Gaschütz, G., D. Pauly and N. David. 1980. A versatile BASIC program for fitting weight and seasonally oscillating length growth data. International Council for the Exploration of the Sea. Council Meeting 1980/D: 6 Statistics Committee, 14 p.

This paper not to be cited without prior reference to the author.

International Council for the Exploration of the Sea C.M. 1980/D:6 Statistics Committee Ref: Pelagic, Demersal and Shellfish Cttees.

A versatile BASIC Program for fitting weight and seasonally oscillating length growth data^T)

by

G. Gaschutz²⁾, D. Pauly³⁾ and N. David⁴⁾

Abstract

A computer program is presented which allows for fitting growth curves of the von Bertalanffy type to any set of weight- or length-at-age data. The data may be weighted by sample size, need not be spaced at regular intervals, and a forcing value for the asymptotic size may be used. The goodness of fit is estimated. An allometry in the length/weight relationship can be accounted for in the case of weight growth, and seasonal growth oscillations can be accounted for in the case of length growth. Both the normal (3 parameters) version and a more generalized (4 parameters) version of the von Bertalanffy growth formula can be fitted. All equations used in the program are derived, and a full program listing is given.

- 1) All correspondence concerning this paper should be addressed to D. Pauly.
- 2) Institut für Landwirtschaftliche Betriebslehre, Kiel University, Kiel, Fed. Rep. of Germany.
- 3) International Center for Living Aquatic Resources Management, MCC P.O. Box 1501, Makati, Metro Manila, Philippines.
- 4) Computer Center, University of the Philippines, Quezon City, Metro Manila, Philippines.

Introduction

The study of fish growth, and of phenomena related to such growth, are central to fishery biology; indeed, it is largely with growth studies that fishery biology established itself as a field of its own (see Mohr, 1927; 1930; 1934; Went 1972).

2

Since the pioneering feats of Hederström (1759) and Petersen (1892), the various methods used to obtain size-at-age data have greatly improved and in fact, it has even been shown possible to age various fish by means of daily otolith rings (Panella, 1971; Brothers et al., 1976).

Despite often virulent, yet strangely ineffectual criticism (e.g. Knight, 1968, or recently by Roff, 1980), the majority of fishery biologists, since publication of Beverton and Holt's classical text (1957) have preferred the von Bertalanffy Growth Function (VBGF) over all other equations suitable for expressing the growth of fish. Therefore, in the present contribution, we aim at briefly presenting two improved versions of the VBGF, and a simple but versatile BASIC program which can be used to fit the standard versions of the VBGF as well as the new versions presented here.

The first of the new versions is the "generalized VBGF", which overcomes biologically inappropriate constraints which von Bertalanffy incorporated in his formula, while the second is a "seasonalized" version of the VBGF which allows for the fitting of seasonally oscillating length growth data.

Derivation of the generalized VBGF

Most commonly, the VBGF is given in the case of length growth the form

 $L_{t} = L_{\infty} (1 - e^{-K (t - t_{0})})$

... 1)

where L_{∞} is the mean length the fish would reach if they were to grow

to a very old age (indefinitely, in fact)

K is a growth constant

t is the "age" the fish would have had at size zero \underline{if} they had always grown according to the equation and where

L_t is the length at age t.

The corresponding equation for weight growth is

$$W_t = W_\infty (1 - e^{-K(t - t_0)})^3$$
 ... 2)

where W_{∞} and W_t are the weights corresponding to L_{∞} and L_t , respectively (see above), where K and t_0 are defined as above and where 3 is a commonly occurring value for the exponent of a length-weight relationship of the form

$$W = a \cdot L^{D} \qquad \dots 3$$

Carlander (1969) has shown, on the basis of an exhaustive compilation of length-weight relationships, that 3 is indeed the value most often reported. However, he also reports that values of b other than 3, down to 2.5 and up to 3.5, occur quite frequently. Thus, the equation used to describe the weight growth of fish should allow for allometric growth, especially if the values of K obtained from a given stock are to be similar, irrespective of their being based on length- or weight-at-age data (see Ricker, 1958, p. 200-201).

The VBGF, it may be recalled, results from the integration of the relationship

$$\frac{d_{w}}{d_{t}} = Hw^{d} - kw^{m} \qquad \dots 4)$$

where $\frac{d_W}{dt}$ is the growth rate with Hw^d and kw^m representing the synthesis of body substance (or anabolism) and the degradation of body substance

(or catabolism) respectively, both being assumed proportional to a certain power (d and m) of the fish weight (v. Bertalanffy, 1934).

Von Bertalanffy (1934) and Beverton and Holt (1957) integrated expression 4) with values of d and m assumed equal to 2/3 and 1, respectively. However, since this is but a special case, we shall call the resulting equations (expressions1 and 2) versions of the "special VBGF".

