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Bertalanffy function and Ford-Walford formula

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Introduction

Fishery biologists have very intensively investigated the possibilities of a mathematical description of growth processes. The growth of fish, unlimited and apparently not complicated by any discontinuity after larval development, seems a particularly suitable example for the study of growth processes. I shall not discuss the variety of suggested functions, but rather limit myself to the problem of the relationship between the Ford-Walford formula and the Bertalanffy function. Both functions have proved very useful and have been applied fairly extensively. The far-reaching agreement between the numerical results has induced BEVERTON & HOLT (1957) and TAYLOR (1958) to clarify the mathematical relationship between the two formulae.

The constancy of growth rates in consecutive years, discovered by FORD (1933) and later by WALFORD (1949), is based on a simple representation of the lengths which are the only values with which this procedure operates. On standard graph paper (graded in millimeters) the individual lengths are plotted on the abscissa, with the respective next higher length values as ordinates. The coordinate points obtained in this manner usually form in very good approximation a straight line. According to FORD (1933) this relationship is based on the following mathematical function:

$$l_{n+1} = a + b \cdot l_n \quad .. \quad .. \quad .. \quad .. \qquad (1)$$

where l = length and n = age in years. In using a and b for the 194
parameters I follow the formulation by HOHENDORF (1966).

This method of representing growth processes is not restricted to fish growth only, but can be applied also to mammalian growth, as already WALDORF (1949) has shown.

If weight data are to be evaluated, their cube roots must be found and the resultant weight lengths $\left[\sqrt[3]{w}\right]$ inserted into the representation or computation. These weight lengths do not give the actual lengths, but can be converted into them by a suitable factor. The method requires however isometric growth, which usually is the case with good approximation. The Ford-Walford method assumes measuring series with the ages equally spaced. GULLAND & HOLT (1960) have described the method for irregular age spacing.

Also the Bertalanffy function

$$y_\tau = L_\infty \left(1 - e^{-K(\tau - \tau_0)}\right) \quad \ldots \ldots \quad (2)$$

permits the representation of lengths only. Weight values, as with the Ford-Walford method, must be introduced as weight lengths. In this function the computation of parameters presents certain difficulties. Therefore BEVERTON & HOLT (1957) tried to determine the decisive parameter of this function - L_∞ - by means of the Walford method. The graphical method proposed by them yields only approximate values. More useful is the method already suggested by TAYLOR (1958) to compute L_∞ on the basis of the relation

$$L_\infty = \frac{a}{1 - b} \quad \ldots \ldots \quad (3)$$

from the Ford-Walford formula. This gives the maximum value of the function. For the parameter K of the Bertalanffy function, TAYLOR has established the following relation:

$$b = e^{-K} \quad .. \quad .. \quad .. \quad .. \qquad (4)$$

In most recent times HOHENDORF has tried to bring more detailed proof for the relation postulated by TAYLOR (Hohendorf does not quote that author) between the parameters of the two functions, and has worked out several examples with these values. He explained his method by means of one example in greater detail and has made it thus accessible even to mathematically less versed biologists.

He starts by computing the regression lines of the Ford-Walford relation whose parameters, according to him, can be computed comparatively easily and with accuracy without using function tables. Then he converts the Ford-Walford parameters into the Bertalanffy parameters by equations (3) and (4).

Mathematical evaluation 195

For the first test of the method suggested by HOHENDORF I used an example worked out by v.BERTALANFFY (1934), namely the numerical series of DERJAVIN (1922) for the longitudinal growth of the male sturgeon (*Acipenser stellatus*). I found that the parameters introduced by v.BERTALANFFY yielded considerably better results than the parameters computed according to HOHENDORF (Table 1).

Table 1. Comparison between the growth values of *Acipenser stellatus* (♂) computed by the method of HOHENDORF (1966) and the results obtained by v.BERTALANFFY (1934)

