon \sim N (0, \sigma^2) \)) were added to all lengths. To guide the selection of \( \sigma \), the standard deviations of residual errors of fitted length-at-age curves were obtained from available literature and from fitting standard von Bertalanffy growth curves using non-linear least squares regression to raw growth data of various exploited fish stocks. Based on nine stocks, estimates of \( \sigma \) ranged from approximately 3 to 10\% of the individual estimates of \( L_\infty \), with mean \( \sigma = 7.1 \% \) (Table 2). Although these nine estimates may not be fully representative of the possible variability in length-at-age of fish stocks, they provide reasonable estimates of the magnitude of this variability.

Variability in length-at-age for a species of fish likely depends on the maximum size achieved by the species (i.e., larger fish species are likely to exhibit larger absolute variability in lengths than smaller species). Therefore, the constant \( \sigma \) was scaled in proportion to the specified \( L_\infty \) in the simulations. This proportional scaling of variation to \( L_\infty \) essentially eliminated the influence of \( L_\infty \) on the simulation and results were comparable for fishes of any asymptotic size,
provided the $\sigma$ scaling factor (% $L_\infty$) was identical for the simulations. For the rest of this paper, $\sigma$ is expressed as a percentage of $L_\infty$.

The second approach to generating growth variability was to assume a constant coefficient of variation (CV) across all ages. This is based on the suggestion that variability in size at age may increase with age. In the datasets we examined, there is evidence to support both approaches to simulating growth variability (see Appendix 1b). For the second approach, errors in length-at-age, ($e_t \sim N(0, \sigma_t^2 = (CV_tL_t)^2$) were added to all lengths where $L_t$ is the mean length at age $t$ specified by the von Bertalanffy growth curve. We used the $\sigma$ estimates to guide the selection of CV values. Hence, all the simulation scenarios were conducted with both $\sigma$ and CV = 7%, with the exception of the species-specific simulation sets (described below). A single realization of the variability in length at age for $\sigma = 7\%$ and CV = 7\% is shown in Figure 2.

In the initial runs of the simulation, the values of the actual $t_\lambda$ were fixed across scenarios. However, the results were difficult to interpret because a given $t_\lambda$ may be extremely important when $Z$ is low and unimportant when $Z$ is high since few animals will attain $t_\lambda$ when $Z$ is high. Hence, the $t_\lambda$ values were scaled to the specified $Z$ rate such that the actual $t_\lambda$ corresponded to the age at which the population is at 10\% of the initial size as follows:

$$0.1 N_0 = N_0 e^{-Zt_\lambda} \quad (5)$$

Likewise, the age of lower truncation $t_c$ was also scaled such that $t_c$ corresponded to the age at which the population is at 70\% of the initial size. The
scaling of age $t_c$ was especially critical in high $Z$ scenarios where the corresponding age range is rather narrow.

According to Ehrhardt and Ault (1992), the value of $L_\lambda$ to be applied should correspond to the actual $t_\lambda$ via equation (2), but since ages are not examined when analyzing a length-frequency dataset, the exact value of $L_\lambda$ an analyst would use in equation (4) is not known. We evaluated the effects of the data analyst adopting six possible choices of $t_\lambda$, and thus of $L_\lambda$, on the $EA(\tilde{Z})$. Given an imposed $L_\lambda$, the simulation discards all lengths in a sample $> L_\lambda$ and uses the imposed $L_\lambda$ in equation (4). The six imposed $L_\lambda$ values corresponded to three situations where the analyst imposed (1) the actual $L_\lambda$ (i.e., the length corresponding to the expected size at age $t_\lambda$), (2) two $L_\lambda <$ actual $L_\lambda$ (over-truncation of length samples where more length measurements were discarded than necessary according to the EA model) and (3) three $L_\lambda >$ actual $L_\lambda$ (under-truncation where the imposed upper length truncation was insufficient to appropriately reflect the actual age structure). The under-truncation situations corresponded to ages of 1, 2 and 3 greater than the true $t_\lambda$, while the over-truncation situations resulted in no more than 40% of lengths being discarded from the right tail.

Performance of the estimators was evaluated based on two metrics: percent bias (% Bias) and percent root mean square error (% RMSE) as follows

\[
\text{% Bias} = 100\times \left( \frac{\tilde{Z} - Z}{Z} \right)
\]  

(5)
\[
\text{% RMSE} = 100 \times \sqrt{\frac{\sum_{i=1}^{N} (\hat{Z} - Z)^2}{N-1}} / Z 
\]  \hspace{1cm} (6)

where \(\bar{Z}\) is the mean of the estimates and \(N\) is the number of simulated datasets (\(N = 10,000\), see below).

Preliminary assessment was performed to determine the number of simulations required to obtain stable variances of both estimators at various sample sizes of lengths (500, 1000, 5000 and 10,000). Variances generally stabilized at the simulation size of 10,000 datasets such that further increase in the numbers of simulated datasets did not improve the accuracy of estimation appreciably. The bias and RMSE for each estimator were also relatively insensitive to the sample size of lengths simulated, indicating that bias from failure of assumption was the major component of the RMSE rather than sampling variability.

Performance metrics of the BH(\(\hat{Z}\)) were calculated based on 10,000 estimates from length samples of 1,000 fish. The large sample size allowed us to focus on a best case scenario in the sense that performance would not be expected to improve appreciably if sample sizes were increased. Note that the sample sizes of lengths used for the EA(\(\hat{Z}\)) estimation were mostly < 1000, depending on the degree of length truncation imposed. Also, for certain sets of sample lengths generated, it was not possible to solve for \(Z\) in the EA equation, particularly in scenarios of severe imposed length truncation (see Appendix 1a). Hence the summary statistics presented for EA(\(\hat{Z}\)) may be based on less than 10,000 datasets.
All simulations, analyses and plotting were performed using the R statistical computing platform (R Development Core Team 2011).
RESULTS

Effects of varying imposed $L_\lambda$ at different combinations of $Z$ and $K$

When right truncation exists and $\sigma = 7\%$, the BH estimator consistently overestimates $Z$ across most combinations of $Z$ and $K$ scenarios, with $\%$ Bias $< 40\%$ (Figure 3, top row). The rare combination that yields negative bias in $BH(\hat{Z})$ is $Z = 2.0$ and $K = 0.1$, which may occur infrequently in real life. For a given $Z$ level and constant $\sigma$, the degree of bias of the BH estimator is not very sensitive to the magnitude of $K$ rates simulated. This is also true for the $\%$ RMSE, which appears to be primarily driven by the bias component. The $BH(\hat{Z})$ $\%$ Bias does not exceed $40\%$ in our simulated scenarios, with lower positive $\%$ Bias observed when $Z$ is low.

In contrast, $\%$ Bias for the EA estimator using the $\bar{L}_{EA}$ method for computing mean length varies from -80% with over-truncation to 140% with under-truncation of length samples (Figure 3, top row) and appears to be sensitive to the magnitude of $K$ for a given $Z$ level. The EA estimator exhibits complex behavior in the sense that the magnitude and direction of the $\%$ Bias and $\%$ RMSE depends on the specific combination of $Z$, $K$, and imposed $L_\lambda$. Generally, the EA estimator is more negatively biased with increasing severity of over-truncation of lengths. As the imposed $L_\lambda$ value rises higher above the actual $L_\lambda$,
(under-truncation), the magnitude and direction of the $EA(\hat{Z})$ bias generally approach that of the $BH(\hat{Z})$ bias (Figure 3, top row). With under-truncation, fewer lengths are omitted from the EA analyses, i.e., the length samples are more similar to those used for the BH estimator, yielding $EA(\hat{Z})$ that are more similar to the $BH(\hat{Z})$.

Across a number of scenarios, the EA estimator exhibits a counterintuitive behavior in that the optimal imposed $L_{\lambda}$ for the EA estimator (i.e., the imposed $L_{\lambda}$ that yields the lowest % RMSE) frequently does not coincide with the simulated actual $L_{\lambda}$. An example of this can be seen in Figure 3(c) where the minimum % RMSE of $EA(\hat{Z})$ at all levels of $K$ does not occur at the actual $L_{\lambda}$ (which corresponds to age $t_{\lambda} = 4.5$). In other words, an analyst who imposes the correct (actual) $L_{\lambda}$ value for the EA estimator may not obtain the $EA(\hat{Z})$ with the lowest RMSE.

Performance of the EA estimator relative to the BH estimator depends strongly on the specific combination of $Z$ and $K$ in the simulation as well as the degree of truncation imposed on the length samples for the EA estimator. Out of 10,000 datasets for each scenario, real-valued solutions of the $EA(\hat{Z})$ estimator existed for only about 6 to 44% of these datasets when generated with high $Z$ rates (1.0 and 2.0) in combination with the most extreme imposed over-truncation of lengths. This may be little cause for concern since over-truncation of length samples may not be preferred by most analysts. When considering the more plausible scenarios of under-truncation of lengths, the BH estimator appears to be
preferred in lower $Z$ scenarios ($Z = 0.1$ and $0.25$; Figures. 3 (a) and (b)) while the EA estimator generally performs better in terms of % RMSE in higher $Z$ scenarios ($Z = 1.0$ and $2.0$; Figures. 3 (d) and (e)).

*Effects of method of calculating mean length on the EA estimator*

When $\bar{L}_{BH}$ is used as the input mean length for the EA estimator, the maximum biases of the $EA(\hat{Z})$ is capped by the biases of the $BH(\hat{Z})$ (Figure 4, top row). The net effect of using $\bar{L}_{BH}$ instead of $\bar{L}_{EA}$ is the downward shifting of the $EA(\hat{Z})$ bias, resulting in more negatively biased $EA(\hat{Z})$ for simulated $Z$ rates $< 1.0$ (compare Figures 3 (top row) and 4 (top row) for scenarios (a), (b) and (c)). Interestingly for $Z = 1.0$ and $2.0$, real-valued $Z$ parameter estimates do not exist for the EA estimator for a number of over-truncation scenarios and even with under-truncation of lengths at $K = 0.1$ (Figure 4 (d) and (e)). Similar to the results of using $\bar{L}_{EA}$ for the EA estimator, the minimum % RMSE of $EA(\hat{Z})$ for all scenarios does not coincide with the actual $L_\lambda$ (Figure 4, bottom row).

*Variability in growth using a constant coefficient of variation*

% Bias and % RMSE for $BH(\hat{Z})$ with constant $\sigma$ is similar to $BH(\hat{Z})$ with constant CV at low $Z$, and likewise for $EA(\hat{Z})$, but the dissimilarities are more apparent at high $Z$ ($Z = 0.5$, $1.0$ and $2.0$; compare Figures 3 and 5 (c), (d) and (e)). % Bias and % RMSE for the $BH(\hat{Z})$ is higher across all combinations of $Z$ and $K$.
when using a constant CV instead of $\sigma$ to simulate growth variability. The behavior of the EA estimator is more stable at high $Z$ rates (1.0 and 2.0) when a constant CV rather than $\sigma$ is used; % RMSE of the $\hat{EA}(\hat{Z})$ is lower than the $BH(\hat{Z})$ across all $K$ levels when $Z = 1.0$ and 2.0 and the minimum % RMSE for the EA estimator coincides consistently with the actual $L_0$ (Figure 5 (d) and (e)).

Effects of varying $\sigma$ and degree of upper age truncation (species-specific simulations)

When applied to simulated length data with underlying truncated age structure (see Table 1 for actual parameter values), the $BH(\hat{Z})$ generally improves with increasing $\sigma$ level, which is unexpected given that the assumption of no individual variability in growth for the BH estimator is violated (Figure 6). As $\sigma$ increases, the bias in $BH(\hat{Z})$ becomes less positive which lowers the % RMSE; in the case of Lutjanus vitta, the bias in $BH(\hat{Z})$ eventually becomes negative, which explains the initial decrease in % RMSE prior to increasing again as $\sigma$ increases (Figure 6 (2)).

On the other hand, the EA estimator appears to perform worse with increasing realism in $\sigma$. For C. cristiceps the bias in $EA(\hat{Z})$ becomes increasingly negative (Figure 6, (1) (a) and (b)). However for L. vitta the bias of $EA(\hat{Z})$ generally increases positively as $\sigma$ increases (Figure 6 (2)); when $F = 0.3$ and lengths are over-truncated (Figure 6, (2) (b) in the shaded region), the bias is 0
when $\sigma = 0$, drops to -60% when $\sigma = 3$ and becomes less negative when $\sigma$ increases from 6 to 9. Again, the EA $Z$ estimator displays complex behavior with respect to % RMSE as the length samples shift from being over-truncated to under-truncated. When $\sigma = 0$, the EA $Z$ estimator exhibits zero bias but only under the condition of over-truncation of length samples. The BH $Z$ estimator generally performs as well or better than the EA $Z$ estimator when the unrealistic simulation of $\sigma = 0$ is omitted from the comparison.

It is unclear if using $L_{\text{max}}$ instead of actual $L_{\lambda}$ as the imposed $L_{\lambda}$ improves the performance of the EA estimator on simulated length data with underlying truncated age structure (see Appendix 2). For $C. \text{ cristiceps}$ the % RMSE is considerably lower when using imposed $L_{\lambda} = L_{\text{max}}$ than when imposed $L_{\lambda} = \text{actual } L_{\lambda}$, especially so when $F = 0.3$; on the other hand, for $L. \text{ vitta}$, examination of the % RMSE suggests that using imposed $L_{\lambda} = \text{actual } L_{\lambda}$ is preferred especially when $F = 0.3$.

When both the BH and EA estimators are applied to length samples that are generated from non-truncated age distributions, there is no penalty in applying the EA estimator over the BH estimator in the case of $C. \text{ cristiceps}$. However the results are less clear for $L. \text{ vitta}$: % RMSE of $EA(\hat{Z}) > BH(\hat{Z})$ when $F = 0$ but the reverse is observed when $F = 0.3$. Additional simulation results with other combinations of parameter values and more levels of variability in length-at-age, $Z$ and $K$ are documented in Appendix 2.
DISCUSSION

Both the BH and EA estimators have been applied primarily to fisheries lacking substantial amounts of age data, e.g., BH: tilapia in Nigeria (King and Etim 2004), pomfret in Kuwait (Morgan 1985), ribbonfish in India (Chakraborty 1990), spiny lobster in South Africa (Groeneveld 2000); EA: coral reef fishes in Florida (Ault et al. 2005) and in Puerto Rico (Ault et al. 2008). While the BH estimator and associated properties have been fairly well studied, the same cannot be said of the EA estimator. Our simulation study shows that the EA estimator, developed to correct the BH estimator in applications to truncated length frequencies, does not necessarily perform better than the original BH estimator. The property of zero bias of the EA estimator under equilibrium conditions does not hold when incorporating realistic scenarios involving individual variability in size at age.

Our simulation results do not show clear support for the use of $\overline{L}_{BH}$ (mean length of samples $> L_c$) over $\overline{L}_{EA}$ as input mean length for the EA estimator (compare Figures 4 to 3). Use of the former mean length generally results in more negatively biased and less conservative $EA(\hat{Z})$ than the latter. Issues with non-existent, positive solutions for the EA estimator using $\overline{L}_{BH}$ are also apparent.
under higher $Z$ rates and plausible length truncation scenarios. Given the above, we prefer the use of the $\bar{L}_{EA}$ as input mean length when using the EA estimator.

The BH method appears robust to violation of the assumption of no individual variability in growth, and its performance generally improves with increasing realism in $\sigma$ (Figure 6, bottom row). While the performance of the EA estimator relative to the BH estimator is highly dependent on the parameters of the simulation, particularly on the combination of $Z$ and $K$, the EA estimator performs increasingly poorly as $\sigma$ increased (Figure 6, bottom row).