As shown by Richard (1959), Taylor (1962), or Pauly (1979), equation 4) can also be integrated when the assumptions that d = 2/3 and m = 1 are relaxed, which results in a "generalized VBGF" of the form

$$L_t^{D} = L_{\infty}^{D} (1 - e^{-KD(t-t_0)})$$
 ... 5)

or

$$L_{t} = L_{\infty} (1 - e^{-KD(t-t_{0})})^{1/D} \qquad \dots 6)$$

and for weight

$$W_t = W_{\infty} (1 - e^{-3/b \text{ KD} (t-t_0)})^{b/D}$$
 ... 7)

which, when b is equal to 3 can simplified to the relationship

$$W_t = W_{\infty} (1 - e^{-KD(t-t_0)})^{3/D}$$
 ... 0)

where, with m > d,

$$D = 3 \cdot (m - d)$$
 ... 9)

٥١

[It will be noted that when d = 2/3, m = 1 and b = 3, the value of D becomes equal to unity, in which case the generalized VBGF (equations 6-8) becomes identical to the special cases in equations 1 and 2.]

While it seems reasonable to assume that catabolism in fishes should be proportional to weight (hence, m = 1 in equations 4) and 9), setting d at 2/3 implies - among other things - that the 0₂-consumption of fish should be proportional to the 2/3 power of their weight ("2/3 rule of metabolism"), the link between anabolism and 0₂-consumption being established by the fact that fishes are aerobic heterotrophs.

It has been repeatedly demonstrated, however, since von Bertalanffy (1934) conducted his respiratory experiments (on guppies!) that the power linking body weight and 0_2 consumption (hence, anabolism) generally ranges in fishes between 0.5 (in small fishes such as guppies) and 0.9 (see Winberg 1960, 1961). Also, the power linking gill surface area and body weight (which, since it determines the scope of 0_2 consumption, also determines the scope of anabolism) has been shown to take values generally averaging 0.8 (De Jager & Dekkers, 1975), with values of up to 0.9 in large fishes such as tuna (Muir, 1969).

In fact, it can be demonstrated that high values of d (and consequently low values of D) occur mainly in fishes capable of reaching a very large size, while low values of d (and high values of D) occur in fish the adult size of which remains very small (Fig. 1).

This provides a method for obtaining preliminary estimates of D from size data alone - independently of growth data - by means of the empirical equation

$$D = 3 \cdot [1 - (0.6742 + 0.03574 \log_{10} W_{max}) \qquad \dots 10)$$

where W_{max} is the maximum weight recorded from the fishes of a given stock, in grams(see Fig. 1). Expression 10 is incorporated in the BASIC program presented here.

- 5 -



The use of distinct value of D for each stock (rather than assuming that D = 1 in all fishes) considerably extends the flexibility of the VBGF, besides having the advantage of making the other parameter estimates $(L_{\infty}, W_{\infty} \text{ and } K)$ easier to interpret in biological terms (Pauly, 1979); for example, the estimates of asymptotic size correspond to the size of the largest specimen recorded from a given stock, as also noted by Mathisen & Olsen (1968 p. 142).

Seasonal growth

Several versions of the VBGF suitable for describing the seasonally oscillating length growth of fish had been presented (e.g. by Ursin, 1963; Pitcher & McDonald, 1973; Daget & Ecoutin, 1976; Cloern & Nichols, 1978) when two of us presented yet another version of a seasonally oscillating VBGF (Pauly and Gaschütz, 1979). This latter version, we believe has several advantages over the versions previously published. In terms of the generalized VBGF, it has the form

$$L_{t} = L_{\infty} (1-e^{-[KD(t-t_{o}) + C \circ \frac{KD}{2\pi} \sin 2\pi (t-t_{o})]})$$
 ... 11)

where L_{∞} , L_t , t, K, D and t_0 are as defined above and where C is a constant with values generally ranging between zero (e.g. in the tropics where seasonal growth oscillation are slight or nonexistent) to unity (in temperate waters, when growth is slowed down or halted in winter). The parameter t_s , in equation (10), finally, expresses the time passed between birth (at t = 0) and the onset of the first growth oscillation (which is modulated by a sine wave curve of period one year). A simple method to fit the generalized VBGF to a set of length-at-age data is to rearrange equation (5) such that

$$\log_{e} (1 - \frac{L_{t}^{D}}{L_{\infty}^{D}}) = KDt_{o} = KD$$
 ... 12)

which has the structure of a linear regression of the form

$$y = a + nx$$
 ... 13)

where

$$\log_{e} \left(1 - \frac{L_{t}^{D}}{L_{\infty}^{D}}\right) = \gamma \qquad \dots 14a$$

and

Thus, the growth parameters K and $t_{\rm O}$ can be estimated, given $L_{\infty},$ D and a set of length-at-age-data, since

and

For weight growth (equation 7) the transformation is

$$\log_{e} (1 - \frac{W_{t}^{D/b}}{W_{\infty}^{D/b}}) = \frac{3}{b} KDt_{0} - \frac{3}{b} KDt \qquad \dots 16)$$

which also has the form of a linear regression from which K and t_o can be estimated, given W_∞ , D, b and a set of weight-at-age data.

This method, which goes back to von Bertalanffy (1934), provides results that can be improved by using different "trial" values of L_{∞} (or W_{∞}) until a value is found which best linearizes the regression (and thus maximizes the correlation between the y and the x values). The latter method, described in detail by Ricker (1958, p. 195-196 and 1975, p. 225) and commonly used in growth curve fitting exercises, forms a part of the program presented here, which may therefore be seen as an extension of the original von "Bertalanffy Plot" (see Table 1).

