A Note on the Inverse Function of the von Bertalanffy Growth Function

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Abstract

Parameter estimates of the von Bertalanffy growth function (VBGF) and its inverse function, based on length-at-age and age-at-length data for *Tilapia rendalli* (Cichlidae) and *Salmo trutta* (Salmonidae) were derived using a variety of "direct" and "indirect" fitting methods. The results obtained by different fitting methods are similar, except when the obvious is ignored: the data must cover the same range of lengths and ages and their weighting factors must be the same.

Introduction

The use of simple mathematical equations to express the biological growth of fishes has helped to understand this biological process. Also, growth equations are useful for predicting the size of fish at a given time (age). An example of a simple mathematical model of growth is the von Bertalanffy growth function (VBGF) (von Bertalanffy 1934). However, the VBGF has been criticized by some authors (Knight 1968; Bailey 1977; Schnute 1981) because it does not express well the growth of some fishes.

A related argument is that while the VBGF has *length* as *dependent* variable, this model is often used, when age-at-length is not known, to back-calculate age from length. Kirkwood (1983) and Sanders (1987) argue thus, that when one needs to estimate age from length, then a model whose parameters were estimated with *age* as the dependent variable should be used.

To achieve this, some existing algorithms, e.g., Pauly and Gaschütz (1979), Kimura (1980), Schnute (1981) and Marquardt (1983), which are based on the VBGF, were transformed into routine which fit their respective inverse functions (see below for definitions). Using the modified software, growth parameter estimates from both direct and inverse functions were then obtained based on field samples for tilapia (*Tilapia rendalli*) and trout (*Salmo trutta*); the results are then compared and discussed.

Methods

The direct and indirect forms of the von Bertalanffy growth function

The direct form of the von Bertalanffy growth function is written as:

$$L_t = L_\infty [1-e^{-K(t-t_0)}] \quad ...1)$$

where L_t is the length at age t, L_∞ is the asymptotic size, and K is a growth constant.

The inverse of the VBGF, which uses the same parameters, is the reciprocal of the equation above. It has the form:

$$t = -1/K * \ln(1-L_t/L_\infty) + t_0 \quad ...2)$$

Growth parameter estimates can be obtained for both **(1)** and **(2)**. In the former case, length-at-age data or "direct" data are used. In the latter case, age-at-length data or "inverse" data are used. The question asked here is whether the estimates of L_∞, K and t_0 estimated by various approaches from these two equations, using different types of data, will be different from each other.

Type and source of data

The samples of *Salmo trutta* from the Viau River in France were adapted from Abad (1982), while the samples of *Tilapia rendalli*, from Lake Mantasoa, Madagascar, were adapted from Moreau (1979). Fish lengths were measured in centimeters and age in years, as determined by scalimetry. The direct data were assembled from these samples and grouped into 0.5-year age class intervals for trouts and 0.25-year age for tilapia, while the inverse data, based on the same samples, were grouped into 1-cm length classes (Tables 1 and 2).

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Table 1. Field data for *Salmo trutta* obtained from the Viau River, France, arranged as "direct" (A) and "inverse" data (B).

(A) Age (year)	Length (cm)	Numbers
0.5	6.7	280
1.0	8.3	456
1.5	13.3	392
2.0	14.8	350
2.5	17.4	300
3.0	19.5	345
3.5	21.0	120
4.0	22.7	151
4.5	25.1	37
5.0	26.6	62
5.5	28.5	21
6.0	30.5	34
6.5	32.9	13
7.0	34.0	16
7.5	36.0	6

(B) Length (cm)	Age (year)	Numbers
7	0.72	434
8	0.83	457
9	0.91	222
10	0.97	70
11	1.50	68
12	1.60	200
13	1.66	347
14	1.76	452
15	1.84	345
16	2.38	275
17	2.72	396
18	2.80	380
19	2.91	184
20	3.34	196
21	3.72	153
22	3.82	158
23	3.89	97
24	4.22	65
25	4.77	62
26	4.93	68
27	4.92	49
28	5.39	37
29	5.79	32
30	5.86	32
31	6.29	21
32	6.40	17
33	6.79	11
34	6.83	9
35	7.13	7
36	7.75	6

Table 2. Field data for *Tilapia rendalli* obtained from Lake Mantasoa, Madagascar, arranged as "direct" (A) and "inverse" data (B).