The EA estimator displays better behaved patterns of $\%$ Bias and $\%$ RMSE in scenarios where growth variability is simulated with a constant CV rather than constant $\sigma$ (compare Figures 3 and 5). Results from scenarios with a constant CV show more support for the use of the EA estimator rather than the BH estimator, particularly at high $Z$ rates (Figure 5). However, two issues need to be considered when an analyst chooses to apply the EA estimator to a length frequency distribution: the performance of the EA estimator will depend on: (1) whether the underlying growth variability is more reflective of a constant CV or a constant $\sigma$, and (2) whether the value of $Z$ is high. Erzini (1994) suggested, based on empirical evidence, that the standard deviations in length at age generally increase to a maximum at some intermediate age, followed by a leveling or decrease. Our examination of select datasets found cases consistent with constant CV and others consistent with constant $\sigma$ (Appendix 1b). The reality may lie somewhere between the two. For the second issue, without knowledge that the
true $Z$ is high (i.e., greater than 1 yr$^{-1}$), one should probably use the BH estimator instead.

The complex behavior of the EA estimator with varying imposed $L_\lambda$ values, particularly the observation that the best input value for $L_\lambda$ often does not coincide with the actual $L_\lambda$, renders it difficult to characterize the magnitude and direction of the bias. Another important point is that the best choice of imposed $L_\lambda$ and direction of bias cannot be determined without knowing the generally unknowable or unknown parameters— the $Z$ rate, the actual $L_\lambda$ (if age truncation is occurring) and the nature of the variability in length at age. Sensitivity analysis is strongly recommended when considering the use of the EA estimator, especially with respect to the input value of $L_\lambda$ as well as the method of calculating mean length.

The most likely scenario for an analyst applying the EA estimator is to use either the maximum length in the sample $L_{\text{max}}$ as the $L_\lambda$ value (provided $L_{\text{max}} < L_\infty$) or apply minimal upper length truncation to avoid data wastage. There appears to be some support for the former practice based on the species-specific simulations even when the EA method is applied to length samples without underlying upper age truncation. However, our results indicate that under-truncating length samples in the right tail of the distribution yields $EA(\hat{Z})$ that approach the $BH(\hat{Z})$. Given that under-truncation of lengths is likely the more common practice, the $EA(\hat{Z})$ bias would be similar to that of the BH estimator. This implies that the
gain from applying the EA method diminishes with less severe upper truncation applied to length samples.

Our results demonstrate that the EA estimator is not uniformly superior to the BH, even under simulated conditions that mimic tropical fisheries. Although the BH estimator often overestimates $Z$ when right truncation exists, this bias, arguably, may be preferred to underestimation of $Z$ or to unknown directionality of bias as exhibited by the EA estimator. Given the unpredictable performance of the EA estimator, we do not advocate its application in tropical or other data-poor fisheries without specific case-by-case evaluation through simulation. This recommendation is important given that these fisheries have little option for validation of resulting mortality estimates. Simulation and sensitivity analyses are strongly recommended for scientists and fishery managers who find the level of accuracy of either method to be acceptable and wish to apply these methods.
REFERENCES


Then, A. Y. (this dissertation). Estimating fishing and natural mortality rates, and catchability coefficient, from a series of observations on mean length and fishing effort (Chapter 2).


TABLE 1. Parameter values for species-specific simulations based on two tropical fish species. $M =$ natural mortality rate (yr$^{-1}$), $F =$ fishing mortality rate (yr$^{-1}$), $K =$ von Bertalanffy growth parameter (yr$^{-1}$), $L_\infty =$ von Bertalanffy asymptotic length (mm), $t_0 =$ von Bertalanffy location parameter (yr), $t_c =$ age of full recruitment (yr) and $t_\lambda =$ actual age of upper truncation (yr). Values for $t_c$ and $t_\lambda$ for both species were assumed because no information was available in the source publication. Note that $t_\lambda$ was not used when generating length samples with no underlying age truncation.

<table>
<thead>
<tr>
<th>Species</th>
<th>$M$</th>
<th>$F$</th>
<th>$K$</th>
<th>$L_\infty$</th>
<th>$t_0$</th>
<th>$t_c$</th>
<th>$t_\lambda$</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Chrysoblephus</em></td>
<td>0.209</td>
<td>0, 0.3</td>
<td>0.081</td>
<td>654.7</td>
<td>-2.35</td>
<td>2, 1</td>
<td>11 (F=0), 5 (F=0.3)</td>
<td>Buxton (1993)</td>
</tr>
<tr>
<td><em>cristiceps</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lutjanus vitta</em></td>
<td>0.342</td>
<td>0, 0.3</td>
<td>0.853</td>
<td>245.3</td>
<td>-0.18</td>
<td>2, 1</td>
<td>7 (F=0), 4 (F=0.3)</td>
<td>Newman et al. (2000)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
TABLE 2. von Bertalanffy asymptotic length, $L_\infty$ (cm), standard deviation (SD) of length-at-age and $\sigma$ (100*SD/$L_\infty$) of various exploited fish stocks. Growth parameters were estimated using non-linear least squares regression.

<table>
<thead>
<tr>
<th>Common name</th>
<th>$L_\infty$ (cm)</th>
<th>SD (cm)</th>
<th>$\sigma$ (%)</th>
<th>Data source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summer flounder</td>
<td>70.6</td>
<td>4.30</td>
<td>6.10</td>
<td>Rago, P. (NMFS)</td>
</tr>
<tr>
<td>Scup</td>
<td>44.4</td>
<td>2.59</td>
<td>5.83</td>
<td>Rago, P. (NMFS)</td>
</tr>
<tr>
<td>Cod</td>
<td>111.0</td>
<td>9.16</td>
<td>8.25</td>
<td>Rago, P. (NMFS)</td>
</tr>
<tr>
<td>Haddock</td>
<td>59.2</td>
<td>5.90</td>
<td>9.96</td>
<td>Rago, P. (NMFS)</td>
</tr>
<tr>
<td>Striped bass</td>
<td>182.1</td>
<td>4.65</td>
<td>2.55</td>
<td>Hoenig, J.M. (VIMS)</td>
</tr>
<tr>
<td>Yellowedge grouper</td>
<td>98.7</td>
<td>8.37</td>
<td>8.48</td>
<td>Walter, J.F. (NMFS)</td>
</tr>
<tr>
<td>Gag grouper</td>
<td>134.4</td>
<td>6.95</td>
<td>5.17</td>
<td>Walter, J.F. (NMFS)</td>
</tr>
<tr>
<td>Red grouper</td>
<td>74.0</td>
<td>6.77</td>
<td>9.15</td>
<td>Walter, J.F. (NMFS)</td>
</tr>
<tr>
<td>Tropical emperor*</td>
<td>36.8</td>
<td>2.71</td>
<td>7.36</td>
<td>Pilling et al., 2001</td>
</tr>
</tbody>
</table>

* Pilling et al. (2001) derived the variances directly from back-calculated length at age for ages 1 to 12 (in Table 1). The square root of the pooled variances was reported for SD.
FIGURES

FIGURE 1. Left: Data generation process to yield length samples with growth variability of either a constant magnitude (σ) across ages or a constant coefficient of variation (CV) across ages, where \( \sigma_t^2 = (CV_t \cdot \bar{L}_t)^2 \) and \( \bar{L}_t \) is the mean length at age. The length samples are either age-truncated on the right or otherwise. Right: Data analysis flowchart representing the decisions to be made in applying the Beverton-Holt (BH) or the Ehrhardt-Ault (EA) estimator of \( Z \) when analyzing a length sample. Effects of varying imposed upper length truncation, \( L_i \), for applying the EA estimator are examined in the simulation (see dashed box). Other parameters: \( Z \) = total instantaneous mortality rate (yr\(^{-1}\)); \( t_c \) = age at first capture (yr); \( L_c \) = length at first capture (mm); \( K \) = von Bertalanffy growth coefficient (yr\(^{-1}\)), \( L_\infty \) = von Bertalanffy asymptotic length (mm), \( t_o \) = year-axis intercept (yr), \( t_i \) = actual upper age truncation. Mean length \( \bar{L}_{EA} \) is computed on lengths \( L, \) with \( L_c < L < \text{imposed } L_i \) while \( \bar{L}_{BH} \) is computed on lengths \( L > L_c. \)
FIGURE 2. von Bertalanffy growth curves generated with the parameters of total mortality rate $Z = 0.25 \, \text{yr}^{-1}$, growth coefficient $K = 0.4 \, \text{yr}^{-1}$, $L_\infty = 400 \, \text{mm}$ and length at first capture = 1 yr. Variability in length at age generated with a constant magnitude of error $\sim N(0, \sigma^2 = (7\% \cdot 400)^2 = 28^2)$ (left) and constant coefficient of variation, $CV = 7\%$ across ages, implying $\sigma_i^2 = (7\% \cdot L_i)^2$ (right). Note that above age 3, the constant $\sigma$ and constant $CV$ growth variability patterns appear similar.
(a) $Z = 0.1$  (b) $Z = 0.25$  (c) $Z = 0.5$  (d) $Z = 1.0$  (e) $Z = 2.0$

FIGURE 3. Percent bias (% Bias) and percent root mean square error (% RMSE) of the total mortality rate ($Z$) estimates of the Beverton Holt (in dashed lines) and Ehrhardt-Ault (in solid lines) estimators when applied to simulated length frequency data, generated with a constant variability in length at age, $\sigma = 7\%$, and various combinations of $Z =$ (a) 0.1, (b) 0.25 (c) 0.5, (d) 1.0, and (e) 2.0 $\text{yr}^{-1}$ and von Bertalanffy growth coefficient $K$ ($K = 0.1$ (denoted with A), $K = 0.4$ (B), $K = 0.7$ (C) and $K = 1 \text{ yr}^{-1}$ (D)). The x-axis is shown in age scale ($t_\lambda$) for clarity but the corresponding length $L_\lambda$ is imposed on the length samples when applying the EA estimator. Shaded region denotes over- truncation ($\text{imposed } L_\lambda < \text{ actual } L_\lambda$), unshaded region denotes under- truncation and the boundary denotes actual age of upper truncation $t_\lambda$ in each simulation, which is a function of $Z$. The mean length for the EA estimator, $\bar{L}_{\text{EA}}$, was computed on lengths $L$, with length at first capture $L_c < L < \text{imposed } L_\lambda$. 

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FIGURE 4. Percent bias (% Bias) and percent root mean square error (% RMSE) of the total mortality rate ($Z$) estimates of the Beverton Holt (in dashed lines) and Ehrhardt-Ault (in solid lines) estimators when applied to simulated length frequency data, generated with a constant variability in length at age, $\sigma = 7\%$, and various combinations of $Z = (a) 0.1$, (b) 0.25, (c) 0.5, (d) 1.0, and (e) 2.0 yr$^{-1}$ and von Bertalanffy growth coefficient $K (K = 0.1$ (denoted with A), $K = 0.4$ (B), $K = 0.7$ (C) and $K = 1$ yr$^{-1}$ (D)). The x-axis is shown in age scale ($t_\lambda$) for clarity but the corresponding length $L_\lambda$ is imposed on the length samples when applying the EA estimator. Shaded region denotes over-truncation (imposed $L_\lambda <$ actual $L_\lambda$), unshaded region denotes under-truncation and the boundary denotes actual age of upper truncation $t_\lambda$ in each simulation, which is a function of $Z$. The mean length for the EA estimator, $\overline{L}_{BH}$, was computed on lengths $L >$ length at first capture, $L_c$. 

(a) $Z = 0.1$  
(b) $Z = 0.25$  
(c) $Z = 0.5$  
(d) $Z = 1.0$  
(e) $Z = 2.0$
FIGURE 5. Percent bias (% Bias) and percent root mean square error (% RMSE) of the total mortality rate (Z) estimates of the Beverton Holt (in dashed lines) and Ehrhardt-Ault (in solid lines) estimators when applied to simulated length frequency data, generated with a constant coefficient of variation, CV = 7%, in length-at-age and various combinations of Z = (a) 0.1, (b) 0.25 (c) 0.5, (d) 1.0, and (e) 2.0 yr⁻¹ and von Bertalanffy growth coefficient $K (K = 0.1$ (denoted with A), $K = 0.4$ (B), $K = 0.7$ (C) and $K = 1$ yr⁻¹ (D)). The x-axis is shown in age scale ($t_\lambda$) for clarity but the corresponding length $L_\lambda$ is imposed on the length samples when applying the EA estimator. Shaded region denotes over-truncation (imposed $L_\lambda <$ actual $L_\lambda$), unshaded region denotes under-truncation and the boundary denotes actual age of upper truncation $t_\lambda$ in each simulation, which is a function of $Z$. The mean length for the EA estimator, $\bar{L}_{Ea}$, was computed on lengths $L$, with length at first capture $L_c < L <$ imposed $L_\lambda$. 
FIGURE 6. Percent bias (% Bias) and percent root mean square error (% RMSE) of the total mortality rate (Z) estimates of the Beverton Holt (dashed lines) and Ehrhardt-Ault (solid lines) estimators when applied to species-specific simulated length frequency data for two tropical species (1) *Chrysoblephus cristiceps* and (2) *Lutjanus vitta*. Constant variability in length at age, \( \sigma \), was simulated at four levels (0, 3, 6, 9 %); other parameters given in Table 2. Two fishing mortality scenarios were presented: (a) \( F = 0 \) and (b): \( F = 0.3 \). Shaded region denotes over-truncation (imposed \( L_\lambda < \) actual \( L_\lambda \)), unshaded region denotes under-truncation and the boundary denotes actual age of upper truncation \( t_\lambda \). The mean length for the EA estimator, \( \bar{L}_{EA} \), was computed on lengths \( L \), with length at first capture \( L_c < L < \) imposed \( L_i \).
CHAPTER 3

Estimating fishing and natural mortality rates, and catchability coefficient, from a series of observations on mean length and fishing effort
ABSTRACT

Despite requiring restrictive assumptions, length-based methods for estimating mortality rates remain widely used, especially for data poor fisheries, due to ease of application and minimal data requirements. Gedamke and Hoenig (2006) developed a non-equilibrium version of the Beverton and Holt estimator of total mortality rate, $Z$, based on mean length and thereby increased the usefulness of length-based methods. In this study, we extend their model by replacing period-specific $Z$ parameters with the year-specific parameterization $Z = qf_y + M$ where $q$ is the catchability coefficient, $f_y$ is the fishing effort in year $y$, and $M$ is the natural mortality rate. Thus, the problem reduces to estimating just three parameters: $q$, $M$ and residual variance. If annual fishing effort is not available, one can substitute $f_y = \text{catch}_y / \text{cpue}_y$ where $\text{catch}_y$ is the total catch in the fishery in year $y$ and $\text{cpue}_y$ is the catch rate in a reference gear sector or survey in year $y$. We used Monte Carlo simulation to study the model behavior. Estimates of $q$ and $M$ are highly correlated and may or may not be reliable; however, the estimates of corresponding $Z$'s are not correlated with each other and are generally reliable, even when uncertainty about the mean lengths is high. This length-based method appears to work best for stocks with rapid growth rate. Contrast in fishing effort data may not be necessary for reliable estimates of $Z$'s. This approach forms a bridge between extremely data-limited models and more complex models.
INTRODUCTION

Reliable and representative age information remains scarce for assessing the status of many fished stocks. Size information, on the other hand, is almost ubiquitously collected and much more readily available especially for data-poor stocks. Utilizing the latter information to obtain reasonably useful estimates of stock parameters, such as total mortality rate, \( Z \), is highly desirable especially when limited resources and prohibitive costs prevent collection of age data. Hence continual research to improve and extend the utility of existing length-based methods is warranted and urgently needed for many unassessed stocks.

A number of length-based estimators of \( Z \) require restrictive assumptions which are generally untenable for real fisheries settings. One such estimator was developed by Beverton and Holt (1956) to estimate \( Z \) from sample mean length and von Bertalanffy growth parameters. The Beverton and Holt estimator assumes equilibrium length composition such that the mean length reflects the current \( Z \) rate experienced by the stock.

Gedamke and Hoenig (2006) modified the Beverton and Holt estimator by relaxing the strict assumption of equilibrium. This was done by modeling the transition of mean length from one equilibrium period to the next, following abrupt changes in \( Z \). Using a time series of mean length observations, the Gedamke-Hoenig estimator yields period-specific estimates of \( Z \) and the
corresponding years of change in mortality (Gedamke and Hoenig, 2006). The number of parameters depends on the number of ‘breaks’ or \( Z \) changes modeled. Using this methodology, Cardinale et al. (2010) were able to detect a total of seven changes in \( Z \) in the plaice stock of the Kattegat–Skagerrak area from a century-long time series of mean length data.

