

Back-Calculation of Fish Lengths Based on Proportionality between Scale and Length Increments

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The assumption underlying linear back-calculation of fish lengths (L) from scale measurements (S) is that annual increments of length (ΔL) are proportional to annual increments between the annuli on scales (ΔS) for each fish–scale combination. A sample from a fish population that provides measurements of fish length and scale radius at time of collection should be symmetrical transversely to its central axis when plotted with an absolute slope of 45° ; if not, it can be made symmetrical by either of two easy methods. The slope of the central axis can be estimated using either an arithmetic mean regression or (preferably) the geometric mean regression; either should be made to pass through the centroid of the whole sample. Average lengths at each age are unbiased if computed from average annulus distances using one of the above symmetrical statistics whereas biased estimates are obtained using either of the ordinary regressions between S and L , especially when part of the range of ages (older than 0) is missing at either end of the sample. Lengths of individual fish can be back-calculated throughout their life by using either the Whitney–Carlander or (preferably) the Fraser–Lee procedure, with the fixed parameter estimated from a symmetrical regression line.

Selon l'hypothèse sous-jacente au calcul à rebours de la longueur des poissons (L) à partir de valeurs mesurées des écailles (S), les accroissements annuels de longueur (ΔL) sont proportionnels aux accroissements annuels des distances entre les anneaux des écailles (ΔS) de chaque combinaison poisson–écaille. Un échantillon d'une population de poissons à partir duquel on a mesuré la longueur des poissons et le rayon des écailles au moment du prélèvement devrait présenter une symétrie transversale par rapport à son axe central lorsque reporté en utilisant une pente absolue de 45° , mais si ce n'est pas le cas, deux méthodes d'application facile permettent d'obtenir la symétrie. La pente de l'axe central peut être estimée à partir d'une régression de moyennes arithmétiques ou, de préférence, de moyennes géométriques, les deux pentes devant passer par le centroïde de l'ensemble de l'échantillon. Les longueurs moyennes de chaque âge ne sont pas biaisées si elles sont déterminées à partir des distances moyennes entre les anneaux en utilisant l'une des méthodes statistiques symétriques ci-dessus, mais elles sont biaisées si l'une des régressions habituelles entre S et L est utilisée, surtout lorsqu'une partie de la gamme des âges (plus que 0) est absente à l'une ou l'autre des extrémités de l'échantillon. Les longueurs de poissons donnés peuvent être calculées à rebours pour tout moment de leur vie en appliquant la procédure Whitney–Carlander ou, de préférence, celle de Fraser–Lee, le paramètre fixe étant estimé à partir d'une droite de régression symétrique.

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1. Introduction

The recent paper by Francis (1990) contains a valuable review of the literature concerning the calculation of fish lengths at successive ages from marks on scales, otoliths, etc., which should be read by everyone in the field. However, his conclusions require modification in one important respect. This paper will show that the point of origin of proportional back-calculations should either be determined biologically or be located on a central axis that is symmetrical with respect to fish length and scale radius, computed from a sample that is symmetrical transversely to that axis when plotted with an absolute slope of 45° .

The argument will be in terms of radial distances measured on a scale from the central focus to successive annuli and to the scale margin, which is the measurement usually used for ctenoid scales. However, the treatment applies equally to such other scale measurements as may be appropriate for individual species. It will not necessarily apply to growth *during* any growing season, almost certainly not if this includes more than

one “stanza” of development (Ricker 1979), although this rarely occurs at ages beyond 0, certain anadromous fishes being the principal exception.

Terms and abbreviations to be used are as follows:

- L = length of a fish,
- \bar{L} = average length of an age-group or a population
- ΔL = an increment of length during 1 yr
- S = radius of a scale, measured from focus to margin
- \bar{S} = average radius of scales used for age determination
- ΔS = an increase in radius during 1 yr, measured between successive annuli on a scale
- FSC = a fish–scale combination used in back-calculation
- C-sample = an assemblage of FSCs that constitute a sample taken from a fish population for the purpose of back-calculation; also called, when plotted, an array of (L_C , S_C) observations
- Centroid = the point described by the mean of L and S in a C-sample, or in any portion of it
- L_C = length of a fish in a C-sample

S_C = radius of a scale from the above fish
 L_i = length of a fish at age i
 S_i = radius of a scale at age i
 OR = an ordinary least-squares regression line, or its slope
 GMR = the geometric mean regression line, or its slope; also called the standardized, or reduced, major axis (of an L - S array)
 AMR = see Appendix 2
 K = the intercept of an L - S regression line on the L -axis
 Q = the intercept of an L - S regression line on the S -axis.

Symbols and concepts to be used are as follows, where L and S are measured from their means:

Σ = summation symbol
 N = number of FSCs in an age-group or in a whole C-sample
 b = OR of L on S : $\Sigma LS / \Sigma S^2$
 d = OR of S on L : $\Sigma LS / \Sigma L^2$
 r = coefficient of correlation between L and S : $(bd)^{1/2}$
 s_L = standard deviation of L : $[\Sigma L^2 / (N - 1)]^{1/2}$
 s_S = standard deviation of S : $[\Sigma S^2 / (N - 1)]^{1/2}$
 v = GMR of L on S : $[\Sigma L^2 / \Sigma S^2]^{1/2} = (b/d)^{1/2} = s_L / s_S$
 $1/v$ = GMR of S on L .

2. The Basis of Linear Back-Calculation

Back-calculations of fish length (L) from scale annuli (S) are made from a sample of fish taken from a population, here called a "C-sample." The necessary characteristics of such a sample are discussed in Section 4. The basic premise to be used is that which is stated or implied in most if not all linear back-calculations, namely, that after the first annulus is formed, for each fish-scale combination (FSC) the annual increment of $S(\Delta S)$ is directly proportional to the annual increment of $L(\Delta L)$. This of course implies that there will be a linear relation between L and S . However, L will not necessarily be proportional to S . In other words, a line relating L and S need not pass through the origin of the graph. Usually it will intersect the L -axis at a positive value of L ; call this K .

