Length-Converted Catch Curves and the Seasonal Growth of Fishes*

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Abstract

A brief review of studies on the seasonal growth of fish is presented, followed by an equally brief review of length-converted catch curves. A new method for constructing catch curves from representative length-frequency data is presented. This new method explicitly accounts for seasonal growth and thus eliminates the bias in Z caused by such growth. Some practical and theoretical implications of the new method are discussed.

Introduction

That the growth of fishes displays seasonal growth oscillations was well known to the pioneers of fishery biology, notably to T.W. Fulton (1901, 1904), who along with C.G.J. Petersen, invented length-frequency analysis.

This awareness faded away, however, when fishery scientists gradually switched away from the analysis of length data and used "annuli" (on otoliths, scales and other bones) to estimate growth rate and draw growth curves (Went 1972). Thus, Beverton and Holt, in their classic of 1957, did not consider seasonal growth oscillations in more than a cursory manner, and particularly, saw no point in modifying the basic von Bertalanffy growth function (VBGF) to express such oscillations, although they occur in all the fishes they studied.

Following a discussion of seasonal growth by von Bertalanffy and Müller (1943), the first version of the VBGF allowing for such oscillation was that of Ursin (1963a, 1963b). Other modifications of the VBGF were those of Pitcher and MacDonald (1973) and Daget and Ecoutin (1976). Improvements of these earlier models and various approaches for fitting them then followed in quick successions (Cloern and Nichols 1978; Antoine et al 1979; Pauly and Gaschütz 1979; Hoenig and Chaudary Hanumara 1982; Sager 1984a, 1984b, 1984c; Appeldoorn 1987; Moreau 1987; Somers 1988; Soriano and Jarre 1988; Soriano and Pauly 1989; Chaudary Hanumara and Hoenig 1990; Gaschütz et al. 1990). The application examples presented by these authors made it quite obvious that growth models which do not explicitly consider seasonal oscillations fail to capture an essential aspect of the growth process (Longhurst and Pauly 1987 and see Fig. 1).

This is also true for tropical fishes, since winter-summer temperature differences as small as 2°C are sufficient to induce detectable seasonal growth oscillations (Pauly and Ingles 1981 and see Fig. 2).

This and evidence presented in Pauly (1985) suggest that not accounting for growth oscillations will lead to biased growth parameter estimates everytime one bases such estimation on growth data other than derived from annuli. This applies to, e.g., tagging/recapture data, or to length-frequency samples collected at monthly or quarterly intervals. (Note that this point applies irrespective of whether other phenomena, such as migration, also affect one's samples).

It is not surprising, thus, that a number of computerized approaches for the analysis of length-frequency data explicitly consider growth oscillations (see, e.g., Sparre

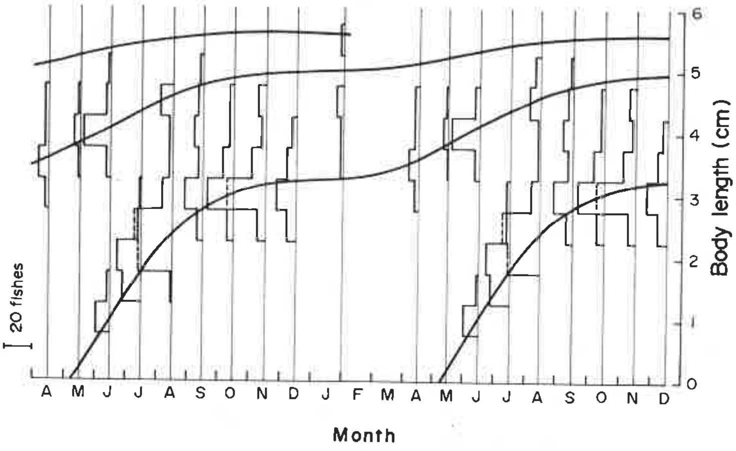

Fig. 1. Length-frequency data on the gobiid *Chasmichthys dolichognathus*, fitted with a seasonally oscillating growth curve by means of ELEFAN I. The original length-frequency data, gathered from April to December 1974 (with the exception of the January-February sample, obtained in 1970), have been here plotted twice to show that the forward projection of the growth curve meets the modal class(es) of most samples. The curve has the parameters L_∞ = 6 cm, K = 1.0 year^{-1}, C = 1.0 and WP = 0, the latter two values suggesting a period of no growth at the turn of the year. Adapted from Pauly and David (1981), based on data in Tamura and Honma (1977).