This simple approach provides - as opposed e.g. to the Ford-Walford Plot statistically unbiased parameter estimates, allows for data at different time intervals to be used, and for data to be weighted by sample size (Table 1). Also, it is well suited for use with a small computer, which will rapidly perform the few iterations needed to achieve a suitable level of precision. Moreover, the advantages of this simple approach can be retained when fitting seasonally oscillating length growth data. In analogy to equation 12), we may rewrite equation 11) in the form

$$\log_{e} (1 - \frac{L_{t}^{D}}{L_{\infty}^{D}}) = - [KD (t-t_{o}) + C \cdot \frac{KD}{2\pi} \cdot \sin 2\pi (t-t_{s})] \qquad \dots 17)$$

Since

$$\sin (\alpha - \beta) = (\sin \alpha \cdot \cos \beta) - (\sin \beta \cdot \cos \alpha) \qquad \dots 18)$$

we have

$$\log_{e}(1 - \frac{L_{t}^{U}}{L_{\infty}^{D}}) = -KD(t - t_{0} + \frac{C}{2\pi} \sin 2\pi t \cdot \cos 2\pi t_{s} - \frac{C}{2\pi} \cdot \sin 2\pi t_{s} \cdot \cos 2\pi t_{s} - \frac{C}{2\pi} \cdot \sin 2\pi t_{s} \cdot \cos 2\pi t_{s} - \frac{C}{2\pi} \cdot \sin 2\pi t_{s} \cdot \cos 2\pi t_{s} - \frac{C}{2\pi} \cdot \sin 2\pi t_{s} \cdot \cos 2\pi t_{s} - \frac{C}{2\pi} \cdot \sin 2\pi t_{s} \cdot \cos 2\pi t_{s} - \frac{C}{2\pi} \cdot \cos 2\pi t_{s} -$$

- 9 -

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

$$y = a + b_1 x_1 + b_2 x_2 + b_3 x_3$$
 ... 20)

where

$$y = \log_e (1 - \frac{L_t^D}{L_{\infty}^D})$$
 ... 21a)

$$x_2 = \sin 2\pi t$$
 ... 21c)

and $x_3 = \cos 2\pi t$... 21d)

Equation 20) thus yields coefficient values which can be used to estimate the growth parameters by means of the relationships:

 $a = KDt_0 \qquad \dots 22a)$

$$b_1 = -KD$$
 ... 22b)
 $b_2 = -KD \frac{C}{2\pi} \cdot \cos 2\pi t_s$... 22c)
 $b_3 = +KD \frac{C}{2\pi} \cdot \sin 2\pi t_s$... 22d)

$$t_s = \frac{arc \tan (-b_3/b_2)}{2\pi}$$
 ... 22e)

while the best value of L_{∞} here is the one which maximizes the multiple correlation between y and x₁, x₂ and x₃.

This best value is produced by the program presented here along with the corresponding values of R^2 , K, C, t_o and t_s after a few iterations only, given a value of D and a set of seasonally oscillating length-at-age data.

Table 1. Comparison of some methods used for fitting the von Bertalanffy Growth Formula (VBGF) to sizeat-age data.

·					
PROPERTY	Von Bertalanffy Plot ¹)	Ford-Walford Plot ²⁾	Non-Linear Regression3)	ETAL 1	
Is the asymptotic size determined?	no ⁴⁾	yes ⁵⁾	yes	yes	
ls t _o estimated?	yes	no	yes	yes	
Are the estimates of asymptotic size and K accurate?	no ⁴⁾	no ⁵⁾	yes	yes	
Can unequal time intervals be used?	yes	no	yes, in most versions	yes	
Can the size-at-age values be weighted by sample size?	yes	no	yes, in most versions	yes	
Can seasonally oscillating length growth data also be fitted?	no	no	no	yes	
Does the method allow for the use of a 4-parameter version of the VBGF?	yes6)	yes ⁶)	yes ⁶⁾	yes, it is incor- porated in ETALI.	

1) Von Bertalanffy (1934 p. 627), Beverton and Holt (1957 p. 283).

2) Ford (1933), Walford (1946) and see Ricker (1975) for review.

3) Tomlinson and Abrahamson (1961), Fabens (1965), Allen (1966, 1967), Misra (1980) and others.

4) A first trial value of the asymptotic size may be improved iteratively, however, and this results in accurate estimates of K (see text).

- 5) Because the first and last values are used only once, and the others twice, because the values are grouped predominantly on the right side of the plot and because the FW-Plot is generally used in conjunction with an inappropriate statistical model (a predictive or type I regression instead of a functional or type II regression), the estimates of both L_∞ (or W_∞) and K obtained from FW Plots are generally biased (see Ricker 1973, 1975).
- 6) All methods used to fit the special VBGF can be used to fit the generalized VBGF when D is known (see e.g. Taylor, 1962) for examples of Ford-Walford Plots used in conjunction with the generalized VBGF). Ricker (1975, p. 225 and 1979, p. 719) gives references to papers and programs which can be used to fit a generalized form of the VBGF in which the (empirical) parameter corresponding to D, however, can take any value and is unrelated to W_{max} (see e.g. the models presented by Richard, 1959; Chapman, 1960 or Turnbull, 1964).

-

Application examples

Three aspects of the versatility of the program presented here which is called ETAL I (see Appendix) will be illustrated by means of examples:

- 1) fitting weight-at-age data when weight growth is allometric;
- 2) fitting of size-at-age data with the generalized VBGF;
- fitting lenght-at-age data with a seasonally oscillating version of the VBGF.

