

Back-calculation of fish length: a critical review

R. I. C. C. FRANCIS

Fisheries Research Centre, Box 297, Wellington, New Zealand

(Received 18 April 1989, Accepted 22 December 1989)

A review is made of the literature on the back-calculation of fish body length from marks on scales or other hard parts (otoliths, vertebrae, fin rays, etc.). Though the technique is widely used it does not appear to be well understood. Regression methods are commonly used, apparently in ignorance of the more realistic proportional methods. It is not generally recognized that there are two equally plausible back-calculation hypotheses which can lead to significantly different back-calculated lengths. The Fraser-Lee equation, the most commonly used back-calculated formula, follows neither of these hypotheses but is based on a misuse of linear regression. It is recommended that back-calculation be restricted to procedures following one of the proportional hypotheses; that the difference between lengths calculated using the two hypotheses is a useful measure of the minimum uncertainty in back-calculation lengths; and that more attention be paid to validating back-calculation hypotheses by comparing observed and back-calculated lengths for individual fish. The pattern of heteroscedasticity in body length–scale radius plots is noted as a useful diagnostic in evaluating back-calculation hypothesis.

I. INTRODUCTION

Back-calculation is a technique that uses a set of measurements made on a fish at one time to infer its length at an earlier time or times. Specifically, the dimensions of one or more marks in some hard part of the fish, together with its current body length, are used to estimate its length at the time of formation of each of the marks. The hard parts used were originally scales (Lea, 1910; Lee, 1920) but the technique has since been applied to otoliths (Hickling, 1933; Graynoth, 1987), opercular bones (Le Cren, 1947; Lauzanne, 1978), vertebrae (Tweddle, 1975; Clay, 1982) and fin rays or spines (MacCrimmon, 1979; Antoine *et al.*, 1983; Berkeley & Houde, 1983). The marks are generally annual rings associated with growth checks, but back-calculation has also been used in association with marks caused by the stress of liberation of hatchery fish (Davies & Sloane, 1986) and tetracycline injections in tagged fish (Rijnsdorp & Visser, 1987).

Back-calculated lengths have been used for a variety of purposes. Often the technique is simply a method of increasing the number of length-at-age data to be used in fitting some growth curve (e.g. Shafi & Jasim, 1982; Grudtsev & Korolevich, 1986). For some species, back-calculation allows the estimation of lengths at ages that are rarely observed (e.g. Hickling, 1933; Morales, 1984). Growth curves derived from back-calculated lengths have been used to compare growth rates between sexes (Kraiem, 1982), cohorts (Frost & Kipling, 1980; Beacham, 1981) and populations of the same species (Gee, 1978; Graynoth, 1987), and to relate growth rates to various exogenous factors (Beacham 1981; references in Casselman, 1987: 230). Miranda *et al.* (1987) used the technique to show that anglers tend to catch faster-growing fish. Back-calculation has also been used to test the ageing of fish with annual (Cayré & Diouf, 1981; Van Leeuwen &

Rijnsdorp, 1986) or daily (Geffen, 1986) rings. Gutreuter (1987) showed that "body length explained approximately eight per cent more of the variation in annual length increments than did age for largemouth bass (*Micropterus salmoides*)".

In this paper I review the literature on back-calculation, with an emphasis on the hypotheses that have been advanced to support the technique, and the extent to which these have been validated. Some problems that are of importance in the application of back-calculation are not relevant to these hypotheses, and so will not be considered. In this category are physiological problems, e.g. resorption of scale tissue or occlusion of annual marks, which are sometimes a problem when fin spines are used (Antoine *et al.*, 1983; Berkeley & Houde, 1983), and ageing errors that cause back-calculated lengths to be associated with the wrong ages. Another matter of great practical, but little theoretical, importance is the selection of hard parts of a given type, e.g. more precise results may be obtained in back-calculation from scales when the scales are chosen from a specific area of the body (the term 'key scales' is used) and measured in a particular way (Hirschhorn & Small, 1987). Nor will I enter into the debate on whether different back-calculation equations should be used for separate populations of a given species (Shentyakova, 1969; Hile, 1970) or an attempt be made to produce a single standard equation for the species (Carlander, 1982).

TERMINOLOGY AND NOTATION

Except when quoting the work of other authors, no distinction will be made here between the various hard parts used in back-calculation (e.g. scales, otoliths, vertebrae, etc.): the word 'scale' will be used to stand for them all. Similarly, 'scale radius' will stand for any hard part dimension (e.g. anterior or posterior radius, diameter, square root of area). Though the practical problems and the precision achieved may differ, the theory of back-calculation is the same for all hard parts, and all dimensions.

Let L and S stand for fish body length and scale radius respectively. L_c and S_c will refer to these measurements at the time of capture, L_i and S_i are the corresponding measurements at the time of formation of the i th scale mark, for $i = 1, 2, \dots, n$. A back-calculation formula (BCF) is one that allows the calculation of L_i from L_c , S_c and S_i . It is important to understand that, for a given population, a BCF generally defines a family of lines (which may be straight or curved). Back-calculation for a particular fish will involve just one of these lines, and this allows the calculation of L_i from S_i . Which particular line is used from the family of lines will depend on the values of L_c and S_c .

The relationship between body length and scale radius (the body-scale relationship, for short) is a central part of back-calculation. Two functions describing this relationship will be denoted as f and g : $f(L)$ is the mean scale radius for fish of length L , and $g(S)$ is the mean body length for fish with scale radius S . These functions may be of any mathematical form (linear, quadratic, exponential, etc.); in their most common form, i.e. linear, they will be written as

$$f(L) = a + bL, \text{ and} \quad (1)$$

$$g(S) = c + dS. \quad (2)$$

f may be calculated from the regression of S and L , and g from the regression of L on S .

II. BACK-CALCULATION: HYPOTHESES AND PRACTICES

I will begin by reviewing the historical development of back-calculation, with an emphasis on the hypotheses put forward to support this practice. Particularly important in evaluating these hypotheses will be seeing how they translate into mathematical terms.

DAHL-LEA

The first account of back-calculation appears to be that of Lea (1910) whose method, derived for use on herring, was based on the hypothesis "that the scale grows in exact proportion to the total length of the individual". This may be written as the set of equations

$$L_1/S_1 = L_2/S_2 = \dots = L_n/S_n = L_c/S_c. \quad (3)$$

From these n equations with n unknowns (L_1, L_2, \dots, L_n) we may describe the BCF

$$L_i = (S_i/S_c)L_c. \quad (4)$$

This was developed jointly by Knut Dahl and Einar Lea and so is known as the Dahl-Lea equation. It describes the family of all straight lines passing through the origin. In back-calculating for a particular fish we choose the line which also passes through the point (S_c, L_c).

FRASER-LEE

The next back-calculation hypothesis came from Lee (1920) who examined plots of S against L for a number of species and concluded that a straight line through the data did not, as the hypothesis of Lea (1910) would indicate, pass through the origin. She put forward a new hypothesis: "that the growth increment of the scale is, on the average . . . , a constant proportion of the growth increment of the fish". In symbols this becomes

$$(L_2 - L_1)/(S_2 - S_1) = (L_3 - L_2)/(S_3 - S_2) = \dots = (L_n - L_{n-1})/(S_n - S_{n-1}). \quad (5)$$

These equations indicate that the back-calculation line for a particular fish is a straight line passing through the point (S_c, L_c), but they do not indicate which line. The reason for this inadequacy is that there are n unknowns but only $n-1$ equations. To obtain her BCF, Lee made the further, tacit, assumption that each line must pass through the point ($S=0, L=c$), where c is as in (2). This results in the BCF

$$L_1 = c + (L_c - c)(S_1/S_c), \quad (6)$$

which is known as the Fraser-Lee equation, since Fraser (1916) first described the approach but Lee (1920) was the first to present the equation explicitly.