The motivation for this work is to increase the generality and reliability of non-equilibrium length-based estimators. Specifically, our paper extends the work of Gedamke and Hoenig (2006) by utilizing additional information from a time-series of fishing effort data, \( f \), to estimate \( Z \) rates. Data required to apply the model are length measurements coupled with a time-series of standardized fishing effort or times series of catch and catch rates. Our model directly estimates three parameters - the catchability coefficient, \( q \), natural mortality rate, \( M \), post-recruitment to the fishery, and residual variance - by assuming constant \( q \) and \( M \) across all fishable ages and years as well as constant (or at least randomly fluctuating) recruitment to the fishery. It is then possible to estimate year-specific fishing mortality rates, \( F (F = qf + M) \), and \( Z \) rates.

Gedamke and Hoenig (2006) showed that for a given change in population \( Z \) rate from \( Z_1 \) to \( Z_2 \), the mean length requires a longer time to reach equilibrium (i.e., to reflect \( Z_2 \)) when the von Bertalanffy parameter \( K \) is low and vice versa. This suggests that the non-equilibrium length based method may be more useful for stocks with relatively higher \( K \) rates. Hence, we utilize a simulation framework with realistic biological parameterizations and plausible scenarios to
assess the accuracy and precision of the extended model. Generalizations and recommendations for application of the extended method are provided.
MODEL DEVELOPMENT AND SIMULATION STUDY

Estimation procedure, assumptions and data requirements

We used an age-structured geometric decline model as the underlying population model. For this model formulation, we assume constant fishery recruitment such that relative abundance at age of full recruitment $N_{t_c} = 1$. In practice, this assumption can be addressed when applying the model to a stock with an available time-series of an index of recruitment (see Gedamke et al. (2008) for an example with the barndoor skate, *Dipturus laevis*). We also assume knife-edge selection of lengths by the fishery gear, such that all lengths $\geq L_c$ corresponding to ages $\geq t_c$ are fully vulnerable to the gear. Other model assumptions include:

1. Mean length at age is known and constant over time.
2. Natural mortality $M$ and catchability $q$ are independent of stock size and constant with age and over time.

Abundance (in numbers) at age $a$ for a given year $y$, $N_{a,y}$ (expressed as a fraction of the recruitment, assumed to be constant) is modeled as:

$$N_{a,y} = \begin{cases} 1, & a = t_c \text{ for all } y \\ N_{a-1,y-1} \cdot e^{-Z_{y-1}}, & a = t_c + 1, \ldots, \infty; \ y = 1, 2, \ldots, n \end{cases} \quad (1)$$
with \[ Z_y = q \cdot f_y + M \] (2)
where \( t_c \) is the age at first capture
\( M \) is the instantaneous natural mortality rate
\( q \) is the catchability coefficient
\( f_y \) is the standardized fishing effort in year \( y \)
\( Z_y \) is the instantaneous total mortality rate for year \( y \), assumed to be linearly related to \( f \)

Estimates of the mean length at each discrete age \( a \) are needed for ages \( \geq t_c \). In this paper, we used mean length-at-age \( \overline{L}_a \) from the von Bertalanffy growth function (3):
\[ \overline{L}_a = L_\infty \left( 1 - e^{-K(a-t_0)} \right) \] (3)
where \( K \) is the von Bertalanffy growth coefficient yr\(^{-1}\)
\( L_\infty \) is the von Bertalanffy asymptotic length
\( t_0 \) is the year-axis intercept

The growth parameters are assumed to be constant over time. In practice, the mean length at age information can be obtained via other models, such as a seasonally varying growth function. The predicted mean length in year \( y \) is modeled as
\[ \overline{L}_{\text{pred}, y} = \frac{\sum_{a=t_c}^{\infty} \left( \overline{L}_{a,y} \cdot \hat{N}_{a,y} \right)}{\sum_{a=t_c}^{\infty} \hat{N}_{a,y}} \] (4)
where \( \hat{N}_{a,y} \) is obtained recursively from (1) using estimates of \( Z_y \).
In theory, the age summations in equation (4) extend to infinity but, for computational purposes, the infinite summation can be approximated to any desired degree of precision by choice of an upper limit of summation. For a long lived species with many age groups, this creates a theoretical problem of requiring a long time series of observations. As a practical matter, the older age groups that are no longer abundant become less important since less weight is given to these age groups in computing the mean length.

To compute predicted mean length in year \( y \), we need the fishing efforts going back in time for an infinite number of years if we assume an infinite number of cohorts are present (see equation (4)). This creates a minor difficulty in specifying the predicted mean lengths for the initial years of the time series. In the absence of fishing effort information for years prior to the first year of mean length observation, one approach is to assume zero fishing effort. Hence the mortality rate depends solely on the parameter \( M \), which is estimable. Another approach is to assume equilibrium conditions at the start of the time series and use the (average) fishing effort(s) in the first year(s) of the time series as the effort prior to the start of the time series. A third approach is to divide the time series into two parts such that the fishing efforts in the first part of the time series are used to compute predicted mean lengths in the second part. Essentially, the observed lengths in the first part of the time series are disregarded. The third possibility may not be a viable option if the time series is too short or the analyst does not wish to ‘waste’ data. In practice, one could explore all possible options
and see if the results are very different from each other. We note that as the time
series grows longer, this problem diminishes.

By the Central Limit Theorem, sample means will tend toward a normal
distribution with increasing sample size. Hence, the sample mean length is
modeled as being normally distributed, i.e., $\bar{L} \sim N(\mu, \frac{\sigma^2}{m})$, with the associated
probability density function $f(\bar{L}; \mu, \sigma^2) = \frac{\sqrt{m}}{\sqrt{2\pi\sigma^2}} e^{-\frac{m}{2\sigma^2}(\bar{L} - \mu)^2}$, where $\mu$ is the
predicted mean length $\bar{L}_{\text{pred},y}$ from equation (4) and $m$ is the sample size of
observed lengths $> L_c$. The product likelihood function for $n$ years of observed
mean lengths with sample size $m_y$ is given as:

$$\Lambda = \prod_{y=1}^{n} \frac{m_y}{\sqrt{2\pi\sigma^2}} e^{-\frac{m_y}{2\sigma^2}(\bar{L}_y - \mu_y)^2}$$

(5)

Maximum likelihood estimation is employed to estimate the parameters $q$ and $M$
from the log likelihood $\log_e(\Lambda)$ which is proportional to $-n \cdot (\log_e(\sigma) -$

$$\frac{1}{2\sigma^2} \cdot \sum_{y=1}^{n} m_y \cdot (\bar{L}_y - \mu_y)^2.$$

Simulation procedure and model evaluation

Various authors have found that estimates of the parameters $q$ and $M$ are
highly, negatively correlated when estimated within a common model framework
(e.g., Fu and Quinn II, 2000; Wang, 1999; Megrey, 1988). They are also difficult
to estimate reliably when there is little contrast in the catch or effort data. Hence
we used simulations to evaluate the performance of our estimator under varying scenarios and to determine if the estimates of \( q, M \) and the corresponding \( Z \)'s (denoted as \( \hat{q}, \hat{M} \) and \( \hat{Z} \)) are useful and reliable.

In addition to reflecting the underlying mortality rates, mean length data are also subject to other sources of variability, i.e., sampling and non-sampling (process) errors, which together we will refer to as pooled errors. The former can be reduced by increasing sample size \( m \) of measured mean lengths, but the latter, such as recruitment variability, may not be accounted for in a like manner. To explore the effect of pooled errors in mean length on the reliability of the model estimates, we added random errors \( \varepsilon \sim N(0, \sigma^2/m) \) to generated mean length data with \( \sigma / \sqrt{m} \) (denoted henceforth as \( \sigma' \)) varying from 1 to 5 in magnitude. A single realization of mean length data generated with three levels of \( \sigma' \) is shown in Fig. 2 (top row). When \( \sigma' = 1 \), the trend in mean length is clear; when \( \sigma' = 5 \), one can still see a decline in mean length although the details of when and how much are obscured.

For clarity, we present scenarios with a single change in \( Z \) over the simulated time-series. Our base case scenario is modeled after a stock with high \( K \) subjected to increasing fishing effort such that the \( Z \) rate of that stock increased by 0.4 yr\(^{-1} \) from \( Z_1 = 0.6 \) to \( Z_2 = 1.0 \) yr\(^{-1} \) (\( \Delta Z = + 0.4 \)). We present additional scenarios with a single parameter modification to systematically examine the effect on the model performance (see Table 1 for details).
In our simulation, the age summations in equation (4) was arbitrarily approximated to an upper age limit \( t_{\text{max}} \) that corresponded to 0.2% of the original population size when subjected to a constant decline rate \( Z = \min \{Z_1, Z_2\} \). The underlying constants for all scenarios were: \( L_\infty = 100 \text{ cm}, t_0 = 0 \text{ yr}, M = 0.2 \text{ yr}^{-1}, q = 0.002 \text{ per unit effort}, t_c = 1 \text{ yr}, t_{\text{max}} = 10 \text{ yrs} \) (i.e., exploitable life span of 9 years), 15 years of mean length observations, and change in fishing effort occurred at the start of the sixth year. The population was in equilibrium (i.e., experiencing \( Z_1 \)) prior to the start of the mean length data collection. These parameters and conditions were used to generate mean length datasets using the population and growth model outlined above. Predicted values of mean length at the start of the time series were calculated consistent with the data generation process, i.e., on the basis that the population was in equilibrium to start. To highlight the negligible effect of the age summation procedure above, the mean length at the start of the time series in the base case computed from nine age groups is 52.04 cm while that computed from 50 age groups is 52.15 cm.

To quantify the reliability of the resulting estimates of the parameters of interest, \( \theta = \{q, M, Z_1, Z_2\} \), we used the measures of percent bias

\[
\text{%Bias} = \frac{100 \cdot \sum (\hat{\theta} - \theta)}{n \theta}, \text{ percent root mean square error,}
\]
%RMSE = \left\lfloor \frac{100 \cdot \sqrt{\sum_{\theta} \left(\hat{\theta} - \theta\right)^2}}{\theta \cdot n} \right\rfloor \text{ and the coefficient of variation (CV = ratio of the standard deviation to the mean of } \hat{\theta}) \text{ based on 5000 simulated datasets. The ratio of } \frac{\hat{Z}_2}{\hat{Z}_1} \text{ was also examined because an estimator may be better at capturing the trend of change in a parameter than it is in quantifying the absolute value of the parameter. Ratio } > 1 \text{ indicates an increase in } Z. 

All analyses and plotting were conducted using the R statistical programming language (R Development Core Team, 2011). We used the nlminb minimization routine for the maximum likelihood estimation.
RESULTS

Estimates of $q$ and $M$ were highly negatively correlated in all scenarios, with the Pearson’s correlation coefficient $r^2 \approx 0.8$ (Fig. 2, middle row). For the base case scenario ($Z_1 = 0.6$, $Z_2 = 1$, $Z_2/Z_1 = 1.67$), $\hat{q}$ and $\hat{M}$ were reliable when $\sigma' = 1$ ($q$: % Bias = 0.06, % RMSE = 7.4, CV = 0.07; $M$: % Bias = -0.5, % RMSE = 6.2, CV = 0.06) but the reliability of the estimates decreased with increasing $\sigma'$ (see Fig. 2, middle row). With $\sigma' = 3$, % RMSE = 21.8 and 18.8 for $\hat{q}$ and $\hat{M}$ respectively and when $\sigma' = 5$, the corresponding % RMSE = 37.1 and 31.2.

The CV values increased from 0.22 ($\sigma' = 3$) to 0.36 ($\sigma' = 5$) for $\hat{q}$ and from 0.19 to 0.31 for $\hat{M}$.

The % RMSE increased linearly with increasing $\sigma'$ across all the scenarios simulated (Fig 3). Relative to the base case scenario (Fig. 3(a), top row), the $q$ and $M$ parameters appeared to be almost as well estimated when a reversed directional change in $Z$ of equal magnitude was simulated (Fig. 3(c), top row). With less contrast in the change in $Z$ (Fig. 3(d), top row), the $q$ and $M$ parameters were less well estimated than the base case, especially for $q$. The least favorable scenario for the performance of the estimator appeared to be the case of a low von Bertalanffy $K$ (Fig. 3(b), top row), with % RMSE as high as 73% for $\hat{q}$ and 55%
for $\hat{M}$ when $\sigma' = 5$. The model appeared to perform better in the estimation of $M$ rather than $q$ across the simulation scenarios based on the % RMSE.

However, simulation results show that the $Z_1$ and $Z_2$ estimates were not correlated with each other and were reliable even at high levels of $\sigma'$ (Figure 2, bottom row; Figure 3, bottom row). For the base case scenario, % RMSE ranged from 2.2% to 11.3% for $\hat{Z}_1$ and from 2.5% to 12.5% for $\hat{Z}_2$ across the levels of $\sigma'$. The CV values were 0.02, 0.07, and 0.11 for $\hat{Z}_1$ and 0.02, 0.07, and 0.12 for $\hat{Z}_2$ when $\sigma' = 1, 3$ and 5 respectively. Histograms of the ratio of $\hat{Z}_2/\hat{Z}_1$ indicated that the center of the distribution coincided with the true $Z_2/Z_1$ ratio and the model reliably predicted an increase in $Z$ over the time series even with increasing $\sigma'$ (ratio $>1$ 100% of the time; see Fig. 2, bottom row).

Relative to the base case scenario (Fig. 3(a), middle row), the $Z_1$ and $Z_2$ parameters were almost as well estimated in the scenarios of decreasing $Z$ (Fig. 3(c), middle row) and less contrast in $Z$ (Fig. 3(d), middle row) with % RMSE of no more than 15%. However, $Z_1$ and $Z_2$ were less well estimated in the case of the low $K$ (Fig. 3(b), middle row), with % RMSE up to 27% when $\sigma' = 5$. Nevertheless $Z_1$ and $Z_2$ were reliably predicted across all the scenarios simulated (ratio was $>1$ for scenarios of an increase in $Z$ and $<1$ for the scenario of a decrease in $Z$ 100% of the time; see Fig. 3, bottom row).

From the scatterplots of Fig. 3 (bottom row), we glean additional information on the behavior of the estimator. $Z_1$ was estimated slightly better than $Z_2$ when an increase in $Z$ was simulated (base case, see Fig. 3(a) bottom row), but
the opposite was observed when a decrease of the same magnitude ($\Delta Z = -0.4$) was simulated (Fig. 3(c) bottom row). In addition, less contrast in $Z$ ($\Delta Z = +0.2$, Fig. 3(d) bottom row) did not appear to affect the reliability of the $Z$ estimates relative to the base case scenario.

Estimates of $q$ were almost always positively biased in our simulation while $\hat{M}$ may be biased negatively or positively depending on the scenario. The magnitude of the % Bias for $\hat{q}$ was greater than that of $\hat{M}$. However, bias appeared to be a negligible component in the RMSE as evidenced by a maximum of 10% bias in the $\hat{q}$ estimates and 5% in $\hat{Z}$ when $\sigma' = 5$ in the least favorable scenario of a low $K$. Although the % RMSE of $\hat{q}$ and $\hat{M}$ can be high when the $\sigma'$ levels are high, the % RMSE of $\hat{Z}$ were often less than 15% with the exception of the low $K$ scenario.

We examined additional scenarios specifically in relation to a low $K$ situation. When adding additional years of mean length and effort data (see Table 1(f)), the % RMSE for all parameters improved, especially for $\hat{q}$ and $\hat{Z}_2$. When less contrast in $Z$ change was simulated (Table 1(e)), the % RMSE for $\hat{q}$ and $\hat{M}$ increased; however the % RMSE for $\hat{Z}$ improved.
DISCUSSION

The model presented in this paper extends the application of non-equilibrium length-based estimators by utilizing additional information on fishing effort. Our simulation study of the model showed that the estimates of $q$ and $M$ are highly negatively correlated and their reliability decreases with increasing variability in mean length information. This is not a surprising result given that other authors have noted the same difficulty in simultaneous estimation of $q$ and $M$ (e.g., Wang, 1999; Fu and Quinn II, 2000). It still may be possible to obtain reliable estimates of $q$ and $M$ when the mean length data appeared to closely reflect the true trend in mortality changes.