1 Alter (Jahre)	2 Meßwerte (cm)	3 Werte von v. Bertalanffy	4 % Abweichung	5 Werte nach Hohendorf	4 % Abweichung
		L_0 = 21,10 L = 201,1 K = 0,06		L_0 = 20,3 L = 209,6 K = 0,056	
1	21,1	21,1	± 0,00	20,3	— 3,79
2	32,0	30,6	— 4,38	30,6	— 4,38
3	42,3	41,5	— 1,89	40,4	— 4,49
4	51,4	50,8	— 1,17	49,6	— 3,50
5	60,1	59,5	— 1,00	58,3	— 2,99
6	68,0	67,8	— 0,29	66,7	— 1,91
7	75,3	75,5	+ 0,27	74,5	— 1,06
8	82,3	82,8	+ 0,61	81,9	— 0,49
9	89,0	89,7	+ 0,79	88,8	— 0,22
10	95,3	96,2	+ 1,10	95,4	+ 0,11
11	101,6	102,3	+ 0,69	101,6	± 0,00
12	107,6	108,1	+ 0,46	107,5	— 0,09
13	112,7	113,5	+ 0,71	113,2	+ 0,44
14	117,7	118,6	+ 0,62	118,4	+ 0,59
15	122,2	123,4	+ 1,00	123,4	+ 1,00
16	126,5	127,9	+ 1,11	128,1	+ 1,26
17	130,9	132,2	+ 0,99	132,5	+ 1,22
18	135,3	136,2	+ 0,67	136,7	+ 1,03
19	140,2	140,0	— 0,14	140,7	+ 0,36
20	145,0	143,5	— 1,03	144,5	— 0,34
21	148,6	146,9	— 1,14	148,1	— 0,34
22	152,0	150,0	— 1,32	151,4	— 0,39
			s_D = ± 1,39 %		s_D = ± 2,13 %

1 - age (in years) 2 - measured values (cm)
3 - v.Bertalanffy's values 4 - deviation (in %)
5 - HOHENDORF's values

This can be demonstrated very well also by the example of the Baltic turbot (Scophtalmus maximus) computed by HOHENDORF. The data on the longitudinal growth of that fish used by him can very easily be represented by the Ford-Walford method, but a much better fit to given data is obtained if 10.5 cm, instead of

the measured value of 10.6 cm, is used as the original value (l_1). In this case the standard deviation s_D = 1.52%, while the one resulting from HOHENDORF's values is 2.44%. (The reason for my 196
s_D value being slightly higher than the one computed by HOHENDORF is the fact that, contrary to him, I subtract three degrees of freedom in the computation).

However, in view of the close relationship between the BERTALANFFY function and the WALFORD formula, it appeared likely that with that function, too, a better fit of observed data could be obtained than HOHENDORF had achieved. Therefore, for control purposes, I applied the graphic method of determining L_∞ described by v.BERTALANFFY (1934), using the values regressed according to the WALFORD computation procedure as a basis. I had the impression that a slightly higher value than 33.3 cm would be more suitable, therefore I chose 33.5 cm as basis for all further computations. The corresponding value for <u>a</u> can be computed by equation (3) and inserted in the WALFORD formula. The goodness of fit can then be tested by means of the values obtained in this manner. I varied L_∞ in steps of 0.1 cm, and again the mathematical optimum for L_∞ was 33.5, i.e. the square deviation was a minimum. These computations were based on a <u>b</u> value of 0.7682 as it resulted from the computation by HOHENDORF. I did not vary that value since such variation would have resulted in substantial computations which could be worked out economically only by a computer. However, a computer programme for this individual case would hardly have made sense.

For τ_0 HOHENDORF suggests a method which is mathematically correct, but yields unsatisfactory values because it is influenced by deviating measuring values and requires accurate values for the two parameters. Via L_0, which can be easily determined when $\underline{l}_1$, $\underline{a}$ and $\underline{b}$ are known, I computed τ_0 = 0.426 with the formula

$$\tau_0 = \frac{\ln L_\infty - \ln(L_\infty - L_0)}{K} \quad .. \quad .. \quad .. \quad (5)$$

Incidentally, for practical work with a computer I prefer L_0 as third parameter; the value of τ_0 proved to be very critical in computations.

No mathematical accuracy is claimed for the BERTALANFFY parameters determined in this manner, but their fit to observed data is still considerably better than that of the values computed by HOHENDORF. In Table 2 the data obtained are compared and the inserted parameters listed.

HOHENDORF's view that, taking the FORD-WALFORD parameters as a basis, it is comparatively easy to arrive at the mathematically accurate parameters of the BERTALANFFY function, is incorrect. His method yields approximate values, but no mathematically satisfactory solution. On the other hand, his suggestion for the computation of the WALFORD parameters is useful since in that manner the uncertainty which accompanies all growth data can be eliminated and the computed figures can be used as the basis of subsequent evaluations. In view of the mostly good approximation of the FORD-WALFORD values to given measuring series, the possibility of regression provided by it seems permissible.

