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Comparative Performance of Three Length-Based Mortality Estimators

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Abstract

Length-based methods provide alternatives for estimating the instantaneous total mortality rate (Z) in exploited marine populations when data are not available for age-based methods. We compared the performance of three equilibrium length-based methods: the length-converted catch curve (LCCC), the Beverton–Holt equation (BHE), and the length-based spawning potential ratio (LB-SPR) method. The LCCC and BHE are two historically common procedures that use length as a proxy for age. From a truncated length-frequency distribution of fully selected animals, the LCCC estimates Z with a regression of the logarithm of catch at length by the midpoint of the length-bins, while the BHE estimates Z as a function of the mean length. The LB-SPR method is a likelihood-based population dynamics model, which—unlike the LCCC and BHE—does not require data truncation. Using Monte Carlo simulations across a range of scenarios with varying mortality and life history characteristics, our study showed that neither the LCCC nor the BHE was uniformly superior in terms of bias or root mean square error across simulations, but these estimators performed better than LB-SPR, which had the largest bias in most cases. Generally, if the ratio of natural mortality (M) to the von Bertalanffy growth rate parameter (K) is low, then the BHE is most preferred, although there is likely to be high bias and low precision. If M/K is high, then the LCCC and BHE performed better and similarly to each other. Differences in performance among commonly used truncation methods for the LCCC and BHE were small. The LB-SPR method did not perform as well as the classical methods but may still be of interest because it provides estimates of a logistic selectivity curve. The M/K ratio provided the most contrast in the performance of the three methods, suggesting that it should be considered for predicting the likely performance of length-based mortality estimators.

Length-based methods for assessing exploited marine populations are of significant interest largely because of their applicability to the study of data-limited stocks for which age-based methods may not be available or suitable (Punt et al. 2013). Hard tissues, such as scales and otoliths, may lack distinct growth marks, for example, in tropical fish species. Such species are often assessed using length-based methods (Pauly 1984c) because length measurements are collected both easily and nonlethally.

Historically, the most common methods used to estimate the total instantaneous mortality rate (Z; year^{-1}) from length composition data have been the length-converted catch curve (LCCC; Pauly 1983, 1984a, 1984b) and the Beverton–Holt equation (BHE; Beverton and Holt 1956, 1957).

These methods are based on a linear regression and a moment estimator, respectively. Improvements in computational power over time have allowed for the development and use of nonlinear models that employ derivative-based optimization methods. Recently, Hordyk et al. (2015b) developed the length-based spawner potential ratio (LB-SPR) method to estimate mortality using a nonlinear model.

An analog of the age-based catch curve (Ricker 1975), the LCCC uses the natural logarithm of catch (C_j) in the jth length interval of a length-frequency distribution (LFD) regressed on the relative age (t'_j) at the midpoint of the length-bin (λ_j). Only fully selected lengths are considered in the analysis. Under the assumption of deterministic growth following a von Bertalanffy function (with parameters constant across time and cohorts), the relative age at the jth length-bin is defined as

$$t'_j = -\log_e\left(1 - \frac{\lambda_j}{L_\infty}\right),\qquad (1)$$

where L_∞ is the asymptotic maximum length from the von Bertalanffy growth function. The regression is of the form

$$\log_e(C_j) = a + bt'_j + \varepsilon_j,\qquad (2)$$

where a and b are the intercept and slope, respectively, of the linear regression; and ε_j is the normally distributed residual error. Total mortality ($\hat{Z}$) is estimated using the estimated slope of the linear regression ($\hat{b}$) and the von Bertalanffy growth rate parameter (K),

$$\hat{Z} = K(1 - \hat{b}),\qquad (3)$$

where the circumflex (^) denotes an estimate. The slope is positive if Z/K is less than 1 and negative if Z/K is greater than 1. The derivation for the LCCC is provided in the Appendix.

Similar to the age-based catch curve, the LCCC assumes a steady-state population, with constant total mortality (over age and time) and constant recruitment (Pauly 1984a). Additionally, all selected fish are assumed to be equally vulnerable to the sampling gear, and the sample size is assumed to be large enough to effectively represent the average population structure over the time period considered (Pauly 1983, 1984a, 1984b). Length-converted catch curves have been criticized for overestimating Z when individual growth varies seasonally (Isaac 1990; Sparre 1990). However, this bias has been overcome by modified LCCCs that accommodate seasonally varying growth (Pauly 1990). Simulations have also shown that individual growth variability creates a negative bias, while reduced size selectivity for smaller sizes produces a

positive bias for the LCCC (Isaac 1990). Analogous to the age-based catch curve, a bend in the regression line could be an indication of a change in mortality with time or with age (Pauly 1984c; Tuckey et al. 2007). However, this method does not generalize easily to account for nonequilibrium conditions.

Beverton and Holt (1956, 1957) derived Z as a function of the observed mean length,

$$\hat{Z} = \frac{K(L_\infty - \bar{L})}{\bar{L} - L_c},\qquad (4)$$

where $\hat{Z}$, K, and L_∞ are as in equations (1) and (3); L_c is the critical length above which all animals are fully selected by the fishery; and $\bar{L}$ is the mean length of animals larger than L_c. Gedamke and Hoenig (2006) provided a recent derivation of the BHE. Similar to the LCCC, the BHE also assumes steady-state conditions, deterministic von Bertalanffy-type growth, a constant mortality rate of all fully recruited fish, and continuous and constant recruitment to the fishery.

A criticism of the BHE is that it tends to overestimate total mortality when the largest size-classes in the population are truncated from the sample (Then et al. 2015). On the other hand, Laurec and Mesnil (1987) and Then et al. (2015) observed that the BHE is generally robust to individual variability in growth. The BHE has also been criticized as overly simplistic because of its stringent equilibrium assumptions (Hilborn and Walters 1992). Gedamke and Hoenig (2006) generalized the BHE to allow for the estimation of total mortality from a time series of mean lengths under nonequilibrium conditions in a maximum likelihood framework. Further extension of this nonequilibrium model has allowed for variable recruitment by incorporating a year-specific index of recruits into the model (Gedamke et al. 2008).

The LB-SPR mortality estimator is an equilibrium age-structured model that converts the predicted age distribution of the catch to a length distribution. Unlike the LCCC and BHE, variability in growth is explicitly modeled, with a coefficient of variation (CV) of length at age generally assumed to be 0.1 (Hordyk et al. 2015b). Ages are converted to lengths via an age–length transition matrix in which the probability of length at age sums to 1.0 for a given age. Logistic selectivity parameters are estimated concurrently with mortality, allowing for the use of the entire LFD in the likelihood function. The method also assumes constant recruitment. Unlike the LCCC and BHE, the LB-SPR method explicitly pairs the mortality estimator with the biological reference points obtained from SPR analyses for management. The same can be done for the LCCC and BHE, although this was not the focus of the current study.

The LCCC has been implemented in ELEFAN II (Pauly 1987; Isaac 1990). Currently, the LCCC can be applied using the FiSAT (Food and Agriculture Organization of the United Nations–International Center for Living Aquatic Resources Management Stock Assessment Tools) software package (Gayanilo et al. 2005). Recently, it has been used to estimate mortality of reef fishes in North Carolina (Rudershausen et al. 2008), Albacore *Thunnus alalunga* in the Mediterranean (ICCAT Secretariat 2012), Japanese Threadfin Bream *Nemipterus japonicus* in the Indian Ocean (Kalhoro et al. 2014), red king crab *Paralithodes camtschaticus* in the Barents Sea (Windsland 2015), Wahoo *Acanthocybium solandri* in the southwest Pacific Ocean (Zischke and Griffiths 2015), blood cockle *Anadara granosa* in Malaysia (Mirzaei et al. 2015), and Red Lionfish *Pterois volitans* in the Gulf of Mexico (Rodriguez-Cortes et al. 2015). Recent applications of the BHE and LB-SPR were cited by Then et al. (2015) and presented by Prince et al. (2015b), respectively. The LB-SPR method can be implemented using the R package "LBSPR" (Hordyk 2017).

