

How Reliable are Growth Back-Calculations Based on Otoliths?

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Growth back-calculations from otoliths assume that the relationship between fish and otolith length is linear through time. The final (or observed) individual fish-otolith ratios are then combined to prepare a fish-otolith regression for the population, upon which the subsequent back-calculations are based. However, recent studies have demonstrated that the fish:otolith size ratio varies systematically with somatic growth rate, resulting in relatively large otoliths in slow-growing fish. Such a growth effect will result in a fitted fish-otolith regression which differs significantly from that of the mean of the individual fish-otolith slopes. Fraser–Lee growth back-calculations made from such a regression consistently underestimate previous lengths at age. The bias may explain the apparent ubiquity of Lee's phenomenon. Back-calculation bias was eliminated through use of an algorithm defining individual fish-otolith trajectories and a biologically determined, rather than a statistically estimated, intercept. Adaptations of the biological intercept back-calculations procedure accurately predicted previous lengths in the presence of both stochastic error and time-varying growth rates. When used to reevaluate some published back-calculations, the biological intercept procedure resulted in more accurate values than those previously estimated, and reduced or eliminated the presence of Lee's phenomenon.

Le calcul inverse de la croissance à partir des otolithes suppose que la relation entre la longueur des otolithes et le poisson est linéaire dans le temps. Les ratios finals (ou observés) otolithes-poisson sont donc combinés en vue de l'obtention d'une régression otolithes-poisson pour la population, à partir de laquelle les calculs inverses ultérieurs se fondent. Cependant, des études récentes ont montré que le ratio poisson-dimensions des otolithes varie systématiquement en fonction du taux de croissance somatique, ce qui correspond à des otolithes relativement gros chez les poissons à croissance lente. Une telle situation conduira à une régression poisson-otolithes particulière qui diffère sensiblement de celle de la moyenne des courbes poisson-otolithes. Les calculs inverses de croissance de Fraser–Lee établis à partir de cette régression sous-évaluent constamment les mesures antérieures de longueur selon l'âge. Le facteur de distorsion peut expliquer l'omniprésence apparente du phénomène de Lee. Le facteur de distorsion des calculs inverses a été supprimé par l'emploi d'un algorithme définissant les circuits otolithes-poisson et un intercept déterminé biologiquement plutôt qu'évalué statistiquement. Les adaptations de la méthode de calcul inverse de recouplement biologique ont permis de prévoir avec exactitude les longueurs antérieures compte tenu de l'erreur stochastique et de taux de croissance variant avec le temps. Utilisée pour réévaluer des calculs inverses rendus publics, la méthode de recouplement biologique a donné des valeurs plus justes que les valeurs estimatives antérieures et a réduit ou éliminé le phénomène de Lee.

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Calculation of true growth rate, as opposed to the population growth rate (Ricker 1975), requires data on individual growth trajectories through a period of time if biases associated with gear selectivity and size-selective mortality are to be avoided. Growth back-calculations from periodic features in bony structures, such as scales or otoliths, serve as a commonly-used proxy for sequential observations of size-at-age for individual fish. Of the two underlying assumptions of growth back-calculations, that dealing with constancy in feature periodicity has been dealt with elsewhere, both on the annular (Beamish and McFarland 1983; Casselman 1987) and the daily level (Campana and Neilson 1985). The second assumption, that the distance between consecutive features is proportional to fish growth, has seldom been adequately tested, but has generally been justified on the basis of empirical correlations between otolith/scale size and fish size. While such correlations certainly indicate a general correspondence between the growth rates of the structure and fish, they by no means demonstrate that the correspondence applies on an individual basis or at a detailed level. Such a correspondence would

require a constant relationship between otolith/scale growth and fish growth, or at the very least, random error around such a relationship.

Virtually all growth back-calculation procedures are based on proportionality between fish length and some measure of otolith (or scale) size (Carlander 1981). The regression method estimates fish length (L) at some previous age (a) through insertion of the measured size of the otolith (O) at age a into a fish length-otolith length regression derived from samples of the population,

$$(1) L_a = b O_a + d$$

where b and d are the slope and intercept of the regression, respectively. Since this procedure assumes no deviation of individual fish and otolith measurements from the overall regression, it has generally been applied when mean back-calculated lengths, rather than individual values, are of importance. In contrast, the more widely-used Lee (or Fraser–Lee) procedure (Carlander 1981) assumes that any deviation of an individual

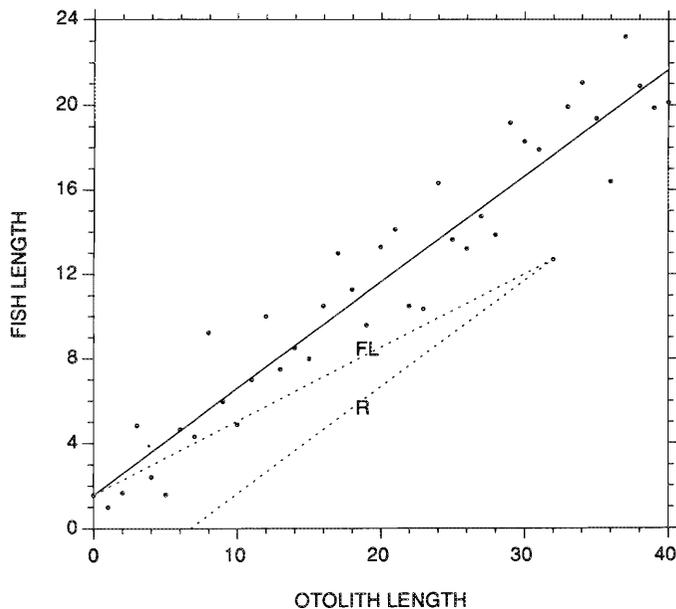


FIG. 1. An example of the regression of fish length on otolith length that is required for the Fraser-Lee and regression growth back-calculation procedures. Regression-based (R) back-calculations from individual fish assume no deviation from the overall regression, while Fraser-Lee (FL) back-calculations assume that individual fish-otolith deviations are maintained proportionally throughout the back-calculation. Both procedures result in mean back-calculated lengths which are equal to the overall fitted regression (solid line).

