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#### **ARTICLE**

# **Evaluation of Age-Length Key Sample Sizes Required** to Estimate Fish Total Mortality and Growth

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#### Abstract

Fisheries assessments often rely on age composition data to infer information about growth, mortality, and the outcome of various management policies. To reduce the costs of estimating the age of all fish collected (i.e., via direct aging), an age-length key (ALK) is often developed by directly aging only a subsample of fish and estimating the ages of the remaining fish based on observed lengths. Although this approach is common, there is little guidance in the literature for determining the appropriate total sample size and numbers of fish needed to directly age for each length bin. We developed a stochastic simulation to evaluate the sample-size requirement for using ALKs to estimate von Bertalanffy growth parameters and the instantaneous rate of total mortality (Z). The simulations accounted for variation in life history characteristics of stocks and exploitation rates of fisheries. Our simulations suggested that for overfished populations, aging more fish per bin provides negligible benefits whereas collecting larger total sample sizes could improve bias and precision of Z estimates. These results also indicated that bias and precision was relatively uninfluenced by fish life history type, which may allow for standardization of field collection methods across a wide range of fish species. In most cases, total sample sizes of 500–1,000 and 10 fish aged per bin provided near optimal performance in accuracy and precision, suggesting that this could be a guideline for many studies.

The ability of fisheries assessments to successfully inform management is dependent on an accurate knowledge of key biological characteristics of stocks. Many contemporary models used to assess the status of fish stocks rely on the collection of accurate age composition data. Information about age composition is useful because it can be used to draw inferences about mortality and growth rates, fishery selectivity, relative cohort strength, and other demographic processes useful to management. However, age information is often costly to obtain. These high costs force many management programs to limit the number of fish aged directly, and to rely on age—length keys (ALKs; Fridriksson 1934, cited in Ketchen 1950) to draw inferences

about the age composition of the stock or catch. Because estimating age composition in this way introduces sampling error into fisheries assessments, it is desirable to understand and minimize this source of error.

The ALK is constructed from a subsample of fish whose individual lengths have been measured and ages have been estimated directly (such fish are said to be aged), usually by examination of annual rings on otoliths or other calcified bony structures. The data are then arrayed by length bin (e.g., centimeter group) and age such that the proportion of fish of each age is calculated for each length bin. These proportions of fish are then used to assign ages to unaged fish in the total sample. By estimating the

age of all fish in a sample using the ALK, the age composition of the entire sample can be used to estimate growth (e.g., von Bertalanffy model [LVB]: von Bertalanffy 1938) or mortality (e.g., catch curve: Ricker 1975) parameters.

Technical and analytical considerations of constructing and applying ALKs have received moderate attention in the literature. One design option for constructing an ALK assumes a fixed and constant number of fish per length bin are chosen to be aged (i.e., fixed-age subsampling). While analysis of such a sample alone will obviously yield biased age composition estimates, Kimura (1977) showed that a fixed-age subsample can be used to construct an ALK and the resulting ALK used to produce unbiased age estimates of the unaged fish. Kimura (1977) also demonstrated that fish chosen proportional to their abundance in each length bin (i.e., proportional-age subsampling) produced an unbiased sample age composition. Similarly, Goodyear (1995) demonstrated that fixed-age subsampling produced biased estimates of mean length at age while proportional-age subsampling produced unbiased estimates (but see Brouwer and Griffiths 2005). While proportional-age subsampling is desirable based on multiple statistical properties, fixed-age subsampling is frequently used because of improved efficiency in field operations. Instructing field personnel to take a fixed number of fish per length bin is easier to execute than having personnel take fish with lengths in proportion to the abundance of each length-group.

The ability of an ALK to provide an unbiased age composition estimate of the sample requires that aged fish are representative of the unaged fish. This implies that aged fish are taken with the same gear, season, and spatial location as the unaged fish (Ricker 1975; Kimura 1977). Failure to meet this assumption can cause the estimated age composition of the sample to be biased relative to the age composition obtained if all fish had been directly aged. Kimura and Chikuni (1987) proposed an iterative method for computing an ALK for cases where aged fish are collected in a different year than are fish for which only length data are obtained. Hoenig and Heisey (1987) also developed an iterative procedure to correct the proportions of fish in each age for application to the unaged fish.