(A) Age (year)	Length (cm)	Numbers
0.75	9.5	160
1.00	12.4	275
1.25	13.5	168
1.50	14.5	124
1.75	15.5	108
2.00	17.0	92
2.25	18.5	52
2.50	19.6	48
2.75	20.0	40
3.00	20.6	38
3.25	21.3	30
3.50	21.5	37
3.75	22.0	25
4.00	22.3	10
4.25	22.7	25
4.50	23.0	23
4.75	23.5	10
5.00	23.8	21
5.25	24.2	3

(B) Length (cm)	Age (year)	Numbers
9	0.80	2
10	1.00	21
11	1.22	99
12	1.24	142
13	1.28	206
14	1.36	118
15	1.52	86
16	1.76	45
17	2.07	92
18	2.48	72
19	2.55	90
20	2.82	74
21	3.29	66
22	4.18	55
23	4.48	43
24	5.47	10
25	5.82	30

Algorithms Used for Comparing the Direct and Inverse Functions

i. The von Bertalanffy plot

The method originally used by L. von Bertalanffy (1934) to estimate the parameters of his equation is based on a linearized version of **(1)**. Thus, estimates of L_∞, K and t_o are obtained by solving a linear regression of the form

$$\ln(1 - L_t/L_\infty) = Kt_o - Kt \quad ...3)$$

where $y = \ln(1 - L_t/L_\infty)$, $a = Kt_o$ and $b = -K$. Initial guesses of L_∞ can be obtained, e.g., from the largest fish (L_{max}) and $L_\infty = L_{max}/0.95$.

The computer program of Gaschütz et al. (1980), which implements this method, was modified to accommodate equation **(2)** where $y = t$, $a = t_o$ and $-b = -1/K$. This program computes for each input value of L_∞ an estimate of the coefficient of determination (r^2), until a maximum is identified and hence, the best value of L_∞ and associated values of K and t_o are determined. The program of Gaschütz et al. (1980) is implemented such that the data points used for the regression can be weighted by any factor, e.g., by the number of fish used to compute the mean lengths at age. This property was retained in the modified version, used for fitting the inverse function.

ii. J. Moreau's modification of Gaschütz et al. (1980)

J. Moreau (unpublished data) replaced the iterative search routine in the program of Gaschütz et al. (1980), which is based on finding the maximum of a parabola, by a routine which scans, in small steps, a wide range of L_∞ for the highest associated value of r^2.

iii. Marquardt (1963)

This is a non-linear curve fitting technique which requires an initial set of seed values; the best curve is obtained by the least-squares minimization method.

iv. Kimura (1980)

In this method, growth parameters are estimated using the method of maximum likelihood. The implementation of this method used here can weigh the mean lengths-at-age (or the mean ages-at-length) by the number of fishes in each group considered. The fit of the curve to the data points is tested by a residual sum of squares.

v. Schnute (1982)

This algorithm implements a non-linear fitting method which minimizes the residual sum of squares by successive iterations defined by what is generally known as the "simplex search method" (Nelder and Mead 1965; O'Neill 1971; Schnute 1982).

Growth parameter estimations

Programs corresponding to each of the fitting methods discussed above were run with direct data to obtain growth parameter estimates that were used as the basis of comparison with estimates obtained using both the inverse data and the inverse functions. The modified routines for the inverse functions were then run using both direct and inverse data.

The same data sets were used for all programs and routines; this allows direct comparison between the resulting sets of growth parameter estimates.

Results and Discussion

Table 3 presents the results of the runs made using each algorithm for both direct and inverse functions of the data sets presented in Tables 1 and 2.

As might be seen, the estimates of L_∞ and t_0 obtained using equation **(2)** are much lower than those obtained using **(1)**, while the converse applies for K. On the other hand, the different fitting methods and data types lead to very similar estimates, the exception being the estimates based on data weighted by sample size, which are very different from the unweighted ones but very similar to each other. Thus, the critical comparisons to make are those between the inverse and the direct versions of the same fitting routine.