Example 1

A

В

Table 2 contains an artificial data set with length-at-age data, and 3 series of weight-at-age data calculated by means of length/weight relationships such as expression 3) and having the same value of a = 1 throughout, with values of b = 2.5, 3.0 and 3.5, respectively.

As may be seen, the values of both K and t_0 are in all four cases exactly the same, while the three values of W_{∞} can be converted back to L_{∞} by raising them by the inverse of the corresponding values of b (Table 2).

Table 2. Data (A) for and results (B) of the comparison of growth parameters obtained from length- and from weight-at-age data. (All computations with D=1).

	1	Weig	ht (in arbitrary uni	ts)
age	<u>length (cm)</u>	b = 2.5	b = 3.0	b = 3.5
1	15	871.4	3375	13071
2	18	1375	5832	24743
3	20	1789	8000	35777
4	21	2021	9261	42439
W _∞		2450 1/2 5	11669 1/2 0	55572 1/3 5
L _∞	22.68	22.68 $(W_{\infty}^{(1)})$	22.68 $(W_{\infty}^{1/3.0})$	22.68 (W_{∞}^{\prime})
ĸ	0.511	0.511	0.511	0.511
to	-1.116	-1.116	-1.116	-1.116
RŽ	0.999	0.999	0.999	0.999

- 12 -

Example 2

In fishes that can grow to a very large size, using the VBGF, with its inherent assumption that d = 2/3, can lead to serious overestimate of asymptotic size, along with biased estimates of the other growth parameters. Thus, in bluefin tuna (<u>Thunnus thynnus</u>), the power which links gill and weight growth is d = 0.9 (Muir, 1969).

Using the data of Table 3, growth parameters have been estimated twice using both the special and the generalized VBGF with the corresponding values of D = 1 and D = 0.3, respectively.

The results are given in Fig. 2, which shows that while both curves fit the data remarkably well, the special VBGF produces an estimate of asymptotic length (L_{∞} =421 cm) that is well beyond the maximum size recorded for bluefin tuna (about 330 m according to Tiews, 1963). On the other hand, the value of L_{∞} = 319 cm obtained by means of fitting the generalized VBGF corresponds quite well with the field data. The value of K corresponding with this new estimate of L_{∞} is quite high and brings in accord the contention of von Bertalanffy that a given value of K is an indicator of metabolic activity (v. Bertalanffy, 1951, p. 293-294) with what is presently known of the physiology of these highly active "migrants of the sea" (Sharp and Dizon, 1978).

Example 3

Table 4 presents literature data on the seasonally oscillating growth of two fishes, one from the subtropics (the halfbeak, <u>Hemirhamphus brasiliensis</u>) the other from temperate waters (the Norway pout, Trisop**t**erus esmarki).

The data were fitted by means of our seasonal growth model, and the resulting growth curves and growth parameter estimates are given in Fig. 3.



Fig. 2. Growth curves at bluefin tuna. Dotted line: special VBGF, with D = 1; solid line: generalized VBGF, with D = 0 at text for further details.

age (years) ²⁾	LF (cm)	age	LF	age	LF
1	64	6	153	11	216
2	82	7	169	12	227
3	98	8	182	13	239
4	118	9	195	14	254
5	136	10	206	-	-

Table 3. Lenght-at-age data for Atlantic bluefin $(\frac{Thunnus thynnus}{1})$

1) from Sella (1929), as given in Hohendorf (1966).

2) the "ages" are presumably age groups.

Table 4. Length-at-age data of two stocks of fish displaying seasonal growth oscillations.

Nr	(relative) age, in months	A (cm)	B (cm)	Nr	(relative) age, in months	A (cm)	B (cm)
		<u></u>					
1	3	16.8	7.3	12	14	23.2	13.8
2	4	18.9	8.8	13	15	23.6	14.7
3	5	19.4	9.4	14	16	25.0	14.5
4	6	20.0	10.6	15	17	-	15.2
5	7	19.8	10.4	16	18	25.5	15.1
6	8	21.0	11.2	17	19	-	15.2
7	9	20.8	11.1	18	20	-	15.3
8	10	21.5	-	19	21	26.4	15.5
9	11	21.5	11.3	20	23	_ ·	15.5
10	12	22.2	11.4	21	24	26.4	-
11	13	22.5	11.8	-		-	-

A) Mean fork length at relative age of half beak (<u>Hemirhamphus brasiliensis</u>, off Florida, as read off Fig. 5 in Berkeley and Houde (1978).

B) Mean total length at age of Norway pout, <u>Trisopterus</u> esmarkii in Scottish waters, as read off fig. 6 in Gordon (1977).

Fig. 3. Two seasonally oscillating growth curves illustrating how the intensity of seasonal growth oscillations are reflected in the estimated values of C.



As may be expected, the growth oscillations in the subtropical fish are less pronounced than in the temperate fish, which is exposed to greater environmental fluctuations (e.g. of temperature). This is reflected in the value of the parameter "C", which took a value of 0.685 in the subtropical and 1.07 in the temperate fish.

Summary and Discussion

The use of our program in conjunction with appropriate data sets allowed, in three cases (example 1, 2 and 3), the demonstration of useful properties of the two new versions of the VBGF.