Most previous work has evaluated the performance of ALKs to accurately represent the actual age structure of the entire sample (e.g., Kimura 1977; Lai 1987). While evaluation of the bias and precision of age composition estimates is important when evaluating the performance of ALK design options, age composition estimates are frequently not of direct interest for management. Instead, the highest utility of age composition information is frequently in estimating growth and mortality parameters that are used in population models. As such, there is a need to evaluate ALK design options based on the bias and precision of growth and mortality parameter estimates (Ricker 1975).

The accuracy and precision of growth and mortality parameter estimates informed by age composition is likely to be influenced by fish life history and the exploitation history of a stock. Fish longevity and growth rate influence the degree to which fish

of a particular length overlap in age, which in turn should influence the accuracy and precision of parameter estimates informed by age composition estimated from an ALK. For example, fish species with high growth rates and small asymptotic length may have many overlapping ages for fish in each size bin. Westrheim and Ricker (1978) showed that the ALK will have no bias only when ages do not overlap between length bins. We predicted that using ALKs for such species would provide more variable and possibly biased estimates of growth and mortality rate than using fish whose length values do not overlap across many ages. Long-lived fish offer more ages for use in a catch curve, which could improve precision of total mortality estimates relative to short-lived fishes, but subsampling the ages for an ALK could influence the estimated age composition for both long-lived and short-lived fishes. Additionally, we would expect heavily exploited stocks to exhibit age structure erosion where the oldest age-classes are absent or greatly reduced. Thus, we expected fish life history, exploitation status, and sample size to interact to affect the performance of ALKs.

While several of the previous papers on ALKs have focused on evaluating the subsampling method (fixed-age versus proportional-age allocation), less effort has been directed at evaluating how sample size for the total number of fish collected and number of fish aged per bin influence parameter estimates (but see Lai 1987). Further, no previous studies have evaluated how fish life history influences the required sample size and parameter estimates derived from models using age composition data estimated using ALKs. The objective of this paper was to evaluate how ALK sample sizes could influence bias and precision of model parameter estimates for mortality rate and growth under two fish life history types and a range of exploitation rates.

# **METHODS**

We constructed a simple age- and size-structured simulation model for our investigation. The two life history types were selected near the end points of a continuum from short-lived, small, and fast-growing (SSF) fish to long-lived, large, and slow-growing (LLS) fish. Each simulated population was exploited at two rates that were predicted to result in spawning potential ratios (SPRs: Goodyear 1989) of either 0.25 or 0.50. Spawning potential ratio is the number of eggs per recruit in the fished condition relative to the unfished condition and is a common metric used to evaluate the potential for recruitment overfishing in fisheries. Values of SPR below 0.35 are often considered to cause recruitment overfishing (Mace 1994). Thus, the populations were exploited at levels roughly corresponding to moderate and highly exploited scenarios, which simulated varying degrees of age structure erosion owing to fishing.

Model structure.—The models were stochastic and allowed annual variation in recruitment and mortality rates such that populations would vary in age composition and abundance through time. This allowed the sampled catch and age composition to reflect variation in population vital rates as well as sampling error.

We simulated a recruitment time series that was independent of parental stock and described by a lognormal distribution with constant mean and standard deviation as

$$N_{1,t} = r\gamma_t$$
 and  $\gamma_t \approx e^{normal(0,\sigma_{rec})},$ 

where  $N_{1,t}$  is the recruit abundance (age = 1 year) at time t in years. We specified the standard deviation ( $\sigma_{rec}$ ) as 0.3 and the median recruitment (r) as one million fish. While this level of recruitment variation is similar to that observed in some wild populations (Allen 1997), and we did not expect recruitment variation to affect the performance of ALKs, we also simulated a population with  $\sigma_{rec} = 1.0$  to confirm our expectations. Similarly, we modeled temporal variation in fishing mortality ( $F_t$ ) as

$$F_t = F \varphi_t$$
 and  $\varphi_t \approx e^{normal(0,\sigma_F)}$ .

We specified the standard deviation of fishing mortality ( $\sigma_F$ ) as 0.1 and 0.3 to evaluate the effect of interannual variation in fishing mortality to mimic either precise or imprecise management control, respectively. The median fishing mortality (F) and natural mortality (F) was based on the life history type (Table 1) and exploitation level modeled in each simulation.