The derivation of the constant c in (6) is important. Both Fraser (1916) and Lee (1920) described c as the length of the fish at the time of scale formation (the assumption being that this length is the same for all scales from all fish in a given population). However, the current practice of most authors (and that followed by Lee herself) is to set c as the L -intercept of the regression line, (2), rather than from observations on juvenile fish. A number of authors have stated that the c cannot be

given a morphological interpretation (Jones, 1958; Monastyrsky, cited by Hile, 1970; Carlander, 1985; Gjøsaeter, 1986).

An interesting variant on Lee's hypothesis was presented by Monastyrsky who stated that "the increases of the logarithms of the lengths of a fish are proportional to the increases of the logarithms of the lengths of its scales" (Chugunova, 1963: 84). Geometrically, this hypothesis says that the points $(\log(S_1), \log(L_1))$, $(\log(S_2), \log(L_2))$, ..., $(\log(S_n), \log(L_n))$ lie on a straight line passing through $(\log(S_c), \log(L_c))$ but, again, does not specify which line. Whereas Lee's tacit assumption was that all back-calculation lines had a common L -intercept, Monastyrsky's practice implies the unwritten assumption that all the lines have a common slope (on a log-log plot). This approach will be discussed further below.

HILE

Hile (1941: 212) produced a back-calculation hypothesis that does not require the body-scale relationship to be linear or, indeed, to take any particular form. His assumption was "that the percentage or relative deviation of the ... radius of any single scale from the theoretical ... radius is constant at the time of formation of all annuli". Mathematically this becomes

$$h(L_1)/S_1 = h(L_2)/S_2 = \dots = h(L_n)/S_n, \quad (7)$$

where $h(L_i)$ is the 'theoretical scale radius' at length L_i .

There are two defects with this assumption. Firstly, to be usable, the hypothesis must be extended by the phrase 'and at the time of capture' so that the equations may be extended to

$$h(L_1)/S_1 = h(L_2)/S_2 = \dots = h(L_n)/S_n = h(L_c)/S_c. \quad (8)$$

This leads to the general BCF

$$h(L_i) = (S_i/S_c)h(L_c). \quad (9)$$

The second defect is that Hile does not specify what is meant by the 'theoretical scale radius' at a given length, i.e. we do not know how h is defined. If h derives from the regression (linear or otherwise) of S on L , then $h(L)$ is the mean scale radius for fish of length L . When the body-scale relationship is linear this interpretation, which I shall call Hile₁, results in the BCF

$$L_i = -(a/b) + (L_c + a/b)(S_i/S_c), \quad (10)$$

where a and b are as in (1). This is the same as the Fraser-Lee equation, (6), except that c , the L -intercept of (2), is replaced by $-(a/b)$, the L -intercept of (1). Standard regression theory (e.g. Ricker, 1973) shows that $-(a/b)$ is always less than c , so that back-calculated lengths from (10) will always be less than those from (6). How much these lengths will differ depends (in part) on the strength of the body-scale correlation and is considered further below.

Alternatively, h may derive from the regression of L on S . This interpretation, which I shall call Hile₂, involves the rather convoluted definition that the 'theoretical' scale radius for a fish of length L is such that the mean length of all fish with scales of that radius is L . When the body-scale relationship is linear, the BCF for Hile₂ is (6), the Fraser-Lee equation.

WHITNEY & CARLANDER

Whitney & Carlander (1956) appear to be the first to have recognized that there are two competing hypotheses for back-calculation. They stated these as: "if the scale were 10 per cent larger when the fish was caught than the average scale for that size of fish, the scale would be 10 per cent larger than normal throughout the life", and "if a fish at time of capture were 10 per cent smaller than the average fish with that size of scale, the fish would be 10 per cent smaller than the expected length for the size of that scale throughout life". These hypotheses assume a constant proportional deviation from the mean size of the scale or body and so I shall refer to them as the 'scale proportional' (SPH) and 'body proportional' (BPH) hypotheses, respectively. They differ from the above hypotheses of Lee (1920) and Hile (1941) in that they are complete: they may be translated, without further assumptions, into BCFs.

SPH is the same as Hile₁; it may be expressed by equation (8), where $h=f$, so the BCF, (9), may be written as

$$f(L_i) = (S_i/S_c)f(L_c). \quad (11)$$

When the body-scale relationship is linear this BCF is (10).

BPH, however, is new. Its mathematical expression is

$$g(S_1)/L_1 = g(S_2)/L_2 = \dots = g(S_n)/L_n = g(S_c)/L_c. \quad (12)$$

which leads to the BCF

$$L_i = [g(S_i)/g(S_c)]L_c. \quad (13)$$

In the linear case this becomes

$$L_i = [(c + dS_i)/(c + dS_c)]L_c, \quad (14)$$

where c and d are as in (2).

It may be seen that the Dahl-Lea method is just a special case of the linear forms of these two hypotheses: it is identical to (10) if $a=0$, and to (14) if $c=0$.

Whitney & Carlander (1956) correctly pointed out that the Fraser-Lee BCF is according to neither of these hypotheses, but would follow SPH if c were the L -intercept of (2), rather than (1). However, their assertion (reiterated by Carlander, 1981), that, when a linear regression is used, BPH produces the same back-calculated lengths as the Fraser-Lee equation is not true, as a comparison of (6) and (14) makes clear. [The geometric relationship between the BCFs (6), (10), and (14) is clarified in the example below.]

Whitney & Carlander's (1956) conclusions are confusing and unconvincing. Firstly, they say that, for use in back-calculation, the regression of L on S is the "proper regression" rather than that of S on L (the reason given I shall discuss and refute below). On this basis they reject SPH. When the body-scale relationship is linear they endorse BPH, saying (incorrectly) that it is the same as the Fraser-Lee approach. When the body-scale relationship is curved, however, they reject BPH because it violates the assumption "sometimes mentioned as necessary" that "estimates of body growth are related to the proportionate growth of the scale and not to the absolute size of the scale". By this they mean that, for example, a large scale and a small scale taken from fish of the same size, and each with annuli at 0.4, 0.6, and 0.8 of their scale radii, should give the same growth history. No

evidence is given to support this assumption. Furthermore, it is violated by the linear version of BPH, which they endorse, but is consistent with SPH (in both linear and curvilinear cases), which they reject.

There appear to have been no other back-calculation hypotheses proposed. Though a wide variety of procedures have been used, their development has mostly been *ad hoc* and unsupported by specific hypotheses. Amongst linear methods there has been some variety in the approach to the calculation of c in the Fraser-Lee equation, (6); in particular, Duncan's method and the GM regression. These approaches will be dealt with in a later section.

NON-LINEAR METHODS

Here I discuss how some of the non-linear methods that have been proposed relate to BPH and SPH.

The most common non-linear method of back-calculation is generally attributed to Monastyrsky (Bagenal & Tesch, 1978). It uses the BCF

$$L_i = (S_i/S_0)^v L_c \quad (15)$$

where the constant v is derived from the body-scale relationship, which is supposed to be of the form

$$L = uS^v, \text{ or, in its logarithmic form,} \quad (16)$$

$$\log(L) = \log(u) + v\log(S). \quad (17)$$

What hypothesis, if any, may be associated with this approach depends on how the constant v is calculated. If it is from a (non-linear) regression of L on S then this BCF is consistent with BPH. Alternatively, if (16) is fitted by the (non-linear) regression of S on L , then (15) follows SPH. Monastyrsky appears to have fitted (16) by eye (Chugunova, 1963: 84). When it is fitted by regression of $\log(L)$ on $\log(S)$ (the most common practice today) the method is BPH if the word 'average' in this hypothesis is interpreted as a geometric mean.

Le Cren's (1947) method, which uses (4) and a table of corrections, is effectively a 'regression' back-calculation procedure (see next section) and thus not to be recommended.

