

Abstract.—The inverse method for mortality and growth estimation (IMMAGE) is a new approach to obtain unbiased estimates of mortality and growth parameters for larval fishes from length-frequency data biased by the size selectivity of plankton nets. The performance of IMMAGE is compared with methods which attempt to eliminate selection bias from sampled length-frequencies. Using Monte Carlo simulations, IMMAGE estimates growth and mortality parameters that are more accurate and precise than those produced by other methods.

Inverse method for mortality and growth estimation: A new method for larval fishes

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Estimation of the growth and mortality rates of larval fishes is complicated by the sampling biases that can result from the size selectivity of plankton nets. Size selectivity due to net avoidance by larvae, for example, results in an underestimation of larval abundance that progressively increases with increasing larval length. This bias leads to an underestimation of mean length-at-age and therefore growth rate, because larger larvae in each age-class are underrepresented relative to smaller larvae. Such bias also leads to an overestimation of mortality rate, because older larvae are underrepresented relative to younger larvae. Size selectivity due to extrusion of larvae results in an underestimation of larval abundance that progressively decreases with increasing larval length and likewise leads to bias in estimates of growth and mortality rates.

Growth studies rarely address such size selection, and when they do, the approach taken is usually to devise a sampling procedure that provides unbiased length-frequencies (Methot and Kramer 1979, Yoklavich and Bailey 1990). Mortality studies, by comparison, almost always address

size selection and do so after the fact by taking one of several approaches to eliminate the selection bias from the sampled length-frequencies. One approach taken by mortality studies is to divide the sampled length-frequencies by length-specific estimates of capture probability. Such capture probabilities have been obtained from field studies and estimated as (1) catch ratios of large to small mesh nets (Lenarz 1972, Leak and Houde 1987), (2) catch ratios of day to night sampling (Houde 1977, Zweifel and Smith 1981, Morse 1989, Somerton and Kobayashi 1989), or (3) catch ratios of plankton nets to purse seines (Murphy and Clutter 1972, Leak and Houde 1987). Capture probabilities have also been based on theoretical escapement models (Ware and Lambert 1985). A second approach taken by mortality studies is to simply eliminate the biased portions of the length distribution. Such elimination may exclude only small (Morse 1989) or large larvae (Houde 1977, Methot and Kramer 1979) or both (Essig and Cole 1986). Elimination of biased length-frequencies also has been combined with the use of capture probabilities (Houde 1977, Morse 1989).

Although the various approaches may differ in the specifics of their application, all are based on the premise that length-frequency data must first be corrected for selection bias before they can be utilized to estimate growth and mortality. Here we introduce a new approach which reorders and joins the processes of data correction and parameter estimation. This approach, which is based on a stock assessment technique known as synthesis modeling (Methot 1989, 1990), will herein be referred to as the inverse method for mortality and growth estimation (IMMAGE). The use of IMMAGE is examined to estimate growth and mortality rates from biased length-frequency data. Additionally, the performance of IMMAGE, using Monte Carlo simulation, is compared with approaches used to correct selection bias in length-frequency data prior to parameter estimation.

Materials and methods

IMMAGE vs. bias correction

To understand how IMMAGE works and why it is an inverse method for obtaining estimates of growth and mortality parameters, the bias-correction approach should first be examined (Fig. 1a-d). One variant of the bias-correction approach might include (1) estimating the unbiased length-frequency distribution (Fig. 1b) by dividing the observed length-frequency distribution (Fig. 1a) by length-specific estimates of capture probability; (2) converting the unbiased length-frequency distribution to an age-frequency distribution (Fig. 1c) using age and length information; and (3) estimating the instantaneous mortality rate (M) as the slope of a straight line fit to the logarithms of numbers at age (Fig. 1d).

The IMMAGE approach, if applied to the same data, would include (1) choosing initial values for M and the number of day-0 larvae (N_0); (2) estimating an unbiased age-frequency distribution (Fig. 1e) based on the values of M and N_0 ; (3) estimating the unbiased length-frequency distribution (Fig. 1f) from the age-frequency distribution using age and length information; (4) estimating the observed (i.e., biased) length-frequency distribution (Fig. 1g) by multiplying the unbiased length-frequency distribution by estimates of capture probability; and (5) iteratively varying M and N_0 , and repeating steps 2-4, until the best fit is achieved between the estimated and observed length-frequency distributions.