measurement from the overall fish-otolith regression will be observed proportionally at back-calculated lengths, as in

$$(2) \quad L_a = d + (L_c - d) O_c^{-1} O_a$$

where L_c and O_c are the fish length and otolith size at capture, respectively. While Eq. 2 does not incorporate the regression slope directly, the value of the regression intercept is, of course, influenced by the slope. Indeed, the regression and Fraser-Lee procedures differ algebraically only in that the latter is intercept-corrected. As a result, the two procedures produce identical mean back-calculated lengths, although back-calculations at the individual level may differ (Fig. 1). Both the regression and the Fraser-Lee procedures are sensitive to age- and sample-dependent variations in the intercept of the fish-otolith length relationship that is employed. Consequently, more sophisticated linear models have been developed to deal with intercept variability (Bartlett et al. 1984; Weisberg 1986; Smith 1987). However, all of the procedures carry the assumption that the fish-otolith length relationship does not vary in a systematic fashion with growth rate, and further, that the regression parameters can be accurately estimated from random samples of the population.

Recent studies of short-term otolith growth have demonstrated that the otolith-fish length relationship can vary systematically with the growth rate of the fish (Mosegaard et al. 1988; Reznick et al. 1989; Secor and Dean 1989a). These studies confirm earlier reports in which otoliths from slow-growing adult fish were consistently larger and heavier than those of fast-growing fish of the same size (Templeman and Squires 1956; Krivobok and Shatunovskiy 1976; Boehlert 1985). The first objective of the current study was to examine the implications of a relationship between growth rate and the otolith-fish size regression: is there any influence on the fish-otolith

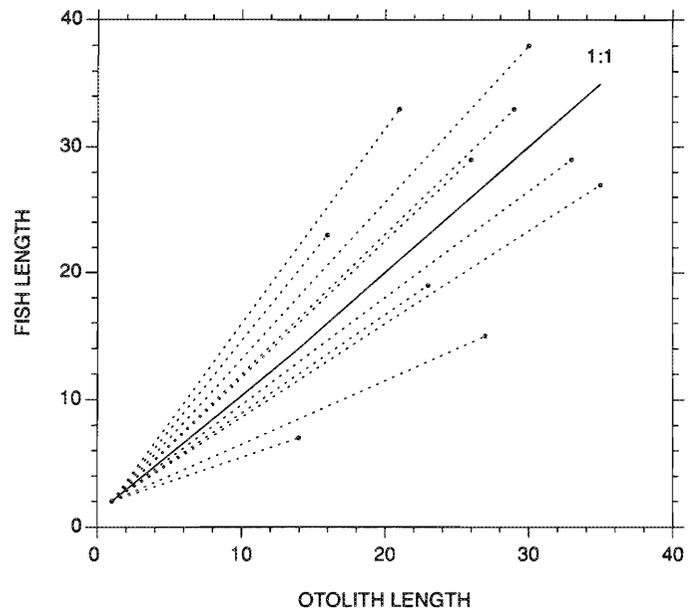


FIG. 2. Conceptual model depicting the trajectories of individual fish lengths relative to otolith lengths. Individual trajectories are not necessarily linear, but on average their slopes are distributed around some mean (1:1) value. Since this is considered to be the traditional (null) model, trajectory slopes are independent of growth rate. The regression predicting fish length from otolith length in the population would normally be calculated using the endpoints of the trajectories, which in this case, would coincide with the mean of the individual slopes.

regression parameters and/or the accuracy of back-calculated values? Also, is there any relationship with the apparent ubiquity of Lee's phenomenon (Lee 1912; Ricker 1969), whereby back-calculated lengths from otoliths of old fish are smaller than the mean lengths actually observed in the population? The second objective is to present a back-calculation procedure with a number of advantages over traditional techniques, including greater accuracy. And the final objective is to use this procedure to re-evaluate some of the conclusions drawn in previous studies which applied back-calculation techniques. While most of the emphasis in this paper will be directed towards growth back-calculations based on daily growth increments, a number of the conclusions will also apply to those based on scale and otolith annuli.

Implications of a Growth Rate Effect upon the Otolith-Fish Length Relationship

Within a population of fish, the trajectories describing individual fish growth relative to otolith growth can be envisioned as having radiated from some common origin (Fig. 2). Positions along the trajectory (which is not necessarily linear) correspond to the size of fish and otolith at a previous time. Smale and Taylor (1987) suggested that an analogous distribution of fish-scale slopes around the mean slope was caused by independent growth rate constants for scale and fish, which covaried in response to some common, controlling mechanism. This suggestion was consistent with the observed increase in the variance of scale size with fish length. A similar process appears plausible for the fish-otolith relationship (Campana and Neilson 1985; Mosegaard et al. 1988). In any event, the concept of individual fish-otolith growth trajectories is well documented (Marshall and Parker 1982; Rosenberg and Haugen 1982; Wil-

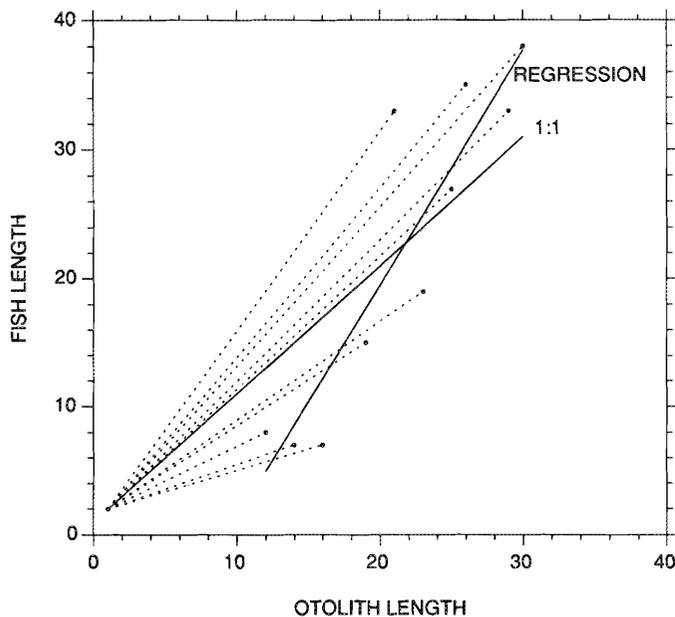


FIG. 3. Conceptual model depicting individual fish-otolith trajectories when faster-growing fish are characterized by smaller otoliths than slower-growing fish of the same size. As in Fig. 2, individual trajectories are distributed around the mean (1:1) slope. However, the trajectories of fast and slow growing fish tend to be segregated above and below the mean, respectively. As a result, the fish-otolith regression calculated on the basis of the trajectory endpoints (e.g. the sampled population) is biased: the calculated slope is too large and the intercept too small.

