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Estimation of Von Bertalanffy Growth Parameters in the Presence of Size-Selective Mortality: A Simulated Example with Red Grouper

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Abstract.—Fish lengths back-calculated to all scale or otolith annuli are often used for estimating parameters of the von Bertalanffy growth equation in an attempt to increase sample size and presumably improve the fitted model. Lengths at early ages back-calculated from younger age-groups sometimes are greater than lengths at the same age estimated from older age-groups, referred to as Lee's phenomenon. Lee's phenomenon can be simulated with use of size-selective mortality and moving averages to incorporate error dependency in lengths at age. To evaluate the appropriateness of using back-calculated lengths at formation of all annuli in growth analyses when size-selective mortality is present, we used simulated data based on von Bertalanffy growth parameters and total mortality for red grouper *Epinephelus morio* from the southeastern U.S. Atlantic coast. Asymptotic length (L_∞) and the growth coefficient (K) showed greater bias when estimated with back-calculated lengths at all annuli than when estimated only with back-calculated lengths at the most recent annuli whenever Lee's phenomenon (or its reverse) was present. One should use only lengths back-calculated to the most recent annuli when estimating growth parameters representative of a population.

Two sets of estimated parameters of the von Bertalanffy growth equation (1938) are presented by Stiles and Burton (in press) for the red grouper *Epinephelus morio* (Serranidae). Growth parameters were estimated with lengths back-calculated to all otolith annuli and simply with lengths back-calculated to the most recent annulus for each fish sampled. The first approach incorporates multiple estimates (repeated measures) per fish; the second relies on a single estimate per fish. The use of lengths back-calculated to all annuli in estimating growth parameters is fairly common (Manooch and Huntsman 1977; Manooch and Haimovici 1978; Ross and Huntsman 1982; Johnson 1983; Hayse 1990).

The statistical assumption of independence of errors in regression analysis is violated when multiple back-calculated lengths per fish are used to estimate parameters for a growth model. This violation can result in biased estimates of the model parameters and inappropriate determination of degrees of freedom in statistical testing (e.g., df = $n - p - 1$, where n is number of measurements and p is number of parameters to be estimated). Netter et al. (1989:568–571) presented an example in which repeated measurements were made in a nonlinear regression setting; an extra variable and two parameters were added to identify two locations on which repeated measures were made over time. However, fishery workers usually are interested in estimating parameters for an equation describing the typical growth of fish in a population,