The three length-based methods have been studied individually, but they have not been directly compared. Importantly, the methods differ in handling selectivity. The LB-SPR method estimates selectivity as a logistic function, whereas the LCCC and BHE assume knife-edge selectivity (i.e., full selectivity of animals greater than a certain length) and, thus, only animals larger than a certain size are included in the analysis. Previous simulations (e.g., Isaac 1990) have not examined the effect of different decision rules for truncating the data on the performance of the estimators. This study compares the performance of the length-based methods in estimating total mortality by applying these methods to populations with known parameters. First, we examined the performance of each of the estimators individually and relative to each other using a common simulation framework. Second, we examined the choice of decision rules in selecting the truncation points for the LCCC and choosing the L_c parameter for the BHE. Third, we examined the robustness of each method to violations in the assumptions of growth and recruitment variability across several life histories and exploitation scenarios. Finally, we conducted sensitivity analyses of the three mortality estimators to total sample size and length-bin width.

METHODS

Simulation design.— Length samples were generated using a factorial design for von Bertalanffy K, fishing mortality (F), growth variability, recruitment variability, and selectivity (Table 1), accumulating to a total of 108 combinations. In this study, the different values of K and F are presented as ratios with respect to natural mortality

(M; i.e., M/K and F/M, respectively), with M set at 0.2 year^{-1} for all scenarios. Ratios were used because the relative values provide a better description of the life history and magnitude of exploitation, respectively, than the absolute values. On a per-recruit basis, the M/K ratio describes the balance between growth and mortality, which affects the shape of the LFD of a population in an unexploited state (Hordyk et al. 2015a), while Z/K describes the shape of the LFD of an exploited population. The F/M ratio can provide an indication of the relative impact of fishing pressure because a scalar multiple of M is often used as a proxy for fishing at maximum sustainable yield (e.g., $F_{MSY} = 0.75\,M$; Zhou et al. 2012).

The simulation used an age-structured model for the population. The model was run for 25 years to burn in deviates in growth trajectories and recruitment strength among cohorts. Fishing was assumed to occur throughout the 25 years, but the length distribution of the catch was only obtained at the end of the 25 years. Growth was assumed to vary among cohorts (Whitten et al. 2013). The mean length ($L_{y,a}$) in year y at age a was

$$L_{y,a} = \begin{cases} L_0 \exp(\nu_c) & a = 0 \\ L_{y-1,a-1} + (L_{y-1,a-1} \\ \quad -L_\infty)[\exp(-K) - 1]\exp(\nu_c) & a = 1, 2, \ldots, A \end{cases}$$

(5)

where L_0 was the expected length at age 0; $c = y - a$ indexes the age-0 recruitment that gave rise to the cohort of age a in year y; and $\nu_c \sim N(-0.5\omega^2, \omega^2)$ is the cohort-specific deviation in growth increments. The L_∞ was set to 500 (arbitrary) units, L_0 was set to 75 units, and ω was set to 0.15 across all factorials. Two values of $K = 0.4$ and 0.1 year^{-1}, corresponding to M/K ratios of 0.5 and 2.0, respectively, were used in the factorial design.

Variability in length at age ($\sigma_{y,a,L}$) assumed a constant CV to the mean length at age,

$$\sigma_{y,a,L} = CV \times L_{y,a}, \quad (6)$$

with three CVs of 0.03, 0.06, and 0.09 in the factorial design. These values were based on the evaluation of size-at-age data of several species by Then et al. (2015).

Lognormally distributed recruitment (R_y) was simulated as a first-order autoregressive process with autocorrelation coefficient (ρ) and residual deviations (δ_y; Thorson et al. 2014),

$$\log_e(R_y) = \begin{cases} \delta_y & y = 1 \\ \rho \log_e(R_{y-1}) + \sqrt{1 - \rho^2}\delta_y & y = 2, \ldots, Y \end{cases} \quad (7)$$

where $\delta_y \sim N[-0.5\tau^2 \times (1 - \rho/\sqrt{1 - \rho^2}), \tau^2]$ (Thorson et al. 2016); and Y is the terminal year of the age-structured model. Two levels of residual standard deviation for

TABLE 1. Parameter values used for data generation in the simulation study. Parameters with multiple values were included in factorial design. Parameters L_{50} and L_{95} are the lengths of 50% and 95% selectivity, respectively, using a logistic function. Parameters μ_d and σ_d are the mean and standard deviation of the normal probability density function, respectively, with values standardized to 1 at age μ_d for dome-shaped selectivity.

Parameter	Symbol	Values
Ratio of the natural mortality rate (M) and the von Bertalanffy growth rate parameter (K)	M/K	Low: 0.5 ($K = 0.4$) High: 2.0 ($K = 0.1$)
Ratio of the fishing mortality rate (F) and M	F/M	Low: 0.25 ($F = 0.05$) Medium: 1.0 ($F = 0.2$) High: 5.0 ($F = 1.0$)
Coefficient of variation of length at age ($L_{y,a}$)	CV	Low: 0.03 Medium: 0.06 High: 0.09
Recruitment residual standard deviation	τ	Low: 0.6 High: 1.0
Selectivity at length	sel_L	Gradual: $L_{50} = 175$ units, $L_{95} = 200$ units Steep: $L_{50} = 175$ units, $L_{95} = 275$ units Dome: $L_{50} = 175$ units, $L_{95} = 275$ units, $\mu_d = 325$, $\sigma_d = 65$
Recruitment autocorrelation coefficient	ρ	0.45
von Bertalanffy asymptotic length	L_∞	500 units
Expected length at age 0	L_0	75 units
Cohort growth standard deviation	ω	0.15
Maximum age	A	23 years

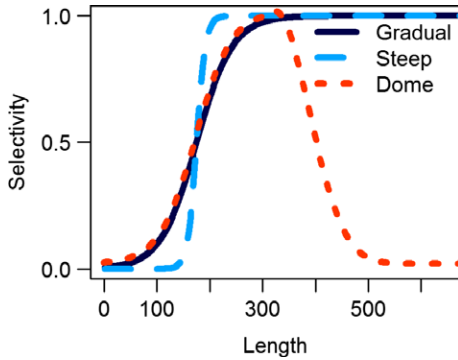FIGURE 1. Length-based selectivity functions (Gradual, Steep, and Dome; see Methods) used in the simulation.

recruitment, $\tau = 0.6$ and 1.0, were included in the factorial design, with $\rho = 0.45$. The values of these parameters were guided by the meta-analysis of Thorson et al. (2014). Mean recruitment was set to 1.0 because the population was stationary over time and the magnitude of recruitment was not relevant for estimating mortality.

Three length-based selectivity patterns were used in the factorial design: a logistic function with a broad ascending limb ("Gradual"), a logistic function with a steep ascending limb ("Steep"), and a dome-shaped logistic-normal function ("Dome"; Figure 1). The logistic function, parameterized by the lengths of 50% (L_{50}) and 95% (L_{95}) selectivity, defines selectivity at length L as

$$sel_L = \left\{ 1 + \exp\left[-\log_e(19) \frac{L - L_{50}}{L_{95} - L_{50}} \right] \right\}^{-1}. \qquad (8)$$

The dome-shaped selectivity function was a piecewise-defined function,

$$sel_L = \begin{cases} \left\{ 1 + \exp\left[-\log_e(19) \frac{L - L_{50}}{L_{95} - L_{50}} \right] \right\}^{-1} & L < \mu_d \\ g(L; \mu_d, \sigma_d) / \max[g(L; \mu_d, \sigma_d)] & L \geq \mu_d \end{cases} \qquad (9)$$

where sel_L is a logistic function for the ascending limb and the right half of a normal probability density function, $g(L)$, with mean μ_d and standard deviation σ_d for the descending limb, with the latter standardized to a value of 1 at μ_d. The Steep and Gradual selectivity functions evaluated the effect of logistic selectivity on data truncation with the LCCC and BHE, while the Dome selectivity function tested the effect of violating the assumption of constant total mortality of fully selected lengths in all three mortality estimators.