son and Larkin 1982; Secor and Dean 1989a, b). In Fig. 2, the endpoints of each growth trajectory, corresponding to the lengths of the fish and otolith at the time of sampling, would be used to calculate the overall fish-otolith regression upon which the subsequent back-calculations would be based. In this case, and in all instances where the slopes of the trajectories are independent of growth rate, the fitted regression line coincides with the mean (1:1) fish-otolith trajectory.

Direction of Bias Induced by Growth Rate Effects

The phenomenon whereby slow-growing fish have larger otoliths than fast-growing fish of the same size is widespread, both at the microstructural (Taubert and Coble 1977; Marshall and Parker 1982; McGurk 1984; Müller and Storck 1984; Neilson et al. 1985; Penney and Evans 1985; Post and Prankevicius 1987; West and Larkin 1987; Mosegaard et al. 1988; Reznick et al. 1989; Secor and Dean 1989a, b; Wright et al. 1990; but see Tzeng and Yu 1988) and the annular (Templeman and Squires 1956; Krivobok and Shatunovskiy 1976; Boehlert 1985) level. The experiments of Rice et al. (1985) also show evidence of the phenomenon (when their otolith-fish regressions are constrained through the point corresponding to size-at-hatch).

When incorporated into the conceptual model of Fig. 2, the growth rate phenomenon would act to segregate the slow and fast growing fish on either side of the mean fish-otolith growth trajectory (Fig. 3). Thus the slower growing fish, characterized by shorter trajectories, would tend to occur below the mean trajectory, while the faster growing fish with longer trajectories would occur above the mean. While the slope of the mean trajectory would probably remain unaffected by any such segregation, the effect upon the calculated regression, which is based upon the trajectory endpoints, is striking (Fig. 3). Irrespective

of the magnitude of the growth effect that is postulated, the slope of the regression will always be greater, and the intercept less, than that of the mean trajectory. On the basis of Fig. 2 and 3, the bias in the fitted regression would appear to be an inescapable product of a population characterized by a range of growth rates in which faster growing fish have relatively small otoliths, and vice versa. Since a fish-otolith regression based upon the trajectory endpoints is the normal predecessor of any back-calculation procedure, bias can also be expected of any subsequent back-calculations, such that back-calculated lengths are smaller than observed at the time. These conclusions are interesting from two perspectives. First, they suggest that bias in back-calculated lengths can arise even when predictions are made within the data range of the regression, and despite random sampling of the population. Indeed, if the growth effect on the fish to otolith length ratio is as universal as now seems likely, these results indicate that back-calculation bias should be an expected result of otolith-based back-calculations. Secondly, the consistent underestimation of fish length at earlier ages would appear to provide a plausible explanation for Lee's phenomenon. The apparent ubiquity of Lee's phenomenon has always been somewhat of an enigma, and although size-selective mortality may well contribute to the phenomenon (Ricker 1969), it now appears that growth effects can produce a similar result in the absence of size-selective mortality.

Magnitude of Bias Induced by Growth Rate Effects

Bias in the fish-otolith regression will result in detectable back-calculation error only if the bias is of sufficient magnitude. To assess the relative importance of the bias on back-calculation accuracy, the conceptual model of Fig. 2 was used to simulate the somatic and otolith growth of a cohort of fish. The objective was to determine the net fish-otolith relationship in a cohort comprised of fish of varying growth rates, where the slopes of the individual fish-otolith trajectories were influenced by their growth rates (e.g. Fig. 3). The cohort ($n = 100$) was assumed to have hatched on a single day with initial fish and otolith lengths equal to zero. Use of non-zero intercepts (e.g. otoliths present in fish at time of hatch) has no influence on the results of this model. To mimic the expected natural variability in growth rates, otolith growth rates were normally distributed among fish. Individual growth rates were kept constant through the 50-d period of growth; a model with time-varying growth rates is presented later. The algorithm for the model is:

- (i) $G \sim N(0.5, 0.1)$ across i fish
- (ii) $O_{it} = G_i \times t$
- (iii) $\text{Ratio}_i = (1 - R) + R \times (G_i/\bar{G})$
- (iv) $L_{it} = O_{it} \times k \times \text{Ratio}_i$

where G_i is the daily growth rate of the i th otolith, \bar{G} is the mean otolith growth rate, O_{it} is the length of the otolith in the i th fish after t days of growth, Ratio_i is the daily fish length increment to otolith length increment ratio in the i th fish, k (set to 1.0 in this model) is the conversion constant between fish and otolith growth rates, R is the magnitude of the growth rate effect on the daily fish to otolith ratio, and L_{it} is the length of the i th fish after t days. Note that this formulation is deterministic in that the daily otolith and fish growth rates are directly linked; a model with stochastic error around both growth rate constants is presented later. The calculation of the daily fish to

otolith ratio (Ratio) results in a value of 1.0 for fish growing at the mean growth rate or for cohorts where the growth effect is absent ($R=0$). However, when $R>0$, faster-growing fish would produce relatively small otoliths, and vice versa. As the value of R is increased, so does the discrepancy in otolith size for fish of a given length but different growth rates. In this model, Ratio is constant within a fish, since individual growth rates have been assumed to be constant through time. The influence of time-varying growth rates (and Ratios) is considered in a later model. Note also that the Ratio calculation is presented as a function of otolith growth, rather than somatic growth, due to the fact that otolith size is the independent variable in the subsequent regression. However, rearrangement of the Ratio calculation as a function of somatic growth does not affect the conclusions which follow. While there are few available data upon which to base the assumption of a linear effect of growth rate on the fish to otolith ratio, use of a nonlinear effect does not alter the implications of the model results.