Fry (1943) described a mechanical apparatus for the back-calculation of fish growth from scales. This is based on the body-scale relationship

$$L - w = u^v S \quad (18)$$

where w is chosen to linearize the plot of $\log(L - w)$ against $\log(S)$. Though he does not describe it explicitly, the BCF implemented by his apparatus is

$$\log(L_i - w) = \log(L_0 - w) + [\log(L_c - w) - \log(L_0 - w)] * [\log(S_i) - \log(S_0)] / [\log(S_c) - \log(S_0)] \quad (19)$$

where (L_0, S_0) is a point arbitrarily chosen on the curve (18). Geometrically, the difference between Monastyrsky's method and this is that, for the former, the family of back-calculation lines is parallel to (17), but for the latter the lines all pass through the point $(S_i = S_0, L_i = L_0)$. Graynoth (1987) also used (19) (though without Fry's apparatus) and Maceina & Betsill (1987) used a special case of (19) where

$S_0 = 1$ and $w = 0$. No back-calculation hypothesis has been presented to support (19) and it follows neither SPH nor BPH.

Hile (1950) showed how to construct a nomograph to implement his back-calculated hypothesis (see above) for body-scale relationships of any mathematical form. Hile (1950) applied it with (16), Carlander (1950) with cubic curves, and Appelget & Smith (1950) with a quadratic. The method attributed by Bagenal & Tesch (1978: 123) to Ricker & Lagler (1942) is simply this method with an empirical body-scale curve. If the body-scale curve is fitted by regression of S on L this method is SPH; if L is regressed on S then the construction of the nomograph may be modified to make it BPH. However, with the widespread accessibility of computers the need for nomographs seems past.

Segerstråle proposed a graphical back-calculation procedure (Chugunova, 1963: 94–98) that has often been referred to in reviews of back-calculation procedures (Lagler, 1956; Bagenal & Tesch, 1978) but, because of its complexity, rarely applied. The method follows neither SPH or BPH, and no other hypothesis appears to have been advanced to support it.

Sherriff (1922) was the first to use a quadratic equation,

$$L = a + bS + cS^2 \quad (20)$$

to describe the body-scale relationship but gave no BCF. Jones (1958) proposed a BCF for (20) and Gutreuter (1987) generalized it for use when the body-scale relationship is a polynomial of arbitrary degree. Neither author gave any hypothesis justifying their formulae, and neither BCF follows either BPH or SPH. If (20) is fitted by (non-linear) regression of L on S , then the BCF according to BPH is

$$L_i = L_c(a + bS_i + cS_i^2)/(a + bS_c + cS_c^2). \quad (21)$$

Thomas (1983a) gave a good statement of SPH and applied it with a quadratic body-scale curve in which S was a function of L , i.e.,

$$S = a + bL + cL^2. \quad (22)$$

REGRESSION METHODS OF BACK-CALCULATION

Carlander (1981) noted that some authors were using a new approach to back-calculation “without evaluation of the method and evidently without recognition that it is different from traditional methods”. In this approach, which Carlander called the regression method, the BCF is simply

$$L_i = h(S_i) \quad (23)$$

where the body-scale relationship is described by the equation $L = h(S)$ for some function h . The key point about this method is that it ignores the size at capture of both the fish and its ‘scales’; a single back-calculation line is used for all fish in the population to which the body-scale curve applies. By contrast, all the above-mentioned methods take into account the proportional deviation of the point (S_c, L_c) from the average body-scale relationship. These methods are accordingly labelled ‘proportional’, as opposed to ‘regression’. Proportional BCFs describe a family of back-calculation lines; for each fish the values of S_c and L_c are used to select a particular line.

It is hard to see any reason for the use of regression methods. They discard information and, for individual fish, will often produce back-calculated lengths

TABLE I. Current practice in back-calculation, as summarized by a survey of 54 papers published since 1978

Body-scale function		Regression used		Back-calculation method	
Linear	40	L on S	29	Dahl-Lea	10
$L = uS^v$	7	S on L	7	Fraser-Lee	25
Polynomial	3	Geometric mean	9	Hile	2
Broken stick	2	Eye	1	Monastyrsky	1
Other	2			BPH	1
				Regression	12

that are greater than the fish length at capture. Whitney & Carlander (1956) compared the variability in back-calculated lengths based on a number of scales from the same fish, using the Fraser-Lee and regression methods. They found lower variability in the results from the former. This, perhaps, is a measure of the information lost when L_c and S_c are ignored in back-calculations.

CURRENT PRACTICE

A survey of papers published since 1978 was used to describe current practice in back-calculation (Table I). Typically, the body-scale relationship was linear (either simple or logarithmic) and obtained by regression of L on S (or $\log(L)$ on $\log(S)$). Of the seven authors who regressed S on L , at least three appear to have done so inadvertently, as they claimed to be using the Fraser-Lee equation. Most (76%) back-calculation methods used were proportional. All authors who used regression methods did so without comment, which supports Carlander's (1981) suggestion that the use of this approach is usually in ignorance of the traditional methods. Many authors modified (either deliberately or inadvertently) standard methods, e.g. 40% of the users of the Fraser-Lee equation calculation c using the wrong regression or Duncan's (1980) procedure (described below).

AN EXAMPLE

A graphical presentation of the linear back-calculation methods illustrates clearly how they differ in practice. For this purpose herring body-scale data from Lee (1920) were used (Fig. 1). The point P represents the capture data for the fish ($L_c = 28.5$ cm, $S_c = 0.41$ cm). The back-calculation lines for this fish are the straight lines joining P to the point of intersection of one of the regression lines with one of the axes. It is a simple matter to check that the SPH line, (10), is PA; the BPH line, (14), is PB; and the Fraser-Lee line, (6), is PC. Since the BPH and Fraser-Lee methods are based on the same regression, they will generally, as shown here, produce very similar results.

III. WHICH REGRESSION?

A major difference between the BCFs associated with SPH and BPH is the regression used to describe the body-scale relationship. In this section I consider two arguments that have been advanced favouring the use of particular

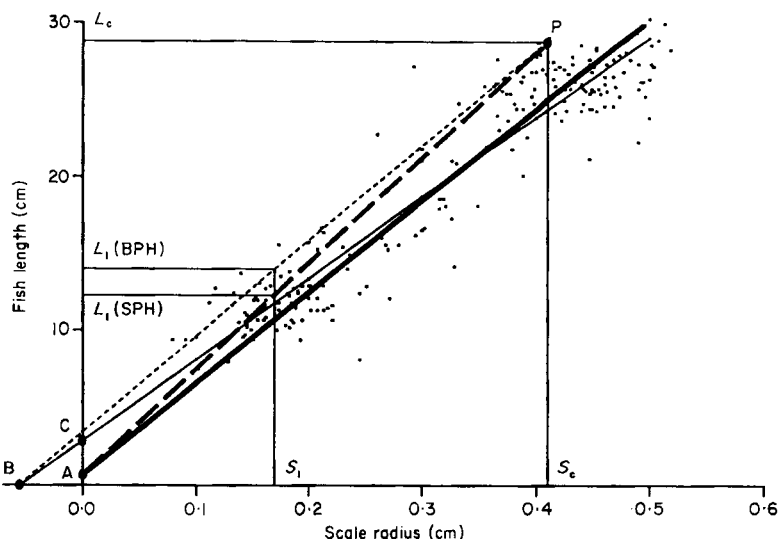


FIG. 1. Example of back-calculation methods using herring data from Lee (1920: Appendix I, Table II) and assuming $L_c = 28.5$ cm, $S_c = 0.41$ cm, and $S_i = 0.17$ cm. Bold and fine lines are used to illustrate back-calculation under the scale proportional (SPH) and body proportional (BPH) hypotheses, respectively. In each case the solid line is the regression line (S on L , and L on S , respectively) and the broken line is the back-calculation line. The Fraser-Lee line (not shown) is PC. (Small random errors, of size equivalent to the measurement rounding error, have been added to Lee's data to separate them in the plot. The original data were used in all calculations.)

regressions, and conclude that neither is valid. A related technical matter and Duncan's (1980) procedure (an alternative to regression) will also be discussed.