However, even with poorly estimated $q$ and $M$, the corresponding estimates of $Z$ appeared to be reliable. The mean length will respond to a change in $Z$ by equilibrating to the new $Z$ more rapidly when (1) the stock growth rate is high, (2) the magnitude of change in $Z$ is small, and (3) the change in $Z$ constitutes an increase in $Z$ rather than a decrease of the same magnitude. Hence the proposed extended model appeared to be most promising when applied to fisheries with such characteristics. These conditions, however, are not prerequisites for reliable $Z$ estimates. Simulation results were also very promising with regard to the model’s ability to capture correctly the trend in change of $Z$ rates even with large noise in the mean length data.
The model yields potentially more detailed information than the original Gedamke and Hoenig (2006) model, i.e., year-specific versus of period-specific mortality rates, while reducing the number of parameters (q and M versus pre- and post-change Z’s and year(s) of change for each time period, depending on the assumed number of breaks in the Gedamke and Hoenig model). By using both length and effort data, this approach constitutes a bridge between data-limited models and more complex models and is potentially useful for checking assessment results from complex models.

Superficially, our procedure of finite summation for obtaining the predicted mean length may seem to follow the logic of Ehrhardt and Ault (1992), who modeled age composition with an upper age truncation (denoted with \( t_{\lambda} \)). However, the two approaches are different in an important way. Their mean length computation is based on the assumption that (1) ages above \( t_{\lambda} \) were absent or present in reduced numbers relative to what would be expected under constant mortality with age and (2) there is no variability in size at age. They then equated this upper age \( t_{\lambda} \) with an upper length \( L_{\lambda} \) and computed the mean of the observed lengths \(< L_{\lambda} \). Essentially they equated the truncated observed mean length with a predicted mean length from a truncated age frequency distribution. The assumption that a truncation in age corresponds to a truncation in length turns out to be critical (Then, this dissertation). The procedure in this paper however does not assume length truncation or zero variability in size at age.

In the absence of direct fishing effort data, one could estimate effort from total commercial catch and a catch rate series. In practice, it may be difficult to
obtain a time series of standardized fishing effort because of multiple and changing fishing gears or management measures aimed at controlling effort. The availability of research survey effort data presents a potential solution to this problem via the equation of \( \frac{\text{Total Catch}_{\text{commercial}}}{\text{CPUE}_{\text{survey}}} = \text{Effective Effort} \) where effective effort is defined as the fishing effort required by the commercial fleet to obtain the given catch if all the fishers fished in a manner similar to the survey boat. Hence, the corresponding estimated \( q \) in the model will be the survey catchability coefficient.

Although the assumptions of constant \( q \) and \( M \) are rather tenuous, especially for stocks with long history of exploitation and diverse fishing patterns, the primary application of length-based estimators is in the realm of data-poor fisheries where the ability to obtain reliable estimates of time-varying \( q \) and \( M \) is unlikely. Others have shown that, even with underlying time-varying \( M \) in the fishery dynamics, the assumption and estimation of a constant \( M \) in the model can be a useful and viable option (Deroba and Schueller, 2013; Johnson et al., in press). Our simulation studies showed that it is relatively harder to obtain reliable estimates of \( q \) than \( M \) when estimated simultaneously; hence one could fix the value of \( M \) in the model in the interest of estimating \( q \). Additionally, if one conceivably has working knowledge of the year or time period in which catchability in the fishery has shifted, one could partition the dataset into two parts and fit the model separately.
Other factors such as the effects of sex-specific differences in growth and varying recruitment were not considered for this paper, but could be incorporated when such information is readily available. With respect to violations of assumptions, an analyst with knowledge of the fishery can parameterize the model specifically to the fishery for further simulation studies of the model performance.

In summary, the extended non-equilibrium mean length-based estimator presented in this paper appeared to be a promising tool in assessing relatively data-limited stocks. While it may be difficult to obtain reliable estimates of the parameters $q$ and $M$ when a lot of noise is present in the mean length data, the corresponding estimates of $Z$ appeared to be useful. In cases where fisheries and stock assessors are interested primarily in trends in changes of $Z$ over the time series, this method appeared to be able to capture this information accurately, given that the other assumptions of the methods are met.
REFERENCES


Table 1
Parameters of total mortality rates $Z$ and von Bertalanffy growth coefficient $K$ used in the simulations. Fishing effort unit is not shown since the actual relevance of the fishing activity is the corresponding impact on the $Z$ experienced by the fished stock. Other parameter constants used in the simulation are natural mortality $M = 0.4$, catchability coefficient $q = 0.002$ and the change in $Z$ rates in the time series of data occurs in the fifth year.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Changes in $Z$</th>
<th>Von Bertalanffy $K$</th>
<th>No. of mean length observations, $n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Base Case</td>
<td>$Z_1 = 0.6$, $Z_2 = 1.0$, $\Delta Z = +0.4$</td>
<td>0.4</td>
<td>15</td>
</tr>
<tr>
<td>(b) Low $K$</td>
<td>Same as above</td>
<td>0.1</td>
<td>15</td>
</tr>
<tr>
<td>(c) Decreased $Z$</td>
<td>$Z_1 = 1.0$, $Z_2 = 0.6$, $\Delta Z = -0.4$</td>
<td>0.4</td>
<td>15</td>
</tr>
<tr>
<td>(d) Less contrast in $Z$</td>
<td>$Z_1 = 0.6$, $Z_2 = 0.8$, $\Delta Z = +0.2$</td>
<td>0.4</td>
<td>15</td>
</tr>
<tr>
<td>(e) Low $K$, $\Delta Z = +0.2$</td>
<td>Same as above</td>
<td>0.1</td>
<td>15</td>
</tr>
<tr>
<td>(f) Low $K$, $\Delta Z = +0.4$, $n = 20$</td>
<td>$Z_1 = 0.6$, $Z_2 = 1$, $\Delta Z = +0.4$</td>
<td>0.1</td>
<td>20</td>
</tr>
</tbody>
</table>
Fig. 1. The contrasting responses in mean length of a stock to trends of (a) a single increase in total mortality rate, $Z$, from 0.6 to 1.0 yr$^{-1}$ versus (b) a single decrease in $Z$ from 1.0 to 0.6 yr$^{-1}$. The stock shown here is simulated with the von Bertalanffy parameter $K = 0.4$ and $L_\infty = 100$ cm.
Fig 2. Top row: Generated mean length data with added variability (σ'); a single realization is shown here for the base case scenario (Z₁ = 0.6, Z₂ = 1, K = 0.4) for σ’ = (a) 1, (b) 3, and (c) 5. Middle row: Scatterplots of 5000 estimates of natural mortality rate $M$ versus estimated catchability $q$. Bottom row: Corresponding $Z₂$ versus $Z₁$ for varying σ’. Dashed lines denote the true parameter values simulated and the dotted lines denote the 2.5th and 97.5th percentiles of the estimates. Insets of histogram (bottom row) show the ratio of $Z₂/ Z₁$ estimates, with dashed lines denoting the ratio of 1 and the solid triangles denoting the true ratio of $Z₂/ Z₁$ estimates (≈ 1.67).
Fig 3. Percent root mean square error (% RMSE) as a function of error in mean length ($\sigma'$), for the estimates of natural mortality rate $M$ and catchability $q$ (top row) and corresponding $Z_2$ and $Z_1$ (middle row) for varying scenarios: (a) Base case, (b) Low $K$, (c) Decreased $Z$, and (d) Less contrast in $Z$ (see Table 1 for actual parameter values). Scatterplots of 5000 estimates of $Z_2$ versus $Z_1$ (bottom row) for varying scenarios, given $\sigma' = 3$. Insets of histogram (bottom row) show the ratio of $Z_2/ Z_1$ estimates, with dashed lines denoting the ratio of 1 and the solid triangles denoting the true ratio of $Z_2/ Z_1$ estimates for each scenario.
CHAPTER 4

Evaluating the predictive performance of empirical estimators of natural mortality rate using information on 201 fish species
ABSTRACT

Numerous methods have been developed in the last 70 years to predict the natural mortality rate, \( M \), of a stock based on empirical evidence from comparative life history studies. These indirect or empirical methods are used in most stock assessments to (1) obtain estimates of \( M \) in the absence of direct information, (2) check on the reasonableness of a directly estimated value of \( M \), (3) examine the range of plausible \( M \) estimates for the stock under consideration, and (4) define prior distributions for Bayesian analyses. The two most cited empirical methods have appeared in the literature over 2500 times. Despite the importance of these methods, there is no consensus in the literature on how well these methods work in terms of prediction error or how their performance may be ranked. We evaluate estimators based on various combinations of maximum age (\( t_{\text{max}} \)), growth parameters and water temperature by seeing how well they reproduce 201 independent, direct estimates of \( M \). We use ten-fold cross-validation to estimate the prediction error of the estimators and to rank their performance. With updated and carefully reviewed data, we conclude that a \( t_{\text{max}} \)-based estimator performs the best among all estimators evaluated. The \( t_{\text{max}} \)-based estimators in turn perform better than the Alverson-Carney method based on \( t_{\text{max}} \) and the von Bertalanffy \( K \) coefficient, Pauly’s method based on growth parameters and water temperature and methods based just on \( K \). It is possible to combine two independent methods by computing a weighted mean but the improvement over the \( t_{\text{max}} \)-based methods is slight. Based on cross-validation prediction error, model parsimony, model residual patterns and biological considerations, we recommend the use of a \( t_{\text{max}} \)-based estimator \( (M = 5.075/ \ t_{\text{max}}, \text{prediction error } = 0.32) \) when possible and a \( K \)-based method \( (M = 1.684K, \text{prediction error } = 0.61) \) otherwise.
INTRODUCTION

One of the most influential stock assessment parameters, natural mortality rate ($M$), is generally believed to be difficult to estimate reliably and directly. By direct, we refer to estimation of $M$ using information strictly pertaining to the species or stock of interest. Five examples are: 1) measuring total mortality in an unexploited stock, 2) relating total mortality to the amount of fishing and extrapolating to zero fishing effort, 3) measuring both total mortality and exploitation rates and solving for components of mortality (e.g. Hewitt et al., 2007), 4) mark-recapture and telemetry studies (e.g. Hoenig et al., 1998; Knip et al., 2012), and 5) estimating $M$ internally in an integrated stock assessment model (see Maunder and Punt, 2013). Direct estimation methods of $M$ are often data-intensive, thus limiting their application to relatively data-rich stocks.

A host of methods have been developed in the last 70 years to estimate $M$ from surrogate life history information. These life history correlates include maximum age $t_{\text{max}}$ (Tanaka, 1960; Bayliff, 1967; Ohsumi, 1979; Hoenig, 1983), von Bertalanffy growth coefficient $K$ (Beverton and Holt, 1959; Ralston, 1987; Charnov, 1993; Jensen, 1996) as well as composites of these variables - for example, the von Bertalanffy asymptotic size $L_\infty$ or $W_\infty$, growth coefficient $K$ and water temperature $T$ (Pauly, 1980), and both $t_{\text{max}}$ and $K$ (Alverson and Carney, 1975). Ecological theory as well as empirical evidence provides strong basis for
prediction of $M$ from surrogate information not only for fish stocks but also for other animals and even plants (Hoenig, 1983; McCoy and Gillooly, 2008).

We use the term indirect or empirical to categorise this suite of methods since their derivation relies on comparative life history studies to borrow strength from numerous species (e.g. Pauly, 1980; Hoenig, 1983). Some models for estimating $M$ have been derived based on theoretical ecological considerations; these models constitute indirect methods by our definition if they rely on empirical data to estimate one or more unknown parameters (e.g. Alverson and Carney, 1975; Gunderson and Dygert, 1988).

Although these empirical methods are often perceived as being less reliable than their data-rich counterparts, a general consensus is that empirical methods are useful and very important particularly in a data-poor setting (e.g. Brodziak et al., 2011). Empirical methods are routinely applied in stock assessments, both for data-poor and data-rich stocks, in the following ways: (1) obtain point estimates of $M$ in the absence of direct information, (2) examine the reasonableness of a directly estimated value of $M$, (3) obtain a range of plausible values for $M$ for the stock by applying a suite of indirect methods, and (4) define prior distributions of $M$ in Bayesian analyses.

A large body of evidence suggests that $M$ varies over age and size (e.g. Peterson and Wroblewski, 1984; McGurk, 1986; Lorenzen, 1996; Gislason et al., 2010) and over time. Nonetheless, most fisheries scientists would agree that a single value for $M$ can provide a useful representation of mortality over much of the lifespan of a species. Recent simulation studies have indicated that the
assumption of a constant $M$ in stock assessments is still very useful even when the simulated populations are subject to age- and time-varying $M$ dynamics (Deroba and Schueller, 2013; Johnson et al., this volume). We proceed on the assumption that it is worthwhile to seek better ways to predict a single value of $M$ for a stock.

Among the empirical estimators of $M$, the Pauly (1980) and Hoenig (1983) log-log linear regression equations are the two most widely applied estimators. The former regression was fitted to 175 fish stocks (113 unique species; see Griffiths and Harrod, 2007) while the latter was derived based on a total of 130 stocks (51 species of fish, 11 of mollusks and 13 of cetaceans). As of February 13, 2014, the number of citations for Pauly (1980) equaled 2016 while Hoenig (1983) had been cited 895 times (Google Scholar http://scholar.google.com). The widespread use of these methods can be attributed to (1) simplicity and ease of application, (2) perceived reliability given the amount of empirical information used to ‘train’ their derivation, and (3) minimal data required to apply them.

Given the importance of empirical estimators, it is surprising there has not been a comprehensive study to compare their performance. Kenchington (2013) described 30 estimators and minor variants and applied them to 12 species of fish and one invertebrate but with a small sample size, it was difficult to draw general conclusions regarding the performance of the methods. Various studies that employed a suite of these indirect estimators have noted a wide disparity in resulting estimates (e.g. indirect $M$ estimates ranged from 0.134 to 0.706 yr$^{-1}$ for the tropical lutjanid *Lutjanus quinquelineatus* (Newman et al., 1996), 0.003 to 0.14 yr$^{-1}$ for *Sebastes variabilis* (Malecha et al., 2007), 0.3 to 2.2 yr$^{-1}$ for the blue
crab (Hewitt *et al.*, 2007)). There is no consensus on why \( M \) estimates from different empirical predictors vary so widely or which should be preferred. The practice in stock assessment applications to utilise these multiple estimates of \( M \) as a means of characterising the uncertainty of \( M \) for a given stock generally assumes implicitly that all the estimates are equally reliable and independent (but see Hamel, this volume).

A major obstacle to such a comparative endeavour is the lack of a comprehensive dataset with all necessary estimates of life history variables used in the empirical estimators of interest. In addition to a comprehensive review of predictive ability, it is perhaps of even greater value to update and improve upon the existing indirect estimators with a more extensive dataset of \( M \) and life history estimates.

The Gunderson and Dygert (1988) and the Pauly (1980) estimators have been ‘updated’ with larger and presumably better datasets (the former by Gunderson (1997) and the latter by Griffiths and Harrod (2007) and Jensen (2001)). Punt *et al.* (2005, Table 14, p. 38) presented updated regression estimators for both Hoenig (1983) and Pauly (1980). Beverton and Holt (1959) and Beverton (1963) noted a relationship between \( M \) and \( K \). Charnov (1993) termed this a “Beverton and Holt life history invariant” relationship; he fitted the model \( M = a/K \) which we refer to as the one-parameter, \( K \)-based method. Jensen (1996) updated this relationship and later proposed a two-parameter \( K \) method using a subset of Pauly’s data (Jensen, 2001). However it is unclear if the updated
estimators predict $M$ rates of fish significantly better than the original formulations of the estimators.