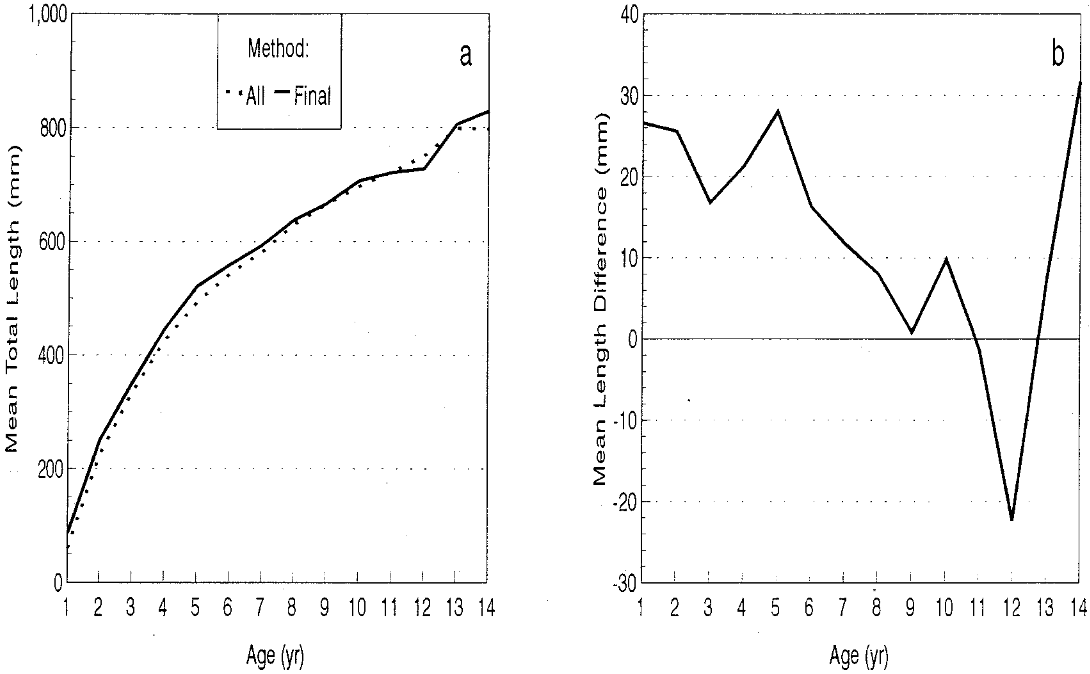

FIGURE 1.—(**a**) Mean total lengths at age for red grouper (Stiles and Burton, in press) from back-calculated lengths at all annuli (all) and back-calculated lengths at the most recent annuli (final). (**b**) Difference in mean calculated lengths at age for red grouper (final − all).

not necessarily the growth of an individual sampled fish. Samples generally contain fish of different ages, so the number of measurements (annuli) can vary among fish. Because of this more complicated situation, we investigated, with Monte Carlo simulations, the appropriateness of using back-calculated lengths at all annuli to estimate growth parameters.

Statistical dependency of estimated lengths at age for individual fish is expected when there is size-selective mortality. If faster-growing fish are selectively removed, then mostly slower-growing fish will survive to the older ages and be available for sampling. Obtaining smaller estimated sizes for younger age-groups when back-calculated lengths at age are estimated from older fish than when they are estimated from younger fish is commonly known as "Lee's phenomenon" (Ricker 1969). The further complication of compensatory growth in response to changing population abundance is not addressed in this paper. The reverse situation of obtaining larger estimated sizes for younger age-groups from older fish is known as reverse Lee's phenomenon. The presence of Lee's phenomenon can be determined by comparing the mean length at age based on back-calculated lengths at all annuli to that based solely on the most recent annulus (Figure 1). For red grouper, the difference in age-specific mean lengths between lengths back-calculated to the most recent annulus and lengths back-calculated to all annuli suggests that Lee's phenomenon is present, at least for the younger ages (ages 1–6).

In this paper, we evaluate whether back-calculated lengths from all annuli or just back-calculated lengths from the most recent annuli (one length estimate for each fish) should be used in estimating growth parameters. We simulated the growth of red grouper such that Lee's phenomenon was explicitly expressed and its effects could be evaluated. This was accomplished by (1) selectively removing fish with faster (or slower) growth in a given year, and (2) incorporating dependencies between length at age and length at prior ages. Varying levels of size-selective mortality were applied to the simulations. Growth parameters for the von Bertalanffy equation were estimated from the simulated growth. Parameter biases—differences between median calculated values and underlying true values of the growth parameters—were compared between estimation procedures. Although other simulation studies of the von Bertalanffy growth equation have been conducted for various reasons (Vaughan and Kanciruk 1982; Parma and Deriso 1990; Mulligan and Leaman 1992), none have addressed the particular question of whether to use back-calculated lengths at all annuli or at only the most recent annuli.

Methods

The basic growth equation under consideration is that of von Bertalanffy (1938), which relates length (L) to age (t):

$$L(t) = L_{\infty}\{1 - \exp[-K(t - t_0)]\} + \epsilon, \quad (1)$$

where L_{∞}, K, and t_0 are parameters to be estimated, and ϵ is independent, normally distributed error with mean 0 and variance σ^2. Stiles and Burton (in press) give the following estimates for red grouper along the southeast U.S. Atlantic coast based on back-calculated total length (TL) at formation of the most recent otolith annulus: L_{∞} = 938 mm TL, K = 0.153/year, and t_0 = −0.099 year. The root mean-squared error (σ) was 60 mm TL.