Irrespective of the period of growth, the simulated cohort was characterized by a normal distribution of both fish lengths and otolith lengths, each centred around a similar mean. Preparation of the standard fish-otolith regression, based upon the individual fish and otolith lengths at the end of the growth period, resulted in populations with a slope of 1.0 and a zero intercept whenever the growth effect (R) was set to zero. As the magnitude of the growth effect (R) was increased, there were proportional increases and decreases in the values of the fitted regression slopes and intercepts, respectively. Back-calculated lengths based on these regression parameters became increasingly biased (too small) as the value of the growth effect was increased above 0. In the presence of a strong growth effect ($R=1.0$), the slope of the fish-otolith regression was more than doubled, indicating the potential for substantial back-calculation error. The degree of bias was virtually independent of the coefficient of variation (CV) in growth rates present in the simulated population. Similar results were observed when the stochastic error ($e_i \sim N(0, 1)$) expected of a natural population was introduced around the fish to otolith ratio calculations (line (iii) in model algorithm), as in:

$$\text{Ratio}_i = ((1 - R) + R \times (G_i/\bar{G})) + e_i$$

Estimation of the Value of the Growth Effect (R)

The model results indicate that back-calculation bias will result from any non-zero value of the effect of growth rate (R) upon the daily fish to otolith ratio. However, small values of R may not produce detectable bias in natural situations. To estimate the magnitude of R that exists under natural conditions, independent estimates were derived from published data, through regression of the slope of the fish-on-otolith regression on growth rate,

$$(3) \quad S = a' + R G$$

where S is the observed slope of the fish length-on-otolith regression, G is the observed absolute linear rate of growth in fish length, and a' and R (the growth effect) are parameters to be estimated. To facilitate the comparison of the regression results among studies, the growth and slope data entered into each regression were first standardized with respect to their means.

Three studies provided sufficient data to estimate the magnitude of the growth effect (R). In the first, Reznick et al. (1989)

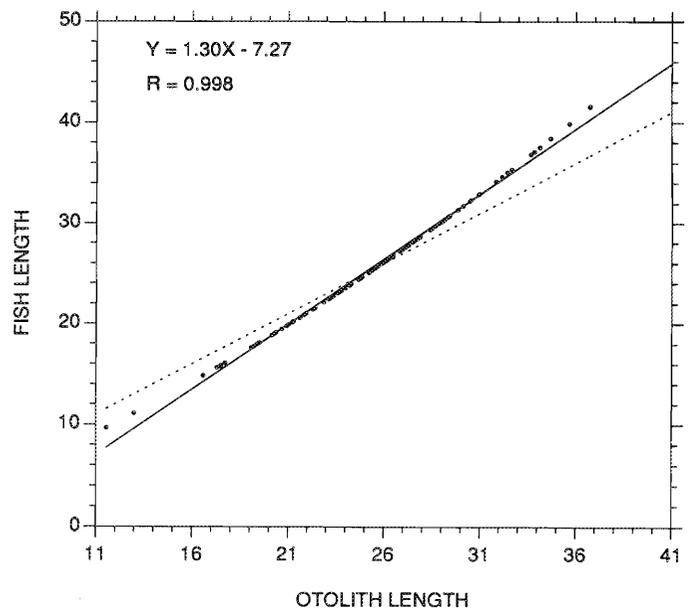


FIG. 4. Example of the distribution of individual fish-otolith trajectory endpoints from a cohort when faster-growing fish are characterized by smaller otoliths than slower-growing fish of the same size (sensu Fig. 3). The value of the growth rate effect ($R=0.3$) was estimated from published data, and was entered into the model deterministically. The fitted regression (solid line) is the normal predecessor to growth back-calculation, yet it is significantly different ($P<0.01$) from that of the mean fish-otolith trajectory (dotted line; slope = 1.0; intercept = 0).

reported only a 4% difference in the adjusted mean length of guppy (*Poecilia reticulata*) otoliths from two treatments where growth rate varied by a factor of 2.3. While statistically correct, their analysis of covariance of the relationship between otolith and fish length assumed homogeneity of slopes and different intercepts between the treatments. Since the environmental and genetic histories of all of the experimental fish were similar and carefully controlled, it is more reasonable to assume that the treatments shared a common intercept, but had different slopes reflecting the different growth regimes. On this basis, and using the regressions presented in their figure 1, the treatment slopes of fish length on otolith length differed by 24%, resulting in a normalized fish-otolith slope which increased at 27% of the normalized rate of increase of growth. A slightly higher estimate of the influence of growth was obtained from four growth treatments in a study of sockeye salmon (*Oncorhynchus nerka*) otoliths by Marshall and Parker (1982) ($R = 0.42$; $n = 4$; $P = 0.16$). However, the most robust estimate of the growth effect was calculated from inverse regressions (which replaced otolith length by fish length as the dependent variable) of the striped bass (*Morone saxatilis*) data of Secor and Dean (1989a). The resulting estimate indicated that the normalized slopes of the fish-on-otolith regression increased at 42% of the rate of increase of growth rate ($n = 12$; $P < 0.0001$). Given the differences among the species and experimental designs used in these three studies, a value of 0.3 would appear to be a conservative estimate of the relative influence of the growth effect on the fish to otolith ratio.