The population abundance ($N_{y,a}$) was defined by

$$N_{y,a} = \begin{cases} R_y & a = 0 \\ s_{y-1,a-1} N_{y-1,a-1} & a = 1, 2, \ldots, A \end{cases} \qquad (10)$$

where $s_{y,a}$ is the survival and A is the maximum age in the model. A maximum age of 23 years, the age when 1% of

a cohort survives given M, was used in the simulation for computational convenience.

To calculate survival due to length-based selectivity, a population length–age matrix ($N_{y,a,\lambda}$) was created for the beginning of each year y, where

$$N_{y,a,\lambda} = N_{y,a}P(\lambda|y,a).\qquad(11)$$

With a normal distribution for variability in length at age, the length-at-age probability vector $P(\lambda|y,a)$ is

$$P(\lambda|y,a) = \begin{cases} \phi(\lambda'_{j+1}) & j = 1 \\ \phi(\lambda'_{j+1}) - \phi(\lambda'_j) & j = 2,\dots,J-1 \\ 1 - \phi(\lambda'_j) & j = J \end{cases}\qquad(12)$$

where λ' is the length at the lower boundary of the length-bin with midpoint λ; $j = 1, 2, \dots, J$ indexes the length-bins; and $\phi(\cdot)$ is the cumulative density function of a normal distribution with mean $L_{y,a}$ and standard deviation $\sigma_{y,a,L}$. The length-bin width in the population model was 5 units (larger bins were subsequently used for mortality estimation).

The abundance of survivors ($N^s_{y,a,\lambda}$) at the end of year y was calculated as

$$N^s_{y,a,\lambda} = N_{y,a,\lambda}\exp[-(sel_\lambda F + M)].\qquad(13)$$

This study used three values of apical fishing mortality, $F = 0.05$, 0.2, and 1.0 year^{-1}, corresponding to F/M ratios of 0.25, 1.0, and 5.0, respectively, with mortality occurring after growth. Survival, which is dependent on age and year due to cohort-specific growth, was calculated as

$$s_{y,a} = \frac{\sum_\lambda N^s_{y,a,\lambda}}{N_{y,a}}.\qquad(14)$$

To approximate continuous recruitment assumed in the mortality estimators, quarterly time steps were used in the simulation. Recruitment occurred quarterly, with all cohorts within a year having the same growth trajectory and recruitment strength. All rate parameters were adjusted accordingly from year^{-1} to season^{-1}, with growth updated after every season.

In the terminal time step of the simulation, the length–age catch matrix ($C_{a,\lambda}$) was created using the Baranov catch equation,

$$C_{a,\lambda} = \frac{sel_\lambda F}{sel_\lambda F + M}N_{y,a,\lambda}\{1 - \exp[-(sel_\lambda F + M)]\},\qquad(15)$$

and the catch-at-length vector (C_λ) was obtained by summing over ages,

$$C_\lambda = \sum_a C_{a,\lambda}.\qquad(16)$$

A data set was obtained by sampling 2,000 individuals from the terminal catch-at-length vector using a multinomial distribution. The sample size of 2,000 was chosen to evaluate the robustness of the estimators to the variables in the factorial design when there is little observation error. For each data set, 2,000 length observations were obtained, and a length frequency histogram was generated by dividing the data set into length-bins with a bin width of 10 units (2% of L_∞). For each factorial combination, 1,000 stochastic data sets were generated.

Mortality estimation.— To use the LCCC, a subset of length-bins from the LFD corresponding to fully selected lengths must be chosen for the linear regression. The LFD typically features an ascending limb, representing some lengths that may not be fully selected to the fishing gear, followed by a descending limb of numbers at length (Figure 2). The first usable length-bin may be defined as the peak of the LFD (hereafter, "Peak"; Wetherall et al. 1987), although Pauly (1983) suggested that the first size-class to be included in the LCCC should be the size-class immediately to the right of the most frequent size-class ("Peak-plus").

Because the LCCC assumes deterministic growth, length-bins greater than L_∞ must be excluded from the analysis. Furthermore, length-bins close to L_∞ may be assigned unreasonably large relative ages. High observation error in length-bins with few observations may affect the slope of the regression line (Isaac 1990; Punt et al. 2013). To combat this, Pauly (1983) recommended that
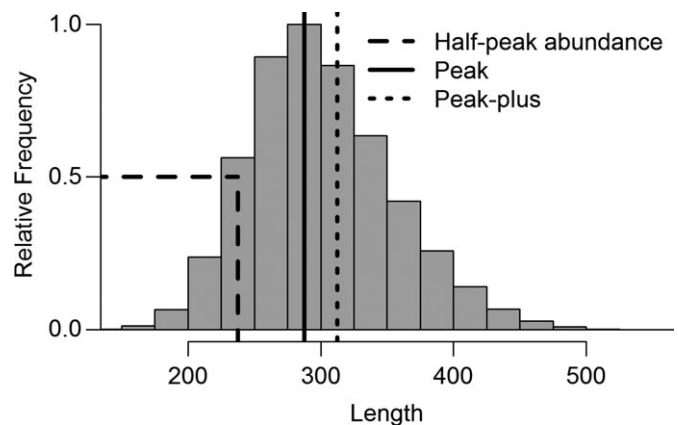

FIGURE 2. Histogram of a length frequency distribution (length is expressed in arbitrary units) with the left-handed decision rules (Half-peak abundance, Peak, and Peak-plus) used to select the length bin of left truncation for the length-converted catch curve and the value of L_c (critical length above which all animals are fully selected by the fishery) for the Beverton–Holt equation in the simulation study.

animals within 5–30% of L_∞ or length-bins with fewer than five individuals be excluded from the analysis. Such approaches sacrifice data in an attempt to avoid bias due to decreased selectivity by the fishing gear and overestimation of the relative age of large individuals. This approach can be problematic, however, when the sample size is low or when only a few size-classes are available.

For the BHE, the length data are usually binned to examine the LFD and identify the critical length L_c. The mean length is then calculated from the subset of animals larger than L_c. Wetherall et al. (1987) suggested that L_c be defined as the length corresponding to the peak of the LFD. Alternatively, Peak-plus truncation can be applied to select a value for L_c. Consequently, length observations from the ascending limb of the LFD are removed from the mean length calculation for the BHE based on the choice of L_c.

To reduce bias associated with the BHE, Laurec and Mesnil (1987) recommended summarizing length data in fine detail and grouping length frequencies in narrow size-bins. Animals within 30% of L_∞ were excluded from their analyses. However, simulation analysis demonstrated that the BHE performed well when all lengths greater than L_c, including those larger than L_∞, were retained (Then et al. 2015).

In this study, three candidate length-bins were selected for left truncation: the first length-bin on the ascending limb of the LFD corresponding to at least half of the frequency of that at the peak ("Half-peak abundance"), the length-bin of the peak ("Peak"), and the first length-bin after the peak ("Peak-plus"; Figure 2). If there are few length-bins larger than the peak, then a portion of the ascending limb of the LFD may consist of fully selected animals (Hordyk et al. 2015a: their Figure 7). Although arbitrary, the Half-peak abundance decision rule can be used to select a length on the ascending limb relative to the Peak across a variety of shapes in the length distribution (Figures 2, 3). This decision rule has also been used in several applications of methods evaluating length data (e.g., ICES 2014).

