Pauly, D. and G. Gaschutz. 1979. A simple method for fitting oscillating length-growth data, with a program for pocket calculator. International Council for the Exploration of the Sea. Council Meeting 1979.G:24. Demersal Fish Ctte, 26 p.

International Council for the Exploration of the Sea

C.M. 1979/G:24
Demersal Fish Cttee.
ref.: Pelagic Fish Cttee.

A simple method for fitting oscillating length growth data, with a program for pocket calculators

by
Daniel Pauly[1] and Götz Gaschütz
Institut für Meereskunde
and
Institut für Landwirtschaftliche Betriebslehre
Kiel University
D-2300 Kiel/Germany

Abstract:
A modification of the von BERTALANFFY Growth Formula is proposed which has the form

$$L_t = L_\infty \left(1 - e^{-\left(K\,(t-t_o) + C \cdot \frac{K}{2\pi} \sin 2\pi\,(t - t_s)\right)}\right)$$

and which can be used to fit seasonally oscillating length-age data. The properties, positive and negative, of the models are discussed. A program for use with the HP 67/97 is provided which estimates K, t_o, t_s and C, and which also can be used to improve preliminary estimates of L_∞. Worked examples are given.

1) to whom correspondence concerning this paper should be adressed, to: Intern. Center for Living Aquatic Resource Management, P.O. Box 1501 Makati, Metro Manila, Philippines.

Introduction

Taking into account seasonal growth oscillations when computing the growth parameters of fishes is not an esoteric game. It is, on the contrary, a method for considerably increasing the accuracy of growth parameter estimates, especially in the case of those temperate fishes which are short-lived. In such cases, and when the length-at-age data at hand stem from different seasons, not considering variations in growth rate can indeed lead to serious errors in the estimation of growth parameters.

Several versions of the von BERTALANFFY Growth Formula (VBGF) have been published in recent years which may be used to describe the seasonally oscillating growth pattern of fishes (URSIN 1963a, 1963b, PITCHER and McDONALD 1973, LOCKWOOD 1974, DAGET and ECOUTIN 1976, CLOERN and NICHOLS 1978), while JONES and JOHNSTON (1977), on the other hand, attempted to relate seasonal variations of food intake to variations of the growth parameters L_∞ and K.

The main drawback of the modifications of the VBGF hitherto published is that their parameters are very difficult to estimate. Thus, for example, the model proposed by PITCHER and McDonald (1973) and that of CLOERN and NICHOLS (1978) both need to be fitted by means of computer programs.

Another drawback of these previous equations is that the parameter which determines the amplitude of the growth oscillations remains undefined, such that it can neither be visualized, nor used for comparative purposes, e.g. for assessing the effects of winter conditions on the growth of different stocks or species of fishes.

The version presented here has three advantages over its predecessors:

1) Its parameters can be estimated easily, e.g. by means of a programmable pocket calculator.
2) It contains a parameter ("C") which was derived such as to express the amplitude of the growth oscillations and to allow for the comparative investigation of the effects of winter conditions on species and for stocks widely differing in their growth parameters.
3) The conditions which limit the applicability of the model are defined.

In order to fully demonstrate these points, a program for use with a HP 97 or a HP 67 calculator is presented, together with worked examples, each of which illustrate (a) different aspect(s) of the model.

Derivation of the equation

The VBGF, for length, has the form

$$L_t = L_\infty (1 - e^{-K (t - t_o)}) \qquad 1)$$

where L_t is the length at age t

L_∞ is the asymptotic length

K is a growth constant

and t_o is the "age" a length zero.

It has been demonstrated by a great number of authors (e.g. by those cited above) that the main abiotic and biotic factors which affect growth (temperature and food availability) tend to fluctuate, in the course of a year in a manner which can generally be well described by a sine curve of wave length one year.

A sine wave can be incorporated into the VBGF such that

$$L_t = L_\infty (1 - e^{-(K (t - t_o) + A \sin 2\pi (t - t_s))}) \qquad 2)$$

where A and t_s are constants whose properties are discussed below.

Equation 2, it may be mentionned, is analogous to equation 6 of PITCHER & McDONALD (1973) and to equation 6 of CLOERN and NICHOLS (1978).

Equation 2, in this form, has the major disadvantage that A is a purely empirical constant which, when estimated does not yield any insight into the magnitude of growth oscillations which it modulates.

This can be corrected by the following considerations: Length growth rate may be completely halted in winter such that: $\frac{dL}{dt} = 0 \qquad 3)$

The first derivative of equation 2) is $\frac{dL}{dt} = p \cdot q \cdot r \qquad 4)$

where $p = L_\infty$

$q = K + A 2\pi \cos 2\pi (t-t_s)$

and $r = e^{-(K (t-t_o) + A \cdot \sin 2\pi (t-t_s))}$

For equation 4 to have zero values, at least one of the values of p, q or r must, at time, come to equal zero. It may be seen, however, that p and r must always remain $\neq 0$.

Hence growth ceases if, and only if

$$q = K + 2\pi A \cdot \cos 2\pi (t - t_s) = 0 \qquad 5)$$

If we now define $A \doteq \left| \frac{C \cdot K}{2\pi} \right|$ 6)

it is assured that equation 5) becomes zero exactly once per year, when $t = t_s + 1/2$ ("winter point").

The multiplier C may be interpreted such that there are no growth oscillations when C = 0, C = 1 when the oscillations produce once per year exactly one zero value of $\frac{dL}{dt}$, and $C > 1$ when the fish actually shrink during the winter period.

This latter case, it may be noted, is very unlikely to happen in nature (as opposed to loss of weight). Only one paper was found in which a significant length loss of 0.67% to 1.23% was reported, after starvation periods of up to 7 weeks (NICKELSON and LARSON 1974). In most cases, therefore, C = 1 will have to be considered the upper biologically interpretable limit for this parameter.
Equation 2) may thus be rewritten in its definitive form

$$L_t = L_\infty \left(1 - e^{-(K(t-t_o) + C \cdot \frac{K}{2\pi} \sin 2\pi (t-t_s))}\right) \qquad 7)$$

where t_s simply sets the start of the sinusoid growth oscillation with regard to t = 0.

Estimation of the parameters

A well-known method for the estimation of K (and of t_o) given length-at-age dates and an independant estimate of asymptotic length was proposed by von BERTALANFFY (1934). It consists of rearranging Equation 1) such that

$$\ln\left(1 - \frac{L_t}{L_\infty}\right) = K t_o - K_t \qquad 8)$$

(which applies only if $L_\infty > L_t$). In this form, K and t_o may be estimated by means of a linear regression

where $y = \ln\left(1 - \frac{l_t}{L_\infty}\right)$

$a = K \cdot t_o$

and $b = -K$

Equation 7), on the other hand may be rewritten as

$$(1 - \frac{Lt}{L_\infty}) = e^{-(K(t - t_o) + C \cdot \frac{K}{2\pi} \cdot \sin 2\pi (t - t_s))} \qquad 9)$$

Since $\sin(\alpha - \beta) = \sin\alpha \cdot \cos\beta - \sin\beta \cdot \cos\alpha$ 10)

we have

$$\ln(1 - \frac{Lt}{L_\infty}) = -K(t - t_o + \frac{C}{2\pi} \sin 2\pi t \cdot \cos 2\pi t_s - \frac{C}{2\pi} \cdot \sin 2\pi t_s \cdot \cos 2\pi t) \qquad 11)$$

which has the structure of a multiple linear regression of the form:

$$y = a + b_1 x_1 + b_2 x_2 + b_3 x_3 \qquad 12)$$

where $y = \ln(1 - \frac{Lt}{L_\infty})$

$x_1 = t$

$x_2 = \sin 2\pi t$

and $x_3 = \cos 2\pi t$

Equation 12) thus yields coefficient values which can be used to estimate the growth parameters by means of the relationships

$$a = K \cdot t_o \qquad 12a)$$

$$b_1 = -K \qquad 12b)$$

$$b_2 = -K \cdot \frac{C}{2\pi} \cdot \cos 2\pi t_s \qquad 12c)$$

$$b_3 = +K \cdot \frac{C}{2\pi} \sin 2\pi t_s \qquad 12d)$$

with $t_s = \frac{\arctan(-\frac{b3}{b2})}{2\pi}$ 12e)

The only parameter which cannot be estimated directly from the seasonally oscillating growth data is L_∞. An estimate of L_∞ has therefore to be computed preliminately, e.g. from a FORD-WALFORD Plot.