If we were dealing with only one fish and one scale that were measured in successive years, obviously $\Delta L / \Delta S$ would be the slope of the line relating L and S . Two or more FSCs can differ in two ways: their L - S relationships can have different slopes,

or different K -values, or both. Among those that have the same $\Delta L / \Delta S$ but different K -values, the L - S relationships (trajectories of Campana 1990) will of course all have the same slope (Table 1; lines 2-4 of Fig. 1). For FSCs that have the same K -value but differ in $\Delta L / \Delta S$, the L - S trajectories radiate from the point K on the L -axis (Fig. 2). Such slope differences are a result of differences in scale size at a given fish length, either because the scales are from different positions on a fish's body or from fish-to-fish variability even at one position. FSCs can of course differ both in slope and in the position of the intercept K (Fig. 1).

Back-calculation of the size of each fish from its own L - S relationship is not practical, and indeed would be pointless: if we know L and S for each age, there is nothing to calculate. However, what is available is not the magnitude of L and S for each FSC at successive ages, but only the magnitude of L and S at capture (L_C , S_C) for fish of as many ages as are available in the C-sample. If the sampled fish were all taken outside of the growing season, so that the edge of the scale marks the position of the final year's annulus, then the average linear relation between \bar{L}_C and \bar{S}_C over several ages can be used to represent the average linear relation between \bar{L}_i and \bar{S}_i in the population. If the sample is taken during the growing season, but all at one time, then the \bar{L}_C - \bar{S}_C relation can still be used, although with slightly less assurance (Section 11c).

In order to obtain a trajectory from which to calculate L from S at all ages, it is only necessary to locate the best value for L when $S = 0$. Because this point cannot be located for each FSC separately, an overall average value must be used. Two types of estimate have been employed: biological and mathematical. Fraser (1916) examined young chinook salmon (*Oncorhynchus tshawytscha*) and found that the average length at which a scale was first formed (more exactly, the length at which its focus was first established) was 2 in. (50.8 mm). This he considered to be the value of \bar{L} when $\bar{S} = 0$, so he made proportional calculations from that point. This implies that $\Delta L / \Delta S$ has the same value *within* age 0 as it has *between* later ages, but there is practically no possibility of significant back-calculation error from failure of this assumption (cf. Section 8). Recently, Campana (1990) has proposed using a biological origin for back-calculating from otoliths, which differ from scales in that they are usually already formed when a fish hatches. Thus, his bio-

TABLE 1. Patterns of increase in length of fish and scale over 4 yr, with means and standard deviations (s). Rows 1-5 compare three FSCs having the same $\Delta L / \Delta S$ but different values of L and S at age 1, with their variability in length increasing from age 1 to age 2 and decreasing from age 3 to age 4. Rows 6-10 compare FSCs having different values of $\Delta L / \Delta S$ but the same length increments throughout life: they could be three different scales from the same fish. L = fish length (cm); S = scale radius (mm).

$\Delta L / \Delta S$	Age 1		Age 2		Age 3		Age 4	
	L	S	L	S	L	S	L	S
10	20	0.5	35	2.0	55	4.0	70	5.5
10	30	1.0	50	3.0	70	5.0	80	6.0
10	40	1.5	70	4.5	90	6.5	95	7.0
Mean	30	1.0	51.67	3.167	71.67	5.167	81.67	6.167
s	10	0.5	17.56	1.258	17.56	1.258	12.58	0.764
40	25	0.5	45	1.0	65	1.5	75	1.75
20	25	1.0	45	2.0	65	3.0	75	3.5
10	25	2.0	45	4.0	65	6.0	75	7.0
Mean	25	1.167	45	2.333	65	3.500	75	4.083
s	0	0.764	0	1.528	0	2.291	0	2.673

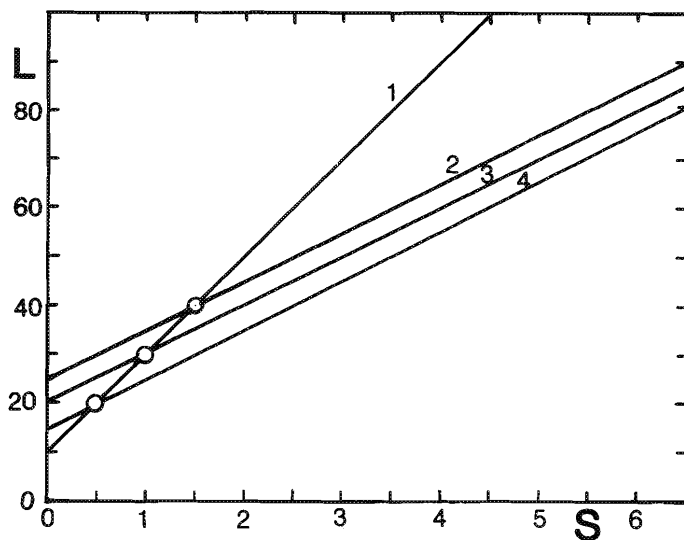


FIG. 1. Diagram of L - S trajectories that pass through three different values of (L_i, S_i) , shown as open circles. Lines 2-4 all have $\Delta L/\Delta S = 10$ and meet the L -axis at three different points: $K = 25, 20$, and 15 . Line 1 has $\Delta L/\Delta S = 20$; it happens to pass through all three values of (L_i, S_i) and meets the L -axis at $K = 10$. L = length (cm); S = scale radius (mm).