To incorporate Lee's phenomenon into the simulation of growth for red grouper, size-selective mortality and dependency of length at later age on length at earlier age must be combined. Size-selective mortality implies that either larger or smaller fish at age are differentially killed. This was accomplished in our simulations by using a logistic model that equated mortality (A) with the error term or residual error (R):

$$A = 1/\{1 + \exp[-(a + bR)]\}; \quad (2)$$

$$a = -\log_e[(1/A_0) - 1],$$

and

$$A_0 = 1 - \exp(-Z_0).$$

The logistic model was selected because it varies between 0 and 1 as R varies between $-\infty$ and $+\infty$. Mortality approaches 1 as residual error becomes more positive and approaches 0 as residual error becomes more negative ($b > 0$) or vice versa ($b < 0$). When $R = 0$, then $A = A_0$. When $b = 0$, total mortality (A) is constant for all values of R.

The parameter b controls whether Lee's phenomenon or its reverse form is present in the simulated data. Because annual mortality (A) approaches 1 as R approaches $+\infty$ when b > 0, faster-growing fish ($R > 0$) have higher mortality ($A > A_0$). Hence, fish with smaller size at the younger ages predominate among the older fish (Lee's phenomenon). Conversely, because A approaches 0 as R approaches $-\infty$ when $b < 0$, slower-growing fish ($R < 0$) have higher mortality ($A > A_0$). Hence, fish with larger size at the younger ages predominate among the older fish (reverse Lee's phenomenon). For the simulations described herein, b took the values −0.2, −0.1, −0.05, 0.0, 0.05, 0.1, or 0.2 (Figure 2).

In these simulations, lengths at age were linked stochastically to lengths at earlier ages by the simulated residual errors; that is, lengths at age n were normally distributed with mean based on equation (1) evaluated at age n and fixed variance (σ^2). The subsequent simulated residual error was modified as follows:

$$R_n^o = R_n + \delta R_{n-1} + \delta^2 R_{n-2} + \delta^3 R_{n-3} + \ldots; \quad (3)$$

R_n^o is the realized residual error of length at age n, R_n, R_{n-1}, R_{n-2}, and R_{n-3} are the simulated residual errors from the normal distribution at ages n, $n - 1$, $n - 2$, and $n - 3$, and δ is a parameter controlling the degree of dependency on earlier ages. Hence, error about predicted growth was described as a moving-average process of order age minus 1 (Nelson 1973). This resulted in length at age 1 not depending on any earlier age, length at age 2 depending on length at age 1, length at age 3 depending on lengths at ages 1 and 2 (but more on length at age 2), and so forth. For faster-growing young fish to have an increased probability of remaining faster growing throughout their lives (and conversely, for slower-growing young fish to remain slower growing throughout their lives), the parameter δ must be positive ($\delta > 0$). Values of δ greater than 1, although theoretically possible, give greater weight to conditions promoting growth of an individual fish during earlier years than during the current year of growth. For the simulations reported here, δ was set at the intermediate value of 0.5.

The combined action of these two processes caused faster-growing fish (larger positive residual error) to die younger ($b > 0$; Lee's phenomenon) and vice versa ($b < 0$; reverse Lee's phenomenon). Mortality was simulated for one fish at a time. At each age, normally distributed error [R_n: NID(0, σ^2)] was generated (RANNOR, SAS Institute 1987), and combined with δ (0.5) times the overall error from the previous age, R_{n-1}^o (except for age 1), to give realized R_n^o, because it follows from equation (3) that