Similarly, there were three candidate length-bins for right truncation: the largest length-bin containing at least five individuals ("5+"), the length-bin at 90% of L_∞ ("90% L_∞"), and the length-bin at L_∞ ("100% L_∞"). The 100% L_∞ was chosen if the 5+ right truncation rule selected a length-bin with a midpoint larger than L_∞. For the 90% L_∞ and 100% L_∞ decision rules, if the bin contained no observations, then we selected the next-smallest bin containing any observations as the truncation point.

Nine methods, labeled L1–L9, were tested with the LCCC using the combinations of left and right truncation (Table 2). For the BHE, the lower boundary of the three candidate length bins for left truncation (Half-peak abundance, Peak, and Peak-plus) was identified as the L_c, comprising methods B1–B3. No truncation was necessary to use the LB-SPR method.

For each data set, total mortality was estimated with the data truncation methods described for LCCC, BHE, and LB-SPR. The values of von Bertalanffy parameters L_∞ and K used in the mortality estimators were sampled from a bivariate normal distribution around the true values with a CV of 0.1 and a correlation of −0.9. This step is designed to simulate the scenario in which only length data are available and growth information is obtained externally (e.g., via a literature search).

Performance analysis.— To quantify the performance of the decision rules for the estimators in terms of bias and precision, the relative percent bias (%Bias) and relative

TABLE 2. Length data truncation methods for estimating total mortality (Z) with the length-converted catch curve (LCCC) and Beverton–Holt equation (BHE). No truncation is associated with the length-based spawning potential ratio (LB-SPR) method. See Methods for a description of each truncation procedure.

Method	Estimator	Left truncation	Right truncation
L1	LCCC	Half-peak abundance	5+
L2	LCCC	Half-peak abundance	90% L_∞
L3	LCCC	Half-peak abundance	100% L_∞
L4	LCCC	Peak	5+
L5	LCCC	Peak	90% L_∞
L6	LCCC	Peak	100% L_∞
L7	LCCC	Peak-plus	5+
L8	LCCC	Peak-plus	90% L_∞
L9	LCCC	Peak-plus	100% L_∞
B1	BHE	Half-peak abundance	N/A
B2	BHE	Peak	N/A
B3	BHE	Peak-plus	N/A
LB	LB-SPR	N/A	N/A

percent root mean square error (%RMSE) for each decision rule in each factorial combination were calculated, respectively, as

$$\%\text{Bias} = \frac{\bar{\hat{Z}} - Z}{Z} \times 100 \qquad (17)$$

and

$$\%\text{RMSE} = \frac{1}{Z} \sqrt{\frac{\sum_i (\hat{Z}_i - Z)^2}{n}} \times 100, \qquad (18)$$

where $\bar{\hat{Z}}$ is the mean of the estimated total mortality rates from n out of 1,000 data sets that produced a feasible estimate; $Z = F + M$ is the true underlying mortality rate for the factorial combination in the simulation; and $\hat{Z}_i$ is the estimated mortality rate from each data set $i = 1, 2, \ldots, n$ within each factorial combination. Unfeasible estimates occurred with the LCCC if only one length-bin was selected using the respective decision rule, in which case the linear regression was not possible, or if the slope of the regression line in equation (3) was greater than 1.0, which resulted in a negative estimate of Z. With the BHE, a negative Z was estimated if the mean length was larger than L_∞.

The %Bias and %RMSE were calculated for each method in all 108 factorials. From this set, the median %Bias and median %RMSE for each method were calculated among factorials with common M/K and F/M ratios. The median %Bias and median %RMSE were further stratified across levels of the other factorial variables (growth variability, recruitment variability, and selectivity) within each group of M/K and F/M. The best decision rules can be identified as those with the lowest absolute values of the median %Bias and the median %RMSE.

Sensitivity analyses.— Sensitivity analyses were performed with respect to sample size, length-bin, and assumed growth parameters. For the sample size analysis, 200 and 500 length observations were selected without replacement as subsets of the original data sets, with a bin size of 10 units in the LFD. This analysis allowed us to test the effect of observation (sampling) error on mortality estimation. For the bin width analysis, mortality was re-estimated by re-binning the data with bin widths of 25 and 50 units (5% and 10% of L_∞, respectively). Sample sizes of 2,000 were used to analyze the effect of bin width separately from observation error. For these two sensitivity analyses, mortality was estimated again using the same decision rules for data truncation, and the %Bias and %RMSE were calculated for each decision rule in each factorial combination. Finally, the variability in individual estimates of mortality was also evaluated when assumed growth parameters were stochastically sampled. All

simulations and analyses were performed in R version 3.3 (R Core Team 2017).

RESULTS

Our factorial design generated several functionally distinct LFDs based on M/K and F/M (Figure 3). Compared to the Gradual and Dome selectivity functions, the Steep selectivity function produced a shorter ascending limb of the LFD, which truncated the length structure of the sample. In contrast, the Dome selectivity function only showed a discernable difference in the descending limb when F/M was 0.25 or 1.0.

Based on a sample size of 2,000, performance of the methods varied the most by M/K and F/M scenarios, with best performance of the methods when M/K was 2 in conjunction with an F/M of 0.25 or 1.0 (Figure 4A). The methods have the least bias in these scenarios, with the magnitude of median %Bias being generally less than 20% and the %RMSE being less than 50%. The ranges of the %Bias and %RMSE among factorials were also relatively small in these scenarios. Most methods performed similarly, although LB-SPR did not perform as well as the LCCC (L1—L9) and BHE (B1–B3) methods.

Performance was worst when M/K was 0.5 in conjunction with an F/M of 0.25 or 1.0 (Figure 4A). Although there were some factorial combinations where the methods produced low %Bias and %RMSE, the range in %Bias and %RMSE of all methods was large (with the performance metrics as high as 300–400%), indicating high variability in performance. In all cases, the bias was positive. The median %Bias and median %RMSE were usually larger than 100%. The best-performing methods were B1 (BHE with Half-peak abundance as the L_c), closely followed by L1 and L3 (both use the LCCC with Half-peak abundance for left truncation).

When F/M was equal to 5, all methods improved in terms of bias for an M/K of 0.5 (the magnitude of %Bias was generally less than 20%) but worsened for an M/K of 2 (the magnitude of %Bias increased up to 40%) relative to lower F/M (Figure 4A). Overall, the sign of the bias trended from positive to negative with increasing F/M, with the trend being most noticeable for an M/K of 0.5. No single method appeared to perform the best when F/M was equal to 5. Although LB-SPR had the lowest bias when M/K was equal to 2, it also had the highest mean square error. In other M/K and F/M scenarios, LB-SPR did not appear to perform as well as the LCCC and BHE.