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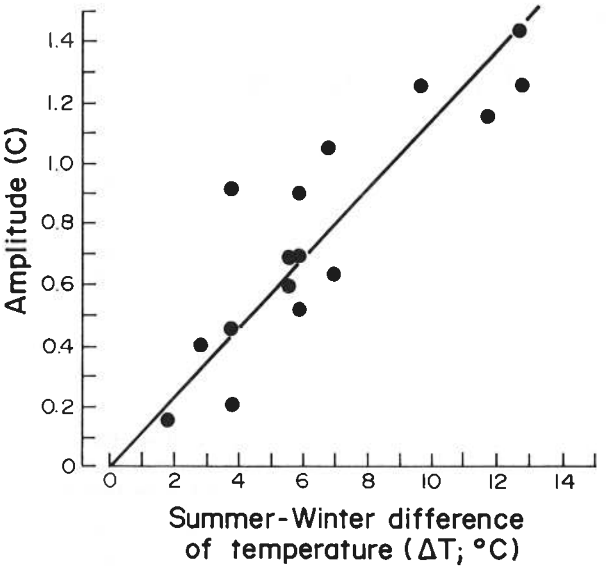

Fig. 2. Relationship between the amplitude of seasonal growth oscillations (C) in fishes, crustaceans and molluscs and the difference between the mean monthly summer and the mean monthly winter temperature of their habitats. The values of C were obtained using ELEFAN I, or the ETAL I program of Gaschütz et al. (1990) (adapted from Pauly 1985).

1987a). In the case of ELEFAN I, seasonal growth oscillations were considered from the very onset (Pauly and David 1980, 1981, and see Fig. 1). Indeed, the seasonalized version of the VBGF documented in Pauly and Gaschütz (1979), and incorporated in the program of Sparre (1987a) and in MULTIFAN (Otter Software 1988) arose in the context of my preoccupation with the analysis of length-frequency data.

As a method for the estimation of mortality (Z), catch curves have a tradition dating as far back as 1908, when T. Edser presented what we would now call a length-structured catch curve. As had happened with studies of age and growth, however, this and other length-based catch curves by Heincke (1913) and Baranov (1918) were gradually replaced by age-structured catch curves, i.e., plots of $\log_e$ (number at age) *vs.* age (Ricker 1975).

Catch curves based on length-frequency data were revived as "length-converted" catch curves in the early 1980s (Pauly 1980, 1982, 1984) and have since found wide utilization (see, e.g., various Fishbyte issues) mainly because they were incorporated as part of various ELEFAN packages (e.g., Brey and Pauly 1986; Gayanilo et al. 1988), in the LFSA package of Sparre (1987b), and because they are part of the curriculum of the continuing and worldwide FAO/DANIDA Training Course in Tropical Fish Stock Assessment (Venema et al. 1988).

There are various views about length-converted catch curves, some of them very positive (Munro 1987). They have also been criticized, however, either

(i) because they share with age-structured catch curves the property of requiring the assumption of steady-state conditions;
(ii) because they have tended to overestimate Z in various simulations; and
(iii) because they overestimate Z when used in conjunction with the parameters of a seasonally oscillating growth curve.

Thus, Shepherd et al. (1987) referring to item (i), i.e., to estimates of Z based on mean length and related methods — such as length-converted catch curves — stated that they "invariably assume a steady-state (equilibrium) age composition, which usually requires both constant mortality with age and time, and constant recruitment. Situations where these conditions are all fulfilled are fairly rare, and since these methods are quite sensitive to violations of the assumptions, their use cannot be generalized except under especially favorable conditions or for very preliminary estimate, for which they are of course still useful".