$$R_n^o = R_n + \delta R_{n-1}^o. \quad (4)$$

Generating a uniform variate over the interval

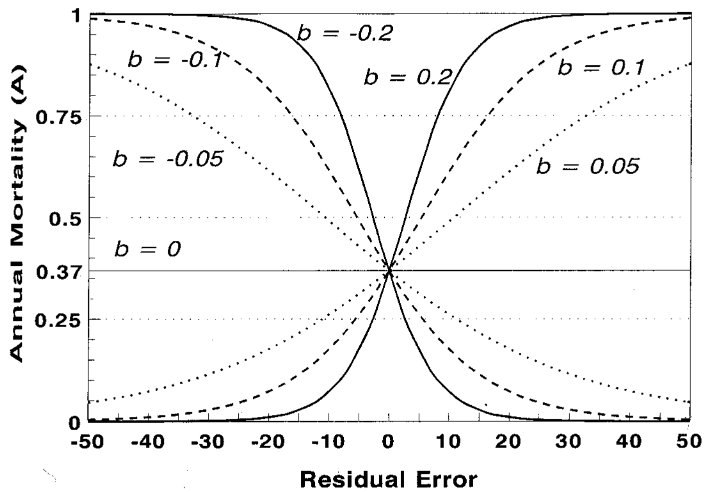

FIGURE 2.—Total annual mortality (A) as a logistic function of the residual error; $A = 1/\{1 + \exp[-(0.369 + bR)]\}$.

(0, 1) (RANUNI, SAS Institute 1987) allowed comparison with calculated A (equation 2), where $R = R_n^o$. If the generated value was less than the calculated value of A, then the fish was killed; otherwise the fish continued growing to the next age.

Parameters for the von Bertalanffy equation in the simulations were approximations of those derived for red grouper by Stiles and Burton (in press): L_∞ = 1,000 mm TL, K = 0.15/year, and t_0 = 0.0 year. Annual mortality (Z_0 = 0.46, A_0 = 0.37) and σ (60 mm) were also from Stiles and Burton (in press). The annual mortality rate (A_0) was used to determine a in equation (2), and the root mean-squared error (σ) was used to generate the normal error (R_n) in equation (4).

Each simulated experiment generally consisted of 100 replicated data sets, each containing lengths at age of 50 fish (representing back-calculated lengths at all annuli). All simulations were explicitly defined by equations (1), (2), and (4) with the parameter values given above. A series of simulated experiments comprised various degrees and directions of Lee's phenomenon (b: −0.2, −0.1, −0.05, 0, 0.05, 0.1, 0.2). The growth coefficient (K: 0.075, 0.15, 0.3) and sample size (number of fish: 10, 50, 100, 200) were also varied. Two nonlinear regressions (PROC NLIN, Marquardt Option, SAS Institute 1987) were applied to each of the 100 simulated data sets of fish lengths. One regression used lengths at all ages (annuli) from the data set (incorporating multiple measurements per fish); the other used only the length at oldest age (most recent annulus) for each fish in the data set. For the purpose of these simulations, the root mean-squared error for red grouper (σ = 60 mm) was assumed to implicitly include the effects of environment, individual genetics, and back-calculation on growth.

Results

Bias in von Bertalanffy parameter estimates was greater when all back-calculated lengths were used than when only the back-calculated length at the most recent annulus for each fish was used. Only in the absence of Lee's phenomenon (b = 0) did the median estimate of L_∞ based on all back-calculated lengths fall nearest the true value (1,000 mm) with bias comparable to that for the most recent back-calculated lengths (Figure 3a). Lee's phenomenon ($b > 0$) tended to cause an overestimate of L_∞; reverse Lee's phenomenon ($b < 0$) tended to cause an underestimate. The magnitude of the bias was greater from Lee's phenomenon than from reverse Lee's phenomenon for the same magnitude of b. Greater increase in bias came from increasing b from 0.0 to 0.05 than from 0.05 to 0.2, probably because of the shape of the logistic mortality function. In general, the true value of L_∞ (1,000 mm) was included within the 90% confidence intervals, except when b was 0.1 or 0.2 and back-calculated lengths at all annuli were used (Table 1).