Performance Across Factorial Variables

In this section and the next section, we present the results for B1 when M/K was equal to 0.5 and for L5 when M/K was equal to 2. Method B1 performed the best
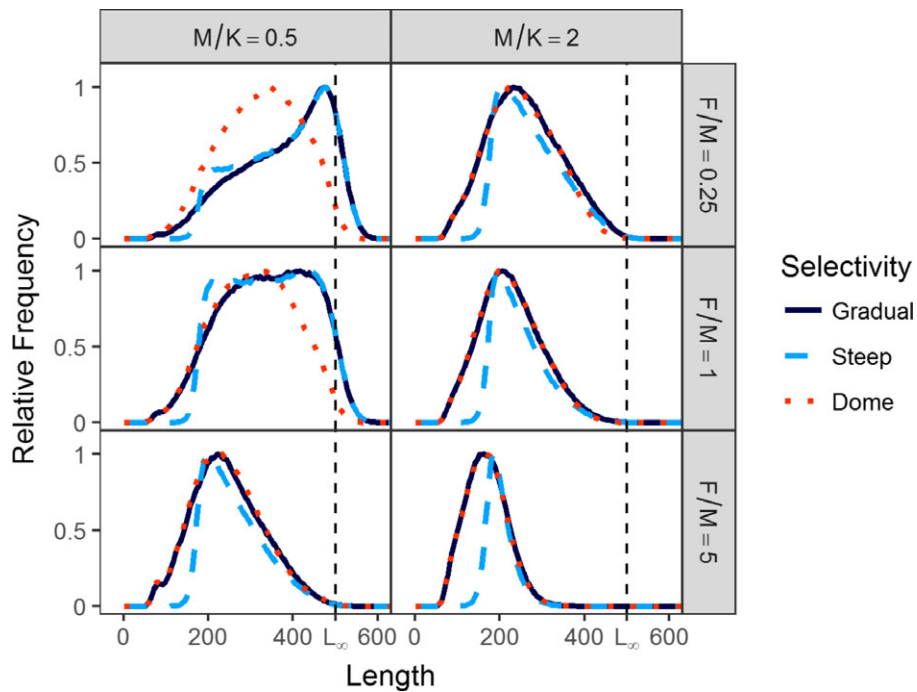
FIGURE 3. Expected length frequency distributions (length is expressed in arbitrary units) obtained from the sum of 1,000 data sets from the simulation stratified by the factorial design for M/K (ratio of natural mortality [M] to the von Bertalanffy growth rate parameter [K]), F/M (ratio of fishing mortality [F] to M), and selectivity. Selectivity functions correspond to those in Figure 1. In all panels, medium growth variability and low recruitment variability were assumed in the sample. Dashed vertical lines indicate an asymptotic length (L_∞) of 500 units (Table 1).

when M/K was 0.5 (and F/M = 0.25 or 1.0). Method L5 was chosen arbitrarily because there was no clear best method when M/K was 2. The performance across factorial variables and sensitivity analyses for individual factorial combinations for all decision rules is described in the main text, with supporting figures and tables provided in the Supplement available separately online.

Within M/K and F/M combinations, the performance metrics were further stratified by growth variability type, magnitude of growth variability, recruitment variability, and selectivity. Observed trends in performance remained similar to those described in the previous section (Tables S.1–S.6).

Bias and precision generally improved with increasing growth variability when F/M was 0.25 or 1.0 (Figure 5, Figures S.1–S.13). When F/M was equal to 5, the differences in bias and precision among different growth variabilities were small to negligible. Larger %Bias and % RMSE were associated with high variability relative to low variability in recruitment (Figure 6, Figures S.14–S.26), although there were negligible differences when F/M was 5. All three methods were much more positively biased with Dome selectivity than with the logistic selectivities (Gradual and Steep) when F/M was 0.25 or 1.0 (Figure 7, Figures S.27–S.39). However, the effect of Dome selectivity was minimal at an F/M of 5. There were

no major differences in performance common to all methods between the Steep and Gradual selectivity functions.

Sensitivity Analyses

At the sample size of 200, most methods had larger bias and less precision compared to use of a sample size of 2,000, but the magnitude of the difference between sample sizes was not particularly large (Figure 4B, Figures S.40–S.52). Methods L4 and L7 were notable in that their median %Bias was lower but their median %RMSE was higher when the sample size was 200 instead of 2,000. However, the general trends remained unchanged.

Length-bin width generally did not affect the %Bias and %RMSE of the mortality estimators (Figure 8, Figures S.53–S.65). Methods L7, L8, and L9 showed improvement in some scenarios when M/K was equal to 0.5 in conjunction with an F/M of 0.25, where larger length-bins performed better, but these scenarios still appeared to be outliers. The magnitude of the performance metrics remained large (%Bias > 100%) for these scenarios.

We examined the correlation of total mortality estimates with the assumed values of L_∞ and K (Figure 9). In general, higher estimates of mortality were obtained with a larger value of L_∞. However, underestimates of Z did not often occur with the low-M/K scenario and when F/M
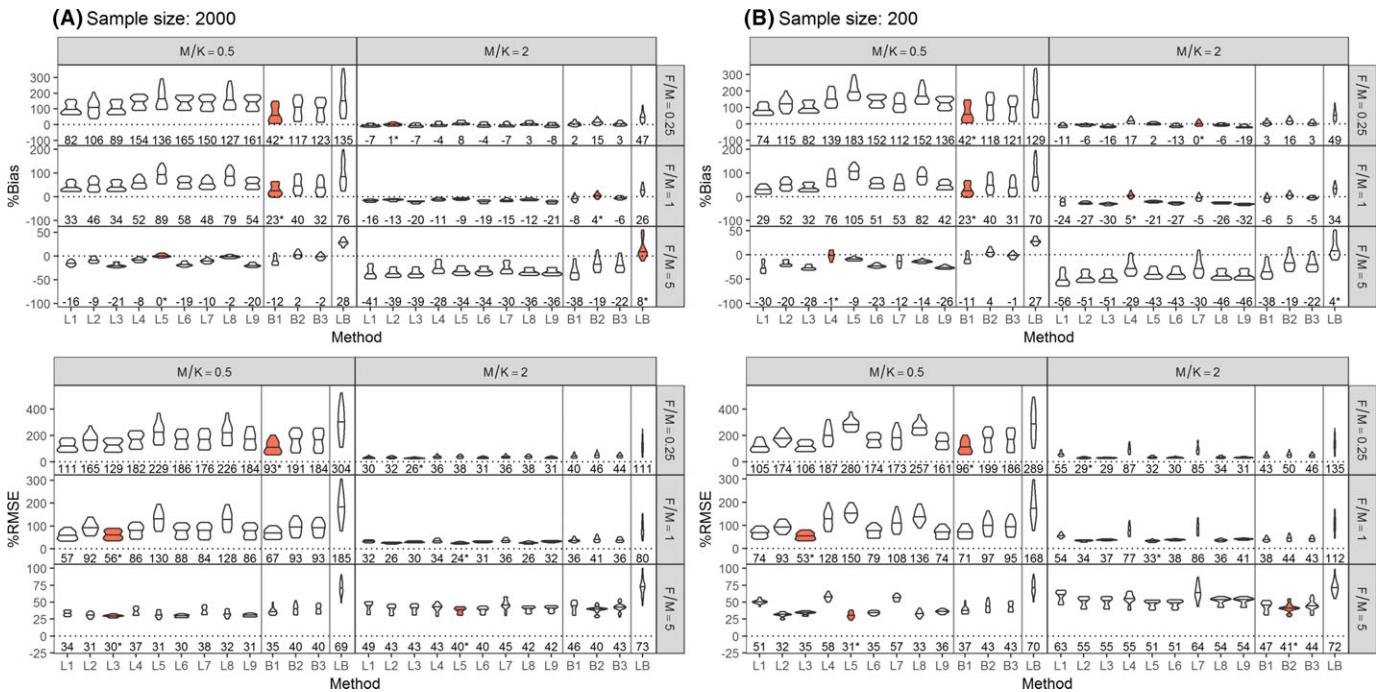
FIGURE 4. Relative percent bias (%Bias; top grids) and relative percent root mean square error (%RMSE; bottom grids) from the simulation study when the data set sample size was **(A)** 2,000 and **(B)** 200. For each method, factorial combinations are stratified by M/K (ratio of natural mortality [M] to the von Bertalanffy growth rate parameter [K]) and F/M (ratio of fishing mortality [F] to M). Numbers and horizontal lines in the violin plots indicate median %Bias and %RMSE, with the numbers rounded to the nearest whole number for clarity. The shape of the violin plots shows the distribution of values. Asterisks and shaded violin plots indicate the method (defined in Table 2) with the lowest median value in each grid cell (not subject to rounding error). Rows in each grid have separate scales on the y-axis to show the shape of the violin plots.

was 0.25 or 1.0. On the other hand, when F/M was 5 (for both M/K scenarios), overestimates of Z did not often occur.