This point is perfectly valid — except for the fact that in the overwhelming majority of cases confronting fishery biologists working in the tropics, potential alternatives to these methods (e.g., virtual population analysis) cannot be used — for lack of the appropriate data; hence we generally have to base our assessment on "preliminary estimates".

With regard to item (ii), Hampton and Majkowski (1987) showed that length-converted catch curves "tend to overestimate Z in experiments where the (individual) growth parameters are highly variable". They also suggested that "there is no reason why this should be so; further work is required to resolve this question".

We now leave item (ii), to which we shall return later, and consider item (iii), i.e., the point so forcefully made by Sparre (this issue of Fishbyte). His point can be decomposed into a number of statements, perhaps as follows:

1) Length-converted catch curves overestimate Z when growth is seasonal;
2) This bias cannot be overcome within the context of approaches assuming a one-on-one correspondence between age and length (such as ELEFAN);
3) Item (2) offers proof, if need be, that these approaches should be abandoned;
4) The bias in (i) can be overcome only within the context of a comprehensive, statistically rigorous approach, such as described in Sparre (1987a).

Statement (1) is obviously true, and this makes his contribution a most useful one. Indeed, his results suggest that the biases in Z encountered by Hampton and Majkowski (1987) may be due to the interaction of seasonal growth oscillations and individual variability of growth parameters, thus providing a "reason why this should be so" (see above).

Statement (2) is erroneous. In the following, I shall briefly present a new, rather simple method, which was largely derived from existing ELEFAN routines, and which eliminates the bias in question. I shall then return, in the Discussion, to the implications of this new method for statements (3) and (4).

Combining Length-Converted Catch Curves and Seasonal Growth

Fishbyte readers have read many times how length-converted catch curves are constructed, but it must be repeated here, for the sake of coherence and clarity.

Essentially a length-converted catch curve is a linear regression, i.e., a plot of

$$\ln(N/\Delta t) = a+bt' \qquad \text{...1)}$$

where N is the number of fishes in a given length class, Δt the time needed for the fish to grow through that length class, a the intercept, t' the mean (relative) age of the fishes in that length class and b, is with sign changed, an estimate of Z. [A "box" is given on page 37 which discusses the choice of points to be included in the regression through which Z is estimated].

The N values used in catch curves must refer to steady-state (or equilibrium) situation (see above). In practice, this amounts to summing up length-frequency data over a longer period (Munro 1982; Hoenig et al. 1987), during which recruitment can be assumed to have been constant, or varied randomly (Ricker 1975). The LFSA (Sparre 1987b) and ELEFAN packages therefore contain various routines to aggregate length-frequency samples across time.

Estimating values of Δt_i is, in case of the standard VGBF, quite straightforward and it implies using

$$\Delta t_i = (-1/K)\ln(L_\infty - L_{i2}/L_\infty - L_{i1}) \qquad \text{...2)}$$

where L_∞ and K are parameters of the VBGF, i.e., of

$$L_t = L_\infty(1-e^{-K(t-t_0)}) \qquad \text{...3)}$$

and where L_{i1}, L_{i2} are the lower and upper limits of length class i, respectively. Note that t_0 is not used in Equation (2), for which reason the "age" (t_i) corresponding to the midpoint of i (L_i) is called "relative age". Values of t' can be obtained from the inverse of the VBGF, i.e.,

$$t' = (-1/K)\ln(1-L_{t'}/L_\infty) \qquad \text{...4)}$$

The features of equation (1) concerning us here are:

- there is only one value of Δt for any length class, i.e., L_{i1}, L_{i2}, L_∞ and K completely determine Δt;
- there is only one value of t' for any length class, i.e., $L_{t'}$, L_∞ and K completely determine t';
- hence class-specific N values can be added across samples (i.e., time) without effect on the values of Δt and t'.