Estimates of K (true value, 0.15/year) were quite biased when all back-calculated lengths were used (except for b = 0.0), whereas essentially no bias

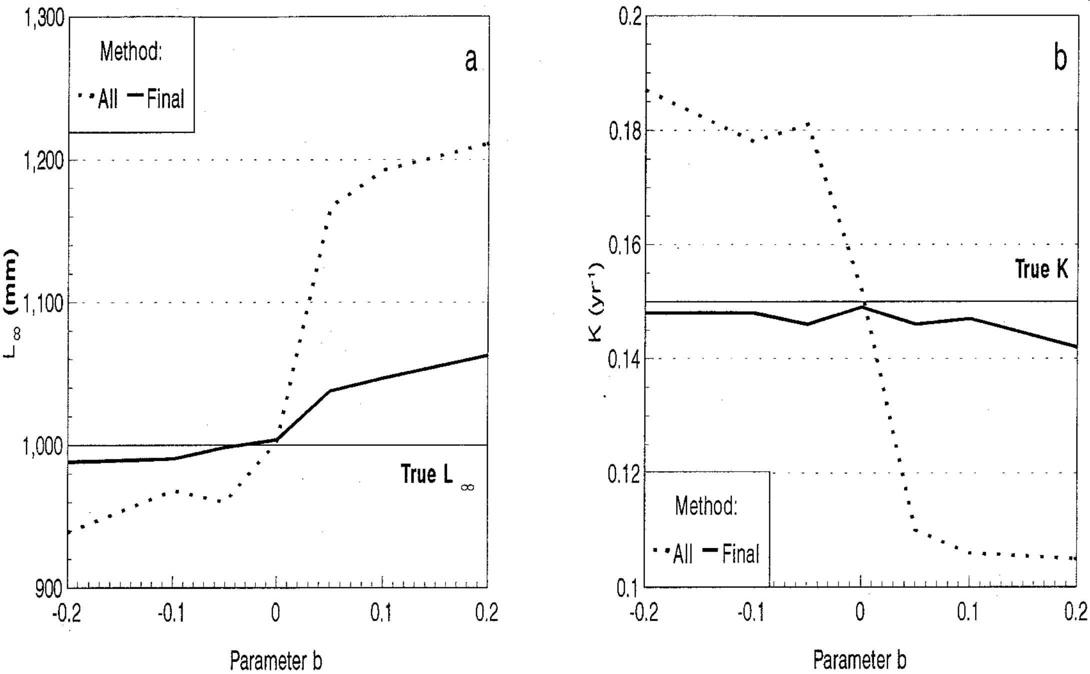

FIGURE 3.—Median values of von Bertalanffy parameter (K) estimated from back-calculated lengths at all annuli (all) and back-calculated lengths at the most recent annuli (final): **(a)** L_∞ and **(b)** K from simulated lengths at age for a range of size-selective mortality (b). For these simulations, the number of fish was 50, true L_∞ was 1,000 mm, and true K was 0.15/year.

was associated with using only lengths at formation of the most recent annuli (Figure 3b). The direction of the bias in K for Lee's phenomenon (and its reverse) was the opposite of that for L_∞ because these parameters are typically inversely correlated. In general, the true value of K was included within the 90% confidence intervals except when b was -0.2, 0.1, or 0.2 and back-calculated lengths at all annuli were used (Table 1).

Increasing the number of fish per replicate within a simulated experiment (Figure 4a) or varying the underlying K (Figure 4b) did not appreciably change the relationship in bias between the two procedures (shown for $b = 0.2$ in Figure 4).