DISCUSSION

Performance of Mortality Estimators

Our simulations suggest that the M/K ratio strongly affects the performance of the three length-based methods, with poor performance at low M/K for all three methods. This finding is consistent with previous simulations on LB-SPR (Hordyk et al. 2015b). When M/K is low, the peak of the LFD may not correspond to the true length of full selectivity (Figure 3). The best decision rules for both the LCCC and BHE used half-peak abundance length as the left truncation point (methods L1 and L3 for the LCCC; method B1 for the BHE), although there was still a large bias associated with them. When M/K was high, there was no clearly superior method in both bias and precision.

The performance of all three length-based methods worsened in situations with extreme shapes in the LFD (i.e., low M/K with low F/M or high M/K with high F/M; Figure 3). In spite of this, if a stock is exploited over a broad range of sizes, then a qualitative assessment of the mortality rate is still possible based on life history and the shape of the LFD. High mortality can be inferred with truncation of the size structure due to low survival of animals to large size-classes. Populations with low M/K and low F/M ratios will have a protracted ascending limb due to the "pile-up" effect, where there are many large animals in the LFD due to low mortality. The use of length as a proxy for age by assuming deterministic growth in the LCCC and BHE did not appear to work well in such scenarios, as a much more substantial portion of the length distribution consisted of lengths larger than L_∞ due to variability in growth (Figure 3). However, contrary to what might be expected, the LB-SPR method, which explicitly models variability in growth and selectivity (removing the need to truncate the data to meet model assumptions), did not perform more reliably than the LCCC or BHE in these situations.

In our study, all three length-based methods were robust to high growth variability. This result is surprising for the LCCC and BHE because both methods assume no variability in growth. Previous simulations with the LCCC showed that the estimator performed better with less growth variability (Isaac 1990), although Then et al. (2015) found that the BHE performed better with higher
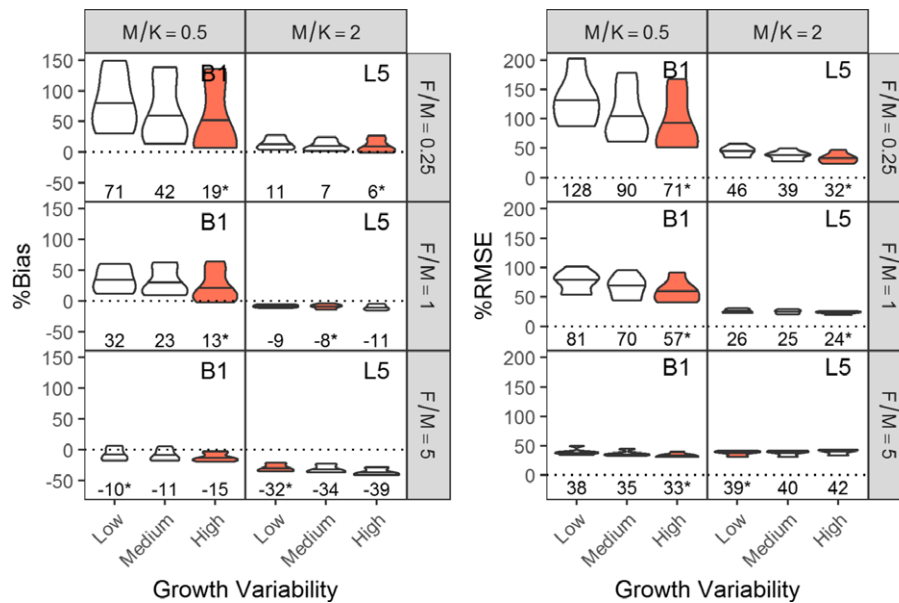
FIGURE 5. Relative percent bias (%Bias; left grid) and relative percent root mean square error (%RMSE; right grid) stratified by M/K (ratio of natural mortality [M] to the von Bertalanffy growth rate parameter [K]), F/M (ratio of fishing mortality [F] to M), and growth variability. Only methods B1 and L5 (defined in Table 2) are shown (text in the corners indicates the method). Numbers and horizontal lines in the violin plot indicate median %Bias and %RMSE, and the shape of violin plot shows the distribution of values. Asterisks and shaded violin plots indicate the method with the lowest median value in each grid cell (not subject to rounding error).

growth variability if the selectivity was dome-shaped. On the other hand, it was not surprising that LB-SPR performed worse when the CV of growth in the population was lower than that assumed in the estimation model. However, this assumption is not as critical in LB-SPR compared to the other two methods because the CV of growth variability can be adjusted in the former when external information from a growth study is available.

The estimators were robust to the magnitude of recruitment variability as long as the recruitments were random. Trends in recruitment are more likely to be a problem because they would be conflated with mortality.

Dome selectivity had a noticeable effect on the bias only when F/M was 0.25 or 1.0, due to the high abundance of large individuals present in the population but missing from the catch (Figure 3). The length-based methods all assume logistic selectivity so that dome selectivity is conflated with high mortality. Thus, dome selectivity must be estimated externally. For example, Ehrhardt and Ault (1992) developed a modified version of the BHE to estimate mortality when there is an upper length truncation in the LFD of the catch (Ehrhardt and Ault 1992), with that length of upper truncation estimated externally and then provided to the equation. Simulations have found the behavior of the Ehrhardt–Ault estimator to be complex (Then et al. 2015). Contrary to the methods tested in our study, the performance of their estimator often worsened with higher growth variability. In some

cases, lower bias but higher variance was observed with using the Ehrhardt–Ault compared to the original equation, although the best input length for upper truncation to obtain minimum bias was often larger than the true length of upper truncation. Then et al. (2015) did not recommend the Ehrhardt–Ault estimator for routine use.

At high F/M, low survival to large size-classes minimizes the effect of dome selectivity. Then et al. (2015) found a positive bias associated with the truncation of large animals in the length distribution when using the BHE for all mortality scenarios, but they assumed knife-edge selection of small animals in their simulations. Our simulations also examined the effect of left truncation for the LCCC and the BHE when selectivity was not knife-edged. In theory, Steep selectivity more closely corresponds to the knife-edge selectivity assumption compared to Gradual selectivity. However, all three methods (including LB-SPR) were robust to different logistic selectivity functions, as indicated by the small differences in performance among truncation methods.