Thus both approaches estimate M by fitting a mortality model. However, in the bias correction approach, the model is fit to numbers-at-age derived from the observed length-frequencies; while in the IMMAGE approach, the model is fit to the observed length-

frequencies themselves. Growth parameters are estimated by IMMAGE in a similar manner, except a growth model rather than a mortality model is fit to the length-frequencies.

To estimate the observed length distribution, IMMAGE requires specification of a process model and ancillary data. The process model contains parameters that are iteratively varied to achieve the best fit to the observed length-frequency distribution; the ancillary data are parameters assumed to be known. For growth estimation, the process model consists of a growth function describing the mean length-at-age and a variance function describing the variance in length-at-age. Ancillary data include estimates of the capture probability at each length. For mortality estimation, the process model consists of a mortality function describing the instantaneous mortality rate at age or length. Ancillary data include the mean and variance in length-at-age, and the capture probability at each length. Growth and mortality process models are not restricted to any particular form and may include linear or nonlinear functions.

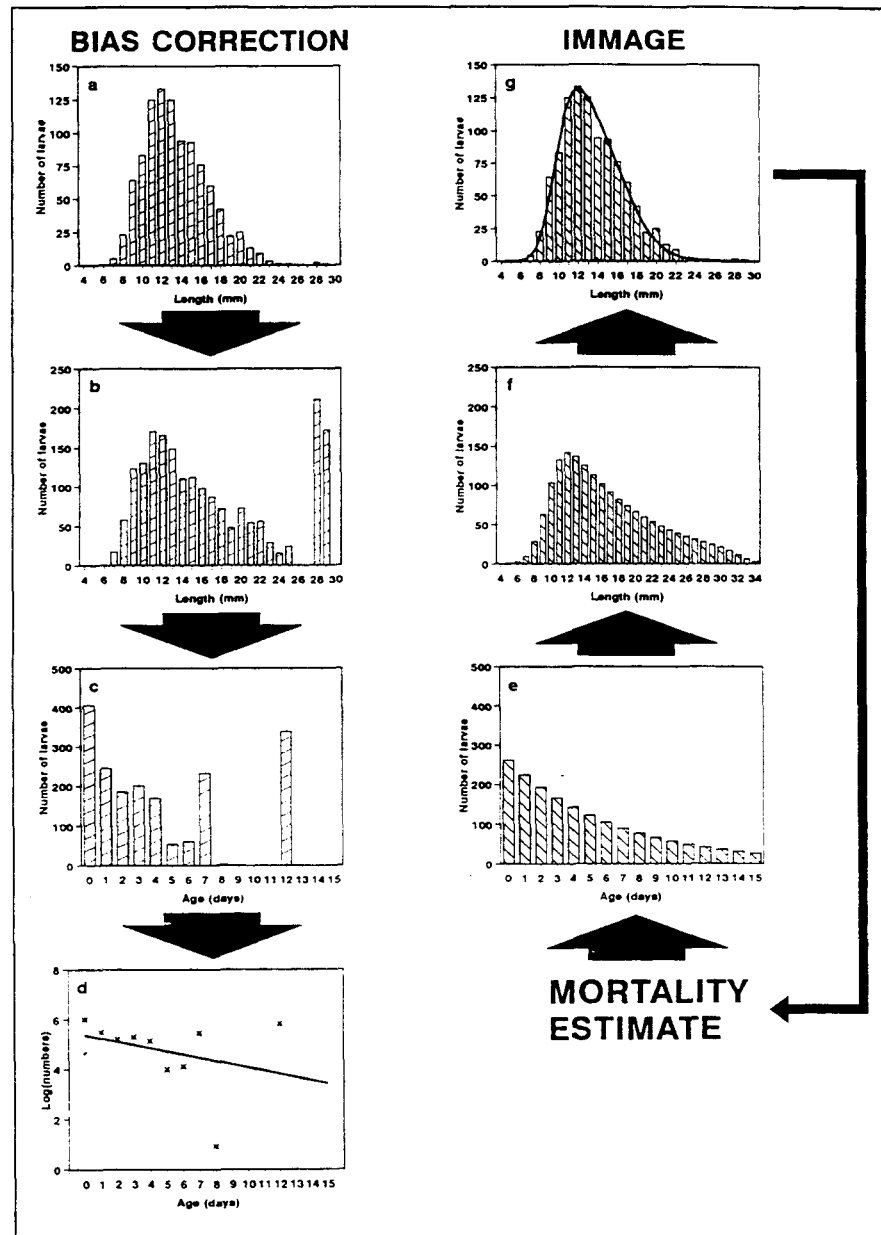
The performance of IMMAGE and several of the bias correction approaches to parameter estimation was examined by using a Monte Carlo simulation model. For growth parameter estimation, bias correction approaches were not examined because no application to larval fishes could be found in the literature. For mortality parameter estimation, three bias correction approaches were examined: (1) elimination of the biased portions of the observed length-frequency distribution, (2) division of the observed length-frequency distribution by estimates of capture probability (correction), and (3) elimination of the biased ages from a corrected age distribution.