Incorporation of $R = 0.3$ as the magnitude of the growth effect in the fish-otolith simulation model demonstrated the amount of bias that would result in the subsequent back-calculation. After a 50-d period of growth, preparation of the

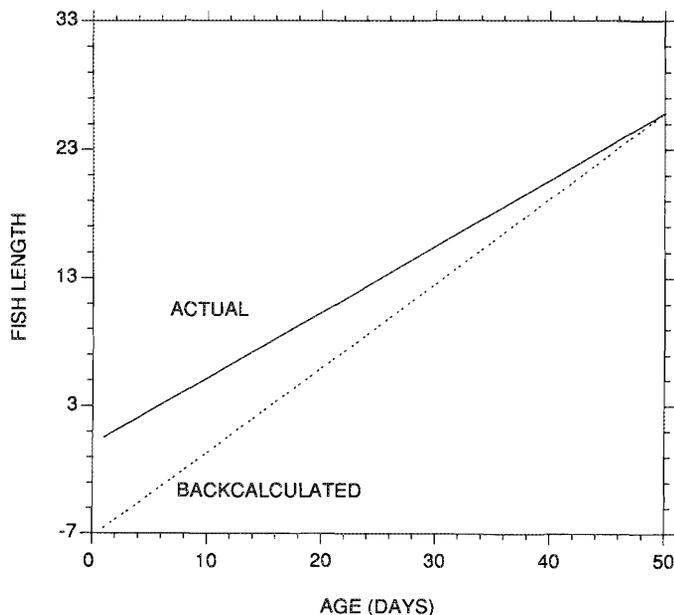


FIG. 5. Fraser-Lee growth back-calculations of mean length based on the fish-otolith trajectory endpoints in Fig. 4. The back-calculated lengths-at-age underestimated the actual lengths in this and all other simulations where growth rate influenced the slope of the fish-otolith trajectories. The actual and back-calculated lengths are significantly different ($P < 0.01$).

standard fish-otolith regression from the "sampled" cohort revealed what would normally be interpreted as a strong and reliable correlation, despite the presence of a barely detectable pattern in the residuals (Fig. 4). However, the slope and the intercept of the regression were significantly ($P < 0.01$) larger and smaller, respectively, than those of the mean of the individual trajectories. A similar result was observed in simulations where a normal error distribution was placed around the growth-ratio relationship. The variance in the latter simulation, which is almost certainly present in the natural environment, effectively obscured any evidence of a pattern in the residuals.

Growth back-calculations of the simulated cohort were made on an individual basis with both the Fraser-Lee and regression methods. Both procedures produced mean back-calculated values which were significantly smaller ($P < 0.01$) than the actual lengths at the time (Fig. 5). Both the absolute and percent deviation from actual values increased as the origin of the regression was approached.

Variations of the fish-otolith simulation model demonstrated that back-calculation bias persisted in the presence of both multiple cohorts and size-selective sampling (mimicking gear selectivity whereby the smallest and/or largest fish in the population were unavailable to the gear). However, the magnitude of the bias was greatly reduced in instances where newly hatched cohorts were present at the time of sampling, presumably through their high leverage on the fish-otolith regression (by forcing the slope through, or near to, the true origin). The latter implies that, in general, back-calculations from daily growth increments in otoliths from juvenile fish collections may be more susceptible to back-calculation bias than those from larval fish. Simulations of multiple annual cohorts, where growth rate declined with age, resulted in significantly different fish-otolith regression parameters among ages, thus providing a plausible explanation for the relative success of back-calculation procedures where age is entered as a variable (Bartlett et

al. 1984; Miller and Storck 1984). However, the age-specific regression parameters were also biased, due to growth rate variability within each age-group.

The relative influence of the fish-otolith regression intercept on the accuracy of growth back-calculations has been presented by several workers (Carlander 1982; Smale and Taylor 1987). The use of species-specific intercepts has been recommended as one means of removing statistical uncertainty due to sampling errors (Carlander 1982). Other researchers have ensured the consistency of their estimated intercept values with independent estimates (Crecco and Savoy 1985; West and Larkin 1987) or have applied procedures which explicitly recognized the possibility of age-specific intercepts (Bartlett et al. 1984; Weisberg 1986). However, to my knowledge, this is the first demonstration that population-wide back-calculation bias can result from other than sampling error, and irrespective of the statistical analysis that is applied.

Minimization of Growth Back-Calculation Bias due to Growth Rate Effects

Use of a Biological Intercept

Under the assumption of proportionality between fish and otolith lengths, the Fraser-Lee back-calculation procedure effectively calculates a separate slope for each fish, using the intercept of the population-based regression as a starting point. By definition, this starting point corresponds to the fish length at which otolith length equals zero, rather than the origin of the fish-otolith trajectories presented in Fig. 2. Independent of the growth effect described earlier, the Fraser-Lee method cannot be used to accurately reconstruct the individual fish-otolith trajectories of Fig. 2; there is no single Y -intercept value (corresponding to a regression intercept) which can be used as an origin for all of the individual trajectories. However, given an appropriate value for the regression intercept, the Fraser-Lee method will correctly predict mean back-calculated lengths, even in the presence of a growth effect. This property suggests that the Fraser-Lee method is an appropriate starting point for the development of a new back-calculation procedure, requiring only a better means of defining the intercept to be complete.

In all of the experiments where growth has been manipulated or monitored, it has been the slope of the fish-otolith trajectories which has varied, rather than the intercept (Marshall and Parker 1982; Rosenberg and Haugen 1982; Rice et al. 1985; Secor and Dean 1989a, 1989b). Indeed, given a common pool from which experimental fish are drawn, all should, by definition, share a common intercept. The common intercept in this case is biologically, not statistically based, and corresponds to the size of the otolith and fish at the beginning of the experiment. Generally, I would define the biological intercept of a fish-otolith trajectory as the fish and otolith length corresponding to the initiation of proportionality between fish and otolith growth. In many species, this point would occur at the time of hatch.

The use of biological intercepts in a modification of the Fraser-Lee back-calculation procedure eliminates the errors and bias that were described in previous sections. When tested in the cohort simulation model, the equation

$$(4) \quad L_a = L_c + (O_a - O_c)(L_c - L_o)(O_c - O_o)^{-1}$$

accurately predicted previous lengths, both at the individual and population level, back to the biological intercept (fish = L_o , otolith = O_o). Equation (4) simply describes the

line connecting an individual fish-otolith coordinate at the time of sampling to that at the biological intercept (sensu Fig. 2 or Fig. 3). In other words, the calculation is intercept-corrected along both X and Y axes. Although the equation was not presented, Smale and Taylor (1987) made a similar recommendation with respect to back-calculations from scale annuli. In contrast, Carlander (1982) concluded that biologically based intercepts might not be reliable, and suggested that back-calculation error be minimized through use of standardized regression intercepts. While the standardization of regression intercepts would almost certainly reduce back-calculation error due to sampling variability, it would not necessarily eliminate bias due to statistical estimation of the standardized intercept. Of course, bias would be minimal if the regression included enough observations near the origin to lever the regression through the biological intercept.