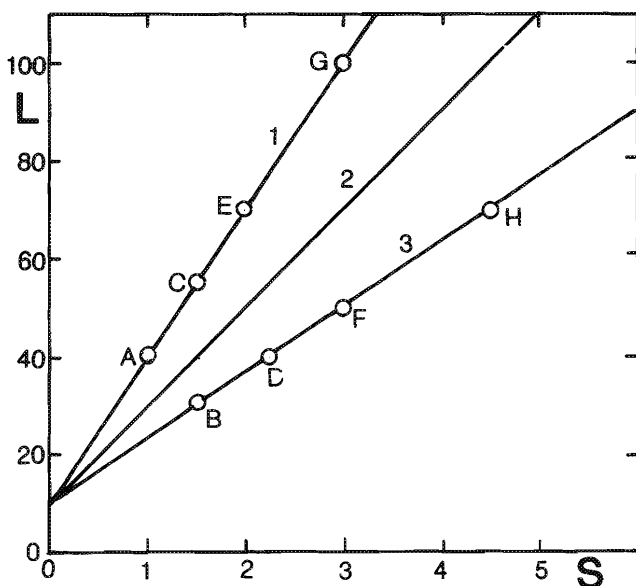


FIG. 2. Diagram of three L - S trajectories, all having a common point of origin ($L = 10, S = 0$) but different values of $\Delta L/\Delta S$, as follows: 1, 30; 2, 20; 3, 13.33. Line 2 has an absolute slope of 45° . See Appendix 2 regarding points A-H. Units as in Fig. 1.

logical origin is "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."

In many investigations, fish of age 0 are not available for study, so these biological methods cannot be used. Lee (1920) was the first to estimate an origin for back-calculation trajectories by extrapolating a linear relation between L_c and S_c back to its intercept on the L -axis. The problem here is, what line should be used? Lee used the ordinary regression (OR) of L_c on S_c , and most later writers have done the same. However, because there is no reason to consider either L or S as dependent on the other, the necessary characteristic of any line that

describes the average relation between the two is that it should be *symmetrical* with respect to L and S , in the sense that if L and S are interchanged, the estimated slope is replaced by its reciprocal. Only if this is true will the line pass through or close to the points (\bar{L}_i, \bar{S}_i) , the average value of L and of S for each age-group represented. And because we need an average value of L at $\bar{S} = 0$ on which to anchor the individual $\Delta L/\Delta S$ trajectories, only a symmetrical axis will be able to provide what is required.

Two types of estimate of this symmetrical axis are available. One is the geometric mean regression (GMR), which is the ratio of the standard deviations of L and S , that is, a measure of the vertical dispersion of the observations divided by their horizontal dispersion (or vice versa, depending on how the coordinate axes are labelled). A second type of symmetrical estimates of the central axis of a sample are the arithmetic mean statistics (AMRs) described in Appendix 2.

3. Frequency Distributions of Fish Length and Scale Radius

Experience with numerous populations of centrarchid, percid, and salmonid fishes has indicated that most of their length distributions are reasonably symmetrical about a central value at each age. Examples are shown for bluegill (*Lepomis macrochirus*) in fig. 3.2 of Ricker (1975) and for yellow perch (*Perca flavescens*) in table 2 of Hile and Jobes (1941); the latter have a much greater dispersion relative to the mean because they include fish taken at different seasons and in different years. In any event, a normal (Gaussian) distribution makes a convenient model for illustration.

Consider then a C-sample taken from all the ages in a fish population. Typically it will consist of a series of near-normal length distributions, most or all of them overlapping. If values of L in an age-group are normally distributed or nearly so, values of S will have a similar shape. If the correlation between L and S were perfect, the points on a graph of L against S would all lie on a single straight line; but because the correlation is always less than perfect, what we get is a series of overlapping elliptical or near-elliptical arrays of observations, one for each age.

The usual pattern for growth in length of a year-class of fish is an increase in variability during the first few years and later a decrease in variability as the initially slow-growing individuals tend to catch up. If all the FSCs in a year-class had the same value of $\Delta L/\Delta S$, the size of the L - S ellipses would first increase and later decrease, following the above trends (upper five rows of Table 1). However, when scales of different sizes are used so that $\Delta L/\Delta S$ varies between FSCs, the ellipses become larger with age. The lower five rows of Table 1 show that an increase in the variability of S would then occur even if all the fish increased in length at the same rate. A similar schedule would show that the fish would increase in length variability even when FSCs are compared whose scales all have the same pattern of increase in radius.

A mortality rate, either natural or from fishing, that varies with size within any age-group of a year-class can also change the shape of an L - S array. However, this may have less effect than one might suppose: Jones (1958) showed that a linear type of size-selective mortality gradient does not change a normal distribution of length in an age-group, or even reduce its standard deviation, although it does shift the mean (illustrated in table 2 and fig. 2 of Ricker 1969).

If the value of $\Delta L/\Delta S$ is independent of the length of each FSC within an age-group, then the major axes of the L - S ellipses for each age will all conform to a single straight line, within limits of sampling error. If, however, $\Delta L/\Delta S$ is correlated with L (and with S) within an age-group, such alignment will not occur. Specifically, if $\Delta L/\Delta S$ is smaller among the slow-growing fish, the slope of the major axis at each age will be less than that of the overall axis that joins the centroids of successive ages. Conversely, if slow-growing fish tend to have relatively larger scales, then the within-age major axes will have greater slopes than the overall axis. The latter situation has been found for the *otoliths* of a number of marine species, in studies cited by Campana (1990), but I know of no similar studies for scales.

In any event the (L_c , S_c) observations in a C-sample form an elongate band. This can be quite narrow if L and S are closely related ($r = 0.96$ – 0.99). This can occur when "key scales" are used, taken from a fixed position on a fish's body (see, for example, fig. 1 of Lindroth 1963), and the range of lengths present is large. If, however, the size of the scales used and hence $\Delta L/\Delta S$ varies considerably, the band of (L_c , S_c) observations will be broader, on the whole, and will probably increase in breadth from age 1 onward.