The focus of this paper is the estimation of $M$ for teleosts and elasmobranchs. The challenge to address appropriately the questions outlined above is the fact that we do not know the true $M$ of any fish. This raises the question: How might we objectively evaluate and rank the predictive ability of these estimators? The approach we took in this paper is to ask which estimator best reproduces what we know about $M$, which is the collection of direct estimates of $M$ in the scientific literature and what we can estimate from both published and unpublished data provided by various fisheries scientists around the world.

Hence, the goal of this paper is to compare and rank the predictive abilities of four major indirect estimation approaches for $M$, namely the $K$-based methods and those of Alverson and Carney (1975), Pauly (1980), and Hoenig (1983), and as well as variants of these estimators. We also explored the possibility of weighting independent estimators to improve $M$ prediction. Specifically, this paper seeks to answer the following questions: (1) How well do the estimators perform in predicting $M$ estimates not used to train the original equation? (2) When evaluated on a common dataset, how do the various methods rank in terms of prediction error? (3) What are the updated model parameters for the preferred estimators when evaluated with a larger, better dataset? (4) Would a weighted combination of estimators improve prediction of $M$?

In conjunction with this research, we have compiled a dataset of direct $M$ estimates and best-matched life history parameters of more than 200 unique fish
species with documentation of the methods used to estimate $M$ as well as the aging methods (where applicable). The need for a well-documented database of $M$ rates of species has been outlined in Brodziak et al. (2011) based on recommendations from a national workshop on estimation of mortality rates.

One fundamental problem with using compilations of parameter estimates is that the quality of individual values can be highly variable and these values are often unknown or controversial. One investigator’s inclusion of a particular stock may be rejected by another investigator (e.g. Gislason et al. (2010) included data for a serranid but Kenchington (2013) rejected those data). This is an inherent and unavoidable aspect of comparative life history studies. Gislason et al. (2010) developed and applied a set of quality control criteria to select usable data. This seemingly logical approach can potentially introduce biases because the accepted species may be the best studied species and these might not be typical of the wider collection of species about which one wishes to make inferences about natural mortality. We have eliminated obviously erroneous data and will make the full, documented dataset publicly available one year after publication of this paper (www.vims.edu/mort.db) so that researchers can filter the data according to whatever criteria they deem appropriate and explore whether the results are robust to choice of data selection criteria.
METHODS

Data compilation and quality control

We included in the dataset fish stocks that are of commercial and sport value as well as those that are presently of no economic importance. We utilized existing compilations of estimates of $M$ (e.g. Gislason et al., 2010; Hoenig, 1982; McGurk, 1986; Pauly, 1980) as well as extensive literature searches of published materials (journal articles, stock assessment reports, grey literature). We also derived new estimates of natural mortality rate using our own data and data supplied by colleagues. We verified that each $M$ estimate was derived from a direct method by examining the original sources of the $M$ estimates. Similarly, the original source document was consulted to verify the supporting life history information. Catch curve-based estimates for stocks that were heavily exploited according to any source document were eliminated.

A noteworthy mention is the heavy reliance of the Pauly (1980) and Hoenig (1982) datasets on the earlier mortality compilation of Beverton and Holt (1959). We examined the original sources of these $M$ estimates and found many of the sources did not themselves provide direct $M$ estimates. Beverton and Holt (1959) most likely estimated $M$ as well as the von Bertalanffy parameters based on the data (mostly some form of numbers-at-age and mean length-at-age data) in these source papers. For some of these stocks, we re-estimated the $M$ and the von
Bertalanffy parameters primarily to validate the published estimates in Beverton and Holt (1959); for catch curve data, $M$ was re-estimated using the Chapman and Robson (1960) estimator based on the recommendations given in Smith et al. (2012). In general, the selected age of full recruitment corresponded to the age with peak catch plus one, with the exception of short-lived species (at least 3 age groups used to estimate $M$) and the cases in which the age of full recruitment was specified by the source authors.

Where available, $M$, growth, $t_{\text{max}}$ and $T$ estimates were extracted from the same study. Otherwise, we searched the literature to find the set of parameters that best matched the $M$ estimates in terms of location and timing of study. When a range of values were given (say $M$ estimates that were based on three different catch curve methods), we used the mean value. When the $M$ estimate was pooled for both sexes but only sex-specific estimates were given for $L_\infty$ and $K$, the sex-specific values were averaged. Mean $T$ for a stock was either obtained from the same mortality-growth study, similar stock area (where $T$ was available for another species in the same area), FishBase (http://www.fishbase.org), or estimated loosely based on the general criteria outlined in Pauly (1980). For certain species, no estimates were available of von Bertalanffy parameters (due to perceived linearity in growth by authors) or $t_{\text{max}}$ (due to lack of ageing work). We did not attempt to ‘borrow’ parameter estimates for these, but left them out of the analysis. Length measurements were not standardized; they were comprised primarily of total (34%) and fork length measurements (33%).
One of the assumptions of fitting a linear regression is that the observations themselves are independent of each other. The inclusion of multiple $M$ estimates for a single species (stocks from multiple locations or separate male and female estimates) very likely violates that assumption. For instance, Pauly (1980) had a total of 9 estimates of $M$ and corresponding parameters for the Atlantic cod while Hoenig (1980) included 8 estimates for the cisco. In order to tackle this issue, one could consider modeling the hierarchical structure, or use only a single observation for a given species. We elected to use the latter approach because most genera and species were represented by single observations, thus making it difficult to estimate components of variability. We selected the best set of estimates for a species based primarily on the aging method, validation of the ages, sample size as well as the author’s and our evaluation of the reliability of the estimates. An exception to this is the lake whitefish ($Coregonus clupeaformis$) where we included both the ‘normal’ ($M = 0.15$) and ‘dwarf’ ($M = 1.3$) forms whose differences in mortality and growth were vast (data from Beverton and Holt (1959)) – we considered these forms as two distinct ‘species’ in the context of this analysis.

**Evaluation and updating of estimators**

We evaluated the approaches of Pauly (1980), Hoenig (1983), Alverson and Carney (1975) and the $K$-based estimators and various variants arising from differences in model formulation and fitting procedures (Table 1). Of note is a one-parameter estimator based on $t_{max}$ given by $M_{est} = a / t_{max}$, where $M_{est}$ denotes
a new prediction of $M$ and $a$ is a coefficient that has been estimated (by least squares) from a compilation of estimates of $M$ and $t_{max}$ from the literature (Bayliff, 1967; Hewitt and Hoenig, 2005; Ohsumi, 1979). This model corresponds to setting the slope to -1 in the model formulation of Hoenig (1983). Some investigators have fixed the value of $a$ at an arbitrary value rather than estimating it but there is little justification for this (see Hewitt and Hoenig 2005) and such estimators are not considered here. Evaluation of taxa-specific estimators (e.g. Serranidae and Lutjanidae (Pauly and Binohlan, 1996; Ralston, 1987); Engraulidae (Bayliff, 1967)) are also not considered here. The full list of all the variants of the estimators evaluated are recorded in Then and Hoenig (2014).

We evaluated the predictive performance of the estimators based on three metrics: (1) ‘Historical Performance’ - how well do the original estimators predict estimates of $M$ that were not used to train the original estimators? (2) ‘Approach Evaluation’ – how well do the different estimators compare with each other when refitted to, and evaluated on, a common dataset? and (3) ‘Updated Performance’ – when updated using the fullest applicable dataset, how well do the estimators reproduce the $M$ estimates? The three metrics differed in the subsets of data used in the evaluation exercise.

The main purpose of the Historical Performance analysis is to determine how well the original estimators have served stock assessment scientists. For the Historical Performance analysis, we applied the original formulas to a new (independent) dataset and calculated the root mean square prediction error.
(RMSE), which is given as
\[ \sqrt{\frac{1}{n} \sum_{i=1}^{n} (M_{\text{est},i} - M_{\text{lit},i})^2} \]
where \( M_{\text{est},i} \) is the predicted \( M \) for species \( i \) from the estimator and \( M_{\text{lit},i} \) is the literature-derived estimate for species \( i \), for \( i = 1, \ldots, n \) species. We evaluated the published log-log regression equations of Pauly (1980) and Hoenig (1983). We did not evaluate the historical one-parameter \( t_{\text{max}} \) or the two-parameter \( K \) models since the same regression form has multiple coefficient estimates by different authors (see Table 1). Alverson and Carney (1975) estimated the constant in their equation based on 63 data points, which were not provided in their paper. Jensen’s (1996) one-parameter \( K \)-based equation was derived from the substitution of a derived equation into another without provision of published data. Hence we evaluate the Historical Performance of the Alverson and Carney (1975) and Jensen (1996) estimators based on the fullest dataset recognizing that a small portion of the data may occur in both the derivation and the evaluation.

The Approach Evaluation was conducted using the common dataset (201 species) with complete sets of parameter estimates available for all estimators. For both the Approach Evaluation and the evaluation of Updated Performance, we also explored fitting the Pauly and Hoenig models using non-linear least squares, thus modeling \( M \) directly, in addition to evaluating the original log-log linear regression formulation (Table 1). This corresponded to fitting the model \( M = aK^bL_\infty^c T^d + \varepsilon \) for Pauly and \( M = a t_{\text{max}}^b + \varepsilon \) for Hoenig where \( a, b, c \) and \( d \) are parameters to be estimated and \( \varepsilon \) is a random error. To distinguish these
estimators from the log-log linear versions, we denoted them as Paulynls and Hoenignls respectively. For the Pauly models, we fitted the full model as well as one excluding the temperature variable T to examine the importance of T in prediction of M. We used the Wald likelihood ratio test to compare the nested models.

For the tests of the Approach Evaluation and the Updated Performance, we used the 10-fold cross-validation technique (Hastie et al., 2009). We used the prediction RMSE as the overall metric of performance (henceforth referred to as cross-validation prediction error CVPE) and also presented as measures of model fit the coefficient of determination (unadjusted $r^2$) and the mean absolute difference (MAD) between the literature estimates and estimator-derived M predictions. In addition we took into consideration the behaviour of resulting model residuals. For the log-log linear models of Hoeniglm and Paulylm, the predicted M estimates used for the model evaluation and calculation of CVPE were the exponentiated log($M_{est}$).

We investigated the possibility of combining the best estimators (with lowest CVPE) using a weighting scheme to create the best linear unbiased combination of estimators. This was based on the fact that for two normally distributed, unbiased and independent estimators, the variance of the optimally weighted combined mean will be lower than the individual estimators’ variances. The updated Hoenig and Pauly estimators could be assumed as independent since there is no overlap in the variables used in each estimator and their M estimates could thus be combined as a weighted mean. The form of the weighted estimator
of $M$ is given as $p \cdot M_{Estimator_1} + (1 - p) \cdot M_{Estimator_2}$ and the weighting factor $p$ was calculated from $p = \frac{Var_{Estimator_2}}{Var_{Estimator_1} + Var_{Estimator_2}}$. We examined the independence of the pairs of estimators via residual and correlation plots.

We used 5000 bootstrap samples to estimate the standard error (SE) and 95% bias-corrected and accelerated (BCa) confidence intervals (CI) of the model parameters for the best set of updated estimators. All analyses and plotting were conducted using the R statistical programming language (R Development Core Team, 2011). The least squares fitting was done using the lm routine while the non-linear least squares fitting was performed with nls. The Wald likelihood ratio test was conducted using the lmtest package (Zeileis and Hothorn, 2002). Geometric mean regressions were computed from the output of the lm routine using the procedure described by Ricker (1975). The bootstrapping was implemented with the ‘boot’ package (Canty and Ripley, 2011; Davison and Hinkley, 1997).
RESULTS

Dataset description

Our ‘common’ dataset with complete parameter estimates for $K$, $L_\infty$, $t_{\text{max}}$ and $T$ is comprised of 201 unique fish species from 23 orders, 66 families and 142 genera with direct $M$ estimates ranging from 0.014 to 7.92 yr$^{-1}$. Most of the $M$ estimates were derived from age-based catch curve analyses (80%), 5% from length-based catch curves, 7% from tagging and 3% from the regression of total mortality rate versus effort (or variants). An additional three species did not have corresponding $t_{\text{max}}$ estimates while 12 were missing corresponding von Bertalanffy growth estimates. These additional species were included in the ‘Updated Performance’ evaluations.

The dataset comprises primarily marine (78%) and temperate (44%) species, but a broad range of reproductive strategies and habitat associations are represented as well. The dataset is largely weighted by stocks from the North American, Australian and European continents and their surrounding water bodies. The von Bertalanffy growth $K$ estimates ranged from 0.012 to 2.56 yr$^{-1}$, $L_\infty$ from 49 to 3164 mm, and $t_{\text{max}}$ from 38 weeks to 205 years. Mean $T$ of stocks ranged from 4.6 to 30°C after accounting for physiological adjustments (as described in Pauly, 1980). The strongest linear predictor for $M$ (in natural log scale) is the log transformed-$t_{\text{max}}$ ($r = -0.91$, Figure 1). This is followed by the log-
transformed $K$ ($r = 0.62$, Figure 1). The literature log($M$) estimates appeared to be fairly normally distributed, suggesting an underlying log-normal distribution for $M$ (Figure 1). When age-based $M$ estimates from the literature were excluded, the correlation between log($M$) and log($t_{\text{max}}$) remained high ($r = -0.91$, $n = 45$). The correlation between $M$ and $K$ is stronger than the log-transformed counterpart ($r = 0.68$), and $M/K$ ratios ranged from 0.06 to 14.8.

**Evaluation of estimators and their performance**

The Historical Performance evaluation of the estimators in Table 1 based on the RMSE indicated that the Hoenig (1983) estimators performed the best, followed by the Alverson and Carney (1975), Pauly$_{\text{lm}}$ (1980) and Jensen (1996) one-parameter $K$-based estimators (Table 2). The Hoenig$_{gm}$ method performed slightly better than that of Hoenig$_{lm}$. The original Hoenig (1983) equation appeared to give lower estimates of $M$ relative to the original Pauly (1980) equation for stocks with literature $M$ estimates less than 0.9 yr$^{-1}$; as the literature $M$ estimates increase, the Hoenig (1983) equation predicted higher $M$ estimates than the Pauly (1980) equation (Figure 2(a)).

For the Approach Evaluation of individual estimators, the Hoenig$_{\text{nls}}$ method performed the best among the $t_{\text{max}}$-based estimators, followed closely by the one-parameter $t_{\text{max}}$, Hoenig$_{\text{lm}}$ and distantly by Hoenig$_{gm}$ (Table 2). Among the estimators that are not based solely on $t_{\text{max}}$, the Alverson-Carney approach performed the best, followed by the Pauly$_{\text{nls}}$, Pauly$_{\text{nls-T}}$, one-parameter $K$, two-parameter $K$, Pauly$_{\text{lm}}$ and Pauly$_{\text{lm-T}}$ approaches. The $K$-based estimators and all
the Pauly-type approaches are comparable to each other performance-wise. With the exception of Hoenig_gm, the $t_{\text{max}}$-based estimators were clearly better than the other types of estimators evaluated, with approximately twice the predictive ability over the $K$-based and Pauly-type approaches. It was also evident that the non-linear least squares fitted estimators of Hoenig and Pauly were better than the log-log regression counterparts, based on the lower CVPE. The CVPE values were very similar for both the Pauly_ln and Pauly_nls approaches with the inclusion and exclusion of $T$, suggesting that $T$ was not a useful variable in predicting $M$ rates.

Model residuals appeared to be generally well behaved for most of the approaches examined (Figure 3). Most of the residual plots exhibit negative residuals for stocks with predicted values of $M > 1$, although one should bear in mind that these are raw residuals that are not scaled to the magnitude of the literature $M$ estimates. The Hoenig_nls and two-parameter $K$ models tended to have negative residuals for stocks with low predicted $M$ values (Figures 3 (b) and (d)). The Alverson-Carney estimator had a number of large positive residuals at low predicted $M$ values (Figure 3 (f)). The one-parameter $t_{\text{max}}$ model showed slightly better residuals than the Hoenig_nls model at low predicted $M$ values. The $K$-based estimators exhibited very similar residual patterns as the Pauly_nls-$T$ method (Figures 3 (c) - (e)), suggesting that the $K$ variable common to all is primarily responsible for the residual patterns.