In order to distinguish between independant estimates, and such estimates of L_∞ that are obtained directly from the length-at-age data, the convention is used here of coding independant estimates of asymptotic length: $L_{(\infty)}$ (PAULY 1978, 1979), the brackets meaning that estimates of this type may be slightly more limited in their accuracy.

A method for obtaining a preliminary value of $L_{(\infty)}$ is to use a good value of L max (greatest length recorded from a given stock) in connection with the relationship.

$$\frac{L\ max}{0.95} = L_{(\infty)} \qquad 13)$$

proposed by TAYLOR (1962) and BEVERTON (1963) and which demonstrably produces good results as long as fishes not larger than about 50 cm are considered (PAULY 1978, and PAULY 1979 for the reason for this size limit).

When reasonable estimates of L max are not available (e.g. when large fishes are not caught by the sampling gear), the following heuristic formula may be used to obtain a preliminary estimate of $L_{(\infty)}$:

$$L_{\infty} = \frac{L_j^2 - (L_{j-i} \cdot L_{j+i})}{2\,L_j - L_{j+i} - L_{j-i}} \qquad 14)$$

where L_j, here, is a centrally located length value and i a time interval chosen as large as possible (In the case of seasonally oscillating data, the value of i should be one year or a whole multiple thereof).

The preliminary value of $L_{(\infty)}$ obtained with either method may be, in any case, subsequently improved by means of a quick trial technique analogous to that proposed by BEVERTON (1954, p. 57) and RICKER (1958, p. 195 ff, or 1975, p. 225) for improving preliminary estimates of $L_{(\infty)}$ used in fitting equation 8) to length-at-age data.

The calculator program proposed here has for this purpose a routine for computing R^2 (multiple coefficient of determination), whose value may be maximized by means of a few plots with varying estimates of $L_{(\infty)}$. (See example 2)

Application examples follow which illustrate various properties of the model.

Example 1: Fit improvement through use of a seasonally oscillating growth curve (Fig. 1)

Data: Growth of Norway Pout, Trisopterus esmarkii in Scottish waters, as read off fig. 6 in GORDON (1977)

age (y)[1]	L (cm)[2]	age	L (cm)
0.250	7.3	1.167	13.8
0.333	8.8	1.250	14.7
0.417	9.4	1.333	14.5
0.500	10.6	1.417	15.2
0.583	10.4	1.500	15.1
0.667	11.2	1.583	15.2
0.750	11.1	1.667	15.3
0.917	11.3	1.750	15.5
1.000	11.4	1.917	15.5
1.083	11.8	--	--

1) birth: set in mid-April

2) mean of several year-classes

$L_{(\infty)}$ is set at 20 cm (see URSIN 1963b and RAITT 1968)

growth	unseasonal[3]	seasonal
r^2 & R^2	0.932	0.979
K	0.670	0.713
t_o	-0.501	-0.380
t_s	--	+0.184
C	--	+1.00

3) as estimated by fitting equation 9)

Residual variance of "unseasonal" curve (Equation 8)

$$1.000 - 0.932 = 0.068 = 6.8\%$$

Residual variance of seasonal curve (Equation 7)

$$1.000 - 0.979 = 0.021 = 2.1\%$$

Percentage of residual variance explained by the seasonalization of the growth curve

$$\frac{6.8 - 2.1}{6.8} = 0.691 = 69\% \qquad 13)$$

That the seasonalization of the growth curve significantly improves the fit may be demonstrated by testing the difference between the two coefficients of determination by means of

$$\hat{F} = \frac{(R^2{}_1 - R^2{}_2) \cdot (n - u_1 - 1)}{(1 - R^2{}_1) \cdot (u_1 - u_2)} \qquad 14)$$

(SACHS 1974, p. 354)

where n is the number of observations, $R^2{}_1$ is the coefficient of (multiple) determination pertaining to equation 12), u_1 is the number of independant variables in equation 12), while $R^2{}_2 (= r^2{}_2)$ the coefficient of determination pertaining to equation 8), and u_2 is the number of independant variables in equation 8). In the present case, $n = 19$, $R^2{}_1 = 0.979$, $u_1 = 3$, $R^2{}_2 = 0.932$, and $u_2 = 1$, which provide an estimate of $\hat{F} = 23.31$. With $v_1 = u_1 - u_2 = 2$ and $v_2 = n - u_1 = 14$, we can reject (at the 99.9% level of confidence) the null-hypothesis of no differences between the R^2 values.

Thus, as far as this example is concerned, the demonstration was made that the use of a seasonally oscillating growth equation removes a highly significant amount of variance over the amount removed by the normal growth equation, hence also increases the accuracy of prediction of length for age and of the growth parameter estimates. The value of C = 1.00, in addition, suggests that T. esmarkii is adapted to the temperature fluctuations of its habitats such that its length growth is completely halted only during a brief period of the coldest month of the year. (Fig. 1). Note also that $t_s + 0.5 = 0.684$, which was defined as "winter point" does indeed fall in the winter time (Fig. 1).

Example 2: Demonstrating that tropical fishes may display a marked seasonal growth pattern (Fig. 2)

Data: Growth of Halfbeak Hemiramphus brasilienses, off Florida, read off Fig. 5 in BERKELEY and HOUDE (1978)

age (months)	LF (cm)	age (months)	LF (cm)
3	16.8	8	21.0
4	18.9	9	20.8
5	19.4	10	21.5
6	20.0	11	21.5
7	19.8	12	22.2

age (months)	LF (cm)	age (months)	LF (cm)
13	22.5	18	25.5
14	23.2	21	26.4
15	23.6	24	26.4
16	25.0	--	--

As L_{max} = 31, in (Fig. 2 in BERKELEY and HOUDE 1978), $L_{(\infty)}$ is set at 32.5 $\approx \frac{31}{0.95}$, which provides the following parameter estimates (with R^2 = 0.988):

$$K = 0.587 \qquad t_s = +0.253^{+)}$$
$$t_o = -1.024 \qquad C = +0.686^{+)}$$

+) Note the conversion (see User Instruction, second part of program)

Example 3: Improving a preliminary value of $L_{(\infty)}$ and showing limitations of the sine wave model (Fig. 2)

Data: *Notropis atheneroides* (Emeral shiner), year class: 1967 length-at-age data read off Fig. 4 in CAMPBELL & MAC CRIMMON (1970)

age (y)	LT (cm)	age (y)	LT (cm)
0.083	1.3	0.750	5.1
0.167	3.1	0.833	5.1
0.250	4.3	0.917	5.5
0.333	4.9	1.000	6.4
0.417	5.0	1.083	7.1
0.500	5.0	1.167	7.8
0.583	5.1	1.250	8.3
0.667	5.1	1.333	8.5

trial values of $L_{(\infty)}$	R^2	K	t_o	t_s	C
10.0	0.993620	1.117	-0.013	0.088	1.49
12.0	0.995783	0.748	-0.132	0.099	1.35
11.0	0.996393	0.910	-0.083	0.094	1.40
11.5	0.996280	0.820	-0.110	0.096	1.37
11.2	0.996411	0.871	-0.094	0.094	1.39
====	========				====

The method produces (after about 30 min. of calculations) an improved estimate of $L_{(\infty)}$ = 11.2 (Fig. 2).