Sensitivity Analyses

We examined the estimators in the ideal situation with large sample sizes and little observation error. The sensitivity analysis indicated that the estimators were generally robust to smaller sample sizes. We assumed that the generated data set was a random sample of animals from the vulnerable population. In reality, data are generally
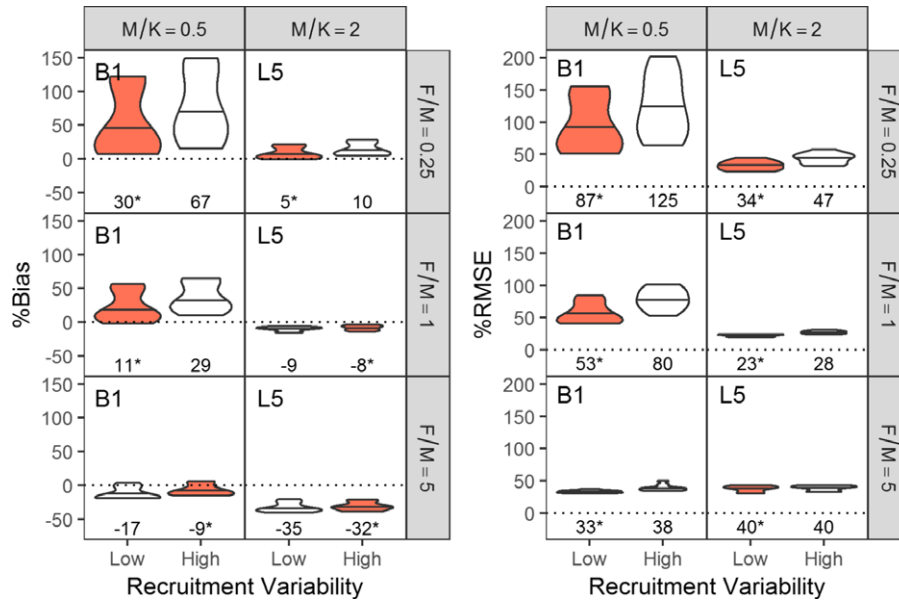
FIGURE 6. Relative percent bias (%Bias; left grid) and relative percent root mean square error (%RMSE; right grid) stratified by M/K (ratio of natural mortality [M] to the von Bertalanffy growth rate parameter [K]), F/M (ratio of fishing mortality [F] to M), and recruitment variability. Only methods B1 and L5 (defined in Table 2) are shown (text in the corners indicates the method). Numbers and horizontal lines in the violin plot indicate median %Bias and %RMSE, and the shape of violin plot shows the distribution of values. Asterisks and shaded violin plots indicate the method with the lowest median value in each grid cell (not subject to rounding error).

collected in clusters from samples of fishing trips or from schools of animals, often with similar lengths and ages within trips or schools. Cluster sampling reduces the effective sample size of the observed LFD and increases the uncertainty surrounding estimates of mortality (Chih 2011). With knowledge of the sampling program used to collect the data, the effective sample size can be estimated via bootstrapping methods (Stewart and Hamel 2014) or design-based formulas (Thorson 2014). Stewart and Hamel (2014) suggested that the number of sampled trips may be an appropriate proxy for the effective sample size. This suggestion may be applicable in a data-limited context if the ratio of within- to among-trip variance is low due to the cluster effect. The effective sample size would be important to determine if an appropriate range of size-classes has been sampled, as the sampling would affect the shape of the LFD used to apply the length truncation methods for the LCCC and BHE and to estimate selectivity in LB-SPR.

The performance of the LCCC and BHE did not appear to worsen with larger length-bins, and in some cases (with low F/M), performance was better. Although sensitivity of length-bins can be examined in individual applications of the equilibrium mortality estimators, low sample sizes may preclude the use of small length-bins to describe the length composition of the catch in data-limited situations.

Our study design assumed that information on growth was stochastic, arising from a bivariate distribution with a

highly negative correlation often associated with estimating parameters of the von Bertalanffy growth equation (Gallucci and Quinn 1979). Sensitivity analyses can be used to determine the influence of growth parameters on mortality estimation. An overestimate of L_∞ may create a positive bias for the estimate of total mortality because fewer large animals are observed than are expected. We examined the correlation of total mortality estimates with the assumed values of L_∞ and K (Figure 9). In light of the systematic biases of the estimators among different M/K scenarios, overestimates of mortality may be more likely and underestimates may be less likely when M/K is low. Similarly, overestimates of mortality are unlikely when M/K and F/M are high. Such information could be used to assess the direction and magnitude of estimation error based on mis-specified growth in future applications of the mortality estimators.

Mortality estimates with length-based methods are dependent on the values of growth parameters. The quality of external growth estimates is affected by, among other things, the choice of the growth model (Gwinn et al. 2010) and the representativeness of the size-at-age data to the population when sampling gears with different selectivity patterns are used (Wilson et al. 2015); this should be assessed in future applications of length-based methods. If size-at-age data are available, integrated modeling approaches for estimating growth simultaneously with mortality and selectivity also exist (Taylor et al. 2005).
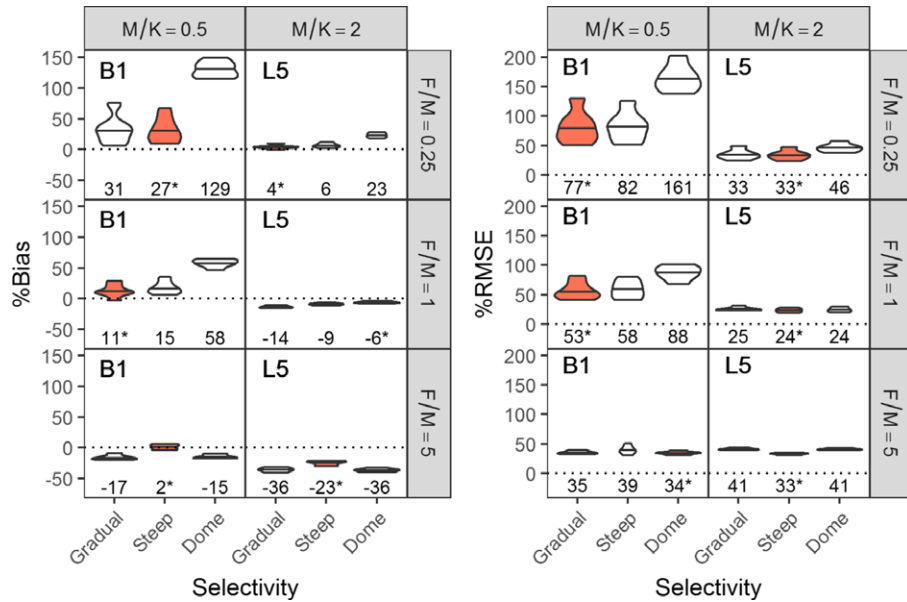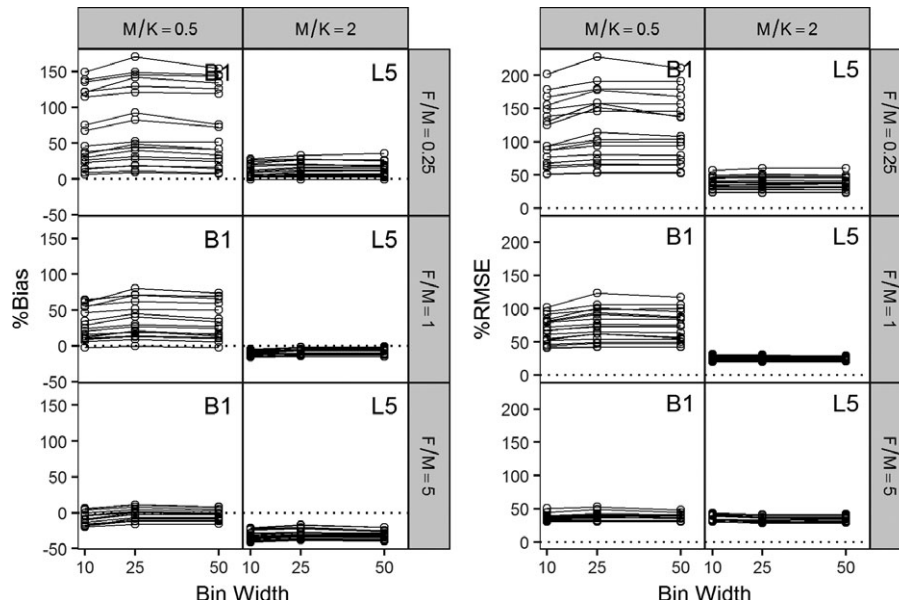
FIGURE 7. Relative percent bias (%Bias; left grid) and relative percent root mean square error (%RMSE; right grid) stratified by *M/K* (ratio of natural mortality [*M*] to the von Bertalanffy growth rate parameter [*K*]), *F/M* (ratio of fishing mortality [*F*] to *M*), and selectivity. Only methods B1 and L5 (defined in Table 2) are shown (text in the corners indicates the method). Numbers and horizontal lines in the violin plot indicate median % Bias and %RMSE, and the shape of violin plot shows the distribution of values. Asterisks and shaded violin plots indicate the method with the lowest median value in each grid cell (not subject to rounding error).