Many early writers developing and using BCFs make no mention of the procedure used to derive a body-scale line (e.g. Hile, 1941; Ricker & Lagler, 1942; Fry, 1943; Lagler, 1956). It is tempting to conclude that a plot of L on S (or S on L) implied the use of a regression of L on S (or S on L), but there are examples where this is not true (Lee, 1920; Le Cren, 1947; Clay, 1982). Some authors fitted lines by eye.

One reason for the popularity of L on S regressions (Table I) is the common argument that, because the purpose of back-calculation is to estimate body length from scale measurements, the appropriate regression is that of L on S (Whitney & Carlander, 1956; Kipling, 1962; Bagenal & Tesch, 1978; Thakur, 1981). This argument rests on two misconceptions. Firstly, there are two ways of using a regression for estimation. For example, the regression of S on L is most commonly used to estimate the mean scale size for a given body length, but it could just as well be used to calculate the body length for which the mean scale size takes a certain value. (An inappropriate use would be to calculate the mean body length for a given scale size.) The second misconception is that back-calculation is a simple one-stage process, estimating L_i from S_i . In fact, under both SPH and BPH it is a four-stage process that uses regression twice.

To illustrate the stages in back-calculation using SPH, I will use the data of Fig. 1. For these data the regression of S on L is

$$S = -0.0134 + 0.0169L. \quad (24)$$

As illustrated in Fig. 1, we will estimate L_1 assuming $L_c = 28.5$ cm, $S_c = 0.41$ cm, and $S_1 = 0.17$ cm. Though the calculation may be accomplished using the single equation (10), this hides the four stages that are implicit in the SPH method:

1. calculate the mean scale radius for fish of length 28.5 cm:
 $-0.0134 + 0.0169 * 28.5 = 0.47$ cm;
2. calculate the ratio of the observed scale radius to this:
 $0.41 / 0.47 = 0.872$;
3. adjust the observed scale radius, S_1 , but this ratio to calculate the expected scale radius for fish of length L_1 :
 $0.17 / 0.872 = 0.195$ cm;
4. calculate the body length for which this is the expected scale radius:
 $(0.195 + 0.0134) / 0.0169 = 12.3$ cm = L_1 .

Stages 1 and 4 use the regression of S on L , both times appropriately. At stage 3, SPH is invoked: since the scale was only 87.2% of the average size at capture, it must have been 87.2% of the average at the time of formation of the first annulus.

The above four stages were described by Whitney & Carlander (1956) as being those used in the Fraser-Lee method, except that regression (1) was used in place of (2) (they called this Procedure A). It is puzzling that, though they realized that the wrong regression was used as stage 1, they never considered the alternative regression. Also, they did not appear to notice that the wrong regression was used at stage 4 of this procedure.

Since the BPH method is rarely used, it is of interest to show how it works with the above data. The regression of L on S is

$$L = 2.93 + 52.4S. \quad (25)$$

Back-calculation using the BCF (14) implies the following four stages:

1. calculate the mean body length for fish with scale radius 0.41 cm:
 $2.93 + 52.4 * 0.41 = 24.4$ cm;
2. calculate the ratio of this to the observed length:
 $28.5 / 24.4 = 1.168$;
3. calculate the mean body length for fish with scale radius 0.17 cm:
 $2.93 + 52.4 * 0.17 = 11.8$ cm;
4. adjust this body length by the above ratio:
 $11.8 * 1.168 = 13.8$ cm = L_1 .

Here the regression of L on S was used in stages 1 and 3. At stage 4, BPH was used to say that, because the fish was 16.8% larger than average for its scale size at capture, it must have deviated by the same amount at the time of formation of the first scale annulus.

The second regression argument to be considered is Ricker's (1973) recommendation of the GM regression for back-calculation. He supported the above argument in favour of the L on S regression but said that, in practice, the slope of this

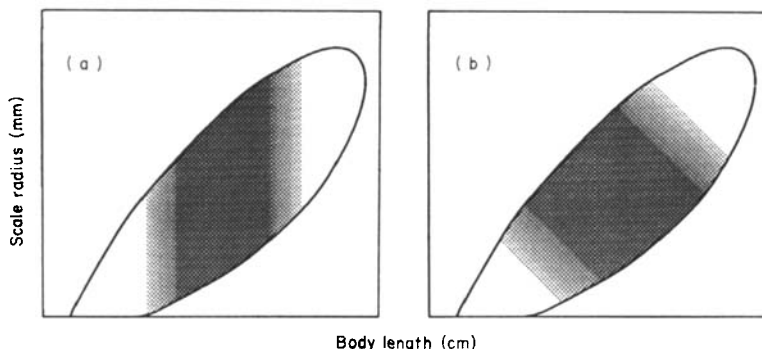


FIG. 2. Schematic representation of the relationship between the range of body length and scale radius values found in a fish population (area bounded by solid line) and in a sample used for back-calculation (shaded area): (a) as suggested in this paper; (b) as described by Ricker (1973) in recommending the GM regression.

regression line is usually an underestimate of the slope of the line describing the true relationship between mean length and scale radius. This is because the sample will not generally cover the entire size range of the population. Ricker argued that the expected slope of the usual predictive regression line will increase as the range of sizes in the sample increases, and will reach the true slope only when the full range is covered. Thus, a predictive regression will produce a biased estimate unless the full population size range is covered by the sample. He thus recommended the GM regression because it is not subject to a similar bias.

However, a consideration of the structure of a typical body-scale sample suggests that one of Ricker's assumptions is not supported. As Smale & Taylor (1987) have pointed out, body-scale samples are typically length-truncated. The reason is that the fishing method used to gather the sample is size selective, the smallest and largest fish being not readily caught. Note that the selectivity acts on body size, not scale size: all fish of a given length are equally likely to be caught, regardless of scale size. The range of such a sample is shown schematically in Fig. 2(a). Ricker (1973, table 8) classified the body-scale sample as one that is "symmetrical with respect to the functional axis". In such a sample [Fig. 2(b)] small fish are more likely to be included if they have big scales; and big fish with small scales are more likely to be included than those of the same length but with bigger scales. This is implausible, so Ricker's (1973) recommendation of the GM regression is not supported. For samples of the Fig. 2(a) type, Ricker (1973) recommended (correctly) the regression of S on L . Both the GM and L on S regressions produce biased estimates with this type of sample.

The above analyses of the BPH and SPH methods show that it is the choice of hypothesis that should determine which regression is used. If SPH is chosen, then the S on L regression is appropriate and will not result in bias. For BPH, the L on S regression should be used but the body-scale sample may need to be modified to avoid bias. This may be done by removing some of the extreme data points until it is felt that, for the smallest and largest scale sizes included, the full range of body sizes is represented in the sample. This will require a subjective judgement that will be based, in part, on a knowledge of the selectivity of the fishing gear used.

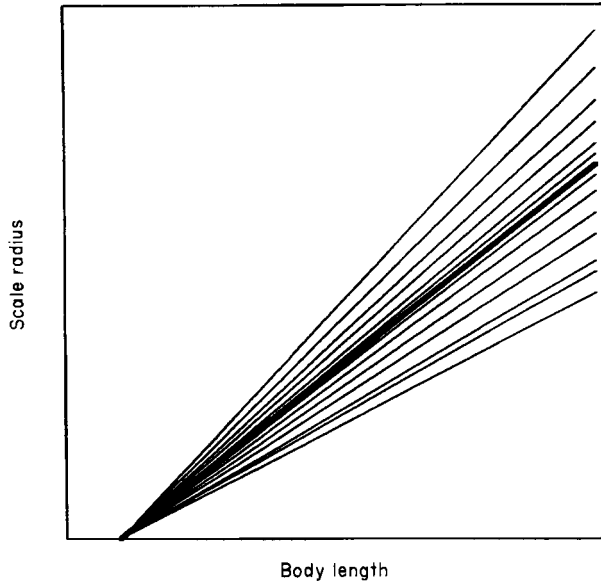


FIG. 3. The pattern of body-scale growth predicted by SPH. The heavy line is the mean scale radius for given body length; the light lines are examples of the growth paths of individual fish. Under BPH the predicted pattern is similar except that the lines meet on the other axis.