These features do not apply in the case of seasonal growth. Such growth can be represented, e.g., by the curve of Hoenig and Chaudhary Hanumara (1982) and Somers (1988), i.e.,

$$L_t = L_\infty(1-e^{-(K(t-t_0)+S(t-t_s)-S(t_0-t_s))}) \qquad \text{...5)}$$

where S = (KC/2π)sinπ.

Here, we have the parameters of equation (3), plus C and t_s; the former expresses the amplitude of the growth oscillations and usually ranges from zero — in which case equation (5) reverts to equation (3) — to unity — in which case the growth rate is zero exactly once a year, when the "winter point" (WP) is reached. The parameter t_s is the time (with regard to t=0) at the onset of a sinusoid growth oscillation; note that t_s = 0.5+WP.

Seasonal growth variations imply that in a given sample, Δt depends not only on L_{i1}, L_{i2}, L_∞ and K, but also on C and, more importantly, on the difference between WP and the date the sample in question was obtained. Hence, N values pertaining to different samples cannot be added across time, because there is no single value of Δt which corresponds to their sum. Thus, the ordinate of the length-converted catch curve is distorted. Similarly, there is no one-on-one correspondence between $L_{t'}$ and t' (as implied by equation 4), because, e.g., one-year old fishes will have very different sizes depending on whether they hatched before or after the winter period of reduced growth. Thus, the abscissa of the length-converted catch curve is also distorted.

I presume it is this apparent dilemma, and the one-on-one correspondence between size and age embedded in ELEFAN I which led to statement (2) above. However, it is often easy to turn liabilities into assets. In this case, the one-on-one correspondence can be used to compute the numbers and (relative) ages of the fishes of various "pseudocohorts" (as opposed to the numbers and ages in various *length* classes), and to plot the log of their numbers against their ages.

This can be done in five steps (Fig. 3A and B):

- Create a length-frequency file in which all fishes are assumed to have been caught within the same period of one year (since no interyear differences of growth or mortality are assumed to occur);
- Estimate, by solving equation (5) iteratively, the (relative) age of the youngest and oldest fish in the file (t'_{min} and t'_{max}, respectively);
- Divide the time difference t'_{max}-t'_{min} by the number of length classes in the file, such as to obtain a number of time intervals (I) equal to the number of data points that would have been obtained from the corresponding regular length-converted catch curve (some value of I has to be used, and the proposed value has the advantages of facilitating comparisons between different catch curves);