The value of C = 1.39 reveals, however, a problematic property of the sine wave model: When the period when $\frac{dL}{dt} = 0$ lasts for several months - as in the present case - the model generates a value of $C > 1$, corresponding to $\frac{dL}{dt} < 0$, although the length-at-age data themselves do not suggest any shrinkage. In the present case, a corrective can be suggested, which consists of setting C = 1 a posteriori, and using this value of C in conjunction with the estimates of the other parameters obtained together with the value of $C > 1$. (Fig. 1).

Alternative models, such as a "switched growth model", which can be used when the situation $\frac{dL}{dt} = 0$ persists over many months have been published by several authors (PITCHER and McDONALD 1973, DAGET and ECOUTIN 1976). However, our perusal of the seasonal growth hitherto published suggested that conditions generating $C > 1$ (prolonged period of no growth) occur predominantly in fresh waters, while marine conditions tend to generate values of $C \leq 1$.

Another limitation of the sine wave model is that it can, in the present form, in no case be applied to weight-at-age data. PITCHER and McDONALD (1973) wrote:

> "The main disadvantage of the sine wave model is that it can generate fish shrinkage during the winter (see above). This is not realistic for fish length. However, it may be of value when dealing with weights, which can easily decrease."

Our attempts to fit the model to weight-at-age data failed miserably, and grossly unrealistic growth curves and parameter values were generated. We consider this a general property of the model when applied to weight-at-age data.

Example 4: A fish with hatching and growth periods that are out of phase (Fig. 3)

Data: *Macrorhamphosus scolopax* (Snipefish), Great Meteor Sea Mount, North Atlantic. EHRICH (1976, Table 3)

age (y)	LT (cm)	age (y)	LT (cm)
0.25	3.7	1.10	9.7
0.30	6.0	1.25	10.6
0.50	8.7	1.50	11.5
0.90	9.0	2.00	14.0
1.00	10.7	--	--

EHRICH (1976) gives for these data the following growth parameters:

L_∞ = 16.5, K = 0.745 and t_o = -0.244; they were obtained by non-linear regression (Fig. 3). The value of L_∞, however, is considerably lower than the value of L_{max} = 19.2 reported by EHRICH (1976, Table 1) from the Great Meteor Bank stock.

The iteration process outlined in Example 2 yields, on the other hand, an improved estimate of $L_{(\infty)}$ = 20.0, which is quite close to $\frac{L_{max}}{0.95}$ = 20.2, hence probably more realistic than L_∞ = 16.5.

Along with $L_{(\infty)}$ = 20 cm went the following other parameter estimates:

K = 0.462, t_o = -0.507, t_s = 0.482 and C = 0.90, R^2 = 0.938 (Fig. 3)

BRÊTHES (1975) gives the following growth parameter estimates for a Moroccan stock of M. scolopax : L_∞ = 16.0, K = 0.36. These values were based on ageing by otoliths, which is unaffected by seasonal growth oscillations. These values suggest that our estimate of K = 0.462 is closer to the true value than the previous, unseasonalized estimate of K = 0.745, especially since there is, in all fish species an inverse relationship between L_∞ and K values (PAULY 1979).

Hatching, in temperate fishes, occurs mainly

a) when food for the larvae becomes abundant (spring plankton bloom)

b) when temperature increases, which accelerates growth.

This pattern is examplified by our examples 1, 2 and 3. Clearly, in the case of M. scolopax, these two phenomena are out of phase, and the fishes are hatched during a period of reduced growth (Fig. 3).

Thus, in spite of the probably limited accuracy of EHRICH's data, (EHRICH 1976, p. 260 - 262) an interesting feature of M. scolopax could be brought to attention simply by seasonalizing the growth curve. It remains to be demonstrated whether this feature is specific to M. scolopax.

Example 5: Demonstrating the use of equation 14) for the estimation of $L_{(\infty)}$

The following length-at-age data were produced by means of the growth parameters L_∞ = 100.0, K = 0.20 and t_o = 0.

age (y)	1	2	3	4	5	6	7	8	9
length (cm)	18.1	33.0	45.1	55.1	63.2	69.9	75.3	79.8	83.5

The most centrally located length value is 63.2 (with t = 5). Thus, we have L_j = 63.2. We choose i as large as possible, i.e. i = 4 and obtain:

$$L_{j+4} = 83.5$$

and

$$L_{j-4} = 18.1$$

These values, inserted into equation 14) produce a value of

$$L_{(\infty)} = 100.1$$

which is almost equal to the value used to generate the length-at-age data.

If the data for the ages 4 to 9 were not available, we would have, on the other hand, only L_j = 33.0, i = 1, with L_{j+1} = 45.1 and L_{j-1} = 18.1. These values, used in conjunction with equation 14) produce

$$L_{(\infty)} = 97.4$$

which is still very close to the real value of L_∞ = 100.0.

Discussion

Several authors had preciously presented versions of the VBGF which could be fitted to seasonal length-at-age data.

Growth in fishes is demonstrably a seasonally oscillating process, and the non-consideration of this feature is likely to produce both erroneous growth parameter estimates as well as misconception on the character of the growth process itself.

Therefore, until an analytical model of fish growth can be proposed which incorporates such seasonal variables as environmental temperature, food availability, migrations etc. a model should be used which at least gives an adequate description of a growth curve. The model proposed here does this job - within certain limits - and its parameters are easy to estimate.

An advantage of this model over its predecessor is - besides the fact that is is easy to fit - that the constants which define the growth oscillations (t_s and C) can be defined in biological terms.

Thus t_s can be understood as an estimator of the amount of out-of-phaseness of hatching in relation to the phase of accelerated growth (see example 4).

The parameter C, on the other hand, is very probably correlated with the magnitude of the temperature fluctuation of the fish habitat (= maximum minus minimum habitat temperature). This is illustrated by our examples:

		C	T. fluctuations+)
1	N. atheneroides	1.39	19
2	T. esmarkii	1.00	7
3	M. scolopax	0.90	4
4	H. brasiliensis	0.67	6
and, by definition:		0	0

+) in °C, based on data in the original papers and/or oceanographic atlas.

More values of C, however, will have to be computed to obtain a reliable quantitative relationship, which when established will allow for the estimation of C for given temperature data. An understanding of the relationship between C and temperature fluctuations, finally should allow for a) improved growth curves, and

b) improved growth parameter estimation, and

c) an improved understanding of the relationship between growth and temperature in general.

References:

BERKELEY, S.A. and E.D. HOUDE (1978): Biology of two exploited species of halfbeaks, Hemiramphus brasiliensis and H. balao from Southeast Florida. Bull. Mar. Sci. 28(4): 624 - 644

BEVERTON, R.J.H., (1954): Notes on the use of theoretical models in the study of the dynamics of exploited fish populations. U.S. Fish. Labor. Beaufort N.C. Misc. Contr. 2: 159 pp.

--- (1963): Maturation, growth and mortality of Clupeid and Engraulid stocks in relation to fishing. Cons. Perm. Expl. Mer Rapp. et Proc.-Verb. 154: 44 - 67

BRÊTHES, J.C., (1975): La becasse de mer des eaux atlantiques marocaines. Premières observations sur la biometrie et la biologie. Trav. & Doc. Dev. Pêches Maroc (15) 39 pp.