With Lee's phenomenon absent ($b = 0.0$), the differences between mean lengths at age obtained by the two procedures should vary around a mean of zero (Figure 5a). For our simulated data ($b = 0.0$), the differences in mean length seemed to be skewed somewhat towards negative values, but no trend with age was evident. With Lee's phenomenon present ($b = 0.05$, 0.1, and 0.2), there was a decreasing trend with age in the differences in mean lengths (Figure 5b–d). This generally decreasing trend was very similar in pattern to that of the

TABLE 1.—Median parameter estimates (in parentheses: 5th, 95th percentiles) of the von Bertalanffy (1938) parameters L_∞ (1,000 mm) and K (0.15/year) from simulated red grouper lengths back-calculated to all annuli and to the most recent (final) annulus under conditions of range of size-selective mortality (logistic parameter b). Sample size was 50 fish and the underlying variability (σ) was 60 mm.

Parameter b	Estimation procedure: All annuli	Final annulus
	L_∞ (true value: 1,000 mm)	
−0.2	938.9 (718.2, 1,044.2)	988.2 (907.9, 1,072.9)
−0.1	968.2 (806.9, 1,096.9)	990.5 (894.0, 1,105.8)
−0.05	960.1 (749.6, 1,084.2)	998.4 (833.0, 1,232.1)
0.0	1,002.5 (876.8, 1,286.6)	1,003.8 (811.1, 1,454.6)
0.05	1,167.0 (985.3, 1,667.9)	1,037.7 (861.8, 1,272.8)
0.1	1,192.5 (1,021.1, 1,939.7)	1,046.8 (912.1, 1,336.5)
0.2	1,211.3 (1,021.8, 1,766.4)	1,062.6 (937.7, 1,295.8)
	K (true value: 0.15/year)	
−0.2	0.187 (0.157, 0.293)	0.148 (0.125, 0.179)
−0.1	0.178 (0.141, 0.243)	0.148 (0.120, 0.179)
−0.05	0.181 (0.143, 0.255)	0.146 (0.101, 0.209)
0.0	0.152 (0.107, 0.191)	0.149 (0.085, 0.220)
0.05	0.110 (0.070, 0.150)	0.146 (0.105, 0.223)
0.1	0.106 (0.055, 0.137)	0.147 (0.098, 0.191)
0.2	0.105 (0.062, 0.138)	0.142 (0.103, 0.185)