The simulation used typical recursion equations to model the age-structured population dynamics as follows:

$$N_{a+1,t+1} = N_{a,t}e^{-Z_{a,t}},$$
 $Z_{a,t} = F_{a,t} + M,$ 
 $F_{a,t} = F_t v_a, \text{ and}$ 
 $C_{a,t} = N_{a,t}(1 - e^{-Z_{a,t}}) \frac{F_{a,t}}{Z_{a,t}},$ 

where  $v_a$  is the vulnerability of age a fish to the fishing gear and  $C_{a,t}$  is the catch of age a in year t. We specified  $v_a = 0$  for fish younger than age at maturity,  $v_a = 0.5$  for fish of age at maturity, and  $v_a = 1$  for fish older than age at maturity.

Mean length at age was modeled with the LVB equation,

$$L_a = L_{\infty} (1 - e^{-K(a - t_0)}),$$

where asymptotic average length  $(L_{\infty})$ , growth coefficient (K), and the theoretical age at zero length  $(t_0)$  were each chosen to portray the life history types. The length of any particular fish sampled at age a was simulated as a normal random variate with mean  $L_a$  and coefficient of variation ( $\text{CV}_L = \text{SD/mean}_L \cdot 100$ ) equal to 10%. This variation in length at age approximates that observed in many exploited fish stocks (Walters and Martell 2004).

Parameter specification.—To assign parameter values to each life history type, we first defined longevity (A) and used published correlations among vital rates and A to specify natural mortality rate, growth parameters, and maturity schedules

TABLE 1. Parameter values used for model simulations. Values are given for the short-lived, small, and fast-growing (SSF) and the long-lived, large, and slow-growing (LLS) species.

Parameter	Description	SSF	LLS
$\overline{A}$	Longevity (years)	8	40
M	Average natural mortality rate (years <sup>-1</sup> )	0.55	0.11
$\sigma_{rec}$	SD of recruitment variation	0.3 or 1.0	0.3 or 1.0
$L_{\infty}$	Average asymptotic length (mm)	300	2,000
K	LVB growth coefficient (years <sup>-1</sup> )	0.37	0.075
$t_0$	LVB age at zero length (years)	0	0
$\mathrm{CV}_L$	Coefficient of variation for length at age	10%	10%
$a_{mat}$	Age at maturity (age in years)	2	10
α	Length-weight constant	0.002	0.002
β	Allometric parameter	3.0	3.0
$\mathrm{CV}_{age}$	Coefficient of variation for estimating age	10%	10%
$F_{0.25}$	Fishing mortality for $SPR = 0.25$	1.40	0.15
$F_{0.50}$	Fishing mortality for $SPR = 0.50$	0.48	0.065
$\sigma_F$	SD of fishing mortality variation	0.1 or 0.3	0.1 or 0.3

(Table 1). We chose a maximum age of 8 years for the SSF species and 40 years for the LLS species. Following Hoenig (1983), we assigned an M of 0.55 years<sup>-1</sup> for the SSF and 0.11 years<sup>-1</sup> for the LLS. We assigned LVB K parameter values of 0.37 for the SSF and 0.075 for the LLS based on Jensen's (1996) relationship between M and K. Average asymptotic length was specified to provide contrast between the life histories (300 and 2,000 mm for SSF and LLS species, respectively). Finally, age at maturity ( $a_{mat}$ ) was specified as 2 years for SSF and 10 years for LLS based on the heuristic that age at maturity is often roughly one-fourth of longevity (Beverton 1992).

Fishing mortality rates ( $F_{0.25}$  and  $F_{0.50}$ ) that provided equilibrium SPR values of 0.25 and 0.5 were determined via the method of incidence functions as described by Walters and Martell (2004, Box 3.1). This method requires estimates of relative fecundity at age that were assumed to be related to weight such that fecundity at any age was simply the positive difference between weight at age and weight at maturity. Weight at age and weight at maturity were computed using

$$W_a = \alpha L_a^{\beta}$$

where  $\alpha = 0.002$  and  $\beta = 3$  for both the SSF and LLS species. Solving for F by iteration yielded fishing mortalities of  $F_{0.25} = 1.40$  and  $F_{0.50} = 0.48$  for the SSF species, and  $F_{0.25} = 0.15$  and  $F_{0.50} = 0.065$  for the LLS species.