HETEROSCEDASTICITY IN BODY-SCALE PLOTS

All proportional back-calculation hypotheses predict heteroscedasticity in the body-scale plot. Specifically, they predict increasing scatter with increasing size (Fig. 3). This connection between the back-calculation assumptions and heteroscedasticity does not appear to have been noted before. Some authors have found heteroscedasticity in a linear body-scale plot and so have decided to remove it with a logarithmic transformation (Gjøsæter, 1981; Maceina & Betsill, 1987). This stabilization of variance after logarithmic transformation is consistent with both BPH and SPH. However, rather than transforming, a more appropriate response would be to use a weighted regression (with weights proportional to $1/L^2$ or $1/S^2$ for SPH or BPH, respectively). This, though, may be too fine a point, considering the current lack of validation of back-calculation. If a weighted regression produces a substantially different result from the usual regression, this is probably evidence that the body-scale relationship is non-linear.

DUNCAN'S PROCEDURE

Duncan (1980) proposed a different method of estimating c in the Fraser-Lee equation, (6). Instead of using the regression of L on S , he gave a formula to calculate a value of c for any pair of fish, and then took the average of c over all pairs of fish "of dissimilar size". This procedure is without theoretical support. No statistical argument or growth hypothesis was advanced and no clear guidelines were given as to which pairs of fish to use. If the aim is to find a value of c that, when used in the Fraser-Lee equation, results in back-calculated lengths

more in agreement with observed data, then it would be easier, and no less sound theoretically, simply to pick c by trial and error.

IV. VALIDATION OF BACK-CALCULATION

The validation of a back-calculation procedure may be divided into three parts, i.e. it must be shown:

- (i) that the radius of a scale mark is the same as the radius of the scale at the time the mark was formed;
- (ii) that the supposed time of formation of the mark is correct; and
- (iii) that the formula used accurately relates scale radius and body size for each fish.

As mentioned above, parts (i) and (ii) are outside the scope of this paper, so in this section I will concentrate on part (iii).

Validation is simply a matter of comparing observed lengths with those predicted by back-calculation, and this comparison may be made for individual fish or with groups of fish. The former is more difficult and more rarely done: I have found only two examples. Rijnsdorp & Visser (1987) tagged and injected with tetracycline 1039 North Sea plaice, *Pleuronectes platessa*. For 43 recaptured fish they compared the observed length at tagging with the length back-calculated to the tetracycline mark in the otolith; growth increments ranged from 1 to 12 cm. They found that, allowing for shrinkage after recapture, there was close agreement between the mean length at tagging and the mean back-calculated length. However, for individual fish, the two lengths differed by as much as 2 cm. They could not say how much of this difference might be attributable to measurement errors rather than a deviation from their BCF. Bradford & Geen (1987) back-calculated lengths for laboratory-reared juvenile chinook salmon, *Oncorhynchus tshawytscha*, using a regression method applied to daily growth rings in otoliths. They found an error of ± 11.3 mm (95% confidence bounds) in back-calculated lengths which, over the size range of fish used, represents a 9–19% deviation.

The most usual method of validation involves the comparison of groups of fish, i.e. the mean back-calculated length of a sample of fish is compared with the mean observed length of another sample of fish. Since it is common to observe large between-cohort variations in mean length-at-age, such comparisons are of little value when they are not restricted to fish of the same cohort. However, even with within-cohort comparisons (e.g. Steinmetz, 1974) there is a problem.

The problem is simply that of establishing that the comparison is of like with like. For example, the collection of all 1-year-old fish is not the same as the collection of all 1-year-old fish that will survive to age 5, say. The latter is what is used in back-calculation. Therefore, the mean length of (a sample of) 1-year-olds need not be the same as the mean back-calculated length of (a sample of) 5-year-olds. These means could be different if mortality is length-dependent, if either sample is not representative, or if the BCF used is inaccurate. But, if the means differ, how can we know which of these possible causes is responsible? If the means do not differ significantly, could it be the result of cancelling errors from two or more of the above sources? For this reason this type of comparison can only be expected to detect gross errors in BCFs.

TABLE II. Approximate maximum differences (Δ) between back-calculated lengths using the linear forms of SPH and BPH [text equations (10) and (14), respectively] for eight published body-scale data sets. These maximum differences will occur when the back-calculation covers the full range of lengths in the body-scale data, i.e. $L_c = L_{\max}$ and $L_i = L_{\min}$. For the purposes of this Table L_{\max} (L_{\min}) was taken as slightly less (greater) than the absolute maximum (minimum) in the respective data sets. Also used in the calculation of Δ were the mean length, \bar{L} , and the correlation, r , in each body-scale data set. Details of the calculation of Δ are given in Appendix I

Data source	r	L_{\min} (cm)	\bar{L} (cm)	L_{\max} (cm)	Δ	
					cm	% of L_{\min}
Rijnsdorp & Visser, 1987	0.98	20	32.5	50	1.0	5
Lauzanne, 1978	0.98	12	18.6	25	0.4	4
Cayré & Diouf, 1981	0.97	30	49.8	75	1.8	6
Lee, 1920	0.94	10	19.7	28	1.5	15
Hunt, 1979	0.91	20	30.5	40	2.5	13
Eknath & Doyle, 1985	0.91	32	39.1	50	2.5	8
Delgado <i>et al.</i> , 1981	0.78	14	18.9	24	3.4	24
Kishida <i>et al.</i> , 1985	0.77	40	70.3	90	17.6	44

The problem of validating back-calculations from within-cohort comparisons is similar to that of assigning a cause to Lee's phenomenon. This phenomenon occurs when the mean back-calculated length at age 1, say, decreases with increasing age of the fish used in the back-calculation. Duncan (1980) listed the following factors which have been cited as possible causes: length-dependent mortality, non-representative sampling, faulty back-calculation, incorrect ageing, and contraction of scale marks. This multiplicity of explanations means that the presence or absence of Lee's phenomenon cannot by itself be taken as evidence against or for the accuracy of a BCF.

The current standard of validation of BCFs does not seem high. In the 54 papers surveyed in Table I, 33 did not mention validation. Where some sort of validation was claimed the comparisons were across cohorts in 17 papers, within cohorts in two, and between individuals in two. Though several papers compared BCFs from different shaped body-scale curves (e.g. linear and logarithmic) none compared BCFs from different hypotheses associated with a particular type of body-scale relationship. In the remainder of this section I will show that BPH and SPH can produce very different back-calculated lengths from the same data set.

If the body-scale relationship is linear, BPH and SPH lead to the BCFs (14) and (10), respectively. An examination of the geometry of Fig. 1 shows that, for a given species, lengths back-calculated from these two BCFs will differ most when the difference between the capture length and back-calculated length is greatest. Approximate maximum differences for eight published body-scale data sets are shown in Table II. As might be expected, the difference increases as the body-scale correlation decreases. In geometric terms this is because the angle between the regression lines (and thus that between the back-calculation lines) increases as the correlation decreases. In the 54 papers surveyed in Table I the median correlation was 0.96.