4. Characteristics of a Good C-Sample

Whereas we want back-calculated lengths to apply to the whole of a fish population, the regression line used in computations has to come from the C-sample taken from that population. Although one or more different segments of a population may sometimes be sampled randomly, using different kinds of apparatus, it is impossible to obtain a random sample of an entire population in the wild, even when age 0 is excluded (as is desirable because they have not yet formed an annulus). Moreover, the relative number of fish of different ages in a population is continually changing. Apart from that, a random sample of an entire population older than age 0 would not be the best C-sample, for fish of age 1 or 2 are sometimes numerous enough to have disproportionate influence. On the other hand, we would not want the sample to include equal numbers of fish of every age because this would give too much weight to the larger ones.

The best solution appears to be to aim at a more or less equal number of L - S observations at equal intervals of length, but it is not important that this rule be followed closely if a symmetrical axis is used for back-calculation and the C-sample is or has been made symmetrical about that axis when at 45° absolute slope (Section 5).

What should be avoided, if possible, is including in the sample fish taken at different times during the growing season. Such mixtures would, strictly speaking, require that $\Delta L/\Delta S$ be constant not only from year to year but also within the year whereas Francis (1990) cited several studies in which small deviations from within-year constancy were observed. But often, of course, an investigator has little choice and must use whatever scales come from routine sampling of sport or commercial catches. A fairly common type is shown in Francis's fig. 1, where there is a concentration of points at either end of the array and fewer in between (Appendix 1).

Although C-samples cannot be random samples of a whole population, it is essential that they be reasonably close to symmetrical transversely to their own (and the population's) central axis when this axis is plotted with an absolute slope of 45° . The reason for this stems from a basic characteristic of an array of

points. Most of the lines that have been fitted to an L_c - S_c array maintain their position, relative to the observations, regardless of the units used for L and S and regardless of the scale intervals chosen for plotting. Examples are the two ORs, the GMR, and the AMRs. These can be called *conformable* lines. However, lines drawn at right angles to a conformable line are *not* conformable. If such a line is used to divide an array into two halves, the identity of the observations in the two divisions will differ, depending on what absolute slope that line may happen to have when plotted (cf. fig. 2 and 3 of Ricker 1984). Thus, a standard slope for the axis is necessary, and the only possible choice for this role is 45° . At this absolute angle the GMR coincides with another well-known (but nonconformable) line, the ordinary major axis or apparent trend of an array. Thus, at 45° the GMR is an estimate of the central axis of a symmetrical array, both in fact and in appearance.

5. Samples Truncated by Length

If a C-sample is truncated at or in the region of a particular length by the nature of the sampling apparatus, the *apparent* extent of the truncation will vary with the absolute slope of any conformable trend line plotted, and at some slopes even the existence of truncation may not be recognizable. When the C-sample is plotted with a slope close to 45° , it is possible to recognize reasonably accurately, by eye, the region affected by truncation and to reject all observations in this region. This may be done either by rejecting the whole of the age-group(s) affected or by drawing a line transversely to the axis of the *unaffected* region when it is plotted at 45° absolute slope.

In general, it is not easy to find measurement units or graph paper intervals that give a set of L_c - S_c points a slope really close to 45° , but a less than perfect line can be used for a preliminary assessment and removal of any obviously asymmetrical points, after which a new line can be fitted and a new assessment made. If an exact diagram of the points with a 45° axis is desired, the observations of L and S can each be divided by its own standard deviation, in which case the plotted axis will have an absolute slope of 45° and a numerical value of 1. Presumably a computer could be programmed to do this work with dispatch.

Once assured that the L - S array is, or has been made, symmetrical, the observations in their original units can be used to estimate either the GMR or an AMR because both are "conformable" statistics.

If two or more sampling methods have contributed to a C-sample, as is usual, there can be truncation by length in the middle of the sample as well as at the ends. However, truncation in this region has much less effect on the overall slope of regression lines than does truncation at the extremes and can almost always be ignored. Moreover, truncation at the upper end of the lower of two component samples will tend to be compensated by truncation at the lower end of the upper one, assuming both types of truncation are present.

6. Which Regression?

The regression line that has most frequently been used to establish an intercept for back-calculation is not either of the symmetrical lines, but is the OR of L on S . The reason is, presumably, that for a bivariate normal C-sample, it provides the best estimates of L from S in that sample. But C-samples are not often close to bivariate normal, and when they are, it

reflects the type of sampling done rather than the structure of the population sampled. Thus, an OR does not estimate a property of a fish population in the way that symmetrical statistics do.

To illustrate, consider a C-sample with observations reasonably symmetrical transversely to the 45° axis of the array and fairly evenly distributed along that axis. Such a C-sample's axis passes through or close to each age's average length in the population whereas the ORs do not. Specifically, the OR of L on S gives estimates of \bar{L}_i that are too large at scale sizes less than the mean of the C-sample (\bar{S}) and too small when S is larger than \bar{S} . The error increases with distance from \bar{S} in both directions, although it will not usually be very large even at the extremes if all ages are included in the sample.

Note that when the OR of L on S is used instead of a symmetrical statistic, the average annual increase in length will be overestimated for age 0, but at all later ages it will be too small, simply because the slope of an OR is always less than that of the array's central axis.

The bias of an OR is more serious when the distribution of observations in the C-sample is not at all uniform over the range of fish and scale sizes in the population. For example, a fairly common deficiency of C-samples is failure to include one or more of the younger annulus-bearing ages. In that case the OR of L and S may give estimates of \bar{L}_i with only a small amount of bias in the ages sampled, but they can become grossly inaccurate when the line is extrapolated to unsampled ages. If observations at the younger ages become available and are added to the sample, the centroid is shifted toward them and the slope of the OR becomes greater, both of which changes will decrease the estimates of \bar{L}_i at the previously missing ages.