Age sampling procedures.—Each simulation run extracted a simple random sample (without replacement) of either 200, 500, 1,000, or 1,500 fish from the catch of the projected population in the terminal year. The simulation then established a set of length bins based on the minimum and maximum observed lengths. The width of each length bin differed between life history types and was calculated by computing  $L_{\infty}/30$  and rounding the result to the nearest 5 mm. This resulted in a bin width of 10 mm for the SSF and a bin width of 65 mm for the LLS species.

To evaluate how the number of fish aged per length bin influenced precision and bias in parameter estimates, the number of fish aged per bin was either 5, 10, or 20. Specifically, each fish was evaluated in random order as to whether the true length placed it in a length bin that did not yet contain the targeted number of fish selected for aging. If the bin already had the target numbers of fish (i.e., it was "full"), the candidate fish did not contribute to the aged subsample. If the bin was not full, the fish was included in that length bin sample and the next fish in the sample evaluated. Note that if this procedure is used to subsample, it is common for some of the length bins to contain fewer than the target number of fish because the total sample size and the underlying length distribution of the catch may limit the total number of fish observed in some length bins. This mimics field sampling where it may not be possible to obtain the target number of aged fish in each bin.

We incorporated aging error for each fish included in the aged subsample by constructing a classification matrix generally following the methods of Richards et al. (1992) and Coggins and Quinn (1998). A discretized and truncated (i.e., to allow only integer ages from the minimum to maximum age) normal distribution was used to compute the probabilities of estimated age given the true age. The distribution was parameterized with a mean equal to the true age and a constant coefficient of variation ( $CV_{age}$ ), which we defined as equal to 10% for both life histories. This level of aging error is near the center of values frequently reported in the literature and across a wide variety of species (e.g., Lai and Gunderson 1987; Kimura and Lyons 1991; Richards et al. 1992; Heifetz et al. 1998; Clark 2004). The estimated age for each fish was a random draw from a multinomial distribution with cell probabilities taken as the vector of the classification matrix corresponding to the fish's true age. The resulting subsample was then used to construct the ALK according to typical methods (e.g., Kimura 1977) and containing the proportions of aged fish in each age-class within each length bin. Thus, the ALK proportions  $(\theta)$  were computed as  $\theta_{l,a} = s_{a,l}/S_l$ , where  $s_{a,l}$  was the number of fish subsampled from bin l that were estimated to be of age a and  $S_l$  was the total number of fish subsampled from bin l. These proportions can also be interpreted as the estimated probabilities of belonging to each age-class conditional on length bin. Finally, the ALK was used to estimate the age of each unaged fish in the sample. The estimated age of unaged fish resulted from a random draw from a multinomial distribution where cell probabilities were taken from the ALK vector associated with the length of the fish being aged. This procedure was then iterated for each unaged fish in the sample.

Simulations.—We conducted 1,000 Monte Carlo replications for each combination of life history type (SSF and LLS), median fishing mortality ( $F_{0.25}$  and  $F_{0.50}$ ), total sample size (200, 500, 1,000, and 1,500 fish), and target age samples per length bin (5, 10, and 20 fish per bin). After age estimation of the sampled fish according to the methods above, the sample data were used to estimate (1) total mortality (Z) using catch-curve methods (Ricker 1975) for ages  $a_{mat} + 1$  to the oldest observed age, and (2) the LVB parameters ( $\hat{L}_{\infty}$ ,  $\hat{K}$ ,  $\hat{t}_0$ ) using maximum likelihood methods with a normal additive error structure. The simulation model was built using program R (R Development Core Team 2012).

#### **RESULTS**

The model performed as expected and produced estimates of growth and mortality that varied from the true values for both short-lived and long-lived life history types (Figure 1). These variations in the outcome of individual model runs were due to the combined variation in the simulated population (i.e., F, total length, and recruitment) and the simulated sampling process (i.e., sample selection, aging error, and application of the ALK). The results presented are conditional on the standard deviation of fishing mortality ( $\sigma_F$ ) and recruitment ( $\sigma_{rec}$ ) specified as 0.1 and 0.3, respectively.

Precision of parameter estimates varied between the fish life history types, with the LLS type having generally greater estimation precision than the SSF type for the overfished population (Figure 2). For the median fishing mortality of  $F_{0.25}$  (overfished status),  $L_{\infty}$  estimates were both more accurate and precise than estimates of K for both life history types (Figure 2). Increasing the number of fish aged per bin from 5 to 20 showed only minor improvements in precision and bias for all parameters and both life history types. However, increasing the total number of fish in the sample improved accuracy and precision for estimates of Z for the LLS history type (Figure 2). Thus, the model suggested that if populations were overfished, aging more fish per bin would provide only minor benefits, whereas obtaining larger sample sizes overall could improve bias and precision of Z estimates. Differences in required sample sizes were not substantial between life history types, indicating that sample sizes to maximize accuracy and precision were relatively invariant of fish life history for overfished fish stocks.