The fact that the computation of the BERTALANFFY parameters from the WALFORD formula suggested by HOHENDORF yielded unsatisfactory results made it necessary to examine the mathematical foundations of this computation in greater detail. The most essential finding 198
was that the FORD-WALFORD function contains a third parameter which HOHENDORF, like the previous authors, did not recognize. In the usual method of application the third parameter is introduced into the computations with the original value.

Derivation of the BERTALANFFY function from the FORD-WALFORD formula

The FORD-WALFORD formula (equation 1) is the equation of a straight line in which b = the slope and a = its point of intersection with the ordinate at the origin; a, however, is not identical with L_0. We get the value for L_0 from

$$L_0 = \frac{l_1 - a}{b} \quad .. \quad .. \quad .. \quad .. \quad .. \qquad (6)$$

Table 2. Comparison between the values computed by HOHENDORF (1966) for the longitudinal growth of the Baltic turbot (Scophthalmus maximus) (Column 3) and the values obtained by changing the parameter c (Column 4) as well as the values obtained if the parameter a is changed too. The heading of the last column also gives the corresponding BERTALANFFY parameters. Data according to KÄNDLER (1944)

1	2	3		4		5		
Alter (Jahre) Age (in years)	Meßwerte (cm) Measured values	Computed values Berechnete Werte (HOHENDORF) $a = 7{,}7195$ $b = 0{,}7682$ $c = 0{,}5548$	% Abweichung Deviation	$a = 7{,}7195$ $b = 0{,}7682$ $c = 0{,}4689$	% Abweichung Deviation	Computed values Berechnete Werte (WALFORD) $a = 7{,}7653$ $b = 0{,}7682$ $c = 0{,}4584$	(BERTALANFFY) $K = 0{,}2637$ $L_\infty = 33{,}50$ $-t_0 = 0{,}426$	% Abweichung Deviation
0				3,62		3,56		
1	10,6	11,01	+ 3,7	10,50	— 0,94	10,50		— 0,94
2	15,5	16,18	+ 4,2	15,79	+ 1,87	15,83		+ 2,13
3	19,7	20,15	+ 2,2	19,85	+ 0,76	19,93		+ 1,17
4	23,5	23,20	— 1,3	22,97	— 2,26	23,08		— 1,79
5	25,5	25,54	± 0,0	25,37	— 0,51	25,50		± 0,00
6	27,7	27,34	— 1,3	27,21	— 1,77	27,35		— 1,26
7	28,7	28,72	± 0,0	28,62	— 0,28	28,78		+ 0,28
8	29,8	29,78	± 0,0	29,71	— 0,30	29,87		+ 0,24
9	30,4	30,60	+ 0,7	30,54	+ 0,46	30,71		+ 1,02
			$s_D = \pm 2{,}58$ %		$s_D = \pm 1{,}52$ %			$s_D = \pm 1{,}46$ %

With the value 10.5 for l_1 and 0.7682 for b and 7.7653 for a, L_0 would be 3.56 cm. Starting from a, we can arrive at L_0 by multiplying with the factor c = 0.4584.

If we insert the parameter c into the FORD-WALFORD formula, we get

$$L_0 = a \cdot c$$
$$l_1 = a + a \cdot b \cdot c$$
$$l_2 = a + a \cdot b + ab^2 \cdot c, \text{ etc.}$$
$$l_n = a \cdot (1 + b + b^2 + b^3 \ldots\ldots + b^{n-1}) + a \cdot b^n \cdot c \quad \ldots \quad \ldots \qquad (7)$$

The brackets contain the descending geometrical progression of b for b < 1, already discovered by FORD (1933). The third parameter appears only in the last member together with a as factor, so that we could also write $b^n \cdot L_0$. Since the value of b^n decreases with increasing exponent, the influence of c, or L_0, on the size reached decreases correspondingly and may become 0.