V. DISCUSSION

This review of the back-calculation literature has shown that, though the technique is widely used, it does not appear to be well understood. Despite the warnings of Carlander (1981) and others, the ill-conceived regression method of back-calculation is still commonly used (Table I), often in apparent ignorance of any alternative. Where proportional methods are used there is no acknowledgment that there are two distinct hypotheses and that these may result in significantly different back-calculated lengths (Table II). No attempt has been made to determine which of these hypotheses is more correct, and the Fraser–Lee method, that most commonly used, follows neither. Validation of BCFs is almost always either missing or weak and the role of regression in back-calculation is widely misunderstood.

The confusion concerning back-calculation is apparent in fisheries text books, where the distinction between BCFs and equations describing body–scale relationships is often blurred (Nikolsky, 1963; Everhart *et al.*, 1975; Bagenal & Tesch, 1978). This can only contribute to the confusion between proportional and regression methods.

Three reasons may be offered to explain why back-calculation has been used so uncritically. Firstly, it is common sense: given the high correlation which often obtains between body length and scale radius, there can be little doubt that the dimensions of marks in its scales contain some information on the growth history of a fish (the proper questions are, how precise is the information and which formula best extracts it?). Secondly, back-calculation is hard to validate properly: it means keeping track of individual fish over long periods of time. Thirdly, fisheries scientists are often, of necessity, pragmatists. Management advice must be given, and it should be based on the widest possible data set. It would be unreasonable to reject back-calculation data simply because a definitive validation was lacking.

What is the recommended approach to back-calculation in the light of this review? A first step would be to restrict back-calculation to BCFs which follow either SPH or BPH. General forms for these are given as equations (11) and (13), with specific examples in equations (10), (14), (15) and (23). (Note that the Dahl–Lea equation, (4), is simply a special case of both (10) and (14), holding when a or c is zero.) In particular, when the body–scale relationship is linear, the Fraser–Lee equation (which is based on a misunderstanding of the role of regression) should be rejected in favour of (10) or (14). It would be naive to expect either of these simple hypotheses to provide an exact description of the relationship between body length and scale size for all fish. However, until they have been shown to be inadequate the use of *ad hoc* procedures cannot be supported. The use of one of these hypotheses should entail the use of the corresponding regression. The GM regression is not recommended for back-calculation.

Secondly, it is recommended that both SPH and BPH methods be used for each fish population, and the difference between the back-calculated lengths be taken as a minimum measure of the imprecision of back-calculation. So, for the fish in the example above, the possible error in back-calculated length at age 1 is at least 1.5 cm (= 13.8 – 12.3). Lee's (1920) hypothesis appears to be the most generally accepted rationale (as well as the 'common sense' explanation) for back-

calculation, and both SPH and BPH are consistent with it. Neither hypothesis seems obviously preferable. Where the two approaches produce widely differing answers it would be appropriate to follow the advice of Gutreuter (1987) and restrict the range of back-calculation.

Thirdly, it is time for some hypothesis testing. In validating back-calculation an attempt should be made not only to compare back-calculated and observed lengths, but also to see which hypothesis, BPH or SPH, leads to more accurate results. Researchers should be aware that little weight can be placed on validations involving group comparisons, especially when the comparisons are across cohorts. Ideally, validations should be based on comparisons of individual fish. For example, the data of both Rijnsdorp & Visser (1987) and Bradford & Geen (1987) could be used to compare BPH and SPH methods. Another approach that could yield useful results is that of Matlock *et al.* (1987) who compared scales taken from fish at tagging and at recapture; their aim was age validation but the data could also be used to compare different back-calculation methods.

The pattern of heteroscedasticity in body-scale plots may be useful in determining species and/or hard parts for which neither of the proportional hypotheses is true, and suggesting modifications of these hypotheses. We need to know why heteroscedasticity occurs very clearly in some data sets (Kipling, 1962; Southward, 1962; Kaakinen & Valtonen, 1976; Gjøsæter, 1986; van Leeuwen & Rijnsdorp, 1986; Lucio, 1986; Rijnsdorp & Visser, 1987) but is not apparent in others (Tweddle, 1975; Lauzanne, 1978; Cayr  & Diouf, 1981; Eknath & Doyle, 1985; Heidinger & Clodfelter, 1987: fig. 3). Another useful diagnostic is a comparison of the standard deviations of observed and back-calculated lengths at age. The large differences found by Antoine *et al.* (1983: table 7) seem most likely to result from a deficiency in the BCF, though length-dependent mortality could be a contributing factor.

The effect of seasonal variation on back-calculation needs further attention. There is evidence that fish and scale growth are not synchronous within a single growing season (Duff, 1929, on the scales of cod, *Gadus callarias*; Reay, 1972, on the otoliths of sandeels, *Ammodytes tobianus*; Casselman, 1983, on the scales and cleithra of northern pike, *Esox lucius*; Thomas, 1983*b*, on the otoliths of pilchard, *Sardinops ocellata*). This has two implications: the body-scale relationship will be different for fish sampled at different seasons, and BCFs will vary in accuracy depending on the season for which lengths are back-calculated. There are currently no modifications proposed to adjust BCFs for this factor. Where possible, it may be sensible to follow the advice of Casselman (1987) and construct the body-scale relationship and perform back-calculation from samples collected just prior to annulus formation. This should influence the design of experiments involving back-calculation to other than annual rings, e.g. tetracycline marks (Rijnsdorp & Visser, 1987) or liberations stress marks (Davies & Sloane, 1986). Certainly, the above findings must cast doubt on descriptions of seasonal growth based on back-calculation to the last annulus (e.g. van Leeuwen & Rijnsdorp, 1986).

Some authors have suggested including age data in the back-calculation process (Lea, 1938; Kang, 1979; Bartlett *et al.*, 1984). This seems reasonable: the expected length of a fish of a given scale size may well depend on its age. Thus back-calculation procedures using age are potentially more precise. The problem though, as with conventional methods, is validation. How will we know if such

methods are better? Since we do not yet know which of the two proportional hypotheses is more accurate, how can we decide which one to extend by the inclusion of age data? Similar comments may be made on more complicated back-calculation procedures, such as those of Smith (1987) and Weisberg & Frie (1987). If we cannot yet properly test simple hypotheses, should we be developing more complex ones?

