ON THE CHOICE OF A GROWTH CURVE FOR INDIAN MAJOR CARPS—von BERTALANFFY OR GOMPERTZ ?

BY

K. K. GHOSH

Central Inland Fisheries Research Institute

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INTRODUCTION

Of the many growth equations developed from time to time for fishes, only two, the von Bertalanffy and the Gompertz, have found favour with fisheries workers. Both the curves are derivable from the generalised empirical growth curve described by Chapman-Richards differential equation (Chapman, 1960) or Taylor's equation (Taylor, 1962). While von Bertalanffy (1938) developed his growth equation for animal organisims from basic physiological considerations, Gompertz (1825) developed his equation in connection with studies on human population growth and mortalities. In recent literature, sufficient evidence exists to challenge the physiological basis of von Bertalanffy's growth equation (Paloheimo and Dickie, 1966a, 1966b). This renders the von Bertalanffy growth curve also an empirical character. Winsor (1932) has very competently analysed Gompertz curve as a growth curve, while Beverton and Holt (1957) have rejected it as 'largely empirical'. The von Bertalanffy growth equation has been applied very widely primarily because the models of theory of fishing advanced by Beverton and. Holt (1957) make use of Bertalanffy growth equation and have justified its use on the grounds of truer physiological acceptance of its basis. In India, all the studies reported on growth of freshwater fishes have used only the von Bertalanffy growth equation for lengths. Natrajan and Jhingran (1963), Kamal (1969), Rao (1972 in press), Gupta and Jhingran (MS-1973), etc., have worked on major carps and have fitted von Bertalanffy growth curve to length at age data, while all have found allometric length-weight relationships. The Gompertz growth curve was first fitted by Weymouth and McMillin (1931) to clam. Since then Silliman (1967) used it in analog computer technique of fisheries dynamics study and

subsequently showed its excellent fit to growth data in a wide group of fishes (Silliman, 1969). The properties of the von Bertalanffy and Gompertz growth curves have been considered here and their suitability for Indian major carps, specially for the weight growth curve, discussed. The growth data of Indian major carps, available in literature, has been analysed to actually examine the suitability of either of them.

A simplified yield equation when Gompertz growth model is valid in the Beverton and Holt (1957) theory of fishing has also been developed.

THEORY

The basis differential equation describing growth was formulated by von Bertalanffy (1938) as

$$\frac{dw}{dt} = HW^n - KW^m \qquad \qquad ...(1)$$

Where H and K were defined as coefficients of anabolism and catabolism. Von Bertalanffy advanced sufficient physiological evidence to postulate that anabolism is governed by surface processes whereas catabolism is governed by mass processes. These postulates under assumption of isometric cubic weight-length relationship led to

$$\frac{dw}{dt} = HW^{2/3} - KW \qquad \qquad ...(2)$$

Equation (2) on integration leads to the well known expression

$$l_t = L\infty(1 - e^{-k(t-t_0)}) \qquad \qquad .. (3)$$

for length growth equation, and

$$W_t = W\infty(1 - e^{-k(t-t_0)})^3 \qquad \qquad ...(4)$$

for weight growth equation,

where $L\infty/W\infty$ is the ultimate attainable size, k is 3 times K of (1) and t_0 is an integration constant, signifying origin of time scale.

If, however, equation (1) is written, under surface law postulation of Bertalanffy, as

$$\frac{dw}{dt} = HS - KW \qquad \qquad ...(5)$$

where S is some physiological surface area, and following Taylor (1962) we put $S = pl^a$ and $W = al^b$, it is easy to see that we reach

$$l_t^{b-a} = L\infty^{b-a}(1 - e^{-k(b-a)(t-t_0)}) \qquad \qquad ...(6)$$

For similarity with (3) and (4), the growth equations may be written as

$$l_t = L\infty\left(1-e^{-k(b-a)(t-t_0)}\right)^{\frac{1}{b-a}} \qquad .. (7)$$

and

$$W_t = W\infty\left(1 - e^{-k(b-a)(t - t_0)}\right)^{\frac{b}{b-a}} \qquad ...(8)$$

Since sufficient evidence exists that $a = 2$ and $b = 3$ are not universally true (1) is more apt to lead to (7) or (8) rather than to (3) or (4). Taylor's generalisation is, therefore, more acceptable. So, under more general conditions, we are concerned with the influence of the parameter

$$\frac{1}{b-a},$$

which was taken as 1 by Bertalanffy (1938), since he put $b = 3$ and $a = 2$. Richards (1959), Taylor (1962), etc., have examined the role of this parameter and have concluded that best fit may be obtained for any value of ($b-a$), sometimes even negative or zero. On the other hand a number of direct studies on physiology of metabolic processes have established that the value of ($b - a$) heavily differs from 1 (e.g. see Paloheimo and Dickie, 1966a).