Differences in accuracy and precision of parameter estimates were less substantial between life history types for fish stocks that were exploited with  $F_{0.50}$  (Figure 3). Bias and precision of parameters were generally similar between life history types, and increasing the number of fish in the entire sample and the number aged per bin showed only modest increases in

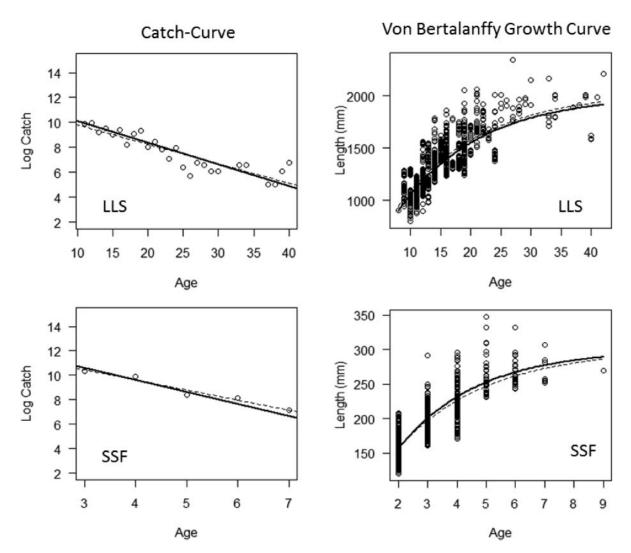


FIGURE 1. Examples of simulated data sets and fitted models for the catch-curve analysis to estimate total mortality (left panels) and the von Bertalanffy analysis (right panels) to estimate length at age. Results for the long-lived, large, and slow-growing (LLS) fish are plotted in the top panels and results for the short-lived, small, and fast-growing (SSF) fish are plotted in the bottom panels. The solid-line curves are the specified or "true" relationships and the dashed-line curves are predictions based on the simulated data sets.

accuracy and precision (Figure 3). Similar to the overfished case, precision in the growth parameters improved slightly with increases in the number of aged fish per bin for both life history types when stocks were only moderately exploited. Overall, precision and accuracy of parameter estimates declined as exploitation increased, and increasing total sample size or number per bin provided only modest improvement in estimation performance across the range of sampling designs evaluated.

We also completed simulations with higher assumed variation in fishing mortality and recruitment. We saw no substantial change in results with higher variation in fishing mortality rate ( $\sigma_F=0.3$ ) and only minimal difference with higher variation in recruitment ( $\sigma_{rec}=1.0$ ). As expected, higher variation in recruitment led to slightly less precise estimates of total mortality

rate, but did not change the relative performance of the ALK under different sample size considerations.

#### **DISCUSSION**

Our results suggest that the choice of how many fish to sample and how many to age per bin was generally invariant of fish life history. DeVries and Frie (1996) outlined procedures to construct and use an ALK, but we found no studies that evaluated the sample sizes required to estimate growth and mortality parameters. Sample sizes of 500–1,000 with 10 fish aged per bin achieved nearly the best possible accuracy and precision in most cases, suggesting that this could be a guideline for most studies. Accuracy of Z estimates did improve at the largest sample sizes for the long-lived life history type, indicating that bias can