In the first example, we demonstrated that the values of K and t_0 computed from corresponding length- or weight-at-age data are the same when the appropriate value of the length/weight exponent is used. The identity of the K values in such cases was previously known (Paloeimo & Dickie, pers. comm. to Ricker, 1958, p. 200); the identity of the t_0 values, on the other hand contradicts the statement by Ricker (1975, p. 231) that the value of t_0 obtained from length growth curves should always be lower than the values obtained from weight growth curves (t_0^2 of Ricker).

In the second example, we demonstrated that the generalized VBGF, while providing a fit that is only slightly better than the special VBGF, has the property, in the case of fishes which reach large size, of generating an asymptotic size which largely corresponds to the largest size actually recorded from the stock in question (L_{max}). This property of the generalized VBGF makes it possible to use values of L_{max} as preliminary estimates of L_{∞} (which may be coded " $L_{(\infty)}$ ") when growth data are scarce or unreliable (Pauly, 1979).

- 17 -

In the third example, finally, we demonstrated that our seasonalized version of the VBGF is not only extremely easy to fit - it can even be fitted by means of a programmable pocket calculator (see Pauly and Gaschütz, 1979) but also that its parameter "C" is interpretable biologically, since it expresses the relationship between environmental fluctuation and the intensity of the growth oscillations these fluctuations generate.

Ricker (1979, p. 719) suggested, while reviewing seasonal growth models, that "the practical value of these expressions remains obscure".

One eminently practical value of the seasonalized version of the VBGF, both in its special on generalized form, is that it generates values of L_{∞} and K very different from those that are obtained when not accounting for seasonal growth. Thus for example, in the case of the Norway pout, the seasonalized VBGF used here generated values which strongly contrast with those commonly used for stock assessment in the North Sea:

	our values	Raitt (1968)
L_{∞}	17.8	19.0 - 19.3
К	1.06	0.44 - 0.59

In the tropics where seasonal growth oscillations are slight, not considering this factor will have less serious effects, however.

Acknowledgements

We would like to thank ICLARM intern Jose Ingles (Univ. of the Philippines, College of Fisheries) for his untiring assistance with the testing of our program and the computation of the examples, and R. Bugay (ICLARM) for drawing the figures.

- 18 -

Allen, K.R., 1967. Computer programs available at St. Andrew Biological Station. Fish. Res. Board Can. Tech. Rep. 20, 32 p. + Append.

23: 163-179.

- Berkeley, S.A. and E.D. Houde, 1978. Biology of two exploited species of halfbeaks, *Hemirhamphus brasiliensis* and *H. balao* from Southeast Florida. Bull. Mar. Sci. 28: 624-644.
- Bertalanffy, L. von. 1934. Untersuchungen über die Gesetzlichkeiten des Wachstums I. Roux' Archiv für Entwicklungsmechanik 131: 613-652.
- Bertalanffy, L. von. 1951. Theoretische Biologie Zweiter Band: Stoffwechsel, Wachstum. A. Franke A.G. Verlag, Bern, 418 p.
- Beverton, R.J.H., and S.J. Holt. 1957. On the dynamics of exploited fish populations. U.K. Min. Agric. Fish., Fish. Invest. (Ser. 2) 19: 533 p.
- Brother, E.G., C.P. Mathews and R. Lasker. 1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull. 74: 1-8.
- Carlander, K. 1969. Handbook of freshwater fishery biology Vol. I. Iowa State University Press, Ames, 752 p.
- Chapman, D.G. 1960. Statistical problems in dynamics of exploited fisheries populations. Proc. Fourth Berkeley Symp. on Math. Stat. and Prob., 153-168.
- Cloern, J.E. and F.H. Nichols. 1978. A von Bertalanffy growth model with a seasonally varying coefficient. J. Fish. Res. Board Can. 35: 1479-1482.
- Daget, J. and J.M. Ecoutin. 1976. Modèles mathématiques de production applicables aux poissons tropicaux subissant un arrêt prolongé de croissance. Cah. O.R.S.T.O.M. ser. Hydrobiol. 10: 59-69.
- De Jager, S. and W.J. Dekkers. 1975. Relations between gill structures and activity in fish. Netherland J. of Zool. 25: 276-308.
- Fabens, A.J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29: 265-289.
- Ford, E. 1933. An account of herring investigations conducted at Plymouth during the years from 1924-1933. J. Mar. Biol. Assoc. U.K. 19: 305-384.
- 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.
- Hederström, H. 1759. [Observations on the age of fishes] reedited 1979 in: Drottningholm Statens Undersknings och Forsaksanstalt for sotvattensfisket 40: 161-164.
- Hohendorf, K. 1966. Eine Diskussion der Bertalanffy Funktionen und ihre Anwendung zur Charakterisierung des Wachstums von Fischen. Kieler Meeresforsch 22: 70-97.
- Knight, W. 1968. Asymptotic growth: an example of nonsense disguised as mathematics. J. Fish. Res. Board Can. 25: 1303-1307.
- Lien, D.A. 1978. The BASIC HANDBOOK. Compusoft Publishing San Diego, U.S.A., 360 p.
- Mathisen, O. and S. Olsen. 1968. Yield isopleths of the halibut, *Hippoglossus hippoglossus*, in Northern Norway. FiskDir. Skr. Ser, HavUnders. 14: 129-159.
- Misra, R.K. 1980. Statistical comparisons of several growth curves of the von Bertalanffy type. Can. J. Fish. Aquat. Sci. 37: 920-926.
- Mohr, E. 1927. Bibliographie der Alters- und Wachstums-Bestimmung bei Fischen, J. du Conseil 2(2): 236-258.
- Mohr, E. 1930. Bibliographie der Alters- und Wachstums-Bestimmung bei Fischen. II Nachträge und Fortsetzung. J. du Conseil 5(1): 88-100.
- Mohr, E. 1934. Bibliographie der Alters- und Wachstums-Bestimmung bei Fischen. III Nachträge und Fortsetzung. J. du Conseil 9(2): 377-391.