After the models were updated with the fullest dataset available, the rank of the estimators performance-wise remained almost unchanged from the
Approach Evaluation results (Table 3). Among the $t_{max}$-based estimators, the updated one-parameter $t_{max}$ performed slightly better in terms of CVPE than the Hoenig methods, with the exception of the Hoenig$_{gm}$ estimator, which was clearly inferior to the other $t_{max}$-based methods (Table 2). The $t_{max}$-based estimators were followed in performance by the updated Alverson-Carney, Pauly$_{nls}$, two-parameter $K$, Pauly$_{nls-T}$, one-parameter $K$, and the Pauly$_{lm}$ estimators. MAD estimates ranged from 0.19 for the three best $t_{max}$-based estimators to 0.39 for the two-parameter $K$ method. Even with the $K$ variable in addition to $t_{max}$, the updated Alverson and Carney model performed worse than the solely $t_{max}$-based estimators. Hence no further results will be presented on this estimator.

The CVPE for the updated Pauly methods indicate that inclusion of $T$ did not improve $M$ prediction. Convergence of the Pauly$_{nls}$ model with $T$ fitted to bootstrap samples was particularly problematic. Bootstrap estimates of the log($T$) coefficient for the Pauly$_{lm}$ model showed high variability and suggested ambiguity of the role of $T$ in predicting $M$ since negative estimates occurred (Figure 4). The Pauly$_{lm}$ model was not significantly better than the Pauly$_{lm-T}$ model ($\chi^2 = 2.71; \text{df} = 1; \text{p-value} = 0.1$). The effect of $T$ in prediction of $M$ is dampened in the present updated Pauly$_{lm}$ model (log($T$) coefficient = 0.207) relative to the original Pauly (1980) estimator (= 0.463); the effect is even less evident when the physiological adjustment described by Pauly for extremely low temperature was not performed for fish with mean $T$ of $< 4^\circ C$ (log($T$) coefficient = 0.136). Hence we focus only on the Pauly models excluding $T$ in the predictive equation since $T$ does not appear very informative.
Among the different pairs of estimators assumed to be independent, the weighted mean from the combination of the updated Hoenig\textsubscript{nls} and Pauly\textsubscript{nls-T} yielded the lowest CVPE (= 0.312) where \( M_{\text{est}} = 0.8M_{\text{Hoenig}_{\text{nls}}} + 0.2M_{\text{Pauly}_{\text{nls-T}}}. \)

Correlation between residuals of the two updated models was relatively weak \( (r^2 = 0.306) \), thus providing some justification for assuming independence and thereby combining the two estimators. However, this best combination estimator offered no advantage in predictive improvement relative to the updated estimators of one-parameter \( t_{\text{max}} \), Hoenig\textsubscript{nls} and Hoenig\textsubscript{im} and we present no further results on this estimation approach.
DISCUSSION

Based on the CVPE alone (Table 2), it was difficult to ascertain the single best $t_{\text{max}}$-based estimator and the best $K$-based estimator. However, the updated two-parameter $K$ equation ($M_{\text{est}} = 0.09 + 1.556K$) imposes a lower bound on $M$ which is rather high such that $M_{\text{est}}$ cannot be $< 0.09$. Based on available $M$ estimates of long-lived species, it is biologically possible for $M$ to be considerably lower than 0.09 and the two-parameter $K$ equation will overestimate $M$ substantially for these species. For this reason, we do not recommend the two-parameter $K$ estimator.

The $L_{\infty}$ exponent in the Pauly$_{\text{tls-T}}$ model appeared to be estimated precisely (Table 3); however inclusion of the $L_{\infty}$ variable in the model did little to improve prediction performance over the one-parameter $K$ model.

Based on the individual CVPE, model residuals, model parsimony principle and biological considerations, we recommend the updated one-parameter $t_{\text{max}}$ estimator, which is the most parsimonious model and one of the best among the $t_{\text{max}}$-based models. In situations where an estimate of $t_{\text{max}}$ is not available we recommend the updated one-parameter $K$ estimator. The updated one-parameter $t_{\text{max}}$ model is $M_{\text{est}} = 5.075 / t_{\text{max}}$ (CVPE = 0.315), based on 213 species (Table 3). The estimated coefficient of 5.075 implies that the $t_{\text{max}}$ estimates from this study corresponded to the age where about 0.6% of the
population survives. The updated one-parameter $K$ estimator is $M_{est} = 1.684K$ based on 204 species.

In examining the pattern of $M$ prediction of the two preferred approaches, the updated one-parameter $t_{max}$ model generally yielded lower estimates of $M$ than the one-parameter $K$ estimator for stocks that appear to have low $M$ rates (according to the literature) but higher $M$ estimates than the one-parameter $K$ method for stocks that experience higher $M$ rates (Figure 2 (b)). It would appear that relative to the differences in the $M$ estimates between original Hoeniglm and Paulylm (Fig. 2(a)), the differences in $M$ estimates between the two preferred updated estimators has shifted upwards such that one may expect considerably higher positive discrepancies for stocks with high literature $M$ and slightly less negative discrepancies for stocks with low literature $M$ (Figure 2 (b)).

In this paper, we definitively ranked and quantified the predictive performance of the most widely used empirical approaches for estimating $M$ using cross-validation on a dataset with over 200 fish species of varying life histories. In addition, we reported the precision of the parameter estimates for the preferred estimators using robust methods. The $t_{max}$-based estimators are unequivocally better in predicting literature $M$ values than the $K$-based estimators evaluated; use of a composite estimator offers no clear advantage over using estimators based on just $t_{max}$. Notably the performance of the one-parameter $t_{max}$, Hoenig$_{slh}$ and Hoenig$_{lm}$ estimators were similar within the group of $t_{max}$-based estimators and the actual ranking may change slightly with addition of new data; the same can be said of the Pauly and the $K$-based methods as well. There was consistency in
predictive performance across the three metrics for evaluation, with agreement based on the CVPE and also on the $r^2$ and MAD values for each estimator. We updated the best performing $t_{\text{max}}$-based estimators as well as the preferred non $t_{\text{max}}$-based estimators and the precision of the associated parameter estimates— the latter are useful alternatives when one lacks age estimates.

Results from our study are generally corroborated by others. Punt et al. (2005) noted in a study of applying information from data-rich stocks to data-poor ones that Hoenig’s (1983) method appears more reliable than Pauly’s (1980) method for the purposes of estimating $M$. It is worth noting that the correlation between $\log(M)$ and $\log(t_{\text{max}})$ was lower in their study ($r^2 = 0.6$) than in ours ($r^2 = 0.9$). MacCall (2009) examined the standard error and coefficient of variation of estimates of $\log(M)$ from both Pauly and Hoenig models and concluded that the latter is the better model. Although based on only 13 species, Kenchington (2013) also showed that the $t_{\text{max}}$-based estimators as a group performed better than the other estimators reviewed.

Among the variables examined in this study ($t_{\text{max}}$, $K$, $L_\infty$, $T$), the most informative one to estimate $M$ empirically for a given fish species is the observed $t_{\text{max}}$ alone. This may be of no real surprise given that $M$ and $t_{\text{max}}$ are functionally related by theory. What may be of greater surprise is that the inclusion of information additional to $t_{\text{max}}$ did not improve $M$ prediction, as observed from the Alverson-Carney model which incorporated $K$ and $t_{\text{max}}$. This was also observed from the weighted Hoenig - Pauly$_{\text{nls-T}}$ estimator; inclusion of the 3-parameter Pauly$_{\text{nls-T}}$ model in the combination offered no additional prediction improvement.
than the stand-alone Hoenig\textsubscript{est} estimator. Our results indicate that despite uncertainties and various issues surrounding $t_{\text{max}}$ estimates (discussed below), the observed $t_{\text{max}}$ is clearly both the best and a sufficient predictor of $M$.

Although various authors have highlighted the issue of sample size in $t_{\text{max}}$ estimates (e.g. Brodziak \textit{et al.}, 2011; Kenchington, 2013; Maunder and Wong, 2011), we did not attempt to ‘correct’ or adjust the observed $t_{\text{max}}$ for sample size. Hoenig (1983) noted that maximum age tends to go up as the logarithm of the sample size and Beverton (1992) noted that the accuracy of $t_{\text{max}}$ appeared to be less dependent on sample size than might be thought. Kenchington (2013) offered two versions of $t_{\text{max}}$-based estimators which purportedly incorporate effective sample size and the age of full recruitment and claimed that they outperformed other $t_{\text{max}}$-based estimators. The main issues with the Kenchington estimators, in addition to the small sample size in his evaluation, are as follows: (1) Hoenig (unpublished proof on file) demonstrated that the derivations of the estimators are mathematically faulty, (2) the assumption of the exponential (or geometric) model underlying the Kenchington estimators is critical and it is unlikely fish stocks conform closely to that assumption, and (3) no guidelines were provided for computing the effective sample size to ‘correct’ the $t_{\text{max}}$ estimate. Kritzer \textit{et al.} (2001) demonstrated that a sample size of about 200 is generally sufficient to obtain a reliable estimate of $t_{\text{max}}$, which is likely a lot less than the sample size of aging for many exploited stocks.

The $M/K$ ratio underlying the one-parameter $K$-based estimator, first discussed by Beverton and Holt (1959) as being relatively invariant within
specific taxonomic groups, has since been reviewed by various authors with mixed conclusions. Beverton (1992) revisited the work and found $M/K$ ratios ranging from 0.2 to 2.5 across four main taxa, with narrower range in individual taxa. Charnov (1993) reported $M/K$ ratios ranging from 1.6 to 2.1 based on Pauly (1980)’s dataset. Frisk et al. (2001) found the $M/K$ ratio to differ significantly between teleosts and elasmobranchs. Vøllestad et al. (2003) found that the originally developed $M/K$ invariant did not hold for 29 brown trout stocks in Norway. Similarly, Purchase et al. (2006) found little evidence of life history invariance for walleye based on 435 stocks in Ontario. These results suggest that the $M/K$ ‘invariance’ may not necessarily hold even within a species and certainly not universally across all taxa, thus limiting its application in predicting $M$ rates.

The mean annual temperature variable $T$ as defined in Pauly (1980) is not a strong predictor of $M$ in our analyses. Griffiths and Harrods (2007) re-examined Pauly’s estimator with a larger dataset derived from FishBase and found that, using path analysis, the effect of temperature on $M$ was only significant indirectly. They also showed that temperature was significant in predicting $M$ of perciform fishes but not for the nonperciforms. In addition to taxa-specific differences, another possible reason why temperature was not important in our analyses is that the mean $T$ was not well estimated. It is possible that a more rigorous definition of $T$ would produce different results.

The process of rigorous quality control and transparent documentation of the dataset is central to any comparative life history study and meta-analytic analyses. One recurring issue that we have encountered when cross-checking
existing mortality compilations is the lack of reproducibility of estimates when referencing the original data sources cited due to (1) the lack of clear documentation on the sources of the $M$ estimates and the methods by which they are derived, especially in stock assessment reports, (2) careless cross-referencing of sources and ‘borrowing of parameters’, and (3) continual referencing of a source paper that appeared to be obsolete. We encountered cases where parameter estimates that were purportedly for a stock were actually taken from a closely related species from an entirely different geographical location. Such practices compromise the quality of a dataset as a useful resource for future investigations. The challenge to maintain an updated and well-documented database of $M$ estimates put forth by Brodziak et al. (2011) is one that we have undertaken for this study.

While we strived to develop and adhere to strict guidelines in building our dataset, we also recognize that utmost stringency would severely truncate the dataset and consequently reduce the usefulness of the resulting analyses in terms of generality across fish of different life history strategies. In determining what constitutes a study of acceptable quality, extracting desired estimates, pooling data, and rejecting some estimates, some degree of subjectivity was unavoidable. Various workers may wish to apply alternative data selection criteria. Hence, the existing dataset should become living documentation that should be reviewed critically and updated constantly as improved estimates are made available. Our database will be maintained on the Internet by an oversight group committed to long-term maintenance of the data.
Given the results from this paper, we make specific recommendations for best practices when estimating $M$ empirically, particularly for data-poor stocks:

1. We recommend the use of the updated one-parameter $t_{\text{max}}$ estimator ($M_{\text{est}} = 5.075/ t_{\text{max}}$) when a $t_{\text{max}}$ estimate is available. This model performed slightly better than the other $t_{\text{max}}$-based estimators, exhibited better looking residuals, and was parsimonious. The use of the Alverson-Carney estimator has no additional advantage over the estimators based solely on $t_{\text{max}}$ and is not recommended.

2. When $t_{\text{max}}$ is not available, we recommend the use of the updated one-parameter $K$ ($M_{\text{est}} = 1.684K$). This estimator is preferred to that of the updated Pauly$_{\text{nls-T}}$ even though the latter had slightly better CVPE, based on model parsimony and similar looking model residuals.

3. The updated Pauly$_{\text{nls}}$ (with $T$ included) is not preferred based on the following:
   (a) the precision of the temperature coefficient in the updated Pauly models is poor, and bootstrapping revealed the coefficient could be positive or negative,
   (b) eliminating temperature from the model provides a more parsimonious model, and (c) the effects of temperature in predicting $M$ appeared to be taxa-specific based on the study of Griffiths and Harrods (2007).

4. The practice of simple averaging of multiple $M$ estimates derived from various empirical estimators is not advocated since this study clearly showed that (a) the empirical estimators are not all equally reliable, and (b) some of the derived $M$ estimates are not independent of each other. The uncertainty of the different estimators evaluated in this study, and their mutual dependencies,
should be given due consideration in applications such as the development of
prior distributions for $M$ for Bayesian analyses.

(5) Stock assessment reports and future meta-analytic research involving
compilations of $M$ and life history parameter estimates should be vigilant in
recording the sources of data and estimates used especially in relation to the
method of derivation of the estimate of $M$.

(6) Previous stock assessments that used an empirical estimator of natural
mortality rate may need to be revisited if the estimator performed poorly in
this study.
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Table 1. The estimation approaches for predicting natural mortality, $M$, investigated in this study. ls = least squares; nls = non-linear least squares; gm = geometric mean or functional regression, as described by Ricker (1975); NA = not applicable.

<table>
<thead>
<tr>
<th>Model name</th>
<th>Formula</th>
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</tr>
<tr>
<td>Pauly$_{\text{lm-T}}^1$</td>
<td>$\log(M) = a + b\log(K) + c\log(L_{\infty})$</td>
<td>ls</td>
<td>this study</td>
</tr>
<tr>
<td>Pauly$_{\text{nls}}$</td>
<td>$M = aK^{bL_{\infty}^{cT^{d}}}$</td>
<td>nls</td>
<td>this study</td>
</tr>
<tr>
<td>Pauly$_{\text{nls-T}}$</td>
<td>$M = aK^{bL_{\infty}^{c}}$</td>
<td>nls</td>
<td>this study</td>
</tr>
<tr>
<td>$K, t_{\text{max}}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alverson-Carney</td>
<td>$M = 3K/(e^{aKt_{\text{max}}} - 1)$</td>
<td>nls</td>
<td>Alverson &amp; Carney (1975)</td>
</tr>
<tr>
<td>Composites***</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weighted $M$</td>
<td>$M = pM_{\text{Estimator1}} + (1 - p)M_{\text{Estimator2}}$</td>
<td>NA</td>
<td>this study</td>
</tr>
</tbody>
</table>
One-parameter $t_{\text{max}}$ refers to the estimator where $a$ is an estimated parameter (not a value assumed for theoretical reasons). Tauchi (1956) apparently proposed that $M$ should be proportional to the reciprocal of $t_{\text{max}}$ (see Ohsumi, 1973). Tanaka (1960) fitted a line to $M$ versus $1/ t_{\text{max}}$ for five species but did not propose an actual empirical estimator as far as we could tell.

** Beverton (1963) and Beverton and Holt (1959) plotted $M$ versus $K$ and established that a relationship exists but did not fit a model.