More generally, if older fish predominate in a sample, the centroid will be situated close to them and the two OR lines will be far apart at the younger ages. If younger ages predominate, the centroid shifts to smaller sizes, and the two ORs come closer together at the younger ages and are farther apart at the older ones. The symmetrical regressions, however, are not changed by such moves, except for random shifts resulting from the improved accuracy provided by each increase in size of the total sample.

Carlander (1982, his fig. 1) shows the distribution of published values of the intercept K that have been estimated from the OR of L on S by various authors for six centrarchid and one percoid species. These typically range from 10 to 50 or 60 mm, with a few even more extreme values. The situation seemed so unlikely and unsatisfactory that Carlander proposed using a standard value of K (his a) for each species (his table 1). These are averages of the estimates that he considered to be most reliable, and he noted that if GMRs had been used, they would have been smaller. Actually, even using the ORs, smaller K -values would have been obtained if all the samples had contained fish of sizes down to the smallest of age 1, so that the slopes of the ORs would be steeper and the centroids of the arrays would be shifted toward the L -axis, both of which reduce the estimate of K . Elimination of any artificial truncation by length that may have been present at either end of the arrays would also reduce K -estimates made from either an OR of L on S or from the GMR. Thus, Carlander's excellent initiative could probably be improved by reducing the standard values of K , perhaps by 10–20 mm for different species. However, it seems best to wait for a few new or revised estimates of K for each species, based on symmetrical L_C - S_C axes of symmetrical C-samples.

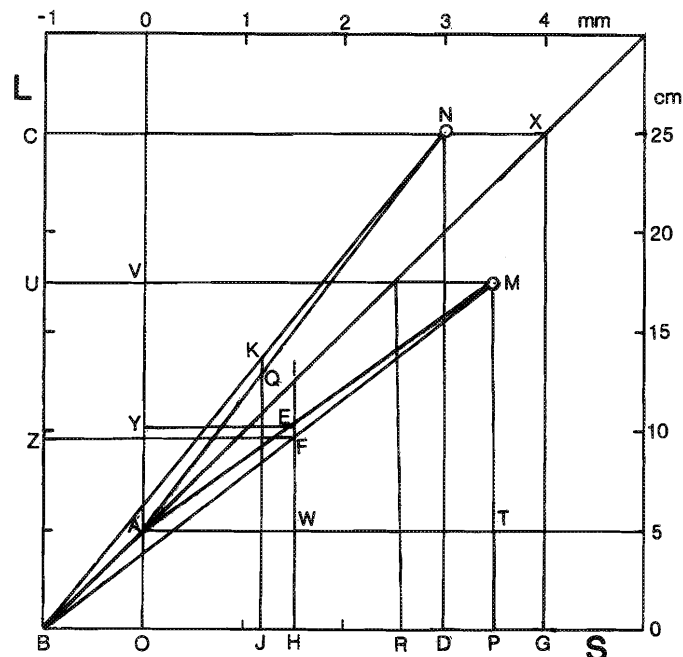


Fig. 3. Illustration of back-calculations of lengths from scales (M and N) that lie on either side of a symmetrical relationship (line BAX) between fish length (L) and scale radius (S).

7. Back-Calculation of Mean Lengths of Age Groups

The principal object of most back-calculations is to estimate the average length of each age-group in a sample at the successive ages indicated on the scales. These can be computed from average annulus measurements using a symmetrical axis directly. The expression for computation of average lengths is

$$(1) \quad \bar{L}_i = K + v\bar{S}_i$$

where v is the slope of the axis of the symmetrical C-sample, estimated by the GM or AM method, K is that axis's intercept on the L -coordinate axis, \bar{S}_i is the mean of the annulus measurements at age i , and \bar{L}_i is the age- i average length to be estimated from \bar{S}_i .

8. Back-Calculation of Length for Individual Fish

Back-calculations for individual fish are usually done along $\Delta L/\Delta S$ trajectories that join each (L_C, S_C) point to an origin where $S = 0$. The value of L when $S = 0$ cannot be estimated for each FSC individually, so an average value must be used. This has been obtained either by direct measurement on age-0 fish or, more often, by extrapolating a line fitted to a series of (L_C, S_C) observations (Section 2).

For example, in Fig. 3, line BAX represents such a (symmetrical) fitted line, and OA is the average value of L when $\bar{S} = 0$. Point M represents a scale whose radius (OP) is greater than the age-group average radius (OR) for a fish of its length (OV) and OH is the distance from its focus to the first annulus. Then because line AEM is a diagonal of both of the similar rectangles $AYEW$ and $AVMT$, $AY/AW = AV/AT$. Changing to the symbols used up to now, and generalizing to any age i , this becomes

$$(2) \quad \frac{L_i - K}{S_i} = \frac{L_C - K}{S_C}$$

where S_C and L_C are scale and fish size at capture, K is the L -axis intercept of a line relating L_C and S_C in a C-sample, and L_i is the fish length to be estimated from a scale annulus at S_i . This method of back-calculation can be called the Fraser-Lee method, using that name in a broad sense to describe any computation whose parameter is an L -axis intercept K , regardless of how the position of K is determined. Some authors seem to restrict the term Fraser-Lee to computations which determine K from the OR of L_C on S_C , but this is inappropriate because Fraser (1916) used a biological method to estimate K whereas Lee (1920) was the first to use a mathematical method, although she too made some reference to observations on age-0 herrings.