Monte Carlo model

The Monte Carlo simulation model is designed to mimic the sequence of steps typically used in growth and mortality studies. A central feature of this model is the simulated collection of three types of data: length-frequency samples, selection samples, and ageing samples.

Length-frequency samples are either unbiased, representing random samples drawn from a larval fish population, or biased, representing samples collected with a plankton net. Selection samples are two independent length-frequency samples, one biased and the other unbiased, used to estimate length-specific capture probabilities. Such samples represent those that might be produced by an experiment to estimate the length-selection characteristics of a plankton net (i.e., day to night catch comparisons). Ageing samples are length-frequency samples in which each length mea-

Figure 1
Comparison of the bias-correction and IMMAGE approaches to estimating instantaneous mortality rate (M) from selection-biased length-frequency data. Bias correction (left column) begins by dividing (a) the observed length-frequency distribution by estimates of capture probability to estimate (b) the unbiased length distribution. The unbiased length distribution is then converted to (c) an age distribution, and M is estimated with (d) linear regression. IMMAGE (right column) begins by creating (e) an unbiased age distribution using initial estimates of M and the number of day-0 larvae, N_0 . The unbiased age distribution is converted to (f) an unbiased length distribution using the ageing sample. (g) The unbiased length distribution is multiplied by the capture probabilities to estimate the sampled length distribution (solid line), then mortality estimates are varied iteratively to minimize the residual sum of squares between the observed (histogram) and the estimated length distributions.



surement is associated with an age. Ageing samples are considered biased when used in growth parameter estimation but are considered unbiased when used in mortality parameter estimation. This distinction is made because mortality parameters can be influenced by

selection bias in ageing samples as well as by selection bias in the length-frequency samples. To simplify interpretation of the results and avoid compounding the effects of the two sources of bias, bias in the ageing samples has been ignored in the mortality estimation.