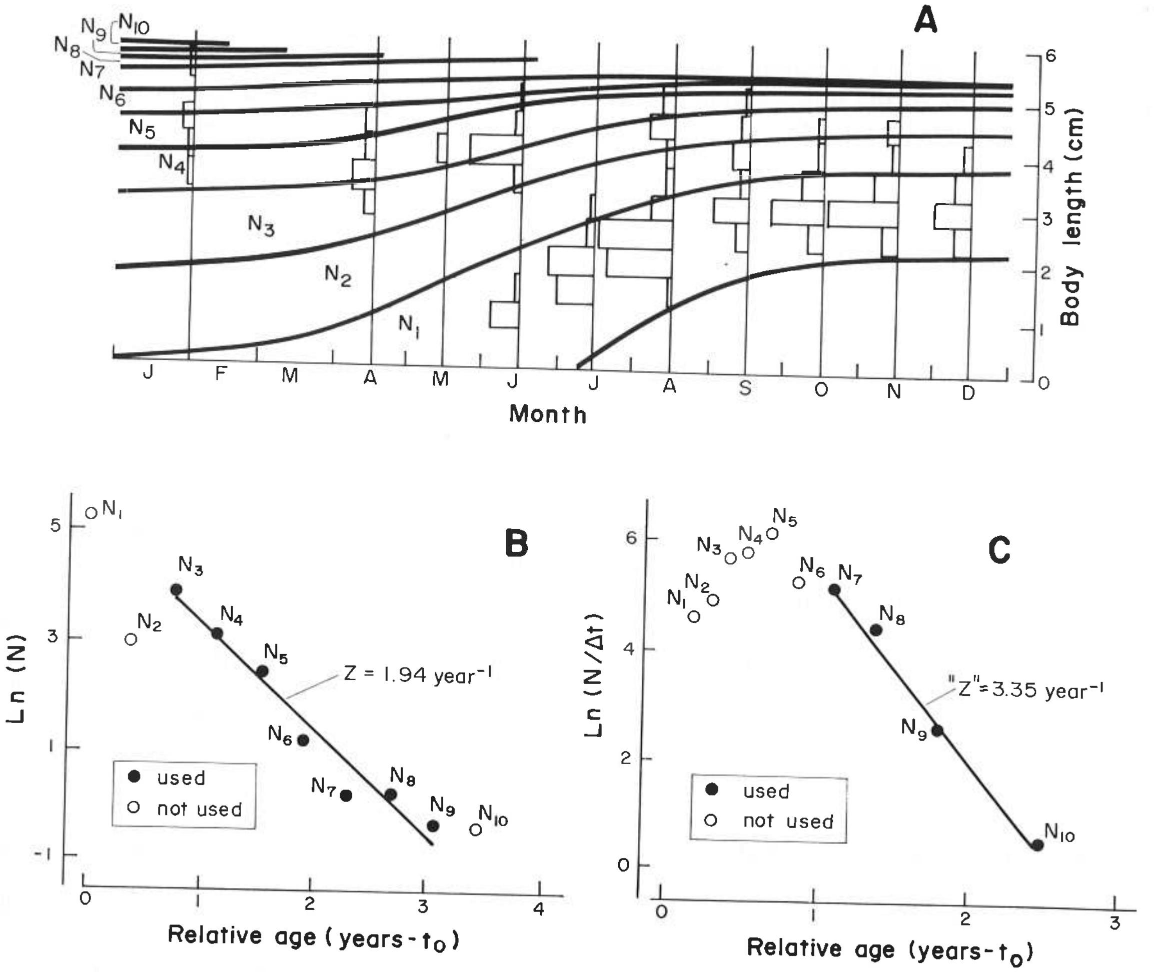

Fig. 3. Schematic representation of the new method for construction of length-converted catch curves which account for seasonality.

A. The first operation is using the parameters of a seasonally oscillating growth curve to identify a number of (pseudo) cohorts, i.e., fish between two successive growth curves; the next step is adding fish belonging to different samples, but to the same (pseudo) cohort to obtain successive values of N_I.

B. Construction of catch curve as a plot of ln(N_I) *vs.* relative ages, and estimation of Z from straight descending arm.

C. Standard length-converted catch curve, also based on data in A, but not accounting for seasonal growth. Note overestimation of Z.

- For each interval, starting from t'_{min}, and moving backward along the time axis, draw successive growth curves at regular (time) intervals, and add up across samples all fishes (N) between the two growth curves defining an interval (this step, which is illustrated in Fig. 3A, is equivalent to adding up, across samples, the fish within defined length class limits).
- Plot the ln N values thus obtained *vs.* the midpoint of the relative age intervals (t'_I), and estimate Z from the slope of the right, descending arm of the curve.

It should be noted that the proposed new method for constructing catch curves from length-frequency data gives exactly the same results as the standard method when C=0, i.e., when growth is not seasonal, and can handle any number of cohorts per year. This would make the new method universally applicable were it not for two disadvantages:

- The new catch curves require a very large amount of computation and therefore cannot be implemented in the absence of a suitable computer program;
- The left, ascending arm of the new catch curve cannot be readily used to assess the impact of size-specific gear selection or recruitment.

Hence, the standard length-converted catch curve will continue to be helpful.

Discussion

The catch curve in Fig. 3B, which documents the new method presented here leads to an estimate of Z = 1.82 year^{-1}. The length-frequency data in Fig. 3A, analyzed with a standard length-converted catch curve would have produced an estimate of Z = 3.25 year^{-1} (see Fig. 3C), i.e., Z would have been estimated with an upward bias of 180%. Thus, Sparre (this issue of Fishbyte) is right in pointing out the biasing effect, for the estimation of Z, of seasonal growth in small short-lived fishes exposed to strongly seasonal changes of their environmental parameters (especially temperature), such as shrimps in Kuwait, or the Japanese goby in Fig. 1.