An alternative, although rarely used, method of computing individual lengths, proposed by Whitney and Carlander (1956), uses the intercept of an average L - S relation on the S -axis as the point from which all the $\Delta L/\Delta S$ trajectories radiate. For example, in Fig. 3 the line BFM is a common diagonal of rectangles $BZFH$ and $BUMP$, so that $BZ/BH = BU/BP$. Bearing in mind that OB is negative, and generalizing to any age i , this becomes the expression

$$(3) \quad \frac{L_i}{S_i - Q} = \frac{L_C}{S_C - Q}$$

where Q is the S -axis intercept of a line relating L_C and S_C , and the other symbols are as for expression (2). The term Whitney-Carlander method also is used here in a broad sense to describe all expressions whose parameter is an S -axis intercept.

In the Fraser-Lee computation, each scale radius is adjusted to the average radius for a fish of its length; hence it has been called a "scale-proportional" or SPH method by Francis (1990). The Whitney-Carlander method he calls "body-proportional" or BPH; in it, each fish length is adjusted to the average length of fish that have the radius measurement of the scale being used. He also suggested that the SPH method requires that the L - S relationship used to estimate K be the OR of S on L rather than the commonly used OR of L on S but that the BPH method should use the OR of L on S to estimate Q . On this basis the two methods tend to give quite different computed values of L_i , especially at the younger ages (Appendix 1). Francis associates the two methods with two different hypotheses but can suggest no criterion for choosing between the two, which leaves everyone in an uncomfortable quandary.

The thesis of this paper is that, whatever their statistical credentials, neither of the ORs is appropriate for establishing an average point from which proportional back-calculations are to be made. The reason is simply the the ORs diverge increasingly from the mean value of fish length and scale radius (\bar{L} , \bar{S}) at the youngest ages; hence, extrapolating them into the age-0 region and beyond cannot possibly estimate either \bar{L} when $\bar{S} = 0$ or \bar{S} when $\bar{L} = 0$. Instead, the same symmetrical axis should be used for both the Fraser-Lee and the Whitney-Carlander methods.

However, there is still the problem of choosing between the two methods, or for that matter, choosing some position on the L - S axis other than K or Q as origin for proportional back-calculations. In the latter event, a computation similar to expression (2) or (3) would require two parameters:

$$(4) \quad \frac{L_i - L_p}{S_i - S_p} = \frac{L_C - L_p}{S_C - S_p}$$

where (L_p, S_p) are the coordinates of the point on the C-sample's central axis that has been chosen to be the origin for propor-

tional back-calculations. (Campana's (1990) similar expression (4) gives the same result, but when rearranged in the form and with the symbols of expression (4) here, it has L_C and S_C instead of L_p and S_p on the left-hand side.)

Fortunately, for practical purposes it is not important to know exactly where the best average point of origin for the individual $\Delta L/\Delta S$ lines is located on the C-sample's central axis. This can be illustrated by comparing the calculation made by the Fraser-Lee and Whitney-Carlander methods in Fig. 3, using two FSCs whose $\Delta L/\Delta S$ trajectories deviate rather widely from the central axis. For the FSC at point M the age-1 computed length using the Fraser-Lee method is HE whereas using the Whitney-Carlander method it is HF , the difference being EF , about 6 mm. Similarly for point N , for the first annulus at J the Fraser-Lee estimate is JQ and the Whitney-Carlander estimate is JK , again a difference of 6 mm. These can be considered unlikely maximum differences, not only because M and N are distant from the axis, but also because $K = 5$ cm and $Q = -1$ mm are rather extreme values for a species of the size indicated. (Compare $K = 1.90$ cm and $Q = -0.341$ mm for the herring of Appendix 1.) The differences at older ages are all less than 6 mm because the $\Delta L/\Delta S$ trajectories converge on points M and N . Also, the differences have opposite signs on either side of the central axis, so that *there is no average difference at all between the two types of calculation* as long as the same symmetrical central axis is used to obtain the intercepts for both.

We may conclude that either the Whitney-Carlander or the Fraser-Lee method will usually or always provide usable back-calculated lengths. However, Fraser-Lee is preferable because K describes, approximately at least, an objective point in the development of the fish: the beginning of scale growth, whereas Q implies a group of fish of zero average length!

9. Random Sampling Variability

As far as I know, there has been no statistical examination of distributions resembling the overlapping ellipse-like arrays suggested above. If from a C-sample, computations of L for individual fish are made using expression (2) or (3), the variances of these estimates at each age can be computed directly, those from expression (3) being slightly larger than those from expression (2). However, in both cases there is additional variability that comes from the sampling error of the position of the C-sample's GMR or AMR line.

The variance of a GMR is the same as that of the corresponding OR, which can be computed by standard methods. Hence, a minimum estimate of the variance of a point on a GMR could be obtained, for orientation, by using the standard formula for the L -variance of a point on the C-sample's OR of L on S . When correlation is large, a GMR and the corresponding OR are not far apart; hence the L -variance of a point on the GMR at a given value of S should be similar to, but somewhat greater than, that of the corresponding point on the OR. Specifically, the L -variance of the point (\bar{S}_i, \bar{L}_i) can then be added to the age- i variance of L that was computed as in the preceding paragraph.

Even the best possible estimates of the variances of computed L_i and \bar{L}_i , when they become available, will not express the whole of the uncertainty in back-calculations. Another source of error, which may be either random or biased, is the misreading of ages. In duplicate tests, different readers rarely if ever agree completely about any long series. Also, the GMR or AMR that is used may be somewhat biased in relation to that of the population, in spite of the precautions and adjustments

discussed earlier. These possibilities make it all the more important to avoid introducing a known source of systematic error by using the wrong line in back-calculations. This is particularly important if L and S are not closely correlated, and C-samples with correlations less than 0.9, or even less than 0.8, have in fact been used.