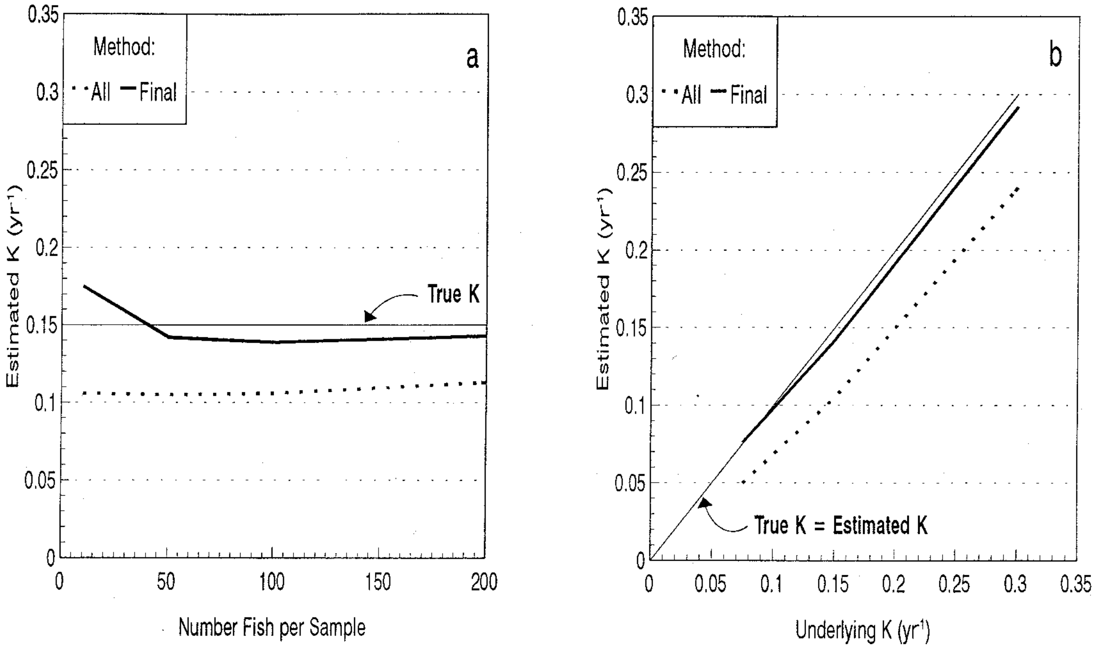

FIGURE 4.—Median values of von Bertalanffy parameter (K) estimated from back-calculated lengths at all annuli (all) and back-calculated lengths at the most recent annuli (final) from simulated lengths at age in relation to **(a)** number of fish per sample and **(b)** underlying value of K (true K). For these simulations, parameter b was 0.2.

actual red grouper data (Figure 1b), particularly for the younger ages for which sample sizes were reasonably large. The increase in mean difference for red grouper lengths between ages 12 and 14 (Figure 1b) was probably a statistical artifact, the result of very low sample sizes at ages 13 and 14 (7 and 2 fish, respectively).

Discussion

These simulations have compared estimates of von Bertalanffy growth parameters derived from using back-calculated lengths at all annuli with lengths at the most recent annuli by capturing the effect of size-selective mortality on growth. How well the effect of Lee's phenomenon is reflected in the simulated sizes at age is, of course, paramount. A comparison of Figures 1b and 5 suggests that the simulations adequately mimicked Lee's phenomenon.

A reason often suggested for using back-calculated lengths at all annuli for each fish is that it improves the precision of the parameter estimates for the fitted growth equation. Our simulations suggest that the use of lengths at all annuli in estimating von Bertalanffy parameters is less accurate. Further, these estimates are generally less precise (Table 1). Only when $b = 0$ (no size-selective mortality) are the confidence intervals for L_∞ and K from using back-calculated lengths at all annuli narrower than confidence intervals from using the lengths at the latest annuli. Hence, confidence intervals obtained from a particular nonlinear regression fit to back-calculated lengths at all annuli are misleading because of the internal dependencies, and they cannot be used to accurately reflect the actual confidence in the estimated parameters. In particular, the degrees of freedom based on back-calculated lengths at all annuli are inappropriate, and the resultant confidence intervals do not accurately reflect the uncertainty in the parameter fits.

The differences in simulated mean lengths at age between back-calculation procedures for fish subjected to greater size-selective mortality ($0.5 < b < 2.0$; Figure 5) were generally greater than the differences in actual red grouper data (Figure 1b). Ricker (1969) noted that Lee's phenomenon can arise from incorrect scale : body relationships and biased sampling in addition to size-selective mortality. Hence, comparing the magnitude of the differences in mean length at age between multiannulus and latest-annulus calculations does not reflect the strength of bias in mortality. For simulated red grouper data, the maximum such dif-