It should be possible mathematically to compute the value for c from the difference between the measured data and the series computed without c. However, the small differences between the two series are so strongly influenced by the uncertainty of measuring results that no satisfactory results are obtained. Therefore there is at first no other way than to determine the parameter L_0 contained in l_1 by empirical variation of l_1 in order to get the best fit to the other measured data. In this case I varied l_1 in steps of 0.1 cm. The sum of the squares of the percent deviations was a minimum at approx. 10.5. This value is very close to the value measured for l_1 and yields a much closer approximation to the measured data than the value of 11.01 computed by HOHENDORF. It seemed useless to me to try and achieve higher accuracy, since the measured data too, have only one decimal.

On account of the circumstance that for $n = \infty$ the influence of $L_0 = 0$, TAYLOR's formula remains valid.

$$L_\infty = \frac{a}{1 - b} \quad .. \quad ... \quad .. \quad .. \qquad (3)$$

Table 3. Computation of length and weight of the Baltic salmon (Salmo salar). Columns 1 and 4 contain the parameters and values computed by HOHENDORF (1966), column 3 the corrected values for weight increase, and column 5 the weights corresponding to column 1, computed by the allometric function. 199

Age group Alters-gruppe	Länge Length: gemessen (cm) measured	Länge Length: 1 computed berechnet (HOHENDORF) $a = 38{,}961$ $b = 0{,}7503$	Gewicht Weight: 2 gemessen (kg) measured	3 computed berechnet: $L = \sqrt[3]{w}$, $a = 0{,}998$, $b = 0{,}685$, $c = 0{,}265$	3 computed berechnet: $W = L^3$	Deviation Abweichung %	4 computed berechnet (HOHENDORF) $a = 1{,}2097$ $b = 0{,}5829$	Abweichung % Deviation	5 Aus den errechneten Längenwerten nach allometrischer Beziehung	Abweichung %
1	53,4	53,39	1,64	1,179	1,64	± 0,00	1,456	— 11,2	1,73	+ 5,49
2	79,6	79,00	5,83	1,805	5,88	+ 0,86	6,539	+ 12,2	5,60	— 3,95
3	97,4	98,21	11,30	2,234	11,15	— 1,33	12,167	+ 7,7	10,49	— 7,17
4	112,6	112,62	16,10	2,527	16,14	+ 0,25	16,000	+ 0,6	16,21	+ 0,68
5	123,6	123,43	20,30	2,728	20,30	± 0,00	19,616	— 3,4	21,44	+ 5,62
	$s_D = \pm 0{,}64\%$				$s_D = \pm 1{,}13\%$		$s_D = \pm 10{,}72\%$		$s_D = \pm 6{,}56\%$	

(However, the relation $L_\infty = \frac{l_1}{1 - b}$ established earlier by FORD and WALFORD and more recently by BÜCKMANN (1967) is not correct). 200

By introducing the third parameter it becomes possible to derive the BERTALANFFY function simply and clearly from the FORD-WALFORD formula. As the basis we take equation (7). Since n corresponds to the number of periods involved, we replace it by τ, and also substitute the bracket by the summation formula for the geometrical progression of b:

$$l_\tau = a \cdot \frac{1 - b^\tau}{1 - b} + b^\tau \cdot L_0 \quad \ldots \quad (7a)$$

according to equation (3) we can substitute $\frac{a}{1 - b}$ by L_∞ and thus get in accordance with the BERTALANFFY function the relation to the maximum quantity:

$$l_{\tau} = L_{\infty} \cdot (1 - b^{\tau}) + b^{\tau} \cdot L_0 \quad .. \quad .. \quad .. \quad (7a)$$

Removing the bracket we get:

$$\begin{aligned} l_{\tau} &= L_{\infty} - L_{\infty} \cdot b^{\tau} + b^{\tau} \cdot L_0 \\ &= L_{\infty} - b^{\tau}(L_{\infty} - L_0) \quad .. \quad .. \quad .. \quad (8) \end{aligned}$$

This is nothing else but the original form of the BERTALANFFY function if, according to TAYLOR's equation (4), we substitute b by $e^{-K\tau}$. This simple derivation shows again that the FORD-WALFORD formula contains three parameters, L_0 or also L_1 acting as parameter. Its value has a decisive influence on the results and must therefore be determined as accurately as possible.

Since HOHENDORF did not recognize that also the WALFORD function contains three parameters, he formulated also his comparative measure s_D incorrectly since when computing it he subtracted only two degrees of freedom. In the WALFORD formula, as in the BERTALANFFY function and in my own suggestion, three degrees of freedom must be taken into consideration when the standard deviation is computed.