CAMPBELL, J.S. and H.R. MAC CRIMMON (1970): Biology of the emerald shiner Notropis atherinoides Rafinesque in Lake Simcoe, Canada. J. Fish. Biol. 2: 259 - 273

CLOERN, J.E. and F.H. NICHOLS (1978): A von BERTALANFFY growth model with a seasonally varying coefficient. J. Fish. Res. Bd. Can. 35: 1479 - 1482

DAGET, J. and J.M. ECOUTIN (1976): Modèles mathématiques de production applicables aux poissons tropicaux subissant un arrêt annuel prolongé de croissance. Cah. O.R.S.T.O.M. ser Hydrobiol. 10(2): 59 - 69

EHRICH, S. (1976): Zur Taxonomie, Ökologie und Wachstum von Macrorhamphosus scolopax (Linnaeus, 1758) (Pisces, Syngnathiformes) aus dem subtropischen Nordostatlantik. Ber. dt. wiss. Kommn. Meeresforsch. 24(4): 251 - 266

EHRICH, S. & H.C. JOHN (1973): Zur Biologie und Ökologie der Schnepfenfische (Gattung Macrorhamphosus) vor Nordwestafrika und Überlegungen zum Altersaufbau der adulten Bestände der Großen Meteorbank. "Meteor"Forsch. Ergebn. (D) 14: 87 - 98

GORDON, I.D.M. (1977): The fish populations of the inshore waters of the west of Scotland. The biology of the Norway Pout (Trisopterus esmarkii). J. Fish. Biol. 10: 417 - 430

JONES, R. & C. JOHNSTON (1977): Growth, Reproduction and Mortality in Gadoid Fish Species. In: I.H. STEELE (ed.) Fisheries Mathematics, Academic Press, 198 pp.

LOCKWOOD, S.J. (1974): The use of the von Bertalanffy growth equation to describe the seasonal growth of fish. J. Cons. int. Explor. Mer 35 (2): 175 - 179

NICKELSON, T.E. & G.L. LARSON (1974): Effect of weight loss on the decrease of length of coastal cutthroat trout. Progressive Fish Culturist 36 (2): 90 - 91

PAULY, D. (1978): A preliminary compilation of fish length growth parameters. Ber. Inst. Meeresk. (55): 200 pp.

--- (1979): Gill size and temperature as governing factors in fish growth: a generalization of the von Bertalanffy Growth Formula. Ber. Inst. Meeresk. (63): 156 pp.

PITCHER, T.J. & P.D.M. MacDONALD (1973): Two models for seasonal growth in fishes. J. appl. Ecology 10(2): 599 - 606

RAITT, D. (1968): The population dynamics of the Norway pout in the North Sea. Mar. Res. (Scotland) (5): 24 pp.

RICKER, W.E. (1958): Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board. Can. 119: 300 pp.

--- (1975): Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 pp.

SACHS, L. (1974): Angewandte Statistik. Springer Verlag, Berlin, 545 pp.

TAYLOR, C.C. (1962): Growth equation with metabolic parameters. J. Cons. int. Explor. Mer 23: 366 - 370

URSIN, E. (1963a): On the incorporation of temperature in the von Bertalanffy Growth Equation. Medd. Danm. Fiskeri-og Havunders. N.S. 4(1): 1 - 16

--- (1963b): On the seasonal variation of growth rate and growth parameters in Norway Pout (Gadus esmarkii) in the Skagerrak. Medd. Danm. Fiskeri-og Havunders. N.S. 4(2): 17 - 29

Von BERTALANFFY, L. (1934): Untersuchungen über die Gesetzlichkeit des Wachstums. I. Allgemeine Grundlagen der Theorie, mathematische und physiologische Gesetzlichkeit des Wachstums bei Wassertieren. Ronx' Archiv Entwickl. mechanik 131: 613-652

Legends for the figures:

Fig. 1: Growth of Trisopterus esmarkii, Scottish waters. Empirical values: data of GORDON (1977)
Above: normal, unseasonalized Von BERTALANFFY curve
Below: seasonalized version of Von BERTALANFFY curve

Fig. 2: Seasonal growth of Hemiramphus brasiliensis (Florida) and Notropis atheneroides (from a Canadian lake). Note that the model, in the latter case does not fit well the prolonged period of no growth occuring between 0.4 and 0.8 years of age.

Fig. 3: Growth of Macrorhamphosus scolopax, Meteor Sea Mount, West Africa.
Above: Growth data and curve as given in EHRICH (1977)
Below: Growth data fitted with seasonal growth curve.
Note that M. scolopax hatches in a period of reduced growth (as opposed to the three previous cases)