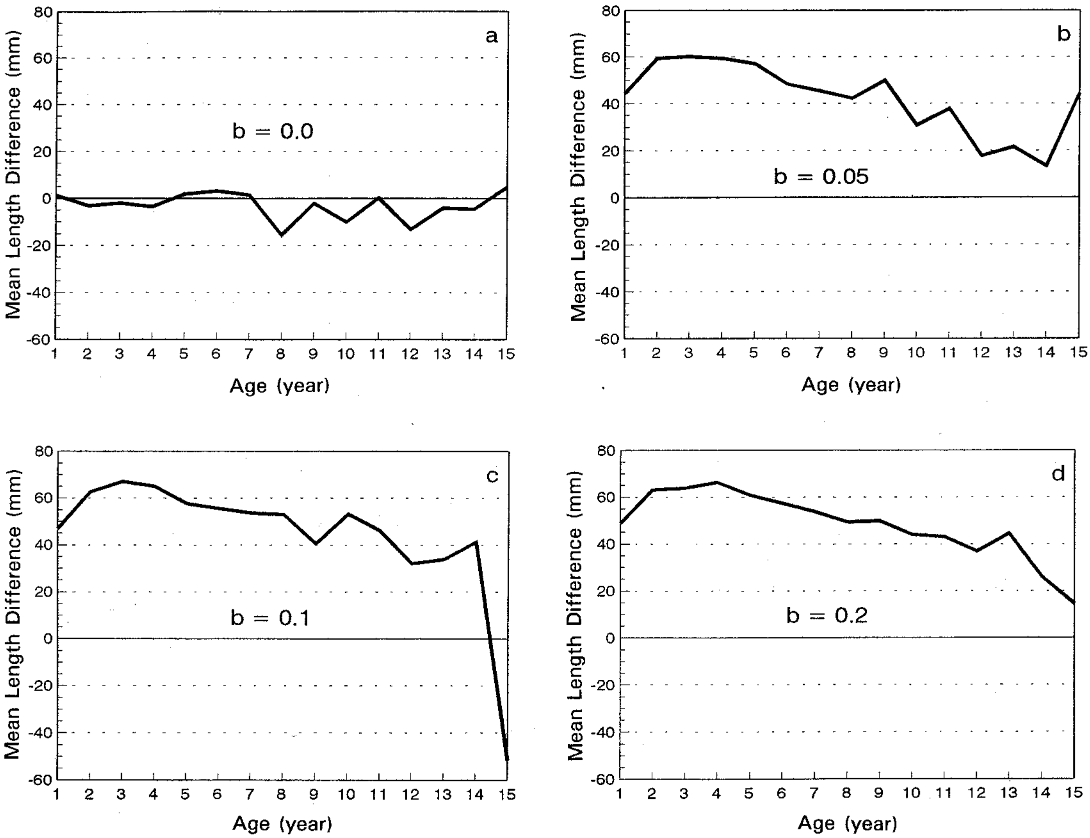

FIGURE 5.—Differences in simulated mean lengths between back-calculations to all annuli (all) and back-calculations to only the most recent annuli (final) for **(a)** no Lee's phenomenon, $b = 0.0$, and for increasing levels of Lee's phenomenon: **(b)** $b = 0.05$; **(c)** 0.1; and **(d)** 0.2. For these simulations, the number of fish was 50 and K was 0.15/year.

ferences ranged from 60 mm for $b = 0.05$ to 67 mm for $b = 0.2$. For actual red grouper data, the same difference was slightly below 30 mm.

Stiles and Burton (in press) obtained estimates for L_∞ and K of 938 mm and 0.153/year from the mean length at age using back-calculated lengths at the most recent annuli, and 922 mm and 0.167/year using all back-calculated lengths. The lower estimate of K resulted from having larger fish at younger ages; when all annuli were used, back-calculated lengths from old fish biased the size of fish at younger ages. The differences in mean length at age between back-calculation procedures suggest size-selective mortality for faster-growing fish (Figure 1b).

These simulations can be generalized to other growth models. The critical parameter of the von Bertalanffy growth model is K, which describes the rate at which length approaches an asymptotic value. When K is large relative to mortality (Z), better estimates of the von Bertalanffy parameters are obtained (Vaughan and Kanciruk 1982). Conversely, when K is small relative to Z, poor estimates (when they converge) are often obtained. The other parameters, L_∞ and t_0, are scaling parameters for the length and age axes, respectively.

In the presence of size-selective mortality (Lee's phenomenon or its reverse), the use of back-calculated lengths at formation of all annuli can lead to relatively large bias in estimates of both L_∞ and K relative to estimates based on only the most recent annuli (i.e., one measurement per fish). Our general advice for estimating von Bertalanffy parameters is to use one measurement per fish, preferably the size at most recent annulus.

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