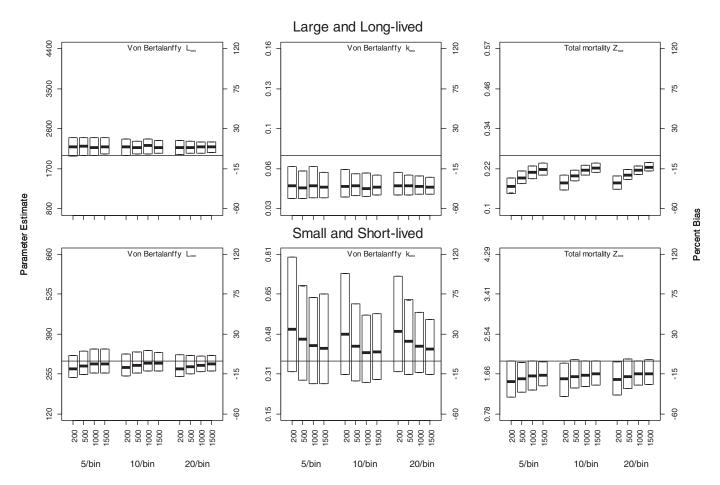


FIGURE 2. Box plots from 1,000 model replications of the von Bertalanffy asymptotic size  $(L_{\infty})$  and growth rate (K) parameters and the instantaneous total mortality (Z). The plots in the top panels are for the long-lived, large, and slow-growing species, and the plots in the bottom panels are for the short-lived, small, and fast-growing species. All estimates are conditional on the population exploitation rate resulting in an average spawning potential ratio of 0.25 (SPR = 0.25) and standard deviation of fishing mortality  $(\sigma_F)$  and recruitment  $(\sigma_{rec})$  specified as 0.1 and 0.3, respectively. The width of the box is the interquartile range and spans the 25th to 75th percentiles of the model runs.

be improved with sample size for long-lived fishes. However, overall results were not strongly influenced by life history type.

Our study added new insight regarding the utility of ALK procedures for parameter estimation. Kimura (1977) and Goodyear (1995) found that proportional-age subsampling of fish ages is superior to fixed-age subsampling for estimating the true age composition of a sample. However, we have found fixed-age subsampling to be far more common in practice because of its simplicity during field collections (e.g., Nate and Bremigan 2005). Monitoring programs could use these results to potentially standardize age-sampling procedures for a range of fish species spanning the life history characteristics we considered.

Estimates of Z were more sensitive to sample size than the LVB parameters, particularly for long-lived fish. The sensitivity occurred because the catch contributions of the oldest ages were positively biased with small sample sizes. This in turn caused a positive bias in the slope of the catch curve and thus an underestimate of the total mortality rate (Z). The proportions of the oldest age-classes were positively biased with small

sample sizes because the minimum nonzero estimated proportion (1/total sample size) exceeded the true proportions of the rarest age-classes. This "flattening" of the catch curve is relatively common in practice and if detected, these data are frequently censored from the analysis (Ricker 1975). This type of data censoring is similar to the practice of censoring the catch-atage estimates for the youngest age-classes due to concerns that those ages are not fully recruited to the capture gear. Analysts should evaluate whether there are multiple old age-classes with only a single sample and, if so, either increase the total sample size or consider removing those age-classes from the analysis.

We found persistent bias in the growth parameters for the LLS where the growth coefficient (K) was underestimated and the average asymptotic size  $(L_{\infty})$  was overestimated. By simulating greater and lesser aging error  $(\text{CV}_{age} = 0.01 \text{ and } 0.5)$  we discovered that this bias was related to the aging-error process expanding the range of observed ages (observed ages younger than the youngest true age and older than the oldest true age) while the range of observed lengths remained unchanged.

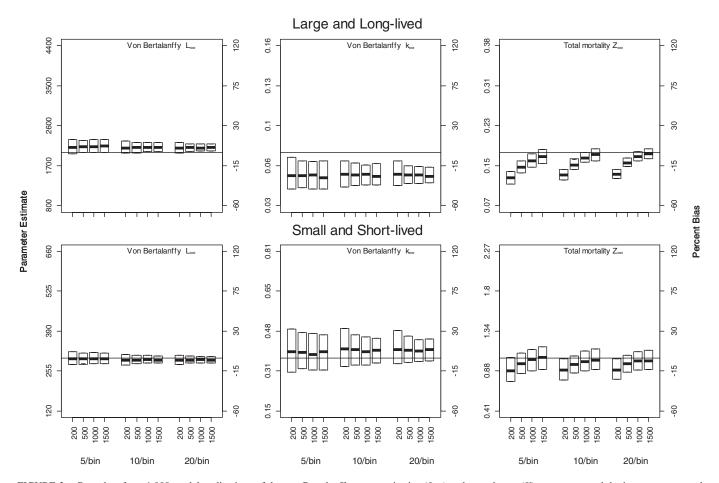


FIGURE 3. Box plots from 1,000 model replications of the von Bertalanffy asymptotic size  $(L_{\infty})$  and growth rate (K) parameters and the instantaneous total mortality (Z). The plots in the top panels are for the long-lived, large, and slow-growing species, and the plots in the bottom panels are for the short-lived, small, and fast-growing species. All estimates are conditional on the population exploitation rate resulting in an average spawning potential ratio of 0.50 (SPR = 0.50) and standard deviation of fishing mortality  $(\sigma_F)$  and recruitment  $(\sigma_{rec})$  specified as 0.1 and 0.3, respectively. The width of the box is the interquartile range and spans the 25th to 75th percentiles of the model runs.