- Muir, B.S. 1969. Gill size as a function of fish size. J. Fish. Res. Bd. Canada 26: 165-170.
- Panella, G. 1971. Fish otoliths: daily growth layers and periodical patterns. Science 173: 1124-1127.
- Pauly, D. 1979. Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy's Growth Formula Ber. Inst. f. Meereskunde (Kiel University) No. 63, 156 p.
- Pauly, D. and G. Gaschütz. 1979. A simple method for fitting oscillating length growth data, with a program for pocket calculators I.C.E.S. CM 1979/G:24, 26 p. (mimeo)
- Petersen, J. 1892. Fiskensbiologiske forhold i Holboek Fjord, 1890-91. Beretning fra de Danske Biologiske Station for 1890 (91), 1: 121-183.
- Pitcher, T.J. and MacDonald. 1973. Two models for seasonal growth in fishes. J. appl. Ecology 10: 599-606.
- Raitt, D., 1968. The population dynamics of the Norway pout in the North Sea. Mar. Res. (Scotland) 5, 24 p.
- Richards, F.J., 1959. A flexible growth function for empirical use. J. exp. Bot. 10(29): 290-300.
- Ricker, W.E. 1958. Handbook of computation for biological statistics of fish populations. Bull. Fish. Res. Board Can. 119, 300 p.
- Ricker, W.E. 1973. Linear regression in fishery research. J. Fish. Res. Board Can. 30: 409-434.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.
- Ricker, W.E. 1979. Growth rates and models, p. 677-743 in:
 W.S. Hoar, D.J. Randall and J.R. Brett (eds) Fish Physiology,
 Vol VIII Bioenergetics and growth. Academic Press 786 p.
- Roff, D.A. 1980. A motion for the retirement of the von Bertalanffy Function. Can. J. Fish. Aquat. Sci. 37: 127-129.
- Sella, M. 1929. Migrazioni e habitat del tonno (*Thunnus thynnus*) studiati col metodo degli ami, con osservazioni su l'accrescimento, etc. Memoria R. Comit. Talassog. ital. 156: 1-24.
- Sharp, G.D., and A.E. Dizon. 1978. (eds) The physiological ecology of tuna. Academic Press 485 p.
- Taylor, C.C. 1962. Growth equations with metabolic parameters. J. du Conseil 27: 270-286.
- Tiews, K. 1963. Synopsis of biological data on bluefin tuna *Thunnus thynnus* (Linnaeus) 1978 (Atlantic and Mediterranean). p. 422-481 in:Proceedings of the world scientific meeting on the biology of tuna and related species, La Jolla, California, U.S.A., 2-4 July 1962. FAO Fish Rep. (6), Vol. 2. Rome
- Turnbull, K.J. 1964. An iterative process for fitting the Chapman-Richards generalized growth model. Univ. of Washington, Forest. Biometry Program No. 8 (Fortran II or IV): 1-9.
- Tomlinson, P.K. and N.J. Abrahamson. 1961. Fitting a von Bertalanffy growth curve by least squares, including table of polynomals. Fish. Bull. Calif. *116*: 1-69.
- Ursin, E. 1963. On the incorporation of temperature in the von Bertalanffy growth equation. Medd. fra Danmarks Fiskeri-og Havundersøgelser 4: 1-16.
- Walford, L.A. 1946. A new graphic method of describing the growth of animals. Biol. Bull. 90: 141-147.
- Went, A.E.J. 1972. Seventy Years Agrowing, a History of the International Council for the Exploration of the Sea 1902-1972. Rapp. P.-V. des Réun, Vol. 165.
- Winberg, G.G. 1960. [Rate of metabolism and food requirements of fishes] Minsk, USSR. 253 p. (1956) Fisheries Research Board of Canada, Translation Series No. 194, 239 p.
- Winberg, G.G. 1961. [New information on metabolic Rate in Fishes] Vopr. Ikhtiol. Vol. 1: 157-165. Fish. Res. Board Can. Transl. Ser. No. 362 11 p.

Appendix: Program listing of ETAL I

Following is a full listing of our program which we have named after Pierre ETAL d'ANON (1914-1980) one of the most inspiring and prolific scientific authors of this century.

The BASIC language has a wide variety of "dialects" and the one we used is Radio Shack BASIC II (we used a TSR-80 Model I Microcomputer). Some of the statements listed here may thus not be understood by your computer. In such cases, "translations" will be necessary, for which purpose we recommend "THE BASIC HANDBOOK" of Lien (1978).