The biological intercept back-calculation procedure has a number of desirable features which recommend its use. Firstly, through incorporation of intercept corrections along both fish and otolith axes, the procedure fits the widely accepted conceptual model of Fig. 2 more closely than any other back-calculation model. Secondly, it is insensitive to bias induced by variable growth rates in the population, although not to growth rate variations through time. Thirdly, the size of the fish and otolith at hatch (or at the time of initiation of a linear fish-otolith relationship) can be precisely measured, and differs little among individuals. Fourthly, back-calculation accuracy is relatively insensitive to normal variation around the intercept value, largely because of the small values involved. Most importantly, use of this procedure does not rely on parameter estimation from a sample of the population. Indeed, back-calculations can be made from an individual fish in the absence of any other fish from the population, other than those used to verify proportionality between otolith and fish growth after the biological intercept. In many cases, the biological intercept could be determined by simple measurements of otolith and fish size in newly-hatched larvae in the laboratory. As for disadvantages of the procedure, I was not able to identify any that were not also associated with other back-calculation techniques. Foremost of these were those linked to nonlinear effects, as discussed in the following section.

Time-Varying Growth Rates

All of the available back-calculation procedures, including Eq. 4, assume linearity in individual fish-otolith trajectories throughout the lifetime of the fish. However, it is unlikely that an individual fish would maintain a constant growth rate through time; thus, the effect of growth rate on the fish-otolith relationship would be expected to introduce curvature into individual fish-otolith trajectories. Here, I will use an enhancement of the fish-otolith simulation model to assess the effect of such nonlinearities on back-calculation accuracy, and suggest improvements to Eq. 4 so as to reduce the influence of time-varying growth rates.

Using the same 100-fish cohort and growth effect ($R = 0.3$) described earlier, individual fish-otolith growth trajectories were modeled over a 150-d period, with a normally distributed error around both the growth rate ($G \sim N(0.5, 0.1)$) and the fish to otolith ratio ($\text{Ratio} \sim N(1.0, 0.1)$). Each fish experienced a "life history transition," characterized by a fourfold increase in growth rate (from 0.25 to 1.0 units/d), at an arbitrary size of 20 units (corresponding to a mean age of 80 d). The variance

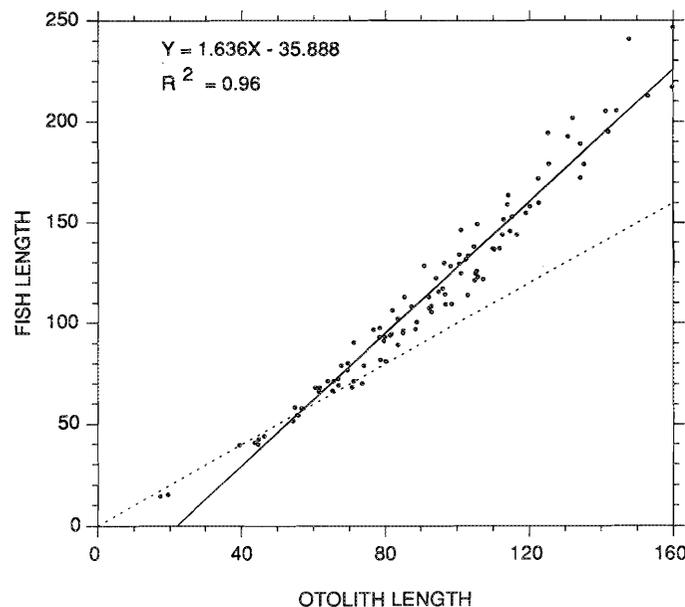


FIG. 6. A fish-otolith regression fitted to simulated data from a 150-d-old cohort which experienced individual life history transitions, characterized by a four-fold increase in growth rate, at a length of 20. The slope and intercept of the regression (solid line) are significantly different from the mean fish-otolith trajectory slope and intercept of 1.0 and 0, respectively (dotted line). The growth rate effect on individual trajectory slopes was set at 0.3, but included a normal error distribution around the mean daily fish:otolith ratio ($\text{Ratio} \sim N(1, 0.1)$).

in growth rates among fish implies that individuals would undergo the transition at different ages. Since the point of transition was designed to simulate natural conditions, it was calculated as a function of size, not age (Policansky 1982; Chambers and Leggett 1987). The extreme case of an abrupt transition was intentionally imposed to maximize the nonlinearity in the individual fish-otolith trajectories. Back-calculations were made on the basis of the "observed" population at the end of the 150-d period.

The characteristics of the net fish-otolith regression (Fig. 6) were similar to those observed in Fig. 4, with the exception that a pattern in the residuals could not be discerned. The slope and intercept were significantly larger and smaller ($P < 0.01$) than 1.0 and 0, respectively. Back-calculations made with both the Fraser-Lee and the biological intercept methods differed from actual values (Fig. 7), although the size of the deviation was much more pronounced and consistently negative in the former. Back-calculations made with the Fraser-Lee method differed from actual values by 159% at the 63-d age corresponding to the lower limit of the regression data in Fig. 6. The percentage deviation increased as the origin was approached. In contrast, the deviation of the biological intercept method never exceeded 42% and was negligible at the time of hatch. Similar results were observed in other simulations where the growth rate transition was a function of age (simulating a sudden environmental effect), and where the fish-otolith relationship was deterministic rather than stochastic.