Fig. 1

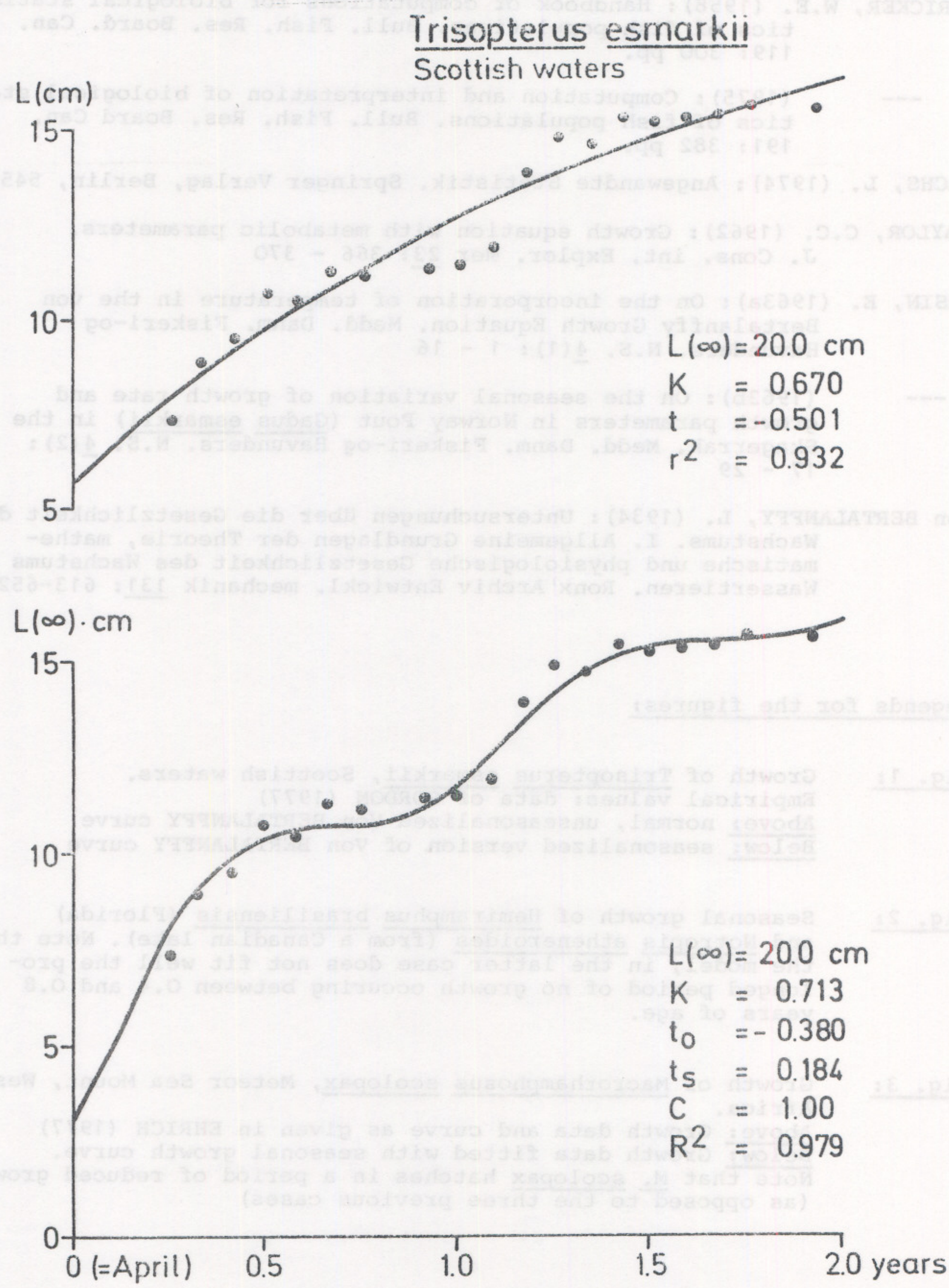
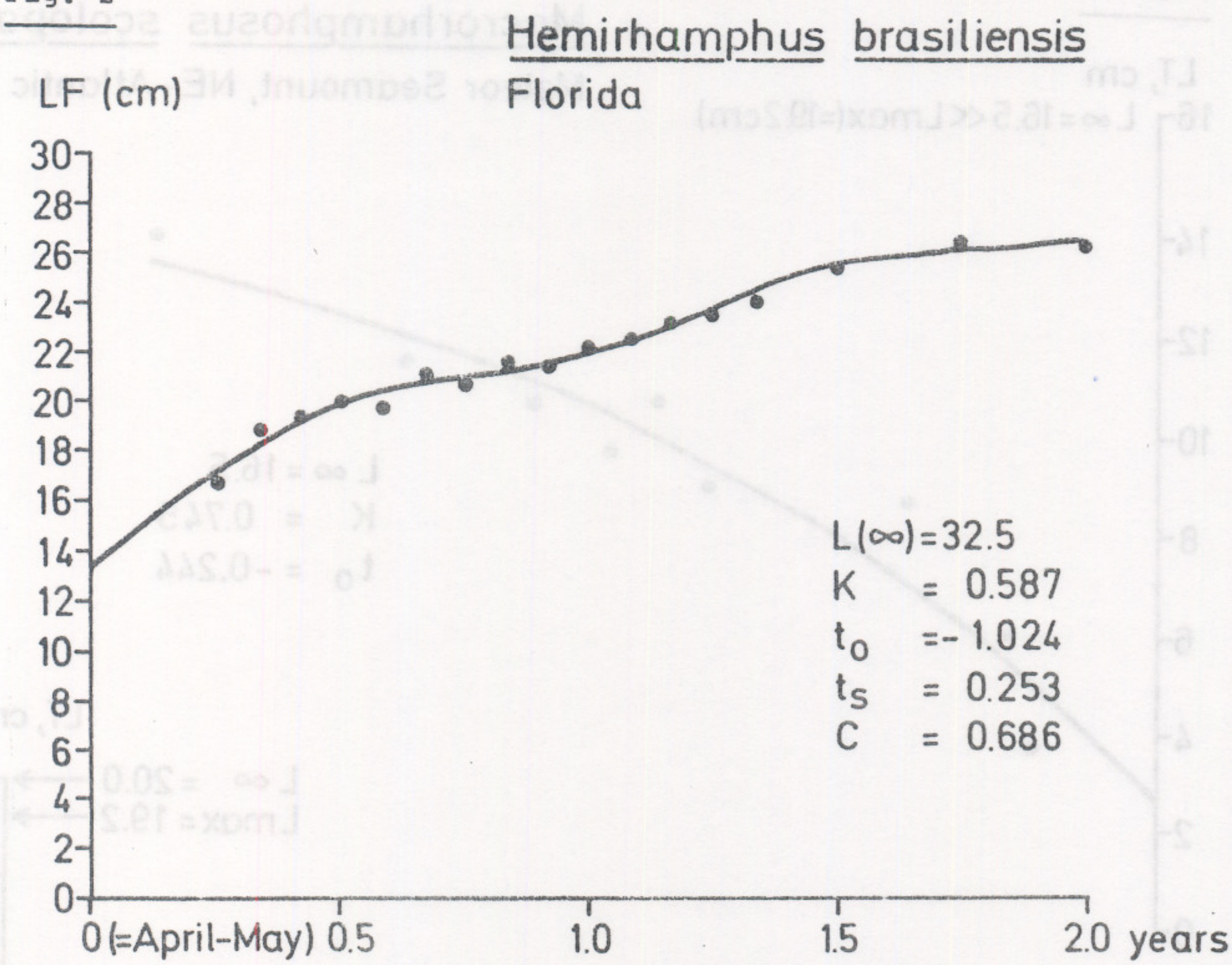

Trisopterus esmarkii
Scottish waters
L(cm)
15
10
5
L(∞)=20.0 cm
K = 0.670
t = -0.501
r2 = 0.932
L(∞)·cm
15
10
5
0
L(∞)=20.0 cm
K = 0.713
to = - 0.380
ts = 0.184
C = 1.00
R2 = 0.979
0 (=April)
0.5
1.0
1.5
2.0 years

Fig. 2


Hemirhamphus brasiliensis
Florida
LF (cm)
L(∞)=32.5
K = 0.587
t0 =- 1.024
ts = 0.253
C = 0.686
0 (=April-May) 0.5
1.0
1.5
2.0 years