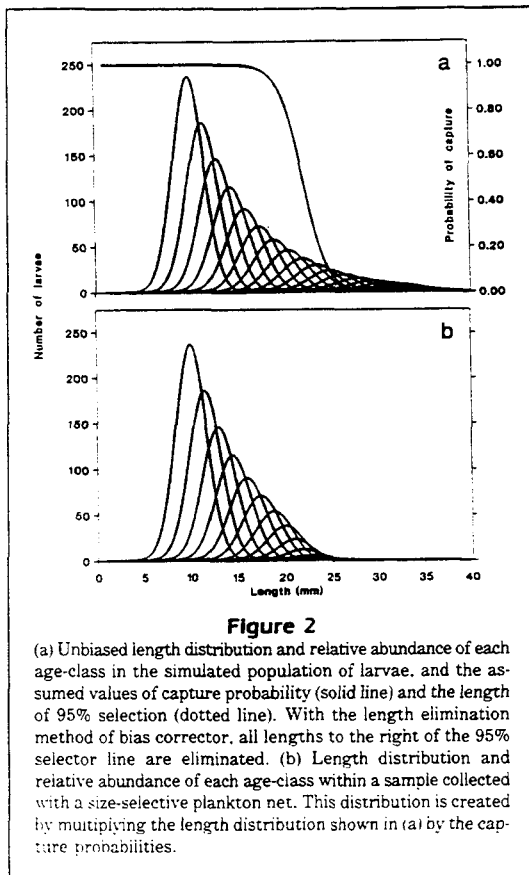


Figure 2

(a) Unbiased length distribution and relative abundance of each age-class in the simulated population of larvae, and the assumed values of capture probability (solid line) and the length of 95% selection (dotted line). With the length elimination method of bias corrector, all lengths to the right of the 95% selector line are eliminated. (b) Length distribution and relative abundance of each age-class within a sample collected with a size-selective plankton net. This distribution is created by multiplying the length distribution shown in (a) by the capture probabilities.

Unbiased length-frequency samples for these three types of data were generated by simulating the random sampling of a larval fish population (Fig. 2a) with a constant daily recruitment, a constant instantaneous daily mortality rate (M) of 0.20, and a length distribution at each age conforming to a normal probability distribution. Mean (l_t) and variance ($\text{Var}(l_t)$) of length-at-age were chosen, for simplicity, to be linear functions of age:

$$l_t = 10.00 + 1.50t, \text{ and} \quad (1)$$

$$\text{Var}(l_t) = 2.50 + 0.25t. \quad (2)$$

where t is age (in days) and l_t is length (in millimeters). Samples were drawn from the cumulative length probability distribution of this population that was constructed by dividing each of the population length-frequencies by the total sample size, then

cumulatively summing across all lengths. Individual lengths within a sample were chosen by determining which category in the cumulative length probability distribution just exceeded the value of a generated uniform random number.

Biased length-frequency samples were generated by simulating the sampling of the model population by using a plankton net, which allowed zero extrusion and produced capture probabilities ($P_{c,l}$) described by an inverse logistic function:

$$P_{c,l} = 1 - \frac{1}{1 + 9.00 \times 10^7 e^{-2.61l}}, \quad (3)$$

where l is length (in mm) [Fig. 2a; parameters in Eq. (1-3) were chosen arbitrarily and were not intended to represent any particular species or sampling gear]. Samples were drawn by using the same procedure as used for unbiased samples except the population length distribution was multiplied by the capture probabilities (Fig. 2b).

Ageing samples were generated similar to length-frequency samples, but after each length was drawn, an associated age was also drawn by using the cumulative age probability distribution at each length and an additional uniform random number. The sample sizes used in the simulations [1000 length-frequency samples, 300 ageing samples, 600 selection samples, with the biased sample size set equal to the unbiased sample size \times the average probability of capture determined from Equation (3)] were arbitrarily chosen but were similar to those used in Somerton and Kobayashi (1989, unpubl. data).

Growth simulations

Growth simulations examining the performance of IMMAGE consisted of 1000 repetitions of the following sequence. First, a biased ageing sample and a selection sample were generated. Second, capture probabilities were estimated from the selection sample by fitting an inverse logistic function of length, using nonlinear regression, to the ratios of the biased to the unbiased length-frequencies. Third, initial parameter estimates for the growth process model [Eq. (1) and (2)] were obtained from the ageing sample by fitting straight lines to length-at-age and variance of length-at-age. Fourth, the unbiased length distribution of each age-class was estimated as a normal distribution with mean and variance predicted from Eq. (1) and (2) evaluated at the current parameter estimates. Fifth, the biased length-frequency distribution of each age-class was estimated by multiplying the unbiased length-frequency distribution by the estimated capture probabilities. Sixth, parameter estimates for Eq. (1) and (2)

were iteratively varied, and steps 4 and 5 were repeated, until the minimum residual sum of squares (RSS) was achieved. The RSS was defined as

$$\sum_j \sum_i (F_{ij} - \hat{F}_{ij})^2, \quad (4)$$

where F_{ij} and \hat{F}_{ij} are the observed and estimated frequency within the i th length interval and the j th age-class.