*** The combination of Estimator 1 (with weighting of p) and Estimator 2 (with weighting of 1-p) examined for the weighted $M$ estimator consists of possible pairs of the estimators listed above that do not have predictor variables in common.

\(^1\)Although the original model formulation in Pauly (1980) was in base 10, we examined variants of the Pauly model in natural log scale for consistency.
Table 2. Cross-validation prediction error (CVPE) of empirical estimators of natural mortality, $M$, evaluated in terms of three metrics: Historical Performance, Approach Evaluation and the Updated Estimators. The mean absolute difference (MAD) and the coefficient of determination (unadjusted $r^2$) of predicted and literature $M$ estimates are presented as well for the updated estimators. n denotes sample size. NA denotes not applicable. See Table 1 for definition of models. The Approach Evaluation column provides a fair test of the approaches. The Updated Estimators column provides an evaluation of each estimator based on the most data for training and checking the estimator.

<table>
<thead>
<tr>
<th>Models</th>
<th>Historical</th>
<th>Approach (n = 201)</th>
<th>Updated</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>RMSE   n</td>
<td>CVPE</td>
<td>$r^2$</td>
</tr>
<tr>
<td>$t_{\text{max}}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>one-parameter $t_{\text{max}}$</td>
<td>NA   -</td>
<td>0.309</td>
<td>0.90</td>
</tr>
<tr>
<td>Hoenig_{lm}</td>
<td>0.34</td>
<td>204</td>
<td>0.323</td>
</tr>
<tr>
<td>Hoenig_{g}</td>
<td>0.32</td>
<td>204</td>
<td>0.504</td>
</tr>
<tr>
<td>Hoenig_{nl}</td>
<td>NA   -</td>
<td>0.286</td>
<td>0.90</td>
</tr>
<tr>
<td>$K$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>one-parameter $K$</td>
<td>0.60</td>
<td>204</td>
<td>0.591</td>
</tr>
<tr>
<td>two-parameter $K$</td>
<td>NA   -</td>
<td>0.591</td>
<td>0.46</td>
</tr>
<tr>
<td>$K, L_{\infty}, T$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pauly_{lm}</td>
<td>0.57</td>
<td>185</td>
<td>0.622</td>
</tr>
<tr>
<td>Pauly_{lm-T}</td>
<td>NA   -</td>
<td>0.628</td>
<td>0.49</td>
</tr>
<tr>
<td>Pauly_{nl}</td>
<td>NA   -</td>
<td>0.584</td>
<td>0.54</td>
</tr>
<tr>
<td>Pauly_{nl-T}</td>
<td>NA   -</td>
<td>0.590</td>
<td>0.50</td>
</tr>
<tr>
<td>$K, t_{\text{max}}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alverson-Carney</td>
<td>0.42</td>
<td>201</td>
<td>0.409</td>
</tr>
<tr>
<td>Weighted $M$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hoenig_{nl} - Pauly_{nl-T}</td>
<td>NA   -</td>
<td>0.312</td>
<td>0.86</td>
</tr>
</tbody>
</table>

Evaluation of Historical Performance was not conducted for the one-parameter $t_{\text{max}}$ or the two-parameter $K$ models (see main text for rationale) and was done based on the published equation of Jensen (1996) for the one-parameter $K$ method.

$^1$The log($M$) estimates from the log-log linear models of Hoenig and Pauly were directly back-transformed (i.e. exponentiated) when calculating the CVPE for these models.
Table 3. Selected updated estimators based on the fullest dataset (sample size n). Model and bootstrap-based estimates of standard error (SE) and the bootstrap bias-corrected and accelerated (BCa) 95% confidence interval (CI) for the model parameter estimates are presented. coef. = coefficient; exp. = exponent. All length measurements ($L$) are in mm.

<table>
<thead>
<tr>
<th>Models</th>
<th>Updated equations</th>
<th>n</th>
<th>Parameter</th>
<th>Model SE</th>
<th>Bootstrap SE</th>
<th>BCa 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>$t_{\text{max}}$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>one-parameter $t_{\text{max}}$</td>
<td>$M_{\text{est}} = 5.075 / t_{\text{max}}$</td>
<td>213</td>
<td>Scaling</td>
<td>0.10</td>
<td>0.23</td>
<td>(4.67, 5.55)</td>
</tr>
<tr>
<td>Hoenig$_{\text{lm}}$</td>
<td>$\log(M_{\text{est}}) = 1.686 - 1.0003\log(t_{\text{max}})$</td>
<td>213</td>
<td>Intercept</td>
<td>0.09</td>
<td>0.08</td>
<td>(1.54, 1.85)</td>
</tr>
<tr>
<td>Hoenig$_{\text{ols}}$</td>
<td>$M_{\text{est}} = 4.895^{t_{\text{max}}^{-0.922}}$</td>
<td>213</td>
<td>Scaling</td>
<td>0.11</td>
<td>0.33</td>
<td>(4.36, 5.62)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$t_{\text{max}}$ exp.</td>
<td>0.02</td>
<td>0.04</td>
<td>(-1.02, -0.85)</td>
</tr>
<tr>
<td>$K$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>one-parameter $K$</td>
<td>$M_{\text{est}} = 1.684K$</td>
<td>204</td>
<td>$K$ coef.</td>
<td>0.08</td>
<td>0.17</td>
<td>(1.36, 2.02)</td>
</tr>
<tr>
<td>two-parameter $K$</td>
<td>$M_{\text{est}} = 0.09 + 1.556K$</td>
<td>204</td>
<td>Intercept</td>
<td>0.06</td>
<td>0.06</td>
<td>(-0.03, 0.23)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$K$ coef.</td>
<td>0.12</td>
<td>0.25</td>
<td>(1.03, 2.02)</td>
</tr>
<tr>
<td>$K$, $L_{\infty}$, $t_{\text{max}}$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pauly$_{\text{ln-T}}$</td>
<td>$M_{\text{est}} = e^{1.461K^{0.741}L_{\infty}^{-0.347}}$</td>
<td>204</td>
<td>Scaling</td>
<td>0.21</td>
<td>0.46</td>
<td>(0.63, 2.45)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>K exp.</td>
<td>0.08</td>
<td>0.17</td>
<td>(0.37, 1.03)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$L_{\infty}$ exp.</td>
<td>0.08</td>
<td>0.16</td>
<td>(-0.67, -0.05)</td>
</tr>
</tbody>
</table>
Figure 1. Scatterplot of pairs of log-transformed variables in the upper half of the panel, with locally weighted scatterplot smoothing (LOWESS) lines added (smoothing parameter \( f = 2/3 \)). Variables: Natural mortality rate \( M \), maximum age \( t_{\text{max}} \), von Bertalanffy growth parameters \( K \) and \( L_\infty \), mean temperature \( T \). Kernel density plots of the log-transformed variables are shown in the diagonal panels. Correlation coefficients (\( r \)) for variable pairs are shown in the lower half of the panel, where the font size corresponds to the magnitude of the \( r \) values.
Figure 2. Difference in the predicted $M$ estimates between (a) the original Hoenig (1983) and the Pauly (1980) estimators as well as (b) the updated one-parameter $t_{\text{max}}$ and the one-parameter $K$ estimators, plotted against literature $M$ estimates ($n = 201$). (a)' and (b)' depict the enlargement of the boxed regions in (a) and (b), respectively. Locally weighted scatterplot smoothing (LOWESS) lines (dashed) shown in each panel (smoothing parameter $f = 2/3$).
Figure 3. Model residuals for the updated estimators of (a) one-parameter $t_{\text{max}}$ (b) Hoenig$_{\text{als}}$ (c) one-parameter $K$ (d) two-parameter $K$ (e) Pauly$_{\text{als-T}}$ and (f) Alverson-Carney, based on the common dataset (n = 201). Locally weighted scatterplot smoothing (LOWESS) lines shown in each panel (smoothing parameter $f = 2/3$).
Figure 4. 5000 bootstrap estimates of the coefficient for log-transformed temperature $T$ coefficient in the Pauly$_{lm}$ (log-log regression) model. log($T$) coefficient estimates for the original Pauly (1980) ($= 0.4634$) and the updated Pauly$_{lm}$ ($= 0.207$) are shown for comparison. Coefficient estimates $< 0$ constitute 5% of the 5000 bootstrap estimates.
Chapter 5

Conclusions
The research work in this dissertation addresses specific knowledge gaps pertaining to the application of existing length-based and indirect methods to estimate the vital stock parameters of natural, $M$, and total mortality rates, $Z$. Results from these studies are expected to influence directly stock assessment methods to estimate $Z$ and $M$, and ultimately fishery management of both relatively data-rich and data-poor stocks.

If the goal for data-poor stocks is to provide reasonable assessments with the existing data collection scheme (e.g., only length samples), the research priority should be to evaluate and improve existing methods that are applicable (e.g., length-based methods). The evaluation study in Chapter 2 advocates the use of the Beverton and Holt estimator of $Z$ over the Ehrhardt and Ault estimator given the generally known directional bias in the former estimator. Results from this chapter highlight the challenges posed in using simple length-based models with restrictive assumptions to estimate vital and influential mortality parameters. Improvement to the original Beverton and Holt (1956) estimator, by relaxing the equilibrium assumption, renders length-based estimators more useful (see Gedamke and Hoenig, 2006).

On the other hand, if the goal is to determine priorities for data collection to improve stock assessment, development of methods that bridge the gap between data-poor and data-rich stocks is warranted. We present a promising
methodology in Chapter 3 that advances the application of length-based
estimators in non-equilibrium situations using additional information on fishing
effort, $f$. The estimator directly estimates two parameters, i.e., catchability, $q$, and
$M$; corresponding $Z$ estimates are then obtained via the equation of $Z = qf + M$.
Results from the simulation study with respect to the behavior of the extended
non-equilibrium model are encouraging. While the reliability of $q$ and $M$
estimates depend on the amount of variability in the mean length data, reliable
estimates of time-varying $Z$ appear possible even when the variability is large.

Future work for this non-equilibrium length-based model is to explore via
simulation the sensitivity of violations of key model assumptions by
parameterizations based on an existing fishery. I seek to demonstrate application
of the model on actual data-rich fishery data to examine how well the parameter
estimates of $q$, $M$ and $Z$ replicate those from more sophisticated age-based
models. Such cross-checking and verification of results will provide reassurance
that the proposed extended model does indeed perform well in real fisheries.
Considerations for other factors such as the effects of sex-specific differences in
growth and varying recruitment could be incorporated when such information are
readily available.

Chapter 4 constitutes possibly the most important piece of work in this
dissertation. Empirical estimators of $M$ are routinely used in stock assessments,
but the manner of choosing which one(s) to use has been contentious due to a lack
of objective, holistic comparison. Our study provides definitive ranking,
quantification of prediction error, and updated equations of widely-used empirical
estimators of natural mortality. The results showed that maximum age-based estimators should always be preferred when estimates of maximum age are available. The maximum age-based estimators are about twice as reliable as those that rely on other life history variables.

Another important contribution of this chapter is the development of a quality-controlled database containing sets of parameter estimates for $M$ and other life history variables. This often overlooked aspect is an important one when the database itself is used to develop empirical predictive estimators for key stock parameters such as $M$. The dataset and subsequent updated versions will be hosted on the VIMS website.

Further investigations along the lines of empirical estimation of $M$ using the developed dataset (some are underway) include the following questions: (1) Can other variables, such as higher order taxonomic groups, habitat categories, reproductive types, trophic levels, etc., account for a substantial amount of variability observed about the mortality-maximum age regression? (2) How do the updated point estimators compare with size-based estimators (e.g. Gislason, et al., 2010)? (3) Can the use of more advanced statistical modeling techniques, such as recursive partitioning, improve our ability to estimate $M$? These future works are anticipated to provide additional insights and useful recommendations in estimation of $M$ for stock assessments.
REFERENCES


APPENDIX 1

a. Conditions under which the Ehrhardt and Ault estimator of instantaneous total mortality rate, Z, may not yield a real-valued, positive solution

The Ehrhardt and Ault (EA) equation is given as

\[
\left( \frac{L_{\infty} - L_\lambda}{L_{\infty} - L_c} \right)^{(2)} \frac{Z}{K} = \frac{Z(3) L_c - L \lambda) + K(4) L_c - L \infty}{Z(5) L_\lambda - L \lambda) + K(6) L_{\infty} - L \infty}
\]

where the superscripted numbers in parentheses are used to number the different terms of the equation.

Note that:
1. For the left hand portion of the equation, terms (1) and (2) are always positive, given that \( L_\infty > L_\lambda > L_c, Z > 0 \) and \( K > 0 \). Note that zero is a possible solution for \( Z \).
2. For the denominator of the right hand side of the equation, terms (5) and (6) are always positive, given that \( L_\infty > L_\lambda > L \).
3. For the numerator of the right hand side of the equation, term (4) is always positive but term (3) is always negative, given that \( L_c < L \). The conditions where the EA estimator may not have positive solutions for \( Z \), i.e., the numerator < 0, are:
   (i) \( L_c >> L \) and \( Z >> K \)
   (ii) \( L \) approaches \( L_\infty \) (i.e., term (4) approaches 0) and \( Z >> K \)
b. Variability in length at age displayed by eight fish species

The plots below are fitted von Bertalanffy growth curves (blue lines) to length-at-age data (left column) and the corresponding model residuals plotted against age (right column; locally weighted scatterplot smoothing (LOWESS) lines in blue) for eight fish species listed in Table 2 (Chapter 2). Visually, the patterns in variability in length-at-age vary considerably: (1) relatively constant magnitude across ages (e.g., summer flounder and striped bass), (2) general increase with age (e.g., cod), (3) increase to some intermediate age before decrease (e.g., haddock, yellowedge, gag, and red groupers), and (4) decrease with age (e.g., scup).
APPENDIX 2 -

Additional simulation results for Chapter 2

(this section will be issued as a VIMS Data Report upon acceptance of paper)

Effect of the values of total mortality rate, $Z$, von Bertalanffy growth coefficient, $K$, type of growth variability, and varying imposed upper age truncation $t_\lambda$

The following section contains results for percent bias (% Bias) and percent root mean square error (% RMSE) of the estimates of $Z$ from the Beverton-Holt and Ehrhardt-Ault estimators. Simulations were based on a factorial design with five levels of $Z$ and four levels of $K$ and two different methods to simulate variability in length at age: (1) constant variability in length at age across ages, $\sigma$ (expressed as a percentage of the von Bertalanffy asymptotic length $L_\infty$), and (2) constant coefficient of variation, CV (expressed as a percentage of mean length at age), across ages. Three levels of variability in length at age were examined: 0, 3 and 7 %. The mean length for the Ehrhardt-Ault estimator was calculated using two different methods: (1) $\bar{L}_{EA}$ - based on lengths, $L$, with length at first capture $L_c < L <$ imposed $L_\lambda$ and (2) $\bar{L}_{BH}$ - based on lengths $L >$ length at first capture $L_c$. Simulated age distributions were generated with truncation and length samples were analyzed with six different values for imposed $L_\lambda$, corresponding to scenarios of over-truncation, actual truncation and under-truncation of lengths. Important simulation conditions are highlighted as headers for the following figures to facilitate ease of reading.
Simulation Conditions: variability, $\sigma = 0$; mean length for the EA estimator = $\bar{L}_{EA}$

(a) $Z = 0.1$
(b) $Z = 0.25$
(c) $Z = 0.5$
(d) $Z = 1.0$
(e) $Z = 2.0$

FIGURE 1. Percent bias (% Bias) and percent root mean square error (% RMSE) of the total mortality rate ($Z$) estimates of the Beverton Holt (in dashed lines) and Ehrhardt-Ault (EA, in solid lines) estimators when applied to simulated length frequency data, generated with no variability in length at age and various combinations of $Z = (a) 0.1, (b) 0.25 (c) 0.5, (d) 1.0, and (e) 2.0 \text{yr}^{-1}$ and von Bertalanffy growth coefficient $K (K = 0.1 \text{ (denoted with A), } K = 0.4 \text{ (B), } K = 0.7 \text{ (C) and } K = 1 \text{ yr}^{-1} \text{ (D)})$. The x-axis is shown in age scale ($t_\lambda$) for clarity but the corresponding length $L_\lambda$ is imposed on the length samples when applying the EA estimator. Shaded region denotes over- truncation (imposed $L_\lambda < \text{actual } L_\lambda$), unshaded region denotes under-truncation and the boundary denotes actual age of upper truncation $t_\lambda$ in each simulation, which is a function of $Z$. The mean length for the EA estimator, $\bar{L}_{EA}$, was computed on lengths $L$, with length at first capture $L_c < L < \text{imposed } L_\lambda$. 