However, negative or zero value of ($b - a$) would mean a collapse of Bertalanffy's postulations, in so far as quantifying the processes and their measurements are concerned, Bertalanffy himself realised the too restrictive nature of his postulation $b=3$ and $a=2$ and was not scrosanct about them (Bertalanffy, 1964), when he advocated the use of his basic equation as

$$\frac{dw}{dt} = HW^n - KW \qquad ...(9)$$

where n stood for suitable matabolic rate body size relationship. He even showed that n may take values over a wide range and concluded, 'We shall expect all sorts of allometric relationships of metabolic measure and body size with a certain preponderance of 2/3 power functions, considering the fact that many metabolic processes are controlled by surfaces. In other words, 2/3 is not a magic number, nor is there anything sacred about the 3/4 the power which more recently has been preferred to the classical surface Law'.

Thus, the shape of the length growth curve (7), which is not violate of Bertalanffy's postulations, needs examination. When

$(a-b)=1$, we have the simple growth equation (3).   But if $(a-b)$ lies between 0 and 1 then we have an inflexion at a length defined by

$$l_t = L\infty \left[1 - (b-a) \right]^{\frac{1}{b-a}} \qquad \text{...(10)}$$

As $(a-b)$ decreases the point of inflextion rises along the length axis.   When $(a-b)$ is very small or zero, the maximum length at inflexion point is reached, which is given by

$$\text{Max } l_t = L\infty. \underset{(b-a)\to 0}{\text{Lim}} \left[1 - (a-b) \right]^{\frac{1}{b-a}}$$

$$= L \infty e^{-1} = .368 \, L\infty$$

It is at this stage that the Gompertz equation becomes pertinent. Richards (1959) has shown that when $(b-a)=0$, equation (6) becomes

$$l_t = L\infty e^{-b} e^{-k(t-t_0)} \qquad \text{...(11)}$$

or the well known Gompertz growth curve.

Bhattacharya (1966) in a very lucid derivation, proved that the basic equation (5) reduces to Gompertz under some specific conditions. He also showed that the general class of growth curves defined by

$$y = (\alpha + \beta\gamma^t)^\delta \qquad \text{.. (12)}$$

where α, β, γ and δ are constants, reduces to Bertalanffy or Gompertz and δ takes the value 1 or ∞.   Thus, by fitting equation (12), the value of δ provides a good measure to choose between the two.   If δ is close to 1, Bertalanffy is more apt, while if δ is high, Gompertz is indicated.   Finding a value of $\delta = 5.6785$, Bhattacharya stated "This* may not be adequate and suggests that Gompertz curve is worth consideration" (Bhattacharya, 1966).

Thus we find, the fundamental differential equation (5) can lead to any one of the forms.

(i) the Bertalanffy growth curve (i) when $b-a=1$

(ii) the Gompertz growth curve, (ii), when $b-a=0$

(iii) the simple exponential :

$$l_t = l_0 \, . \, e^{-k'(t-t_0)}, \text{ where } \frac{a}{b} = 1,$$

and l_0, k', t_0 are constants carrying usual meanings.

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* "This" referred to the modified exponential i.e. Bertalanffy growth curve.

Southward and Chapman (1965) have estimated the parameter $(b-a)[(b-a)$ in their notation equals $(1-m)]$ using a computor, for Pacific hlibut, walleye and largemouth bass and have found the most probable ranges of the parameter as 0.22-0.40 for halibut, 0.20-0.41 for largemouth bass and $0.46-0.62$ for walleye. Thus the parameter $(b-a)$ instead of being close to 1 is closer to zero. In fact the 3/4 power law, instead of the classical surface law of 2/3rd power appears to be more apt. This points to the possibility of finding a closer fit to Gompertz in case of such fishes where growth is faster in early life with its rate touching a maximum at a point sufficiently high up on the length or weight axis.

The above treatment reveals some basic aspects of Gompertz curve that revives one's interest in this curve.

(i) The Bertalanffy growth curve assumes isometric weight-length relationship involving a cubic. In almost all fishes, more so in Indian major carps, the cubic has been found insufficient. Natrajan and Jhingran (1963) have shown the exponent to differ significantly from 3. Gompertz is free from such assumption.

(ii) Both curves do not seem to violate the basic principles of growth as enunciated by Bertalanffy and others.

(iii) Both curves require estimation of three parameters $[G, g$ and W_r for Gompertz and $K, t_0, W\infty$ for Bertalanffy]. So estimation problem, theoretically, appears to be equal.

(iv) The Gompertz curve is simpler to combine with other exponential expressions so prevalent in population studies.