10. Lee's Phenomenon

Lee's phenomenon (LP) of "apparent change in growth rate" is a tendency for back-calculated lengths at any age to be smaller, the larger the fish from which they were calculated. It was reported for sprats by Sund (1911) and for herring, haddock, and trout by Lee (1912). Both authors had made their back-calculations assuming direct proportionality between L and S . Later, Lee (1920) showed that part of what they observed was a computational artifact. When lengths are calculated by direct proportion, so that K of expression (2) is put equal to 0 when in fact it has a positive value, back-calculated lengths automatically become smaller, the larger the fish from which they are calculated. More generally, LP occurs whenever K is assigned a value less than the best one, estimated biologically or from a symmetrical regression line. Conversely, if K is assigned a value greater than the above, it produces "inverse LP," a tendency for calculated lengths to be larger, the larger the fish from which they are calculated.

Much the commonest departure from best back-calculation procedure has been putting K equal to the L -axis intercept of the OR of L_C on S_C instead of to the (always smaller) intercept of a symmetrical regression line. By itself, this produces *inverse* LP. In spite of this, *direct* LP is of very frequent and widespread occurrence among published back-calculations, while *inverse* LP is uncommon. This indicates that there is some other mechanism causing direct LP, usually powerful enough to reverse the effect of using too large a value of K . Lee (1920) suggested that this could be the effect outlined by Lea (1913), based on successive annual recruitments, of the larger of the still unrecruited members of a year-class, to the mature schools that were sampled. A more generally applicable explanation is the one proposed by Sund (1911) that the faster-growing members of a year-class have a greater mortality rate (natural or from fishing) than slow-growing ones, during part of their life at least. It is also possible for a stock to exhibit *inverse* LP in early life, when the smaller fish are more vulnerable to predation, and *direct* LP later (Ricker 1975, section 9.4.1).

11. Discussion

(a) Campana (1990, his fig. 3) showed that when faster-growing fish have smaller otoliths (T) at any given length (L) within an age-group, any line describing the trend of (L , T) observations for that group will deviate from the average value of $\Delta L/\Delta T$; hence, it would not be a suitable line for establishing a point of origin for proportional back-calculations. Campana was interested especially in the growth of fish during their first year of life, for which this effect could be important, so he proposed using the biological point of origin described in Section 2 above. It has yet to be shown that fast-growing fish have relatively smaller (or larger) scales, but even for otoliths the effect will be very much less important when an axis is fitted to (L_C , T_C) observations for several ages, as compared with a single age. And if the axis is fitted to the *means* of the (L_C , T_C)

observations for each age, there should be no bias at all (Appendix 2).

(b) We of course wish all back-calculated lengths to refer to a standard time of year: the period between the formation of an annulus and the start of the next year's growth. If the scales available were taken *during* a growing season, it becomes necessary to know or to assume that $\Delta L/\Delta S$ is constant throughout that interval, although small deviations from within-age linearity have been described in several papers cited by Francis (1990). However, trial calculations suggest that, for practical purposes, the assumption of within-age uniformity of $\Delta L/\Delta S$ will almost always be satisfactory. Only part of the final year's increment in length is affected for each FSC; for all earlier years the complete year's growth is obtained from the annulus-to-annulus distance.

(c) As defined here, ΔL and ΔS are increments of length and of scale radius during 1 yr. This needs to be modified slightly because it has been observed, for some populations at least, that growth of a scale beyond an annulus begins somewhat later in the growing season as a fish becomes older. Thus, an annulus-to-annulus year may be longer than a calendar year by up to a week or so. This effect emphasizes the need for caution in determining ages during the early part of the growing season, especially among the larger fish.

(d) The development of a fish from the fertilized egg onward can be divided into several stages of *stanzas* that are separated by some abrupt change in morphology or rate of growth. The transition between stanzas may be either severe (as in eels) or merely a change in the relative growth rate of body parts (Ricker 1979). The latter kind of change happens in some species of salmonid fishes when they enter salt water. If this occurs during or at the end of the first year of growth, as in many *Oncorhynchus*, it is not a problem for back-calculations that go back only as far as the first annulus. However, there are species or stocks that spend 2 or more yr in freshwater before going to sea, for example many *O. nerka* and most stocks of *Salmo salar*. For the latter, Lindroth (1963, his fig. 2-4) showed that scale measurements, plotted against fish length, have a greater slope during their freshwater life at 40-200 mm than they have later in the ocean. Hence, back-calculations would have to be made separately for these two stanzas.

(e) If all age-groups in a population were to be randomly sampled at the end of a growing season, and if the survival of fish in an age-group is not related to their size, then \bar{L}_C should be an estimate of \bar{L}_i at each age i , in which event it would not be necessary to make back-calculations. Thus the reasons that back-calculations are needed are three: (1) most samples are taken within a growing season, so back-calculation is needed to estimate length at the end of the last complete year of growth; (2) *random* samples of all ages in a population are rarely available; in particular, samples from the younger ages often include more of the larger individuals of those ages, and sometimes one or more ages are completely absent; (3) growth rate and survival rate frequently are correlated, usually negatively, in which event the mean back-calculated size at a given age is smaller, the greater the age of the fish from which it was calculated ("natural" LP, assuming unbiased back-calculation procedure). The correlation may have a physiological or ecological cause, or be a result of selective fishing, or any combination of these. Hence, back-calculated sizes should be separated on the basis of the total age of each FSC, in order to determine whether natural LP is present. If it is, then the problem of decid-

ing what is to be an average growth rate at each age is difficult, but must be faced (Ricker 1969, 1979). Under these conditions, comprehensive expressions like the Gompertz or Pütter (Brody-Bertalanffy) curves, fitted to the observed lengths of the survivors at each age, will indicate growth that is slower than the actual from age 1 onward.