10 DIM D(50), D1(50), X(50), XV(50), E(50), EV(50), S(50), C(50), A(4,4), R(4,4): P1=3.141 59:CLS:R\$="N" 20 GOSUB1250:REM DATA INPUT 30 N1=2:IF L\$ ="L" THEN INPUT SEASONAL FIT (Y/N)";S\$:IF S\$="Y" THEN N1=4 ELSE IF S\$ () "N" THEN 30 40 INPUT"TIME UNITS IN YEARS (Y/N)";S\$:IF S\$="Y" THEN M1=1 :GOTO70ELSE IF S\${}"N THEN 40 50 INPUT"TIME UNITS IN MONTHS (Y/N)";S\$:IF S\$="Y" THEN M1=12:GOTO70: ELSE IF S\${ >"N" THEN 50 60 INPUT TIME UNITS IN DAYS (Y/N) "; S\$: IF S\$="Y" THEN M1=365 ELSE IF S\$="N" THEN 40ELSE 60 70 INPUT"ESTIMATE D (Y/N)";S\$:IF S\$="N" THEN 110 80 IF S\$ () "Y" THEN 70 90 INPUT"MAXIMUM WEIGHT IN GRAMS";WX:D=3*(1-(0.6742+0.03574*LOG(WX)/LOG(10.))) 100 PRINT"ESTIMATED D =";D 110 PRINT TYPE VALUE OF D, ELSE TYPE 1"; INPUTD0 120 IF L#="L" THEN B0=1 ELSE INPUT"EXPONENT OF L/W RELATIONSHIP (B)";B0 130 DØ=DØ/BØ 140 IF M=1 THEN INPUT"USE WEIGHTING FACTORS (Y/N)";S\$:IF S\$="Y" THEN FOR I3%=1 T O N:D(I3%)=D1(I3%):NEXT I3%:GOTO170 150 IF M=1 THEN IF S\$ <> "N" THEN 140

160 IF M=1 THEN FOR I3%=1 TO N:D(I3%)=1:NEXT I3% 170 IF L\$="L" THEN INPUT"ENTER FORCING VALUE OF L(00), IF NONE TYPE 0";L2:GOTO19 Ø 180 IF L\$="W" THEN INPUT"ENTER FORCING VALUE OF W(00), IF NONE TYPE 0";L2 190 INPUT"PROCEED (Y/N)"; S\$; IF S\$="N" THEN 30 ****** WAIT ******* 200 CLS:PRINT" 210 B(1)=1 220 Y1=0:Y2=0:FOR 18%=1 TO 4 :FOR 19%=1 TO 4 :A(18%,19%)=0:NEXT 19%:NEXT18% 230 L1=0 260 L(I)=EXP(D0*LOG(LV(I))) 270 Y1=Y1+L(I)*D(I) 280 Y2=Y2+L(1)*L(I)*D(I) 290 B(2)=X(1) - exc 300 IF N1=2 THEN 350 310 B(3)=SIN(2*P1*X(I)) 320 B(4)=COS(2*P1*X(I)) 330 S(I) = B(3)340 C(I)=B(4) 350 I1=D(I) -360 FOR K=1 TO N1 370 FOR J=1 TO N1 380 A(K,J) = A(K,J) + B(K) + B(J) + I1390 NEXT J 400 NEXT K 410 IF L(I) (=L1 THEN 430 420 L1 = L(I)430 NEXT I 440 N3=A(1,1) 450 Y2=Y2-Y1*Y1/N3 460 FOR I=1 TO 4 470 B(I)=0 480 FOR J=1 TO 4 490 R(I,J) = 0(† 4) 500 NEXT J 510 R(I,I)=1 520 NEXT I 530 FOR I1=1 TO N1 540 P=A(I1, I1) 550 IF P()0 THEN 580 560 PRINT"EQUATIONS CANNOT BE SOLVED WITH DATA ENTERED." 570 STOP 580 FOR J=1 TO N1 590 A(I1, J)=A(I1, J)/P 600 R(I1, J) = R(I1, J) / P610 NEXT J 620 FOR I=1 TO N1 630 IF I=I1 THEN 690 640 P = A(I, I1)650 FOR J=1 TO N1

- 21 -

```
660 A(I,J) = A(I,J) - P * A(II,J)
670 R(I,J) = R(I,J) - P * R(I1,J)
680 NEXT J
690 NEXT I
700 NEXT I1
710 D4=2
720 F2=Y2
730 L2=L2+D0
740 W$="N": IF L2>L1*1.001 THEN W$="F":GOTO760
750 L2=1.5*L1
760 D3=L2-L1
770 LØ=L2
780 FOR I=1 TO 4
790 B(I)=0
800 W(I)=0
810 NEXT I
820 FOR I=1 TO N
830 P=D(I)*LOG(L0-L(I))
840 B(1) = B(1) + P
850 B(2) = B(2) + P \times X(1)
860 B(3) = B(3) + P + S(1)
870 B(4) = B(4) + P * C(1)
880 NEXT I
890 FOR I=1 TO N1
900 FOR J=1 TO N1
910 W(I)=W(I)+R(I,J)*B(J)
920 NEXT J
930 NEXT I
940 52=0
950 FOR I=1 TO N
960 G=W(1)+W(2)*X(I)+W(3)*S(I)+W(4)*C(I)
970 G=L0-L(I)-EXP(G)
980 \ S2=S2+G*G*D(I)
990 NEXT I
1000 IF LO()L2 THEN 1170
1010 IF S2>F2 AND W$="N" THEN GOTO 1140
1020 F2=S2
1030 T0=(LOG(L0)-W(1))/W(2)
1040 K=-W(2)/(D0*B0)
1050 IF L$="L" THEN PRINT"L00 =";EXP(LOG(L0)/D0);" T0 =";T0;" K =";K;:GOTO1070
1050 IF L$="W" THEN PRINT"W00 =";EXP(LOG(L0)/D0);" T0 =";T0;" K =";K;
1070 IF N1=2 THEN C0=0:T1=0:GOT01110
1080 T1=ATN(-W(4)/W(3))/(2*P1)
1090 C0=W(3)*2*P1/(W(2)*COS(2*P1*T1))
1100 IF CO ( 0.0 THEN T1=T1+.5; CO=CO*(-1.0)
1110 PRINT" C=";C0;" TS=";T1
1120 PRINT"***** SUM OF SQUARES=";52;:PRINT " r*r=";1-52/Y2;"
                                                                      ****** * PRINT
1130 IF W#="F" THEN 1220
1140 51=52
 198 10-13+1.001
1160 0010 700
                14
```