FIGURE 8. The effect of bin width on relative percent bias (%Bias; left grid) and relative percent root mean square error (%RMSE; right grid) for the length-based estimators. Only methods B1 and L5 (defined in Table 2) are shown (text in the corners indicates the method). Each line represents individual factorial combinations stratified in separate cells by *M/K* (ratio of natural mortality [*M*] to the von Bertalanffy growth rate parameter [*K*]) and *F/M* (ratio of fishing mortality [*F*] to *M*).

Life History Considerations

Overall, our study found that life history as expressed in the *M/K* ratio was a good predictor of the performance of length-based mortality estimators, with better performance in high-*M/K* scenarios compared to low-*M/K* scenarios. This result supports those in previous studies of length-based methods (e.g., Hordyk et al. 2015b). Two features unique to low-*M/K* populations may result in
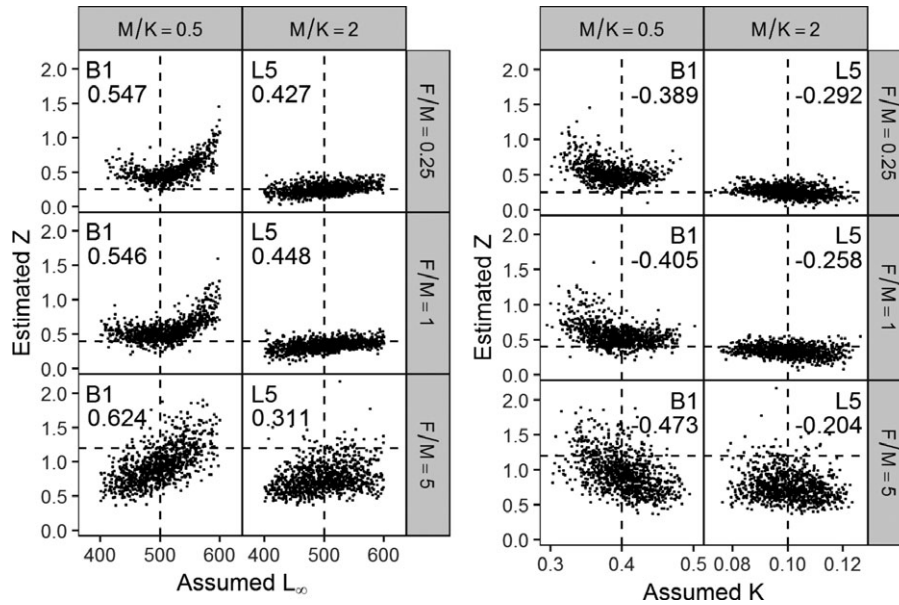
FIGURE 9. Individual estimates of total mortality (Z) based on the assumed values of von Bertalanffy parameters L_∞ (asymptotic length; left grid) and K (growth rate parameter; right grid) in the estimation model (parameters are sampled from a bivariate normal distribution around the true values with a correlation of -0.90). Only methods B1 and L5 (defined in Table 2) are shown (text in the corners indicates the method). Plotted estimates are from the simulations with medium growth variability, low recruitment variability, and the gradual selectivity function stratified in separate cells by M/K (ratio of natural mortality [M] to K) and F/M (ratio of fishing mortality [F] to M). Dotted lines indicate the true value of mortality and the growth parameter in the respective cell.

their poor performance. First, the protracted ascending limb of the length composition in the population conflates selectivity with abundance at length. It may be difficult to select appropriate truncation lengths or estimate selectivity. Second, there is a high abundance of large animals from the "pile-up" effect. In a low-M/K population, a large age range is encompassed in a small spectrum of lengths, and the length structure is a poor proxy for the age structure of the population. We recommend caution when using length-based methods in low-M/K situations, as the results are likely to be positively biased even in equilibrium situations. From a management standpoint, this behavior can dictate data collection priorities for alternative data types in assessments of low-M/K stocks. In a data-limited context, meta-analyses can be used to identify taxa with low M/K ratios (Prince et al. 2015a). Nevertheless, if length-based methods are to be used, our study suggests that classical methods (LCCC and BHE) remain viable options for mortality estimation.

CONCLUSIONS

Our study examined the performance of three length-based mortality estimators. When M/K is low ($M/K = 0.5$ in our simulation), we recommend using the BHE with half-peak abundance as the L_c, although the method is still likely to be positively biased and imprecise. When M/K is high ($M/K = 2$ in our simulation), both the LCCC and BHE performed well and were robust to variation in commonly used truncation rules. For optimal performance, the length-based estimators require some a priori judgment of the life history and expected fishing pressure on the stock of interest. We recommend caution in using length-based methods for populations with low M/K. Overall, this study demonstrated that relative to LB-SPR, both the LCCC and BHE produced less-biased and more precise estimates of total mortality. Although LB-SPR did not perform as well as the other two methods when estimating mortality, the method has an advantage of providing estimates of selectivity if desired. The LCCC and BHE methods performed comparably, and no firm recommendation is made for choosing between these two methods.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.

Appendix: Derivation of the Length-Converted Catch Curve

The age-based catch curve is of the form

$$\log_e(C_t) = a - Zt, \tag{A.1}$$

where C_t is the catch at age t; Z is total mortality; and a is a constant. In a length frequency distribution (LFD), length-bins of larger animals contain more age-groups than bins with smaller ones due to the decreasing growth rate of older individuals. Thus, abundance at size in an equilibrium population is a function of individual growth rate and mortality over time (Ricker 1975; Van Sickle 1977; Pauly 1983). Assuming the length-bins are narrow, the length-based catch curve is of the form

$$\log_e\left(C_i \frac{dL_{t_i}}{dt}\right) = a - Zt_i, \tag{A.2}$$

where C_i is the catch in the ith length-bin; t_i is the age at the midpoint of the ith length-bin in the LFD (assuming deterministic growth); $L_{t_i} = L_\infty\{1 - \exp[-K(t_i - t_0)]\}$ is the von Bertalanffy growth equation for length at age t_i; and $\frac{dL_{t_i}}{dt}$ is the instantaneous growth rate evaluated at the

corresponding midpoint of the ith length-bin. The following substitutions are made:

$$\log_e\left(\frac{dL_{t_i}}{dt}\right) = \log_e(KL_\infty) - K(t_i - t_0), \tag{A.3}$$

and

$$t' = K(t_i - t_0), \tag{A.4}$$

where t' is the relative age defined as a variable transformation. After substitution and simplification, equation (A.2) reduces to

$$\log_e(C_{t'}) = \tilde{a} + \left(1 - \frac{Z}{K}\right)t', \tag{A.5}$$

where $\tilde{a}$ is a nuisance parameter of all constant terms. Equation (A.5) is a linear equation of the form

$$\log_e(C_{t'}) = \tilde{a} + bt', \tag{A.6}$$

where $\tilde{a}$ and b are the intercept and slope, respectively. Using equations (A.5) and (A.6), total mortality (Z) is

solved:

$$Z = K(1 - b). \qquad (A.7)$$

$$t' = -\log_e\left(1 - \frac{L_{t_i}}{L_\infty}\right), \qquad (A.8)$$

From an LFD, the midpoint of the length-bins can be converted to relative ages t', also defined by the von Bertalanffy growth equation:

with the logarithm of the catch in that length-bin used in a linear regression to estimate the slope of equation (A.6) and, thus, Z in equation (A.7).