Incorporating aging error resulted in a "flattening" of the growth curve that subsequently caused the growth coefficient to be underestimated and the asymptotic length to be overestimated. While the SSF results exhibited a bias directionally opposite from that observed with the LLS, the magnitude of the bias was much smaller. We found that the discrepancy between the SSF and LLS results is explained by recognizing that with a constant CV<sub>age</sub> and a much shorter longevity, the likelihood of aging error larger than  $\pm 1$  year is much lower for the SSF than for the LLS life history. Additionally, we specified the minimum observed age as 1 year for both life history types thus limiting the scope for underestimating the minimum observed age for the SSF much more than for the LLS. Perhaps most importantly for this study, this bias is due to imprecision in directly estimating the age of fish and is not related to the relative performance of ALK sampling design options.

In contrast to previous work that focused on evaluating how the number of fish aged per bin affects the bias and precision of age composition estimates (Kimura 1977; Lai 1987; Quinn and Deriso 1999), our work suggests that total sample size is generally more important than the sample size of aged fish. This result should not be interpreted to mean that the sample size of aged fish is not influential in parameter estimation. Indeed, close inspection of our results does indicate modest improvements with increasing numbers of fish aged per bin, particularly in the precision of the growth parameter estimates. However, a much greater source of bias occurs with small total sample sizes, which cause positive bias in the proportion of oldest ages and lead to a negative bias in estimates of *Z*. Thus, the influence of various ALK design options is strongly related to how the age composition data are to be used.

DeVries and Frie (1996) and Bettoli and Miranda (2001) demonstrated that using only the aged fish from fixed-age subsampling would cause bias in mean length-at-age estimates. The bias results from the fixed-age subsample because the number of fish in each length bin is not weighted by the true abundance of fish in the whole sample. Our model randomly assigned ages to all unaged fish based on the ALK, and thus our results are

not influenced by the bias highlighted in Bettoli and Miranda (2001).

This study documents results from a simulation model, and thus interpretation should include caveats regarding the model structure and input parameters. We used two generalized life history types that probably underrepresent the vast range of characteristics of specific fish species. The life history types varied widely in maximum age, growth parameters, and mortality, suggesting that values within the range we used would show similar results. Fish species that vary substantially from our short- or long-lived life history types should be assessed individually. We evaluated multiple levels of recruitment and fishing mortality variation through time based on empirical observations and found ALK performance invariant to these assumed levels. However, our results may not accurately represent results from populations with extreme variation in these or other parameters. For example, periodic high natural mortality events (e.g., fish kills) that substantially alter age composition were not considered in our models.

We considered the effect of subsampling on parameter estimation, but biases can occur in parameter estimates even if all fish are aged. Age structure, growth, and mortality estimates can be biased owing to selectivity of the sampling gear (Vaughan and Burton 1994; Goodyear 1995; Taylor et al. 2005; Gwinn et al. 2010). Sampling gears that underrepresent small fish (e.g., Vaughan and Burton 1994) or have dome-shaped selectivity curves (Gwinn et al. 2010) can cause bias in growth parameters. Meeting the required sample size in an age-length key does not preclude bias that occurs via sampling from size-selective fishing methods. Our model considered only increasing (logistic) vulnerability of the gear with fish becoming vulnerable to the gear after maturation. Results would vary if selectivity were dome-shaped or decreased with fish size. Therefore, the effect of both the sample size for an age-length key and the selectivity of the sampling gear should be considered as factors that can influence the bias and precision of growth and mortality estimates.

This study was the first to evaluate how sample size in an age-length key could interact with fish life history to influence parameter estimation. The results indicated that bias and precision were relatively uninfluenced by fish life history type, and, thus, required sample sizes could potentially be consistent in field collections for a wide range of fish species. Future work should address the caveats highlighted above (e.g., highly variable natural mortality and selectivity pattern of the fishing gear), but the results of this study should prove useful to investigators questioning the required sample size for age-length key construction and parameter estimation.

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