Mortality simulations

Mortality simulations examined the performance of IMMAGE and three bias-correction approaches: length elimination, division by capture probabilities, and age elimination. Each of the 1000 repetitions of a simulation began by generating a biased length-frequency sample, an unbiased ageing sample, and a selection sample. For all simulations, except those examining IMMAGE, mortality estimation began with an attempt to derive an unbiased age distribution. If length elimination was used, this was accomplished in two stages. First, an unbiased length-frequency distribution was estimated by eliminating all length categories with a capture probability of <0.95 [based on capture probabilities defined by Equation (3), length-classes 3-18 were retained; Fig. 2a]; a probability of 0.95 was used instead of 1.00 because it is better defined. Second, the age-frequency distribution was estimated from the unbiased length-frequency distribution by using the ageing sample and a procedure known as age-slicing (Mesnil and Shepherd 1990). To do this, lengths from the ageing sample were regressed on the ages, and the fitted linear regression equation was evaluated to determine the length corresponding to each age boundary (i.e., 0.5, 1.5, 2.5 days, and so on). Age-frequencies were then estimated by summing length-frequencies between age boundaries.

If division by capture probabilities was used, the age-frequency distribution was estimated by first dividing the observed length-frequency distribution by estimates of capture probability, then converting the length-frequencies to age-frequencies using age-slicing. If age elimination was used, age-classes with a capture probability of <0.95 at the mean length also were eliminated from the age-frequency distribution (age-classes 0-5 days were retained; Fig. 2a). For all three cases, instantaneous mortality rate was then estimated as the slope of an unweighted linear regression to the natural logarithm of numbers-at-age (Ricker 1975).

For simulations examining IMMAGE, mortality estimation proceeded as follows. First, initial values of M and N_0 were obtained from the ageing sample by fitting a straight line to the logarithm of numbers-at-

age. Second, values of l_t and $\text{Var}(l_t)$ were estimated from the ageing sample by fitting straight lines to length-at-age and $\text{Var}(l_t)$ -at-age, using linear regression, and then evaluating the fitted regression equations at each t . Third, capture probabilities were estimated from the selection sample. Fourth, the unbiased age distribution was estimated as $N_t = N_0 e^{-Mt}$. Fifth, the unbiased length distribution of each age-class was estimated as N_t times a normal probability distribution with a mean equal to l_t and a standard deviation equal to the square root of $\text{Var}(l_t)$. The unbiased length distribution for the population was then estimated by summing the age-specific length distributions over all age-classes. Sixth, the biased (observed) length distribution was estimated by multiplying the unbiased population length distribution by the estimated capture probabilities. Seventh, N_0 and M were iteratively varied, and steps 4-6 repeated, until the minimum RSS was achieved. The RSS was defined as

$$\sum_j (F_j - \hat{F}_j)^2, \quad (5)$$

where F_j and \hat{F}_j are the observed and estimated frequencies within the j th length interval.

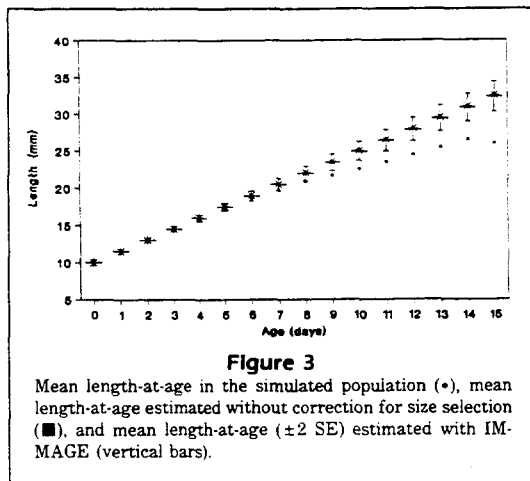
The IMMAGE application used in the simulations (i.e., one that assumes linear growth and constant mortality) is available from the authors as a stand-alone program (IMMAGE, written in Microsoft QuickBasic) designed to run on IBM-compatible microcomputers.