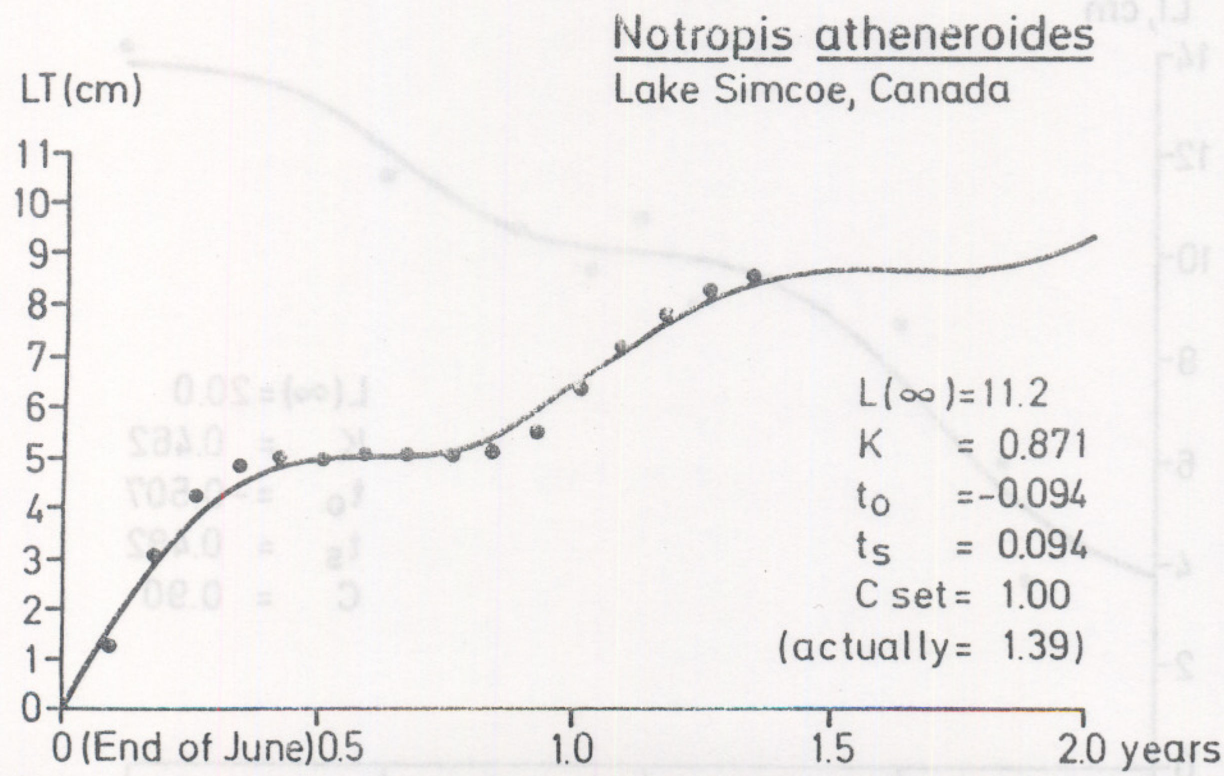
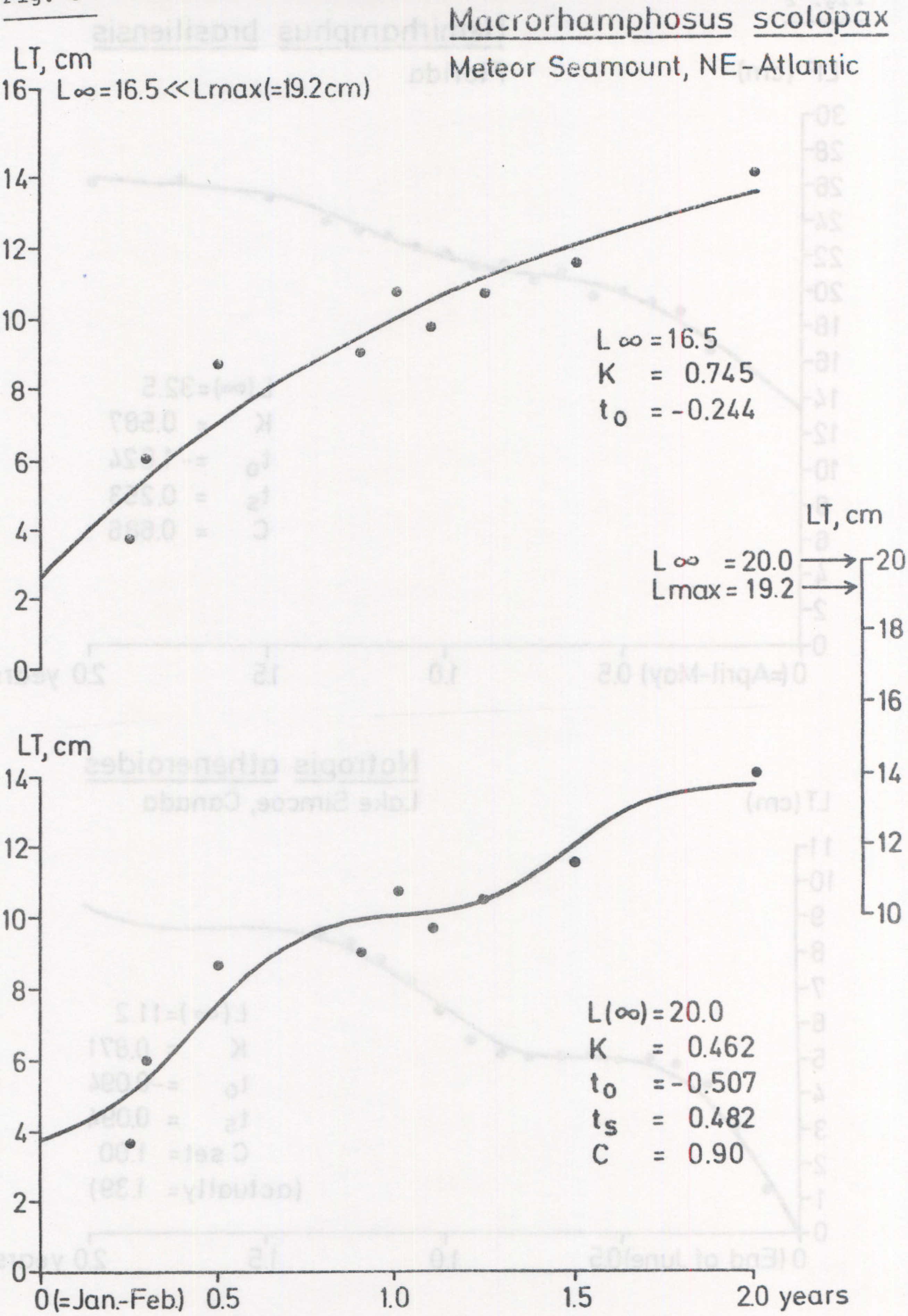

Notropis atheneroides
Lake Simcoe, Canada
LT (cm)
L(∞)=11.2
K = 0.871
t0 =-0.094
ts = 0.094
C set = 1.00
(actually= 1.39)
0 (End of June) 0.5
1.0
1.5
2.0 years

Fig. 3


Macrorhamphosus scolopax
Meteor Seamount, NE-Atlantic
LT, cm
L∞ = 16.5 ≪ Lmax (=19.2 cm)
16
14
12
10
8
6
4
2
0
L∞ = 16.5
K = 0.745
t₀ = -0.244
LT, cm
L∞ = 20.0
Lmax = 19.2
20
18
16
14
12
10
LT, cm
14
12
10
8
6
4
2
0
L(∞) = 20.0
K = 0.462
t₀ = -0.507
tₛ = 0.482
C = 0.90
0 (=Jan.-Feb.)
0.5
1.0
1.5
2.0 years

User Instructions

◀1 Fitting seasonally oscillating growth data I 2▶

Initialize/Input

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS		OUTPUT DATA/UNITS
1	Read side 1 and 2 of card I and initialize:	10	10	↑	10.00
		5	5	y^x	100000.00
			f	a	100000.00
2	Enter data	t	↑		t
	repeat until all data are entered	L_t	↑		L_t
		$L(\infty)$	A		n
3	Read side 1 and 2 of card II and go to User Instructions, Part II.				

Notes:

1) Input routine takes about 15 seconds per data triplet.
2) Note that $L(\infty)$ is entered with each set of length-at-age values.

STEP	KEY ENTRY	KEY CODE	COMMENTS
001	*LBLa	21 16 11	
	CLRG	16-53	
	STO0	35 00	
	STO4	35 04	
	STO7	35 07	
	STO9	35 09	
	P⇄S	16-51	
	CLRG	16-53	
	RAD	16-22	
010	RTN	24	
	*LBLA	21 11	These steps (and also step 009) may be deleted, and the program may then be used for multiple linear regression analysis. 24 steps are available for linearizing transformations (e.g. taking log).
	STOD	35 14	
	÷	-24	
	CHS	-22	
	1	01	
	+	-55	
	LN	32	
	STOD	35 14	
	X⇄Y	-41	
020	STOC	35 13	
	2	02	
	x	-35	
	Pi	16-24	
	x	-35	
	SIN	41	
	RCLC	36 13	
	X⇄Y	-41	
	RCLC	36 13	
	2	02	
030	x	-35	
	Pi	16-24	
	x	-35	
	COS	42	
	RCLD	36 14	
	ST+8	35-55 08	
	X²	53	
	ST+9	35-55 09	
	R↓	-31	
	GSBD	23 14	
040	−	-45	
	STOE	35 15	
	P⇄S	16-51	
	RCL3	36 03	
	RCLC	36 13	
	x	-35	
	RCL2	36 02	
	RCLB	36 12	
	x	-35	
	+	-55	
050	RCL1	36 01	
	RCLA	36 11	
	x	-35	
	+	-55	
	RCL0	36 00	
	+	-55	
	RCL6	36 06	