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Appendix 1. Statistics from the Herring Example of Lee (1920) and Francis (1990)

Lee's appendix table II includes 200 North Sea herring. Francis plotted these as an L - S array in his fig. 1, and his regression equations for them are (1) OR of L on S : $L = 2.93 + 52.4S$ and (2) OR of S on L : $S = -0.0134 + 0.0169L$ (both L and S are in centimetres). The centroid of the array is where these lines cross at $\bar{S} = 0.3156$, $\bar{L} = 19.47$, found by solving the

simultaneous equations. The correlation between L and S is $(52.4 \times 0.0169)^{1/2} = 0.941$, and the GMR of L on S is $(52.4/0.0169)^{1/2} = 55.68$. Passing a line of this slope through the centroid gives the GMR equation for L on S as $L = 1.897 + 55.68S$ and that for S on L as $S = -0.03407 + 0.01796L$, two expressions for the same line.

The observations used in the herring back-calculation are $L_C = 28.5$ cm, $S_C = 0.41$ cm, $S_1 = 0.17$ cm. Using the Fraser-Lee or SPH method with the OR of S on L , so that K of expression (2) is $0.0134/0.0169 = 0.793$, Francis (p. 892) computed $L_1 = 12.28$ cm; using Whitney-Carlander or BPH with the OR of L on S , so that Q of expression (3) is $-2.93/52.4 = -0.0559$, he obtained $L_1 = 13.82$ cm, a difference of 1.54 cm.

Using the GMR equation above, the L -axis intercept is $K = 1.897$; hence, from expression (2), $L_1 = 12.93$ cm. Similarly the S -axis intercept of the GMR line is $Q = -0.03407$; and from expression (3), $L_1 = 13.10$ cm. Thus the difference between these Whitney-Carlander and Fraser-Lee computations, using the GMR line, is only 0.17 cm at age 1 and would be progressively smaller at older ages. Also, the difference would be negative for any scale from that fish that was larger than 0.48 cm, which is the average scale size computed from the GMR line using $L_C = 28.5$ cm.

It may be worth noting that if the two ORs were to be used in the traditional manner, i.e. opposite to Francis's recommendation, the difference between their computed values of L_1 is reduced, but not by much. In that case, for SPH, $K = 2.93$ and $L_1 = 13.53$ cm and for BPH, $Q = -0.0134$ and $L_1 = 12.35$ cm. The difference is 1.18 cm instead of 1.54, and the SPH value is of course now larger than the BPH.

Appendix 2. Comparison of Arithmetic Mean and Geometric Mean Regression Lines

Seeking a central trend line or axis that would be symmetrical with respect to Y and X variates, Wald (1940) proposed dividing an array of Y - X observations into two halves and joining their centroids. A little later, K. R. Nair and colleagues (e.g. Nair and Banerjee 1942) proposed dividing the array into three parts and joining the centroids of the two outer portions. Bartlett (1949) adopted Nair's proposal and improved it slightly by passing a line of Nair's slope through the centroid of the entire array. All of these procedures were shown to be consistent estimates of the same central axis, the Nair-Bartlett procedure being somewhat more efficient, at least for large samples. It is also true that any other symmetrical division of a symmetrical array, with or without omission of a section of it, will produce a consistent, although less efficient, estimate of the same central trend line (Wald 1940).

However, as originally described, these AM methods all overlooked a practical difficulty. In order to be symmetrical, they must divide an array transversely to a central axis plotted at 45° absolute slope, which axis's position has yet to be established. To meet this, a trial division can be used first, its position corrected by successive iterations; usually, one is sufficient. Another problem is that with large arrays there can be difficulty in deciding on which side of a division line a particular observation lies.

These problems can be avoided if an array is naturally subdivided into segments, which may even overlap somewhat. Because (L_C, S_C) observations in a C-sample are structured by age, a simple way to apply the Wald method is to combine the

ages into two groups having numbers of observations as nearly equal as possible and then join their centroids to obtain an estimate of the symmetrical slope of the array. With this procedure, it is not necessary that the individual ages be symmetrical about the C-sample's 45° axis, although they may well be so; it is only necessary that their means lie on that axis, within limits of sampling variability. Hence, this method could be used if there is appreciable deviation from overall symmetry of the C-sample caused not by selective sampling, but by the existence of a correlation between $\Delta L/\Delta S$ and L within age-groups, or because of an effect of a length-related mortality rate. All AMRs are of course conformable lines, in the sense of Section 4.

The GMR too is conformable and symmetrical. In addition, it is analogous to a least squares estimate in that it minimizes the sum of the areas (all considered positive) of the triangles formed by projecting each observation horizontally and vertically onto the line. Also, if a sample is perfectly symmetrical (i.e. for each point on one side of the 45° axis there is a point opposite and at the same absolute distance from that axis on

the other side) the GMR and the AMRs estimate the same line exactly.

To illustrate this, in Fig. 2 the two pairs of symmetrical points AB and CD have a centroid at ($\bar{L} = 41.25$, $\bar{S} = 1.5625$); similarly, EF and GH have a centroid at ($\bar{L} = 72.5$, $\bar{S} = 3.125$). Thus the Wald estimate of the slope of their central axis is

$$(72.5 - 41.25)/(3.125 - 1.5625) = 20.$$

At the same time the GMR of all the points $A-H$ is

$$s_L/s_S = 22.510/1.1255 = 20.$$

In practice the exact symmetry described above never occurs. We can only make sure that an array *appears* symmetrical transversely to its central axis when that axis is plotted with an absolute slope of 45°. Thus, there are always small differences between AM and GM estimates of a central axis. I prefer the GMR because of its simple form (the ratio of two standard deviations), because it coincides with the ordinary major axis at 45°, because of its similarity to a least squares estimate, and because there is no need to decide how an array should be divided up.