If even in the relatively simple computation of lengths HOHENDORF's parameters do not give really satisfactory results, this applies in particular to the weight computations carried out by him. Since in the latter case the results enter the final results in the third power, even the slightest deviations become extremely noticeable.

HOHENDORF uses the Baltic salmon (<u>Salmo salar</u>)(Table 3) as an example to demonstrate his method. His parameters yield very good values for longitudinal growth; if they are used to compute the corresponding weights via the allometric length-weight relation, the approximation to given data is noticeably better than the one achieved by HOHENDORF. For this reason I worked out this example again. The parameter values I obtained for the weight lengths were different from those used by HOHENDORF. A graphical check confirmed the correctness of the WALFORD parameters I had used; they are listed in Table 3. It was to be expected that in this case the third parameter must not be disregarded because L_0 differs greatly from $\underline{a}$. Graphically, an approximate value of 0.3 was found for L_0. A 201
variation of L_0 resulted in a surprisingly good fit to the cube roots of the weights with L_0 = 0.265. Since in this case $\underline{a}$ is almost 1.000, $\underline{c}$ and L_0 are practically identical. The weight lengths computed from these three parameters hardly differ from the observed data even in the weights. HOHENDORF's evaluation, on the other hand, yielded very great deviations (Table 3). I did not determine the BERTALANFFY parameters in this case, but they presumably would result in a similarly good approximation. Apparently the method suggested already by BERTALANFFY (1934) makes a very good representation

of weight data possible.

If the maximum weight of the Baltic salmon is computed from the weight-length relationship, the approximate value is 31.64 kg. If, however, the maximum value of longitudinal growth is taken as the starting point, the maximum weight computed via the allometric function is 43.68 kg. Thus the two methods for computing the maximum weight differ greatly from each other. Neither do the other parameters of the length and weight functions reveal any clear mathematical relations, a fact which already HOHENDORF had pointed out. In this respect the function suggested by me (KRÜGER 1965) has a distinct advantage since the allometric parameters can be inserted into it.

Discussion

The above statements have shown that by introducing the third parameter L_0 (= $a \cdot c$) the relationship between the FORD-WALFORD formula and the BERTALANFFY function can be demonstrated very easily. The relationship between the parameters of the two functions formulated by TAYLOR also becomes clear. In spite of this, several facts complicate the mathematical relation between the parameters of the two functions.

The first complication is caused by the presence of the third parameter. In the usual application of the FORD-WALFORD formula it is contained in the original value $\underline{l}_1$ and is introduced into the computations by the latter. HOHENDORF then tries to compute the value of $\underline{l}_1$ by means of the BERTALANFFY function, making the mistake of inserting the parameter $\underline{a}$ of the WALFORD function in the place of $\underline{l}_1$ in the course of his derivation (his equation 4). In this manner he does arrive at a value for $\underline{l}_1$ which deviates from $\underline{a}$, but is in no way optimal. It cannot be optimal for the simple reason that its WALFORD parameters are optimal only for the growth series on which the computation is based, but not for a series with a deviating original value. In this way it changes the value of the third parameter which has a functional relationship with $\underline{l}_1$.

The theoretical possibility of computing the value for $\underline{c}$ from the measured data fails on account of its inevitable uncertainty. There remains only the possibility of determining on a completely empirical basis, by inserting different values for $\underline{l}_1$, the value which will yield the smallest square deviations from the measured values. With a given slope $\underline{b}$, an approximate value for $\underline{l}_1$ is found
which can be used as a basis for computing the approximate value 202
for $L_0 = a \cdot c$. Then $\underline{a}$ is varied in order to obtain an even better fit to the measured data, if possible. In this manner it was possible to reduce almost to half of HOHENDORF's evaluation the mean square deviation of the data of the given example. I took only the value for $\underline{b}$ from the parameters computed by HOHENDORF. For technical reasons I was not in a position to examine whether it was optimal.

HOHENDORF has made still another mistake. The FORD-WALFORD formula is a linear function and therefore the regression computation used by him yields the parameters for a minimum linear deviation from the measured values. He, however, tests the goodness of fit with the percent deviation, although the regression line for the relative deviations does not coincide with that for the linear deviations. In this respect logarithmic functions are better. The WALFORD formula depends mainly on the values of the classes of greater magnitude, while the classes of smaller magnitudes are decisive for the relative approach. It is an indication of a very accurate control of the growth process if even in linear formulation the computed figures show such good approximation to the growth curves. However, as long as no mathematical solution has been found which minimizes the relative deviations in the FORD-WALFORD formula, its parameters can be regarded merely as approximate solutions for the parameters of the BERTALANFFY function on the basis of which the accurate parameters can be found only empirically by iterative computations.