Results and discussion

Growth

The type of size selection examined in the simulations (i.e., a decrease in the probability of capture with increasing larval length) complicates the estimation of growth and mortality in slightly different ways. For growth estimation, the primary effect is that the largest larvae in each age-class are undersampled relative to the smallest larvae, and the mean lengths-at-age are therefore underestimated (Fig. 2b). Since the bias progressively increases with age, plots of mean length against age are curvilinear and falsely indicate a declining growth rate (Fig. 3). Such curvilinear or even asymptotic growth patterns are often reported in studies of wild-caught larvae (Bailey 1982, Laroche et al. 1982, Lough et al. 1982, Thorrold 1988, Warlen 1988). Although there may be biological reasons to expect such a pattern, especially for species with pronounced ontogenetic changes in body form, length-selective sampling may be a contributing factor.

IMMAGE estimates of the slope (1.499 ± 0.005 ; \bar{x} 1000 replicates ± 2 SE) and intercept (10.002 ± 0.012)



of the linear growth function [cf. Eq. (1)] were both unbiased, as were all of the estimates of mean length-at-age over the entire age range (Fig. 3). This indicates that, at least for linear growth, IM-IMAGE provides unbiased estimates of growth parameters from biased length and age samples.

Mortality

For mortality estimation, the primary effect of the decrease in capture probability with increasing larval length is that relative abundance is progressively underestimated with increasing age (Fig. 2b). If ignored, such a progressive underestimation would result in positively biased mortality estimates. In the simulated population, for example, mortality estimates obtained from the observed length-frequency samples ($M = 0.450 \pm 0.004$) had a highly significant positive bias of 125% (Fig. 4a).

Elimination of the biased length-frequencies was only partially effective in reducing the bias in estimated mortality rates, because the mortality estimates ($M = 0.364 \pm 0.007$) still had a highly significant positive bias

of 80% (Fig. 4b). In practice, length elimination is likely to be even less effective than it appears here, because it is usually applied to cases where the capture probabilities are crudely known, whereas exact knowledge is assumed in the simulations.

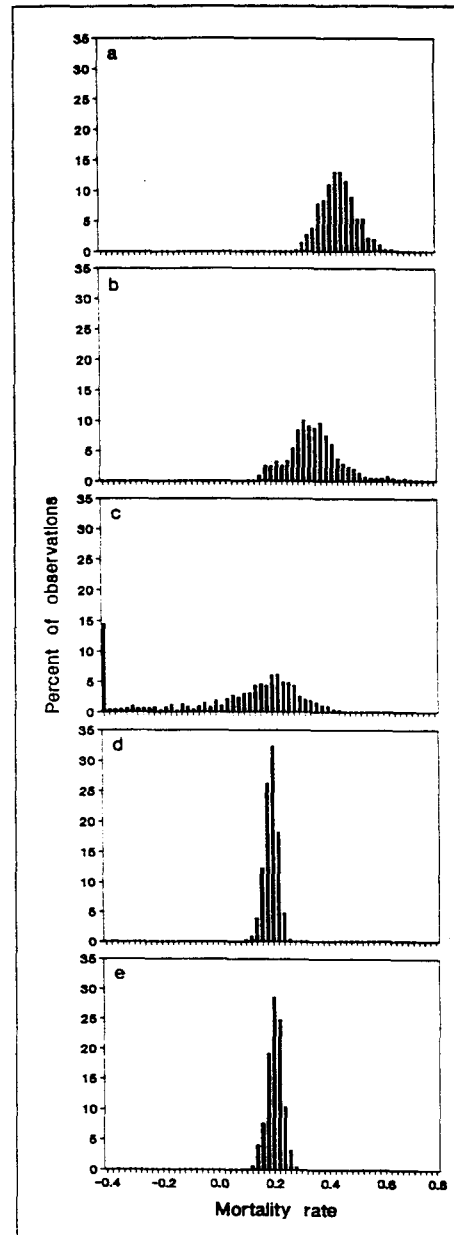


Figure 4 (right)

Frequency distribution of 1000 simulated estimates of instantaneous mortality rate computed from (a) observed length-frequency data, (b) observed length-frequency data after eliminating all length-frequencies with a capture probability of < 0.95 , (c) observed length-frequency data divided by estimates of capture probability, (d) corrected age-frequency data after eliminating all age-frequencies with a capture probability of < 0.95 , and (e) observed length-frequency data using IM-IMAGE.