1170 IF S1>S2 THEN 1190

1180 D4=0.5 1190 D3=D3+D4 1200 L2=L2-SGN(S2-S1)*D3 1210 IF D3>L2*0.001 THEN 770 1220 INPUT"REPEAT WITH DIFFERENT PARAMETERS (Y/N)";5\$ 1230 IF S\$="Y" THEN R\$="Y":GOT030 1240 END 1250 CLS:PRINT" **** DATA INPUT ROUTINE 1260 INPUT"NUMBER OF OBSERVATIONS";N 1270 INPUT DATA WEIGHTED BY SAMPLE SIZE (Y/N) "; S\$: IF S\$="N" THEN M=0 ELSE IF S\$= "Y" THEN M=1 ELSE 1270 1280 INPUT"LENGTH GROWTH OR WEIGHT GROWTH (L/W)";L\$:IF L\$()"L" AND L\$()"W" THEN 1280 1290 CLS:PRINT" ***** ENTER";N;"OBSERVATIONS ****** 1300 FOR I=1 TO N 1310 PRINT"ENTER AGE(";I;")=";;INPUTX(I) 1320 IF LS="L" THEN PRINT"ENTER LENGTH(";I;")=";:INPUT L(I):GOTO1340 1330 IF Ls="W" THEN PRINT"ENTER WEIGHT(";I;")=";:INPUT L(I) 1340 D(I)=1:IF M=1 THEN PRINT"ENTER WEIGHTING FACTOR(";I;")=";:INPUT D(I) 1350 PRINT:NEXT I ***** CHECK FOR ERRORS ***** 1360 CLS:PRINT" 1370 IH=1 1380 FOR I=1 TO N 1390 PRINT"AGE(";I;")=";X(I); 1400 IF Ls="L" THEN PRINT TAB(14);"LENGTH(";I;")=";L(I); 1410 IF Ls="W" THEN PRINT TAB(14); "WEIGHT("; I; ")="; L(I); 1420 PRINTTAB(38); "WT.FACTOR(";I;")=";D(I) 1430 IF I=14*IH THEN INPUT"PRESS 'ENTER' KEY TO CONTINUE";5\$:IH=IH+1 1440 NEXT I 1450 INPUT"DISPLAY AGAIN (Y/N)";S\$:IF S\$="Y" THEN 1360 1460 INPUT"CORRECTION NEEDED (Y/N)";S\$ 1470 IF S\$="N" THEN 1640 1480 IF S\$ () "Y" THEN 1460 1490 PRINT" ***** CORRECTION ROUTINE ***** 1500 INPUT"CORRECTION FOR AGE NEEDED (Y/N)";S\$:IF S\$="N" THEN 1540 1510 PRINT"TYPE SEQUENCE NUMBER OF ERRONEOUS AGE"; INPUT K* 1520 PRINT"AGE(";K%;") =";:INPUT X(K%) 1530 GOT01500 1540 IF LS="L" THEN INPUT"CORRECTION FOR LENGTH NEEDED (Y/N)";SS;IF SS="N" THEN 1600 1550 IF LS="L" THEN PRINT TYPE SEQUENCE NUMBER OF ERRONEOUS LENGTH";: INPUT K% 1560 IF LS="L" THEN PRINT"LENGTH(";K%;") =";:INPUT L(K%):GOTO 1540 1570 INPUT"CORRECTION FOR WEIGHT NEEDED (Y/N)";S\$:IF S\$="N" THEN 1600 1580 PRINT"TYPE SEQUENCE NUMBER OF ERRONEOUS WEIGHT"; : INPUT K% 1590 PRINT"WEIGHT(";K%;") =";:INPUT L(K%):GOTO 1570 1600 IF M=1 THEN INPUT"CORRECTION FOR WEIGHTING FACTOR NEEDED (Y/N)";S\$:IF S\$=" N" THEN 1360 1610 IF M=0 THEN 1360 1520 PRINT TYPE SEQUENCE NUMBER OF ERRONEOUS WEIGHTING FACTOR"; : INPUT K% 1630 PRINT"WT. FACTOR(";K%;") =";:INPUT D(K%):GOTO 1600 1640 FOR I3%=1 TO N: D1(I3%)=D(I3%):LV(I3%)=L(I3%):XV(I3%)=X(I3%): NEXT I3% 1650 RETURN

.