Sanders (1987) used methods similar to those presented above for his analysis of the inverse VBGF. However, there is a crucial difference between his and our applications, specifically in the nature and range of the data sets: we used data covering the same age and length range for both functions, and he did not.

Table 3. Estimates of growth parameters for the VBGF using direct and inverse algorithms with direct and indirect files.

Method	(Eq.)	Direct Program						Inverse Program					
		Direct data			Inverse data			Direct data			Inverse data		
		L_∞ (cm)	K ($year^{-1}$)	t_0 ($year^{-1}$)	L_∞ (cm)	K ($year^{-1}$)	t_0 ($year^{-1}$)	L_∞ (cm)	K ($year^{-1}$)	t_0 ($year^{-1}$)	L_∞ (cm)	K ($year^{-1}$)	t_0 ($year^{-1}$)
von Bertalanffy Plot	(1)	81.1	0.070	-0.79	81.3	0.071	-0.78	82.8	0.068	-0.79	86.3	0.064	-0.80
Gaschütz et al.	(2)	25.9	0.483	-0.25	25.1	0.558	0.03	26.1	0.456	-0.31	25.5	0.536	-0.07
Moreau's modification	(1)	82.5	0.07	-0.80	86.3	0.064	-0.82	82.5	0.070	-0.78	86.2	0.064	-0.80
von Bertalanffy Plot	(2)	26.2	0.45	-0.36	24.7	0.586	-0.06	26.2	0.451	-0.35	25.6	0.500	-0.09
Marquardt (1983)	(1)	81.0	0.070	-0.79	83.2	0.068	-0.79	67.4	0.095	-0.60	86.5	0.064	-0.80
	(2)	27.2	0.380	-0.26	24.7	0.584	-0.05	26.1	0.457	-0.32	25.6	0.501	-0.08
Schnute (1982)	(1)	61.1	0.078	-0.79	83.2	0.067	-0.79	82.3	0.069	-0.78	86.5	0.064	-0.80
	(2)	25.8	0.490	-0.24	24.7	0.586	-0.06	26.2	0.456	-0.32	25.6	0.500	-0.09
Kimura (1980)	(1)	74.8	0.078	-0.75	74.5	0.078	-0.71	54.0	0.137	-0.34	52.0	0.142	-0.14
	(2)	25.5	0.509	-0.21	25.4	0.535	0.01	25.7	0.487	-0.25	25.8	0.454	-0.21
von Bertalanffy weighted	(1)	55.1	0.121	-0.55	56.1	0.117	-0.53	59.0	0.110	-0.56	62.1	0.101	-0.58
Gaschütz et al.	(2)	25.7	0.491	-0.26	25.2	0.525	-0.05	25.9	0.471	-0.29	25.2	0.527	-0.06
Kimura (1980) weighted	(1)	52.7	0.121	-0.54	43.9	0.159	-0.33	45.3	0.169	-0.36	48.7	0.151	-0.24
	(2)	25.6	0.497	-0.25	25.0	0.568	0.03	25.9	0.506	-0.30	24.9	0.518	-0.12

Sanders (1987) used an age range of 1 to 5 years for the direct data and 1 to 4 years for the inverse data. This effectively means that the direct data had an extra age class, and it is not surprising that his two growth curves had very different shapes. If one looks at Fig. 1 of Sanders (1987), it can easily be seen that his curve B (the inverse data) appears to have a higher L_∞ because it does not pass through the fifth and final age group.

The same is apparent for the length data. For the direct data, his range was 55-74 cm, while for the inverse data, it was 58-76 cm. Comparisons of growth parameters should not be made when the two sets of data cover such different ranges. The results show different estimates simply because they have been produced by different data sets.

In conclusion, it appears that it is justifiable to use the inverse function to estimate growth parameters from both length-at-age and age-at-length data. However, it must be emphasized that the inverse function works well only if the data cover a wide range of size/age classes. In such cases, the estimation of ages (or of Δ t values) from lengths (or Δ L values) based on the inverse of the VBGF for e.g., length-structured VPA or the construction of length-converted catch curves (Jones 1981; Pauly 1983) appears appropriate.

Acknowledgments

We thank Ma. Lourdes "Deng" Palomares for her help in the writing of this paper.

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