We have seen that in some instances a purely mathematical approach did not yield satisfactory results. Only with the necessary adjustments do the deviations of observed biological data from the mathematically accurate values permit purely formal computations. The measured values deviating from the theoretical course of the curve influence the computations in a manner which is difficult to to follow; therefore in most cases only approximate values are determined. However, from the latter, values can be obtained, by gradual systematic alteration of the parameters, which provide a better fit to observed data.

In general, biomathematics require approximation methods for useful solutions. This necessitates very frequent repetition of highly complicated computations and is therefore very time-consuming. Modern electronic computers are indispensable aids for the solution of biomathematical problems. Computer programmes for the BERTALANFFY function have been developed e.g. by FABENS (1965) and RADWAY (1966). It would have been an advantage if HOHENDORF had used them to check his method.

Today, with several equally efficient solutions at hand, it is no longer possible to overlook or deny the basic possibility of reproducing animal growth data by a mathematical model.

The present study confirms the identity of the BERTALANFFY function and the WALFORD formula in a very simple and clear manner. I myself suggested a new growth function (KRÜGER 1965) which
apparently runs largely parallel to the BERTALANFFY function. Even with 203
regard to the mathematical values, its goodness of fit to growth data is at least equal to that of the BERTALANFFY function. I pointed that out already previously, and HOHENDORF confirmed that parallel.

Mathematically, however, its basis is completely different.

Therefore at present there exist at least two functions which are suitable in practice for representing the growth of fish. The GOMPERTZ function, also mentioned very frequently, shall be disregarded here. It has been applied only fairly rarely, since the determination of its parameters, and therefore the assessment of its usefulness, is difficult. It is therefore not the goodness of fit to measuring series which decides on the suitability of a growth function, but its mathematical properties and the informative value of the parameters to be used.

My suggestion has two essential advantages over the BERTALANFFY function. For one thing, it contains an inflection point also for the length values, as was to be expected theoretically. For another, and this is the more important advantage, there exists a mathematically determined relationship between its parameters and the allometric function. This permits also a direct evaluation of weight data without the detour via the weight length $\left(\sqrt[3]{w}\right)$. This advantage plays an even more decisive role when physiological problems are involved (KRÜGER 1967).

The mathematical structures of the BERTALANFFY function and of my suggestion:

$$y_x = \frac{y_{max}}{N^{\frac{1}{x+\zeta}}}$$

are very similar. Both contain a maximum quantity as parameter which the organism approaches when growth is unlimited; both also contain a parameter of rate which expresses the slope of the growth curve, and an additive time value τ_0 or ξ. However, a direct comparison of the parameters is not possible. In my function the maximum value is considerably higher than in the BERTALANFFY function, but on account of the greater distance from the measured data it does not so easily run the risk of lying below actually occurring maximum quantities, as HOHENDORF reports for the North Sea turbot.

All parameters which we insert in our computations are at first purely numerical values, and in my opinion it seems pointless to attach too much importance to their biological interpretation. That interpretation is merely a secondary task.

In the BERTALANFFY function the exponent K is the parameter of rate. However, its relation to the rate of growth is not as simple as HOHENDORF (1966) assumes. This is shown by his example for the longitudinal growth of the North Sea turbot (Scophthalmus maximus) (his Table 5).

He reports that for the male turbot the value for K is 0.2690, for the female, 0.2594. Judging from these figures, the males would grow faster than the females. In reality, the females grew from 8.3 cm to 60.82 cm in the observed period, the males only to 53.5 cm. Female growth is therefore undoubtedly faster. This contra-

diction is explained by the fact that K determines the speed with 204
which growth approaches the terminal point. The value for K contains the maximum quantity which differs greatly in the two sexes. According to HOHENDORF it is 53.88 cm for males and 62.17 cm for females. Since in growth comparisons on the basis of the BERTALANFFY function the value for L_∞ in different species or sexes cannot be kept at a constant level, K is not a definite expression of the rate of growth. In this respect the $\underline{b}$ value of the FORD-WALFORD formula is a more useful basis for comparison since it is based on the original value $\underline{l}_1$ which is the same for both sexes. In this case the $\underline{b}$ value is 0.7642 for males and 0.7715 for females. Thus it reflects the relation of the rate of growth more accurately.