In principle, it is possible to use a series of daily growth increment widths to compensate for back-calculation curvature produced by time-varying growth rates. Since the width of a daily increment is a measure of daily otolith growth rate, compensation for the growth rate effect, on a day-to-day basis,

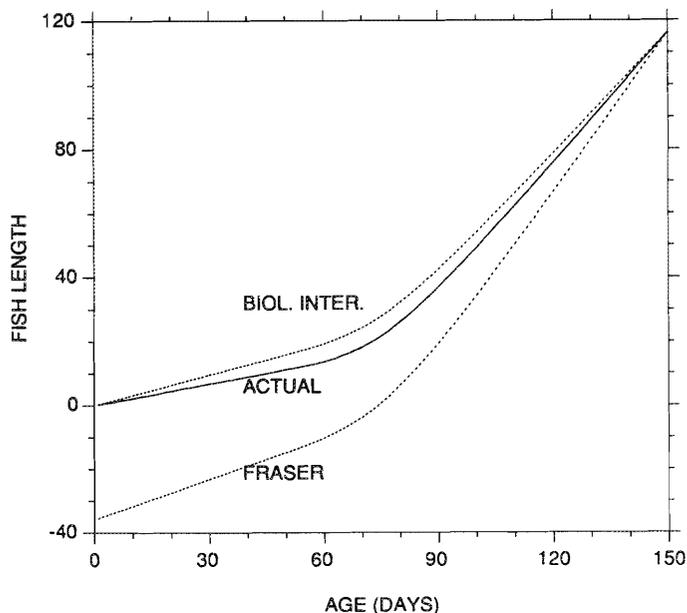


FIG. 7. A comparison of actual mean lengths-at-age with those back-calculated from the observations in Fig. 6, in which individual growth rates varied through time. Back-calculations made with the linear form of the biological intercept procedure (Biol. Inter.) (Eq. 4) were more accurate than those made with the Fraser-Lee method, but both deviated from actual values. Mean back-calculated values made with Eq. (7) were the same as the actual values, although individual back-calculations differed.

should restore proportionality to the increment width series, as in:

$$(5) L_t = W_t \times k \times \text{Ratio}_t$$

In other words, the daily growth in length at age t (L_t) is related to the width of the corresponding increment (W_t) by a conversion constant (k) and the fish-length growth ratio on that day (Ratio_t). If the magnitude of the growth effect (R) is known, and substituting line (iii) of the model algorithm for Ratio_t , the calculation becomes

$$(6) L_t = W_t \times k \times ((1 - R) + R \times (W_t \times \bar{W}^{-1}))$$

with \bar{W} defined as the mean daily increment width (or otolith growth rate) across all fish and ages. Length back-calculation is then the sum of daily back-calculated fish length increments, as in:

$$(7) L_a = L_o + \sum_{t=1}^a (k \times W_t \times ((1 - R) + R \times (W_t \times \bar{W}^{-1})))$$

where L_o is the size of the fish at the origin of the linear fish-otolith trajectory (e.g. biological intercept), and $t = 1$ corresponds to the first day after L_o . The requirement for a continuous series of increment widths, from the time of hatch (or biological intercept) to the point of back-calculation, makes this formulation somewhat more restrictive than Eq. 4. It also does not account for stochastic error around the mean daily fish to otolith ratio. As a result, back-calculations made with Eq. 7 are analogous to those made with the regression method, whereby mean back-calculated lengths are more accurate than those at the individual level.

Despite the above caveats, Eq. (7) accurately predicted mean back-calculated lengths in the cohort simulation which incor-

porated time-varying growth rates (Fig. 7). The maximum absolute deviation from actual lengths for individual fish was only 8%, making the calculation considerably more accurate than either the biological intercept or the Fraser-Lee methods at both the individual and the mean level. However, Eq. (7) should be used with caution, given its potential sensitivity to the untested assumptions concerning the error distribution and age independence of the growth rate effect. The formulation of line (iii) in the model algorithm would also have to be developed with more rigor than was done here, since \bar{G} could be expected to vary ontogenetically or under different environmental conditions.

In practice, estimates of the magnitude of the growth effect can be made without an experimental framework. Given the value of the biological intercept, each fish in a sample could serve as an independent observation in the regression of Eq. 3. Each fish-otolith length trajectory could be used to calculate the dependent variable (the slope of the fish-otolith regression), while examination of the otolith microstructure would provide the age estimate required for calculation of the independent variable (growth rate). Of course, the sample would have to be selected from an environment in which time-varying growth rates were minimized.

It is important to note that Eq. 7 cannot be used to compensate for all sources of nonlinear fish-otolith trajectories. At the daily level, autocorrelated increment widths (Gutiérrez and Morales-Nin 1986; Bradford and Geen 1987) would be expected to reduce the accuracy of detailed growth back-calculations. In principle, a time series model could be developed to account for the autocorrelation, but such would require considerably more research. Deviations from a linear fish to otolith trajectory at a frequency greater than that of the periodic feature being used would also introduce error. Examples of such deviations would include seasonal disruptions of the fish to otolith ratio (Reay 1972; Casselman 1987) and their effects upon back-calculations made from annuli. For this reason, and given inter-annual variations in the timing of annulus formation, Eq. 7 is more likely to be of value when applied at the daily level.

Implications for Previously Published Studies

In many situations, the difference between growth back-calculations made with traditional methods and those made with the biological intercept procedure will be relatively small. Under conditions where the statistical and biological intercepts of the fish-otolith regression are collinear, mean back-calculated lengths will be identical, although individual values may differ. More substantial differences can be expected under the following circumstances: (1) when there are differences between the biological and statistical intercepts, (2) when different fish-otolith regressions are used for different populations, and (3) when the same fish-otolith regression is used for different populations of dissimilar growth rates. Using these criteria, I have re-examined a number of published studies, both as an independent test of the validity of the biological intercept back-calculation procedure, and to determine the implications of its use, if any, on the authors' conclusions.

Differences in the collinearity between the biological and statistical intercept can be a major source of back-calculation error. Both Crecco and Savoy (1985) and West and Larkin (1987) gave careful attention to this problem, and demonstrated consistency between estimated and observed intercept values before their application. However, in a study of redbfish

(*Sebastes* spp) larvae (Penney and Evans 1985), there was a demonstrable difference (evident in the residuals) between the observed and predicted fish to otolith ratios at larval extrusion, which may have had implications for the conclusions that were reached concerning early larval growth.