References

- Antoine, L. M., Mendoza, J. T. & Cayré, P. M. (1983). Progress of age and growth assessment of Atlantic skipjack tuna, *Euthynnus pelamis*, from dorsal fin spines. In *Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks* (E. D. Prince & L. M. Pulos, eds), NOAA Tech. Rep. NMFS No. 8, 91–97.
- Appelget, J. & Smith, L. L., Jr. (1950). The determination of age and rate of growth from vertebrae of the channel catfish, *Ictalurus lacustris punctatus*. *Trans. Am. Fish. Soc.* **80**, 119–139.
- Bagenal, T. B. & Tesch, F. W. (1978). Age and growth. In *Methods for Assessment of Fish Production in Fresh Waters*, 3rd edn (T. B. Bagenal, ed.), pp. 101–136. Oxford, U.K.: Blackwell Scientific Publications.
- Bartlett, J. R., Randerson, P. F., Williams, R. & Ellis, D. M. (1984). The use of analysis of covariance in the back-calculation of growth in fish. *J. Fish Biol.* **24**, 201–213.
- Beacham, T. D. (1981). Variability in growth during the first 3 years of life of cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. *Can. J. Zool.* **59**, 614–620.
- Berkeley, S. A. & Houde, E. D. (1983). Age determination of broadbill swordfish, *Xiphias gladius*, from the Straits of Florida, using anal fin spine sections. In *Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks* (E. D. Prince & L. M. Pulos, eds), NOAA Tech. Rep. NMFS No. 8, 137–143.
- Bradford, M. J. & Geen, G. H. (1987). Size and growth of juvenile chinook salmon back-calculated from otolith growth increments. In *Age and Growth of Fish* (R. C. Summerfelt & G. E. Hall, eds), pp. 453–461. Ames, IA: Iowa State University Press.
- Carlander, K. D. (1950). Growth rate studies of saugers, *Stizostedion canadense canadense* (Smith) and yellow perch, *Perca flavescens* (Mitchill) from Lake of the Woods, Minnesota. *Trans. Am. Fish. Soc.* **79**, 30–42.
- Carlander, K. D. (1981). Caution on the use of the regression method of back-calculating lengths from scale measurements. *Fisheries* **6**(1), 2–4 [with corrections in *Fisheries* **8**(5), 25].
- Carlander, K. D. (1982). Standard intercepts for calculating lengths from scale measurements for some centrarchid and percoid fishes. *Trans. Am. Fish. Soc.* **111**, 332–336.
- Carlander, K. D. (1985). Sampling problems in deriving a body–scale regression for growth calculation for fish scales. *Verh. int. Verein. theor. angew. Limnol.* **22**, 2534–2536.
- Casselman, J. M. (1983). Age and growth assessment of fish from their calcified structures—techniques and tools. In *Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks* (E. D. Prince & L. M. Pulos, eds) NOAA Tech. Rep. NMFS No. 8, 1–17.
- Casselman, J. M. (1987). Determination of age and growth. In *The Biology of Fish Growth* (A. H. Weatherley & H. S. Gill, eds), pp. 209–242. London: Academic Press.
- Cayré, P. & Diouf, T. (1981). Croissance de la thonine *Euthynnus alletteratus* (Rafinesque, 1810), établi à partir de coupes transversales du premier rayon de la nageoire dorsale. *Coll. Vol. Sci. Pap. ICCAT* **15**(2), 337–345.
- Chugunova, N. I. (1963). *Age and Growth Studies in Fish*. Jerusalem, Israel: Israel Program for Scientific Translations. 132 pp.
- Clay, D. (1982). A comparison of different methods of age determination in the sharptooth catfish *Claris gariepinus*. *J. Limnol. Soc. S. Afr.* **8**(2), 61–70.

- Davies, P. E. & Sloane, R. D. (1986). Validation of aging and length back-calculation in rainbow trout, *Salmo gairdneri* Rich., from Dee Lagoon, Tasmania. *Aust. J. Mar. Freshwat. Res.* **37**, 289–295.
- Delgado, A., Fernandez, M. A. R. & Goñi, R. (1981). Contribucion al estudio de la sardina (*Sardina pilchardus* Walb.) en aguas de Africa Occidental. III. Estudio del crecimiento por lectura directa de otolitos y por retrocalculo mediante escalimetria de escamas. *Bol. Inst. esp. Oceangr.* **6**(3), 140–164.
- Duff, G. L. (1929). Factors involved in the production of annual zones in the scales of the cod (*Gadus callarias* Linnaeus). *Contr. Can. Biol. Fish* **4**(21), 289–305.
- Duncan, K. W. (1980). On the back-calculation of fish lengths; modifications and extensions to the Fraser–Lee equation. *J. Fish Biol.* **16**, 725–730.
- Eknath, A. E. & Doyle, R. W. (1985). Maximum likelihood estimation of ‘unobservable’ growth and development rates using scale data: application to carp aquaculture in India. *Aquaculture* **49**, 55–71.
- Everhart, W. H., Eipper, A. W. & Youngs W. D. (1975). *Principles of Fishery Science*. Ithaca, NY: Cornell University Press. 288 pp.
- Fraser, C. McL. (1916). Growth of the spring salmon. *Trans. Pacif. Fish. Soc.* **1915**, 29–39.
- Frost, W. E. & Kipling, C. (1980). The growth of charr, *Salvelinus willughbii* Günther, in Windermere. *J. Fish Biol.* **16**, 279–289.
- Fry, F. E. J. (1943). A method for the calculation of the growth of fishes from scale measurements. *Publ. Ont. Fish. Res. Lab.* **61**, 5–18.
- Gee, A. S. (1978). The distribution and growth of coarse fish in gravel-pit lakes in south-east England. *Freshwat. Biol.* **8**, 385–394.
- Geffen, A. J. (1986). The growth of herring larvae, *Clupea harengus* L., in the Clyde: an assessment of the suitability of otolith ageing methods. *J. Fish Biol.* **28**, 279–288.
- Gjøsæter, H. (1986). Growth of the Barents Sea capelin compared to stock size and geographical distribution. *ICES C.M. 1986/H:38* (mimeo.). 15 pp.
- Gjøsæter, J. (1981). Life history and ecology of the myctophid fish *Notscopelus elongatus kroeyeri* from the northeast Atlantic. *FiskDir. Skr. Ser. HavUnders.* **17**, 133–152.
- Graynoth, E. (1987). Growth of landlocked sockeye salmon (*Oncorhynchus nerka*) in New Zealand. *N.Z. J. Mar. Freshwat. Res.* **21**, 15–30.
- Grudtsev, M. E. & Korolevich, L. I. (1986). Studies of frigate tuna *Auxis thazard* (Lacépède) age and growth in the eastern part of the equatorial Atlantic. *Coll. Vol. Sci. Pap. ICCAT* **25**, 269–274.
- Gutreuter, S. (1987). Considerations for estimation and interpretation of annual growth rates. In *Age and Growth of Fish* (R. C. Summerfelt & G. E. Hall, eds), pp. 115–126. Ames, IA: Iowa State University Press.
- Heidinger, R. C. & Clodfelter, K. (1987). Validity of the otolith for determining age and growth of walleye, striped bass, and smallmouth bass in power plant cooling ponds. In *Age and Growth of Fish* (R. C. Summerfelt & G. E. Hall, eds), pp. 241–251. Ames, IA: Iowa State University Press.
- Hickling, C. F. (1933). The natural history of the hake. IV. Age-determination and the growth-rate. *Fishery Invest., Lond., Ser.2*, **13**(2). 120 pp.
- Hile, R. (1941). Age and growth of the rock bass, *Ambloplites rupestris* (Rafinesque), in Nebish Lake, Wisconsin. *Trans. Wis. Acad. Sci. Arts Lett.* **33**, 189–337.
- Hile, R. (1950). A nomograph for the computation of the growth of fish from scale measurements. *Trans. Am. Fish. Soc.* **78**, 156–162.
- Hile, R. (1970). Body–scale relation and calculation of growth in fishes. *Trans. Am. Fish. Soc.* **99**, 468–474.
- Hirschhorn, G. & Small, G. J. (1987). Variability in growth parameter estimates from scales of Pacific cod based on scale and area measurements. In *Age and Growth of Fish* (R. C. Summerfelt & G. E. Hall, eds), pp. 147–157. Ames, IA: Iowa State University Press.
- Hunt, J. J. (1979). Back-calculation of length-at-age from otoliths for silver hake of the Scotian shelf. *Sel. Pap. ICNAF* **5**, 11–17.
- Jones, R. (1958). Lee’s phenomenon of “apparent change in growth-rate” with particular reference to haddock and plaice. *Spec. Publ. int. Commn NW Atlant. Fish.* **1**, 229–242.