Dividing the observed length-frequency distribution by estimates of capture probability was as ineffective because the mortality estimates (-0.035 ± 0.030) had a highly significant negative bias of 83% (Fig. 4c). The negative bias and the strong negative skew in the frequency distribution are due to the infrequent generation of large larvae. When such larvae occur in a sample, their relative abundance is greatly magnified by their extremely small capture probabilities. The overestimation of large length-classes results in a corresponding overestimation of old age-classes. Because the overestimated age-frequencies are at the extreme of the age range, they exert considerable influence on the slope of the mortality regression and thereby result in the underestimation of M .

Elimination of the biased age-frequencies nearly eliminates this problem and results in mortality estimates (0.192 ± 0.002) with a significant but small negative bias of 4% and a considerable reduction in variance (Fig. 4d). The apparently greater effectiveness of age elimination compared with length elimination is a function of the variance in length-at-age within the larval fish population. For example, when length elimination is applied to the simulated population, essentially all of the undersampled lengths are removed. However, this creates a new bias in the age distribution, because some age-classes experience greater elimination than others (Fig. 2a). Clearly, if no variation exists in length-at-age, length elimination will be identical to age elimination. To our knowledge, the use of age elimination has not been reported in the literature.

Mortality estimates produced by IMMAGE (0.201 ± 0.002) are unbiased and, along with age elimination, have the smallest variance (Fig. 4e). This superior performance is achieved because, unlike length or age elimination, IMMAGE uses all of the sampled length-frequency data and, unlike correction, uses capture probability multiplicatively and therefore avoids magnifying the sampling error.

Practical application of IMMAGE

The application of IMMAGE using the Monte Carlo simulation has been chosen because of its simplicity. Although linear growth, constant mortality, and monotonically increasing size selection may not always be suitable for a particular application, the IMMAGE procedure is extremely adaptable in the way growth, mortality, and size selection can be specified. For example, growth could be specified as an exponential or a Laird-Gompertz function, and size selection could be specified as a double logistic function (Somerton and Kobayashi 1989) describing extrusion and avoidance simultaneously. Mortality could be specified as either a stage-specific function, where the mortality rates of

yolk sac and feeding larvae differ, or an inverse function of age (Lo 1986). More importantly perhaps, mortality could also be specified as a function of length.

Although mortality rates of larvae likely decline with length for many species (Pepin 1991), length-dependent mortality rates are difficult to estimate because such mortality induces a progressive bias in mean length-at-age (if the largest larvae in an age-class survive better than the smallest, the apparent growth rate is positively biased; Methot and Kramer 1979). This problem can be circumvented with IMMAGE by estimating the size-selected length-frequency distribution using a length-based population model (Somerton and Kobayashi 1990) which mimics the growth and survival of individual members of an age-class over time. Using such an approach, the likelihood of size-dependent mortality could be tested against constant or age-dependent mortality based on goodness-of-fit to the observed length-frequencies.

Several variations on the application of IMMAGE described herein may be more appropriate in other cases. First, the estimation of growth and mortality parameters could be accomplished simultaneously rather than separately by allowing the mortality process model to include growth parameters as variables rather than as known quantities. Second, the objective function used for parameter estimation could be specified as a likelihood function rather than a sum-of-squares function. This would be especially appropriate in cases where the errors about the observed length-frequencies are not normally distributed. Third, prior estimates of some parameters could be included in the growth and mortality process models rather than estimating all parameters directly from the three samples (i.e., ageing, length-frequency, and selection samples).

We believe the best way of estimating parameter variances for an IMMAGE application is to use a sample reuse technique known as bootstrapping (Efron and Tibshirani 1991), because all sources of sampling variability can be included. Bootstrapping IMMAGE, however, is computationally intensive and potentially time-consuming. To facilitate variance estimation on slow computers, we have therefore included in the IMMAGE program an approximate technique that is based on the inverse of the information matrix (Ratkowsky 1983).

When obtaining larval fish samples free of selection bias is difficult, IMMAGE can still obtain unbiased estimates of growth and mortality parameters. Not only does IMMAGE provide estimates that are more accurate and precise than other approaches, its greater flexibility in form allows estimation of length-dependent mortality rates that are perhaps biologically more realistic than the constant rates now estimated.

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