While the parameters of rate of the BERTALANFFY function and the WALFORD function permit accurate comparison, such a comparison is not possible with the parameter of rate of my function, since in it the rate of growth is expressed by two parameters: log N and ξ.

In mathematical terms the third parameter which the BERTALANFFY function and my own suggestion contain is the period during which the organism develops from the dimension 0 to the first measured length. Since, however, in both functions the parameters of postlarval growth do not include larval and embryonic development, this "pre-natal" age represents a purely mathematical value which is determined by the mathematical interpretation of the growth curve.

Due to the fact that the BERTALANFFY function has no inflection point, it declines much more steeply in the prenatal range, which results in lower values for the prenatal age than in my function. Therefore the τ_0 values lie rather in the dimension of prenatal age, but also HOHENDORF is rather hesitant about this interpretation.

It is the principal significance of the ξ value of my function that it designates the curvature of the relative growth curve; mathematically it is therefore a parameter of curvature. It also has the advantage of being only slightly critical and lying at comparable magnitudes in more rapidly growing fish. This facilitates a comparison of rates of growth by means of the parameter of rate. I shall discuss this elsewhere. In the BERTALANFFY function τ_0 is very critical and its relation to the curvature of the curve not as clear.

The mathematical interpretation of the parameters of the FORD-WALFORD function still awaits further analysis. Changes of the parameter <u>c</u> cause a displacement of the values on the regression line, while changes of the <u>a</u> value displace the regression line parallel to itself. It cannot be said off-hand what influence this has on the growth curves.

My explanations and mathematical demonstrations have shown that the relationship existing between the parameters of the BERTALANFFY function and the FORD-WALFORD formula cannot be evaluated for the determination of the BERTALANFFY parameters in as simple a manner as suggested by HOHENDORF.

HOHENDORF's statement in his summary (1966) "that a simple and easily applicable method for the accurate determination of the parameter values and growth values by purely mathematical procedures can be established by using this linear relationship as recurrence formula for the BERTALANFFY function" was not confirmed. To clarify 205
the connection between the BERTALANFFY function and my own suggestion, I was interested in a really accurate determination of the BERTALANFFY parameters. Unfortunately, HOHENDORF's suggestion did not meet this requirement. If time-consuming iterative computations on mechanical computers are to be avoided, the only way - at least at present - is the graphical solution which I used for the determination of L_∞. Parameter computations are further facilitated by the utilization of the relations with the FORD-WALFORD formula. I thought it was important to publish my experiences with HOHENDORF's suggestion in order to inform future users on the limitations of his method and its applicability. His method is completely unsuitable for computing $\underline{l}_1$. Only the original value is mathematically correct. For a better percent approximation the optimal value for L_0, or $\underline{c}$, must be determined and given as third parameter.

Again and again, the treatment of biomathematical questions has revealed erroneous formulations in various authors. It will be possible to use mathematical methods for the study of biological phenomena only if all efforts are made to achieve on a mathematically satisfactory basis the best possible fit to observed data. Rough approximations must not be expected to contribute to the progress of our knowledge.

Summary

1. For the characterization of fish growth, HOHENDORF (1966) tried to use the relation between the parameters of the BERTALANFFY function and the FORD-WALFORD formula: $L_\infty = \frac{a}{1 - b}$ and $K = \ln \underline{b}$, formulated by TAYLOR, for computing the BERTALANFFY parameters. By working out several mathematical examples it is shown that his method does not yield parameters which can be regarded as accurate.

2. The FORD-WALFORD formula contains a third parameter, $\underline{c}$, which is introduced into the computation with $\underline{l}_1$.

3. The third parameter permits a very simple derivation of the BERTALANFFY function from the FORD-WALFORD formula and confirms the relationship between the parameters established by TAYLOR.

4. The reasons are studied on account of which HOHENDORF's method yields only approximate values.

5. In this respect the decisive fact is that the parameters of

the regression lines of the FORD-WALFORD formula minimize the linear differences between the computed and measured values, while in growth computations the minimum of the percent deviations is the desired quantity.

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206

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