STEP	KEY ENTRY	KEY CODE	COMMENTS
	RCLC	36 13	
	x	-35	
	RCL5	36 05	
060	RCLB	36 12	
	x	-35	
	+	-55	
	RCL4	36 04	
	RCLA	36 11	
	x	-35	
	+	-55	
	RCL1	36 01	
	+	-55	
	P⇄S	16-51	
070	STO5	35 05	
	RCLA	36 11	
	x	-35	
	X⇄Y	-41	
	STO4	35 04	
	+	-55	
	STOD	35 14	
	P⇄S	16-51	
	RCL8	36 08	
	RCLC	36 13	
080	x	-35	
	RCL7	36 07	
	RCLB	36 12	
	x	-35	
	+	-55	
	RCL5	36 05	
	RCLA	36 11	
	x	-35	
	+	-55	
	RCL2	36 02	
090	+	-55	
	RCL9	36 09	
	RCLC	36 13	
	x	-35	
	RCL8	36 08	
	RCLB	36 12	
	x	-35	
	+	-55	
	RCL6	36 06	
	RCLA	36 11	
100	x	-35	
	+	-55	
	RCL3	36 03	
	+	-55	
	P⇄S	16-51	
	STO7	35 07	
	RCLC	36 13	
	x	-35	
	X⇄Y	-41	
	STO6	35 06	
110	RCLB	36 12	
	x	-35	
	+	-55	

REGISTERS

0	1	2	3	4	5	6	7	8	9
a	b_1	b_2	b_3	used	used	used	used	used	used

S0	S1	S2	S3	S4	S5	S6	S7	S8	S9
C_0	C_1	C_2	C_3	C_4	C_5	C_6	C_7	C_8	C_9

A	B	C	D	E	I
used	used	used	used	used	counter

Program Listing

STEP	KEY ENTRY	KEY CODE	COMMENTS
	RCLD	36 14	
	+	-55	
	1	01	
	+	-55	
	1/X	52	
	STOD	35 14	
	RCLE	36 15	
120	x	-35	
	STOE	35 15	
	RCL7	36 07	
	x	-35	
	ST+3	35-55 03	
	RCLE	36 15	
	RCL6	36 06	
	x	-35	
	ST+2	35-55 02	
	RCLE	36 15	
130	RCL5	36 05	
	x	-35	
	ST+1	35-55 01	
	RCLE	36 15	
	RCL4	36 04	
	x	-35	
	ST+0	35-55 00	
	RCLD	36 14	
	RCL4	36 04	
	x	-35	
140	STOE	35 15	
	RCL4	36 04	
	x	-35	
	RCLE	36 15	
	RCL5	36 05	
	x	-35	
	RCLE	36 15	
	RCL6	36 06	
	x	-35	
	RCL7	36 07	
150	P⇄S	16-51	
	R↓	-31	
	ST-2	35-45 02	
	R↓	-31	
	ST-1	35-45 01	
	R↓	-31	
	ST-0	35-45 00	
	R↓	-31	
	RCLE	36 15	
	x	-35	
160	ST-3	35-45 03	
	P⇄S	16-51	
	RCLD	36 14	
	RCL5	36 05	
	x	-35	
	STOE	35 15	
	RCL5	36 05	
	x	-35	
	RCLE	36 15	

STEP	KEY ENTRY	KEY CODE	COMMENTS
	RCL6	36 06	
170	x	-35	
	RCLE	36 15	
	RCL7	36 07	
	x	-35	
	P⇄S	16-51	
	ST-6	35-45 06	
	R↓	-31	
	ST-5	35-45 05	
	R↓	-31	
	ST-4	35-45 04	
180	P⇄S	16-51	
	RCLD	36 14	
	RCL6	36 06	
	x	-35	
	STOE	35 15	
	RCL6	36 06	
	x	-35	
	RCLE	36 15	
	RCL7	36 07	
	x	-35	
190	RCLD	36 14	
	RCL7	36 07	
	x^2	53	
	x	-35	
	P⇄S	16-51	
	ST-9	35-45 09	
	R↓	-31	
	ST-8	35-45 08	
	R↓	-31	
	ST-7	35-45 07	
200	P⇄S	16-51	
	ISZI	16 26 46	
	RCLI	36 46	
	RTN	24	
	*LBLD	21 14	
	STOC	35 13	
	R↓	-31	
	STOB	35 12	
	R↓	-31	
	STOA	35 11	
210	RCLD	36 14	
	RCL0	36 00	
	RCL1	36 01	
	RCLA	36 11	
	x	-35	
	+	-55	
	RCL2	36 02	
	RCLB	36 12	
	x	-35	
	+	-55	
220	RCL3	36 03	
	RCLC	36 13	
	x	-35	
	+	-55	
	RTN	24	

LABELS

A enter data	B	C	D	E
a initialize	b	c	d	e
0	1	2	3	4
5	6	7	8	9

FLAGS

0	
1	
2	
3	

SET STATUS

FLAGS	ON	OFF
0	☐	☒
1	☐	☒
2	☐	☒
3	☐	☒

TRIG	
DEG	☐
GRAD	☐
RAD	☒

DISP	
FIX	☒
SCI	☐
ENG	☐
n	2

Program Description

Program Title Fitting seasonally oscillating growth data I

Name D. PAULY* and G. GASCHÜTZ
Date JULY 1979
*Address International Center for Living Aquatic Resource Management, P.O. Box 1501
City Makati, Metro Manila State PHILIPPINES Zip Code —

Program Description, Equations, Variables, etc. 1) Given a preliminary value of $L(\infty)$ (or L_∞) and length-at-age data, the program (Part I & II) estimates the values of the parameters K, t_o, t_s and C of the equation

$$L_t = L_\infty \left(1 - e^{-\left(K(t-t_o) + C \cdot \frac{K}{2\pi} \cdot \sin 2\pi \cdot (t-t_s)\right)}\right)$$

which is a version of the von Bertalanffy Growth Formula suitable to describe the seasonally oscillating length growth of animals, e.g. of fishes.

2) The parameter estimation is based on multiple regression analysis; the calculation of the regression coefficients is based on the program "Multiple Regression Analysis" No. 50584, HP 67/97 Users' Library (Europe) by Tapio Westerlund. [By deleting step 009, and steps 012-034, the present program can also be used for solving multiple regression problems involving 3 independent variables (See Program Listing). In such cases, the second part of this program may be used for estimating R^2. (The regression coefficients (a, b_1, b_2 and b_3) are stored in STO 0 to STO 3)].

3) The large number (10^5) used when initializing may be replaced by any large number of similar magnitude.

4) The program accepts only the year as time (age) unit. The appropriate conversions may be performed when entering the data.

Operating Limits and Warnings 1) $L(\infty) - L_t$ must always be a positive number.

2) The values of time (age) must always be expressed in years or fractions thereof.

DO NOT USE THIS SPACE

User Instructions

1 Fitting seasonally oscillating growth data II 2

→ R^2 → L_t → K, t_o, t_s, C

STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS	OUTPUT DATA/UNITS
3	You have already read in side 1 and 2 of this program card. If not, do it now, then press "RAD"			
4	Calculate R^2.		A	R^2
5	Calculate K, t_o, t_s, and C.		E	K t_o t_s C
6	To estimate the length corresponding to a given t value, perform:	$L_{(\infty)}$	STO A	$L_{(\infty)}$
7	Then calculate value of L_t: step 7 may be repeated at will, e.g. in order to draw a seasonally oscillating growth curve.	t	C	L_t
8	If L_t values are to be calculated without the parameters having been estimated internally, perform	$L_{(\infty)}$ K t_o t_s C	STO A STO 4 STO 5 STO 6 STO 7	
	and go to step 7.			
	Notes: 1) When C output is negative, transform C and t_s according to instructions in Program Description II. 2) Setting C=0 in step 8 estimates values of L_t for the unseasonalized von Bertalanffy Growth Formula.			