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Simulation Conditions: variability, $\sigma = 0$; mean length for the EA estimator $= \overline{L}_{BH}$

(a) $Z = 0.1$  
(b) $Z = 0.25$  
(c) $Z = 0.5$  
(d) $Z = 1.0$  
(e) $Z = 2.0$

FIGURE 2. Percent bias (% Bias) and percent root mean square error (% RMSE) of the total mortality rate ($Z$) estimates of the Beverton Holt (in dashed lines) and Ehrhardt-Ault (EA, in solid lines) estimators when applied to simulated length frequency data, generated with no variability in length at age and various combinations of $Z = (a) 0.1, (b) 0.25 (c) 0.5, (d) 1.0, \text{ and (e) } 2.0 \text{ yr}^{-1}$ and von Bertalanffy growth coefficient $K$ ($K = 0.1$ (denoted with A), $K = 0.4$ (B), $K = 0.7$ (C) and $K = 1 \text{ yr}^{-1}$ (D)). The x-axis is shown in age scale ($t_\lambda$) for clarity but the corresponding length $L_\lambda$ is imposed on the length samples when applying the EA estimator. Shaded region denotes over-truncation (imposed $L_\lambda < \text{ actual } L_\lambda$), unshaded region denotes under-truncation and the boundary denotes actual age of upper truncation $t_\lambda$ in each simulation, which is a function of $Z$. The mean length for the EA estimator, $\overline{L}_{BH}$, was computed on lengths $L > \text{ length at first capture, } L_c$. 

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Simulation Conditions: variability, CV = 7%; mean length for the EA estimator = \( \bar{L}_{BH} \)

FIGURE 3. Percent bias (% Bias) and percent root mean square error (% RMSE) of the total mortality rate (Z) estimates of the Beverton Holt (in dashed lines) and Ehrhardt-Ault (EA, in solid lines) estimators when applied to simulated length frequency data, generated with a constant coefficient of variation, CV = 7 %, in length-at-age and various combinations of Z = (a) 0.1, (b) 0.25, (c) 0.5, (d) 1.0, and (e) 2.0 yr\(^{-1}\) and von Bertalanffy growth coefficient \( K \) (\( K = 0.1 \) (denoted with A), \( K = 0.4 \) (B), \( K = 0.7 \) (C) and \( K = 1 \) yr\(^{-1}\) (D)). The x-axis is shown in age scale (\( t_\lambda \)) for clarity but the corresponding length \( L_\lambda \) is imposed on the length samples when applying the EA estimator. Shaded region denotes over- truncation (imposed \( L_\lambda < \) actual \( L_\lambda \)), unshaded region denotes under-truncation and the boundary denotes actual age of upper truncation \( t_\lambda \) in each simulation, which is a function of Z. The mean length for the EA estimator, \( \bar{L}_{BH} \), was computed on lengths \( L > \) length at first capture, \( L_c \).
Simulation Conditions: variability, $\sigma = 3\%$; mean length for the EA estimator $= \bar{L}_{EA}$

(a) $Z = 0.1$
(b) $Z = 0.25$
(c) $Z = 0.5$
(d) $Z = 1.0$
(e) $Z = 2.0$

FIGURE 4. Percent bias (% Bias) and percent root mean square error (% RMSE) of the total mortality rate ($Z$) estimates of the Beverton Holt (in dashed lines) and Ehrhardt-Ault (EA, in solid lines) estimators when applied to simulated length frequency data, generated with a constant variability in length at age, $\sigma = 3\%$, and various combinations of $Z = (a) 0.1, (b) 0.25 (c) 0.5, (d) 1.0, and (e) 2.0 \text{ yr}^{-1}$ and von Bertalanffy growth coefficient $K$ ($K = 0.1$ (denoted with A), $K = 0.4$ (B), $K = 0.7$ (C) and $K = 1 \text{ yr}^{-1}$ (D)). The x-axis is shown in age scale ($t_\lambda$) for clarity but the corresponding length $L_t$ is imposed on the length samples when applying the EA estimator. Shaded region denotes over- truncation (imposed $L_t < \text{actual } L_t$), unshaded region denotes under-truncation and the boundary denotes actual age of upper truncation $t_\lambda$ in each simulation, which is a function of $Z$. The mean length for the EA estimator, $\bar{L}_{EA}$, was computed on lengths $L$, with length at first capture $L_c < L < \text{imposed } L_t$. 

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Simulation Conditions: variability, $\sigma = 3\%$; mean length for the EA estimator $= \bar{L}_{BH}$

(a) $Z = 0.1$
(b) $Z = 0.25$
(c) $Z = 0.5$
(d) $Z = 1.0$
(e) $Z = 2.0$

FIGURE 5. Percent bias (% Bias) and percent root mean square error (% RMSE) of the total mortality rate ($Z$) estimates of the Beverton Holt (in dashed lines) and Ehrhardt-Ault (EA, in solid lines) estimators when applied to simulated length frequency data, generated with a constant variability in length at age, $\sigma = 3\%$, and various combinations of $Z = (a) 0.1, (b) 0.25 (c) 0.5, (d) 1.0, and (e) 2.0$ yr$^{-1}$ and von Bertalanffy growth coefficient $K$ ($K = 0.1$ (denoted with A), $K = 0.4$ (B), $K = 0.7$ (C) and $K = 1$ yr$^{-1}$ (D)). The x-axis is shown in age scale ($t_\lambda$) for clarity but the corresponding length $L_\lambda$ is imposed on the length samples when applying the EA estimator. Shaded region denotes over-truncation (imposed $L_\lambda$ < actual $L_\lambda$), unshaded region denotes under-truncation and the boundary denotes actual age of upper truncation $t_\lambda$ in each simulation, which is a function of $Z$. The mean length for the EA estimator, $\bar{L}_{BH}$, was computed on lengths $L >$ length at first capture, $L_c$. 

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Simulation Conditions: variability, CV = 3%; mean length for the EA estimator = $\bar{L}_{E_A}$

FIGURE 6. Percent bias (% Bias) and percent root mean square error (% RMSE) of the total mortality rate (Z) estimates of the Beverton Holt (in dashed lines) and Ehrhardt-Ault (EA, in solid lines) estimators when applied to simulated length frequency data, generated with a constant coefficient of variation, CV = 3%, in length-at-age and various combinations of $Z = (a) 0.1$, (b) 0.25, (c) 0.5, (d) 1.0, and (e) 2.0 yr$^{-1}$ and von Bertalanffy growth coefficient $K$ ($K = 0.1$ (denoted with A), $K = 0.4$ (B), $K = 0.7$ (C) and $K = 1$ yr$^{-1}$ (D)). The x-axis is shown in age scale ($t_{\lambda}$) for clarity but the corresponding length $L_{\lambda}$ is imposed on the length samples when applying the EA estimator. Shaded region denotes over-truncation (imposed $L_{\lambda} <$ actual $L_{\lambda}$), unshaded region denotes under-truncation and the boundary denotes actual age of upper truncation $t_{\lambda}$ in each simulation, which is a function of $Z$. The mean length for the EA estimator, $\bar{L}_{E_A}$, was computed on lengths $L$, with length at first capture $L_c < L <$ imposed $L_{\lambda}$. 

\[\]
Simulation Conditions: variability, CV = 3%; mean length for the EA estimator = $\bar{L}_{BH}$

(a) $Z = 0.1$
(b) $Z = 0.25$
(c) $Z = 0.5$
(d) $Z = 1.0$
(e) $Z = 2.0$

FIGURE 7. Percent bias (% Bias) and percent root mean square error (% RMSE) of the total mortality rate ($Z$) estimates of the Beverton Holt (in dashed lines) and Ehrhardt-Ault (EA, in solid lines) estimators when applied to simulated length frequency data, generated with a constant coefficient of variation, CV = 3%, in length-at-age and various combinations of $Z = (a) 0.1$, (b) 0.25 (c) 0.5, (d) 1.0, and (e) 2.0 yr$^{-1}$ and von Bertalanffy growth coefficient $K$ ($K = 0.1$ (denoted with A), $K = 0.4$ (B), $K = 0.7$ (C) and $K = 1$ yr$^{-1}$ (D)). The x-axis is shown in age scale ($t_\lambda$) for clarity but the corresponding length $L_\lambda$ is imposed on the length samples when applying the EA estimator. Shaded region denotes over-truncation (imposed $L_\lambda <$ actual $L_\lambda$), unshaded region denotes under-truncation and the boundary denotes actual age of upper truncation $t_\lambda$ in each simulation, which is a function of $Z$. The mean length for the EA estimator, $\bar{L}_{BH}$, was computed on lengths $L >$ length at first capture, $L_c$. 

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Effect of the values of total mortality rate, $Z$, degree of growth variability, and varying imposed upper age truncation $t_\lambda$

The following section contains results for percent bias (% Bias) and percent root mean square error (% RMSE) of the estimates of $Z$ from the Beverton-Holt and Ehrhardt-Ault estimators. Simulations were based on a factorial design with five levels of $Z$ and four levels of constant variability in length at-age $\sigma = 0, 3, 6, 9\%$. The von Bertalanffy growth coefficient was fixed at 0.4 yr$^{-1}$. The mean length for the Ehrhardt-Ault estimator was calculated using two different methods: (1) $\overline{L}_{EA}$ - based on lengths $L$, with length at first capture $L_c < L < \text{imposed } L_\lambda$ and (2) $\overline{L}_{BH}$ - based on lengths $L > \text{length at first capture } L_c$. Simulated age distributions were generated with truncation and length samples were analyzed with six different values for imposed $L_\lambda$, corresponding to scenarios of over-truncation, actual truncation and under-truncation of lengths. Important simulation conditions are highlighted as headers for the following figures to facilitate ease of reading.
Simulation Condition: mean length for the EA estimator = \( \bar{L}_{EA} \)

FIGURE 8. Percent bias (% Bias) and percent root mean square error (% RMSE) of the total mortality rate (Z) estimates of the Beverton Holt (in dashed lines) and Ehrhardt-Ault (EA, in solid lines) estimators when applied to simulated length frequency data, generated with combinations of Z = (a) 0.1, (b) 0.25, (c) 0.5, (d) 1.0, and (e) 2.0 yr\(^{-1}\) and four levels of constant variability in length at age \( \sigma \) (0, 3, 6, 9 %). The von Bertalanffy growth coefficient \( K = 0.4 \). The x-axis is shown in age scale \( t_\lambda \) for clarity but the corresponding length \( L_\lambda \) is imposed on the length samples when applying the EA estimator. Shaded region denotes over-truncation (imposed \( L_\lambda < \) actual \( L_\lambda \)), unshaded region denotes under-truncation and the boundary denotes actual age of upper truncation \( t_\lambda \) in each simulation, which is a function of Z. The mean length for the EA estimator, \( \bar{L}_{EA} \), was computed on lengths \( L \), with length at first capture \( L_c < L < \) imposed \( L_\lambda \).
Simulation Condition: mean length for the EA estimator = $\bar{L}_{BH}$

(a) $Z = 0.1$
(b) $Z = 0.25$
(c) $Z = 0.5$
(d) $Z = 1.0$
(e) $Z = 2.0$

FIGURE 9. Percent bias (% Bias) and percent root mean square error (% RMSE) of the total mortality rate (Z) estimates of the Beverton Holt (in dashed lines) and Ehrhardt-Ault (EA, in solid lines) estimators when applied to simulated length frequency data, generated with combinations of $Z =$ (a) 0.1, (b) 0.25, (c) 0.5, (d) 1.0, and (e) 2.0 yr$^{-1}$ and four levels of constant variability in length at age $\sigma$ (0, 3, 6, 9 %). The von Bertalanffy growth coefficient $K = 0.4$. The x-axis is shown in age scale ($t_\lambda$) for clarity but the corresponding length $L_\lambda$ is imposed on the length samples when applying the EA estimator. Shaded region denotes over-truncation (imposed $L_\lambda <$ actual $L_\lambda$), unshaded region denotes under-truncation and the boundary denotes actual age of upper truncation $t_\lambda$ in each simulation, which is a function of $Z$. The mean length for the EA estimator, $\bar{L}_{BH}$, was computed on lengths $L >$ length at first capture, $L_c$. 
Species-specific simulation: effect of varying $\sigma$ and degree of upper age truncation

The following section contains results for percent bias (% Bias) and percent root mean square error (% RMSE) of the estimates of $Z$ from the Beverton-Holt and Ehrhardt-Ault estimators. Simulations were parameterized using two tropical species, *Chrysoblephus cristiceps* and *Lutjanus vitta*, with different growth spectrum. Simulated age distributions were generated with and without age truncation (Figures 10 and 11 respectively) and length samples were analyzed with input $L_\lambda = \text{maximum length in the samples} < \text{the von Bertalanffy asymptotic length } L_\infty$. The mean length for the Ehrhardt-Ault estimator was calculated using $\overline{L}_{EA}$, i.e., based on lengths $L$, with length at first capture $L_c < L <$ imposed $L_\lambda$. Important simulation conditions are highlighted as headers for the following figures to facilitate ease of reading.
Simulation Conditions: Age-truncated length samples; mean length for the EA estimator = \( \bar{L}_{EA} \); \( L_{\lambda} \) = maximum length in sample

**Chrysoblephus cristiceps**

\( F \approx 0 \)

\( F \approx 0.3 \)

**Lutjanus vitta**

\( F \approx 0 \)

\( F \approx 0.3 \)

FIGURE 10. Percent bias (% Bias) and percent root mean square error (% RMSE) of the total mortality rate (Z) estimates of the Beverton Holt (in dashed lines) and Ehrhardt-Ault (EA, in solid lines) estimators when applied to simulated length frequency data, generated with age truncation, for two tropical species *Chrysoblephus cristiceps* (top row) and *Lutjanus vitta* (bottom row). Constant variability in length at age, \( \sigma \), was simulated at four levels (0, 3, 6, 9 %). Two fishing mortality scenarios were presented: (a) \( F = 0 \) and (b): \( F = 0.3 \). Input \( L_{\lambda} \) for the Ehrhardt-Ault estimator = maximum length in the sample, \( L_{\text{max}} \). The mean length for the EA estimator, \( \bar{L}_{EA} \), was computed on lengths \( L \), with length at first capture \( L_c < L < \text{imposed} \ L_{\lambda} = L_{\text{max}} \). For comparison, the % Bias and % RMSE when input \( L_{\lambda} = \text{actual} \ L_{\lambda} \) were shown as well (solid dotted lines).
Simulation Conditions: Non age-truncated length samples; mean length for the EA estimator = $\bar{L}_{EA}$; $L_\lambda$ = maximum length in sample

$Chrysoblephus cristiceps$

$F \approx 0$

$F \approx 0.3$

$L_{max}$

$\sigma$

$\sigma$

$\sigma$

$\sigma$

FIGURE 11. Percent bias (% Bias) and percent root mean square error (% RMSE) of the total mortality rate ($Z$) estimates of the Beverton Holt (in dashed lines) and Ehrhardt-Ault (EA, in solid lines) estimators when applied to simulated length frequency data, generated with no age truncation, for two tropical species $Chrysoblephus cristiceps$ (top row) and $Lutjanus vitta$ (bottom row). Constant variability in length at age, $\sigma$, was simulated at four levels (0, 3, 6, 9 %). Two fishing mortality scenarios were presented: (a) $F = 0$ and (b): $F = 0.3$.

Input $L_\lambda$ for the Ehrhardt-Ault estimator = maximum length in the sample, $L_{max}$. The mean length for the EA estimator, $\bar{L}_{EA}$, was computed on lengths $L$, with length at first capture $L_c < L <$ imposed $L_\lambda$. 

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