- Kaakinen, R. & Valtonen, T. (1976). The body-scale length relation on the Oulu River population of *Coregonus lavaretus* (Linné) s. str. *Rep. Inst. Freshwat. Res. Drottningholm* **55**, 38–44.
- Kang, Y. J. (1979). A new method for the calculation of the growth of chum salmon, *Oncorhynchus keta*, from scale measurements. *Bull. natn. Fish. Univ. Busan* **19**(2), 43–54.
- Kipling, C. (1962). The use of the scales of the brown trout (*Salmo trutta* L.) for the back-calculation of growth. *J. Cons. perm. int. Explor. Mer* **27**, 304–315.
- Kishida, T., Ueda, K. & Takao, K. (1985). Age and growth of Japanese Spanish mackerel in the central and western waters of the Seto Inland Sea. *Bull. Jap. Soc. scient. Fish.* **51**, 529–537.
- Kraiem, M. M. (1982). Etude comparative de l'âge et de la croissance du barbeau, *Barbus barbus* (L.) [Poissons, Cyprinidés] dans deux rivières françaises, le Rhône et l'Allier. *Arch. Hydrobiol.* **96**(1), 73–96.
- Lagler, K. F. (1956). *Freshwater Fishery Biology*. Dubuque, IA: Wm. C. Brown Company. 421 pp.
- Lauzanne, L. (1978). Croissance de *Sarotherodon galilaeus* (Pisces, Cichlidae) dans le lac Tchad. *Cybiurn 3rd ser.* **3**, 5–14.
- Lea, E. (1910). On the methods used in the herring-investigations. *Publ. Circonst. Cons. perm. int. Explor. Mer* **53**, 175 pp.
- Lea, E. (1938). A modification of the formula for calculation of the growth of herring. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* **108**(1), 14–22.
- Le Cren, E. D. (1947). The determination of the age and growth of the perch (*Perca fluviatilis*) from the opercular bone. *J. Anim. Ecol.* **16**, 188–204.
- Lee, R. M. (1920). A review of the methods of age and growth determination in fishes by means of scales. *Fishery Invest., Lond., Ser. 2* **4**(2), 32 pp.
- Lucio, P. (1986). On the methodology of length back-calculation from otoliths in flatfish with particular reference to brill: *Scophthalmus rhombus*, L. *ICES CM 1986/G: 52* (mimeo.). 36 pp (with errata).
- MacCrimmon, H. R. (1979). Comparative annulus formation on anatomical structures of the white sucker, *Catostomus commersoni* (Lacépède). *Fish. Mgmt* **10**(3), 123–128.
- Maceina, M. J. & Betsill, R. K. (1987). Verification and use of whole otoliths to age white crappie. In *Age and Growth of Fish* (R. C. Summerfelt & G. E. Hall, eds), pp. 267–278. Ames, IA: Iowa State University Press.
- Matlock, G. C., Colura, R. L., Maciorowski, A. F. & McEachron, L. W. (1987). Use of on-going tagging programs to validate scale readings. In *Age and Growth of Fish* (R. C. Summerfelt & G. E. Hall, eds), pp. 279–286. Ames, IA: Iowa State University Press.
- Miranda, L. E., Wingo, W. M., Muncy, R. J. & Bates, T. D. (1987). Bias in growth estimates derived from fish collected by anglers. In *Age and Growth of Fish* (R. C. Summerfelt & G. E. Hall, eds), pp. 211–220. Ames, IA: Iowa State University Press.
- Morales, B. (1984). Aplicacion del retrocalculo en la determinacion del crecimiento de *Genypterus capensis* (Smith 1847). *Coll. Sci. Pap. ICSEAF* **11**(2), 7–12.
- Nikolsky, G. V. (1963). *The Ecology of Fishes*. London: Academic Press. 352 pp.
- Reay, P. J. (1972). The seasonal pattern of otolith growth and its application to back-calculation studies in *Ammodytes tobianus* L. *J. Cons. int. Explor. Mer* **34**, 485–504.
- Ricker, W. E. (1973). Linear regressions in fishery research. *J. Fish. Res. Bd. Can.* **30**, 409–434 [with corrections in Ricker (1984), *Can. J. Zool.* **62**, 1897–1905].
- Ricker, W. E. & Lagler, K. F. (1942). The growth of spiny-rayed fishes in Foots Pond. *Invest. Indiana Lakes Streams* **2**, 85–97.
- Rijnsdorp, A. D. & Visser, T. A. M. (1987). Tetracycline labelling of otoliths in plaice. *ICES CM 1987/G:33* (mimeo.). 11 pp.
- Shafi, M. & Jasim, B. M. (1982). Some aspects of the biology of a cyprinid, *Aspius vorax* Heckel. *J. Fish Biol.* **20**, 271–278.
- Shentyakova, L. F. (1969). The verification by mathematical tests of the hypothesis that the relationship between body growth and the scales of fishes is constant within the species. *Probl. Ichthyol.* **9**, 338–354.

- Sherriff, C. W. M. (1922). Herring investigations. Report on the mathematical analysis of random samples of herrings. *Scient. Invest. Fishery Bd Scotl.* **1**, 25 pp.
- Smale, M. A. & Taylor, W. W. (1987). Sources of back-calculation error in estimating growth of lake whitefish. In *Age and Growth of Fish* (R. C. Summerfelt & G. E. Hall, eds), pp. 189–202. Ames, IA: Iowa State University Press.
- Smith, P. J. (1987). Maximum likelihood estimation of the distribution of length at age. *Biometrics* **43**, 601–615.
- Southward, G. M. (1962). A method of calculating body lengths from otolith measurements for Pacific halibut and its application to Portlock-Albatross grounds data between 1935 and 1957. *J. Fish. Res. Bd Can.* **19**, 339–362.
- Steinmetz, B. (1974). Scale reading and back-calculation of bream *Abramis brama* (L.) and rudd *Scardinius erythrophthalmus* (L.). In *Ageing of Fish* (T. B. Bagenal, ed), pp. 148–157. Old Woking, England: Unwin Bros.
- Thakur, N. K. (1981). Studies on the age and growth of an air-breathing catfish, *Clarias batrachus* (Linn.). *Int. Rev. Hydrobiol.* **66**, 563–573.
- Thomas, R. M. (1983a). Back-calculation and time of hyaline ring formation in the otoliths of the pilchard off South West Africa. *S. Afr. J. mar. Sci.* **1**, 3–18.
- Thomas, R. M. (1983b). Seasonal variation in the relationship between otolith radius and fish length in the pilchard off South West Africa. *S. Afr. J. mar. Sci.* **1**, 133–138.
- Tweddle, D. (1975). Age and growth of the catfish *Bagrus meridionalis* Günther in southern Lake Malawi. *J. Fish Biol.* **7**, 677–685.
- Van Leeuwen, P. I. & Rijnsdorp, A. D. (1986). The analysis of the growth of turbot by backcalculation of otoliths. *ICES CM 1986/G:50* (mimeo.). 17 pp.
- Weisberg, S. & Frie, R. V. (1987). Linear models for the growth of fish. In *Age and Growth of Fish* (R. C. Summerfelt & G. E. Hall, eds), pp. 127–143. Ames, IA: Iowa State University Press.
- Whitney, R. R. & Carlander, K. D. (1956). Interpretation of body-scale regression for computing body length of fish. *J. Wildl. Mgmt* **20**, 21–27.

APPENDIX I. CALCULATIONS FOR TABLE II

We wish to calculate how large the difference may be between back-calculated lengths derived from the BCFs (10) and (14). This difference will depend on the input values (L_c , S_c and S_i) and the regression parameters (a , b , c and d).

In terms of the input parameters, it is clear from Fig. 1 that the difference will be largest when L_c is as large, and L_i as small, as possible. Since the back-calculations should not extend beyond the range of lengths in the body-scale data (L_{\min} to L_{\max}) we will set $L_c = L_{\max}$ and let S_c be the average scale size for a fish of this length, i.e. $S_c = c + dL_{\max}$. Similarly, we assume S_i is the average scale size for a fish with length L_{\min} , i.e. $S_i = c + dL_{\min}$.

Substituting these values of L_c , S_c and S_i in equations (10) and (14) we may calculate that Δ , the approximate maximum difference between the BPH and SPH back-calculated lengths, is given by

$$\Delta = (L_{\max} - L_{\min}) / (1 + bdL_{\max} / (a + bc)).$$

From standard regression theory (Ricker, 1973) it is easy to show that $bd = r^2$ and $a + bc = L(1 - r^2)$, where \bar{L} is the mean length and r is the correlation in the body-scale sample. Thus

$$\Delta = \bar{L}(1 - r^2)(L_{\max} - L_{\min}) / (\bar{L}(1 - r^2) + r^2L_{\max}).$$