STEP	KEY ENTRY	KEY CODE	COMMENTS
001	*LBLA	21 11	
	3	03	
	STO4	35 04	
	P⇄S	16-51	
	RCL7	36 07	
	RCL4	36 04	
	x	-35	
	RCL5	36 05	
	RCL5	36 05	
010	x	-35	
	-	-45	
	STOA	35 11	
	RCL8	36 08	
	RCL4	36 04	
	x	-35	
	RCL6	36 06	
	RCL5	36 05	
	x	-35	
	-	-45	
020	STOB	35 12	
	RCL9	36 09	
	RCL4	36 04	
	x	-35	
	RCL6	36 06	
	RCL6	36 06	
	x	-35	
	-	-45	
	STOC	35 13	
	RCL4	36 04	
030	RCL2	36 02	
	RCL1	36 01	
	P⇄S	16-51	
	RCL8	36 08	
	x	-35	
	RCL1	36 01	
	-	-45	
	STOD	35 14	
	R↓	-31	
	RCL8	36 08	
040	x	-35	
	RCL2	36 02	
	-	-45	
	x	-35	
	STOE	35 15	
	RCL3	36 03	
	RCL8	36 08	
	P⇄S	16-51	
	RCL3	36 03	
	x	-35	
050	-	-45	
	RCL4	36 04	
	x	-35	
	RCLD	36 14	
	RCL6	36 06	
	x	-35	
	+	-55	

STEP	KEY ENTRY	KEY CODE	COMMENTS
	RCLA	36 11	
	x	-35	
	RCLD	36 14	
060	RCL5	36 05	
	x	-35	
	RCLE	36 15	
	-	-45	
	RCLB	36 12	
	x	-35	
	-	-45	
	RCLC	36 13	
	RCLA	36 11	
	x	-35	
070	RCLB	36 12	
	RCLB	36 12	
	x	-35	
	-	-45	
	÷	-24	
	P⇄S	16-51	
	STO5	35 05	
	P⇄S	16-51	
	RCLD	36 14	
	RCL5	36 05	
080	x	-35	
	RCLE	36 15	
	-	-45	
	X⇄Y	-41	
	RCLB	36 12	
	x	-35	
	-	-45	
	RCLA	36 11	
	÷	-24	
	P⇄S	16-51	
090	STO6	35 06	
	RCL5	36 05	
	P⇄S	16-51	
	RCL6	36 06	
	x	-35	
	X⇄Y	-41	
	RCL5	36 05	
	x	-35	
	+	-55	
	RCLD	36 14	
100	+	-55	
	RCL4	36 04	
	÷	-24	
	CHS	-22	
	P⇄S	16-51	
	STO7	35 07	
	RCLI	36 46	
	RCL4	36 04	
	-	-45	
	1	01	
110	-	-45	
	STOA	35 11	
	RCL0	36 00	

REGISTERS

0 a	1 b_1	2 b_2	3 b_3	4 used/K	5 used/t_0	6 used/t_s	7 used/C	8 used	9 used
S0 C_0	S1 C_1	S2 C_2	S3 C_3	S4 C_4	S5 C_5	S6 C_6	S7 C_7	S8 C_8	S9 C_9
A used	B used	C used	D used	E used	I n				

Program Listing

STEP	KEY ENTRY	KEY CODE	COMMENTS
	RCL8	36 08	
	×	-35	
	RCL7	36 07	
	RCL1	36 01	
	×	-35	
	+	-55	
	RCL6	36 06	
120	RCL2	36 02	
	×	-35	
	+	-55	
	RCL5	36 05	
	RCL3	36 03	
	×	-35	
	+	-55	
	RCL8	36 08	
	X^2	53	
	RCLI	36 46	
130	÷	-24	
	STOE	35 15	
	−	-45	
	STOD	35 14	
	RCL9	36 09	
	RCLE	36 15	
	−	-45	
	STOE	35 15	
	÷	-24	
	STOB	35 12	
140	RCLE	36 15	
	RCLD	36 14	
	−	-45	
	RCLA	36 11	
	÷	-24	
	STOC	35 13	
	RCLD	36 14	
	RCL4	36 04	
	÷	-24	
	RCLC	36 13	
150	÷	-24	
	STOD	35 14	
	RCLB	36 12	
	RTN	24	
	*LBLE	21 15	
	RCL1	36 01	
	CHS	-22	
	PRTX	-14	
	STO4	35 04	
	CHS	-22	
160	RCL0	36 00	
	X⇄Y	-41	
	÷	-24	
	CHS	-22	
	STO5	35 05	
	PRTX	-14	
	RCL3	36 03	
	RCL2	36 02	
	÷	-24	

STEP	KEY ENTRY	KEY CODE	COMMENTS
	CHS	-22	
170	TAN^{-1}	16 43	
	Pi	16-24	
	÷	-24	
	2	02	
	÷	-24	
	PRTX	-14	
	STO6	35 06	
	Pi	16-24	
	×	-35	
	2	02	
180	×	-35	
	SIN	41	
	RCL4	36 04	
	×	-35	
	RCL3	36 03	
	Pi	16-24	
	×	-35	
	2	02	
	×	-35	
	÷	-24	
190	1/X	52	
	PRTX	-14	
	STO7	35 07	
	RTN	24	
	*LBLC	21 13	
	STOB	35 12	
	RCL6	36 06	
	−	-45	
	Pi	16-24	
	×	-35	
200	2	02	
	×	-35	
	SIN	41	
	RCL7	36 07	
	×	-35	
	Pi	16-24	
	÷	-24	
	2	02	
	÷	-24	
	RCL4	36 04	
210	×	-35	
	RCLB	36 12	
	RCL5	36 05	
	−	-45	
	RCL4	36 04	
	×	-35	
	+	-55	
	CHS	-22	
	e^x	33	
	CHS	-22	
220	1	01	
	+	-55	
	RCLA	36 11	
	×	-35	
	RTN	24	

LABELS

A $\rightarrow R^2$	B	C $\rightarrow L_t$	D	E $\rightarrow K, t_0, t_s, C$
a	b	c	d	e
0	1	2	3	4
5	6	7	8	9

FLAGS: 0, 1, 2, 3

SET STATUS

FLAGS	ON	OFF	TRIG		DISP	
0	☐	☒	DEG	☐	FIX	☒
1	☐	☒	GRAD	☐	SCI	☐
2	☐	☒	RAD	☒	ENG	☐
3	☐	☒			n	3

Program Description II

Program Title Fitting seasonally oscillating growth data II

Name D. PAULY* and G. GASCHÜTZ Date JULY 1979

*Address International Center for Living Aquatic Resource Management, P.O. Box 1501

City Makati, Metro Manila State PHILIPPINES Zip Code

Program Description, Equations, Variables, etc. (see also Program Description I)

5) The routine for the estimation of R^2 is taken from "Statistics for Multiple Regression Analysis" No. 50585, HP 67/97 Users Library (Europe) by Tapio Westerlund.

6) Due to size limitation, the program may not always produce positive values of C. If a negative value of C is encountered, the following transformations should be applied:

a) change $-C$ to $+C$

and b) add 0.5 to the value of t_s.

(This is easily verified by looking at equations 12c, 12d and 12e.) Although the two sets of C and t_s values (original and transformed) are equivalent in their effects on a growth curve, the use of the transformed values agrees better with the definition of C given in equation 6.

7) Program No. 50585 (see 5 above) may be used subsequently to this program to obtain additional statistics for the multiple linear regression (e.g., to obtain standard deviations and F-values for the regression coefficients).

Operating Limits and Warnings

1) The values of time (age) must always be expressed in years or fractions thereof.

2) Do not forget, when applicable, the transformations recommended in 6).

3) Steps 6, 7 and 8 must follow step 5.

DO NOT USE THIS SPACE