On the other hand, once this source of bias was identified, it turned out to be extremely simple to correct for it. I consider this latter point to be extremely important, taking it to indicate that ELEFAN and other length-based approaches not explicitly accounting for individual growth variability continue to be relevant for tropical stock assessment. One reason for this is the ease with which this approach can be adjusted to changing needs, as shown here; the other is that the statistically rigorous alternatives that have been proposed, continue to remain unavailable to researchers in developing countries (see Sparre, this issue of Fishbyte), and/or have data requirements (such as length-frequency data *weighted by catch/effort*) that will continue to prevent their routine use in tropical situations.

These constraints are not irrelevant; rather, they determine (or at least *should* determine), where our research emphasis should go, and which methods and approaches are worth refining and/or updating.

Acknowledgements

I thank Mr. Felimon "Nonong" Gayanilo, Jr. for programming the new routine described above for construction of "seasonalized" length-converted catch curves.

Selection of Points in Catch Curves

One problem which regularly comes up during lectures and at training courses, related to both age-structured and length-converted catch curves, is the choice of points ($P_1,...,P_n$) to be included in the linear regression from which Z is estimated. The following paragraphs present a set of rules which, jointly, may solve this problem.

(i) One obvious first rule is that only the points pertaining to the right, descending side of the curve must be used, because the location of the points on the left side of the curve are affected by gear selection and/or incomplete recruitment;

(ii) A second rule, proposed by Robson and Chapman (1961), is to use as first point (P_1) that immediately to the right of the highest point (P_{max}), because the latter is likely to be contaminated by selection/recruitment effects;

(iii) The rule is (ii) should be modified: if P_{max} is *above* the leftward projection of an initial regression line that did not include P_{max}, then it was not contaminated, and it should be included;

(iv) Generally, because it includes few fishes, the rightmost point (P_{last}) of a catch curve is less reliable than the others. Also, in length-converted catch curves, P_{last} tends to be shifted to the right, toward high ages, because of the non-linearity of the length-to-age conversion. The proposed rule is, therefore, that P_{last} should be included in the regression only if it lies below the rightward projection of an initial regression line that did not include the last point;

(v) A necessary (though not *sufficient*) condition for a catch-curve estimate of Z to be reasonable is that it should have been derived from a regression line as straight as possible (implying a constant value of Z), and including as many age groups as possible (such as to dampen fluctuations of mortality and/or recruitment);

(vi) In statistical terms, item (v) suggests (a) that a large fraction of the variance of the points $P_1...P_n$ should be explained by the regression, and (b) that the value of n should be as large as possible.

These two requirements can be simultaneously taken into account by basing the regression used for estimating Z on the sequence of points $P_1...P_n$ which maximizes

$$F_{ratio} = \Sigma(\hat{y}_i-\bar{y})^2/((\Sigma y_i^2-((\Sigma y_i)^2/n))/(n-2))$$

where x, y are the coordinates of the points included (Sokal and Rohlf 1981). This can be straightforwardly implemented as a computer routine, by scanning all possible combinations of points leading to a negative slope and for which the criteria in (iii) and (iv) apply;

(vii) The rule in (vi) may still fail in case of curves with a wide, flat plateau, or two (or more) descending sequences of point separated by an ascending sequence, or other pathological cases.

These can be generally identified by eye, however, and/or incorporated into the routine described in (vi), e.g., in the form of a series of "IF statements" which identify such pathological sequences of points, and set their F-ratio at zero.

Mr. Felimon "Nonong" Gayanilo, Jr. has recently implemented the approach described here in the form of a routine which proposes default values of P_1 and P_n when a catch curve is constructed. Numerous trials have shown this routine to propose, in most cases, the very points that we would have selected by eye. This, therefore, may perhaps be seen as the solution to the question as to how to select the points of a catch curve.

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