A more substantial difference between statistical and biological intercepts was apparent in a study of back-calculated growth in sand lance (*Ammodytes dubius*) (Scott 1973). The statistically estimated fish length at which otoliths were formed (e.g. the statistical intercept) was 2.4 cm (Scott 1973), a value which was six times larger than the actual value (0.4 cm; Scott and Scott 1988). The discrepancy was probably the product of the fish-otolith regression bias discussed earlier. As noted by Scott (1973), regression-based back-calculations of mean length underestimated the observed mean lengths-at-age by up to 33%. However, when I repeated the back-calculations using the biological intercept procedure (Eq. 4), virtually all evidence of Lee's phenomenon disappeared: all back-calculated values fell to within 6% of observed values.

Additional support for the validity of the biological intercept procedure was obtained in a re-evaluation of back-calculated growth in multiple year-classes of juvenile chinook salmon (*Oncorhynchus tshawytscha*) (Neilson et al. 1985). While it had no effect on their conclusions, Neilson et al.'s (1985) back-calculated sizes at entry into the estuary by the 1979 cohort underestimated observed values. The underestimation was due to the relatively large calculated value for the fish-otolith regression slope, which in turn was almost certainly due to the regression bias produced by the rapid growth rate of that cohort. Application of the biological intercept procedure to their data produced mean back-calculated lengths that were 12% closer to observed values than were the corresponding back-calculations based on the Fraser-Lee method. There were no significant differences between the biological and statistical intercepts, nor between the corresponding back-calculations, for the remaining year-classes.

Use of a single fish-otolith relationship to back-calculate the growth of two samples with different growth rates appears to be the cause of an interesting anomaly in the study of Wilson and Larkin (1982). After a careful analysis of the sequential growth of a single cohort, Wilson and Larkin (1982) reported a good correspondence between back-calculated and observed fish weights, but noted a parabolic distribution of unknown origin in the residuals. Re-examination of their data indicated that the growth rate declined by over a factor of 2 in the second half of their experiment. Based on my simulations, their residual pattern matched that expected of two disparate growth rates and the corresponding change in the fish to otolith ratio through the course of the experiment. In an unrelated study, Post and Prankovics (1987) also used a single fish-otolith regression to back-calculate the growth of different samples. After combining inshore and offshore collections that were characterized by significantly different growth rates, the authors concluded that size-selective mortality was the cause of differences between observed and back-calculated lengths in one of the lakes. Application of the biological intercept procedure to their digitized data reduced, although it did not eliminate, the size of the discrepancy. In the second lake, where size-selection was not apparent, the revised back-calculated lengths matched those that were observed. In a third study, Beacham (1981) could find no evidence of density-dependent growth after applying a single fish-otolith relationship to samples from a sequence of year-classes. Since density-dependent growth would be expected to

manifest itself as reduced growth of abundant year-classes, and given the growth rate effect on the fish to otolith ratio, it is doubtful that he could have detected density-dependent growth with the regression method that he applied. Further analysis would be required to confirm or reject his hypothesis.

In summary, re-analysis of a variety of independent studies with the biological intercept back-calculation procedure confirmed its effectiveness in estimating previous lengths at age at least as accurately, and generally more so, than was possible with the Fraser-Lee method. In most instances, the revised back-calculation reduced the magnitude of length underestimation and eliminated the need to invoke Lee's phenomenon. The assumptions of the biological intercept procedure were better met than those of the Fraser-Lee method in all studies; in some cases, use of the former produced results which were inconsistent with the conclusions reached through use of the latter.

Conclusions

The realization that the fish to otolith ratio is influenced by somatic growth rate necessitates some rethinking of traditional means of growth back-calculation. This is particularly true given that the effect of growth variability is to induce a bias into the net fish-otolith relationship, upon which all traditional back-calculation procedures are based. The bias is evident at both the daily and the annular level. Fortunately, this information can be used to recommend an alternative, and in many ways easier, back-calculation algorithm. While based upon a different rationale, some of the features of the biological intercept technique are common to those associated with Carlander's (1982) standard intercept formulation. Additional advantages of the former include increased resistance to bias associated with growth rate variations, increased back-calculation accuracy at the individual and mean level, ease of determination of the intercept value, and in particular, insensitivity to the sampling error and truncation effects that can be so influential in other back-calculation procedures (Carlander 1981; Bartlett et al. 1984; Smale and Taylor 1987). The algorithm is applicable at both the daily and the annular level. All techniques can produce error when back-calculations are made outside of the sample range or when curvilinear fish-otolith relationships are left untransformed. However, a further advantage of the biological intercept algorithm is that fish-otolith proportionality can be confirmed in other, independent samples, and need not be repeated in each back-calculation study. Nonlinear fish-otolith relationships formed as a consequence of time-varying growth rates require special handling (e.g. Eq. 7), and in many populations, will probably result in the introduction of some back-calculation error.

The finding that Lee's phenomenon can result from mathematical bias induced by the effect of growth on the fish to otolith ratio is noteworthy, given the number of reports of its existence (Halliday 1969; Scott 1973; Bagenal and Tesch 1978; Neilson et al. 1985; Radtke et al. 1985; Morales-Nin 1988). The fact that similar bias may exist in back-calculations based on scale annuli suggests that further research on the fish-scale relationship may be required (Carlander 1981; Smale and Taylor 1987).

While the influence of growth rate on the fish to otolith ratio has been both quantified and applied in this study, little is known of the underlying mechanisms. It is unlikely that growth rate is the only variable which can influence relative otolith size

(Mosegaard et al. 1988; Secor and Dean 1989a, 1989b; Wright et al. 1990). Identification of other influential variables would not affect the conclusions drawn here concerning statistical bias in the fish-otolith regression, or the overall benefits of the biological intercept procedure. However, it could alter, and presumably improve, our perception of individual fish-otolith trajectories in the presence of conditions promoting time-varying growth rates. It could also improve our ability to back-calculate previous lengths under such conditions.

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