It is recognised that the Indian major carps grow initially much more in length and subsequently in weight, indicating a better Gompertz fit. These fishes are known to have a very fast early growth with the maximum rate of weight growth at a substantial age. The instantaneous growth rate of *Catla catla* is maximum during the second year of its life (Natrajan and Jhingran, 1963). It, therefore, appears worthwhile to examine the growth data of other major carps also as to their closeness to Bertalanffy or Gompertz growth model, specially for the weight growth curve. For this purpose the growth data of lengths or weights at age and weight-length relationships has been taken from published accounts or ready manuscripts.

FITTING OF GOMPERTZ CURVE

Following the form of Gompertz curve suggested by Chapman (1960) for fisheries application, the equation is written as

$$W_t = W_r e^{G - Ge^{-g(t-t_r)}} \qquad \ldots(13)$$

where W_r is the weight at entry to fishery at age t_r, G and g are constants. Further $W\infty = W_r e^G$.

Thus G has a physical meaning denoting the connection between ultimate size and size at recruitment.

It is known that the parameters of Gompertz curve do not admit maximum likelihood estimates (Riffenburgh, 1960). Comparing the well known linear transforms of von Bertalanffy growth curve with those of Gompertz, we find that they are exactly similar, except for a logarithmic transformation of length in the case of Gompertz.

Linear transform	Bertalanffy growth curve	Gompertz growth curve
1.	$l_{t+1} = l_t e^{-k} + L\infty (1 - e^{-k})$	$\log_e l_{t+1} = \log_e l_t \cdot e^{-g} + \log_e L\infty (1 - e^{-g})$
2.	$l_{t+1} - l_t = (L\infty - l_t)(1 - e^{-k})$	$\log_e l_{t+1} - \log_e l_t = (\log_e L\infty - \log_e l_t)(1 - e^{-g})$
3.	$\dfrac{dl}{dt} = k(L\infty - l)$	$\dfrac{d \log l}{dt} = g(\log_e L\infty - \log_e l)$

Similar equation for weight growth curve can also be written.

An examination of the equations reveals the characteristic similarity of g of Gompertz with k of Bertalanffy and, therefore, should have similar physiological significance.

In order to choose the form for fitting Gompertz, it is desirable to take that method which is analogous to the best of von Bertalanffy. Ghosh (MS 1973) has shown that the transform (iii) provides better estimation of von Bertalanffy growth parameters by least squares on statistical grounds as well as to obtain closer fit to observed data. So the transformation.

$$\frac{d}{dt}\left(\log_e W_t\right) = g\left(\log_e W\infty - \log_e W_t\right)$$

for weight growth curve, similar to

$$\frac{d}{dt}\left(\log_e l_t\right) = \left(\log_e L\infty - \log_e l_t\right)$$

is used here for finding g and $W\infty$ by least squares technique. The regression,

$$\log_e W_t = \log_e W_t + G - G e^{-g(t-t_r)}$$

of $\log_e W_t$ on $e^{-g(t-t_r)}$

yields the slope as $-G$,

while

$\log_e W\infty - G$ yields $\log_e W_r$

The t_r value is known to be zero for all the riverine major carp fisheries considered here. However, a different t_r based on breeding period to first entry in catches is also possible. Which could change G and materially alter W_r. Here t_r is taken as zero.

To convert the lengths at age data to weight at age data ; the published weight-length relationships were used. The parameter of Bertalanffy's equation were taken directly from the published papers for estimation of weights at age by equation (4), while those of Gompertz growth model (13) were estimated as indicated above.

Criterion for choosing a method

(i) *From 'δ' value of* (12)

Preliminary choice of criterion was provided by the estimation of δ value in (12) by the method of Bhattacharya (1966) ; putting

$$R_1 = \frac{1}{W} \frac{dW}{dt}, \text{ approximated by } \triangle \log_e W_t$$

and $R_2 = \frac{1}{R_1} \frac{dR_1}{dt}$, approximated by $\triangle \log_e R_1$

the equation (12) reduces to the linear from

$$R_2 = \log_e \gamma - \frac{1}{\delta} R_1$$

which can be expressed as a linear statistical model

$$\triangle \log_e R_1 = \log_e \gamma - \frac{1}{\delta} \triangle \log_e W + \epsilon$$

and the value of δ estimated by least squares technique.

(ii) *From residual sum of squares or lack of fit.* The closeness of fit can also be evaluated from the residual sum of squares.

$$S(\theta) = (W_t - \hat{W}_t)^2$$

and the associated coefficient of determination, r^2, defined by

$$r^2 = \text{correlation } [W_t, \hat{W}_t].$$

Discussion

The criterion for choosing a growth model involved use of length-weight relationship. The pure Bertalanffy form using cubic as

well as the modified Bertalanffy using the allometric relationship were both used for determining lack of fit S (θ) and coefficient of determination r^2. The $W\infty$ values were also correspondingly estimated.

Table 1 present the results of computations done to examine the quality of fit of Gompertz against Bertalanffy growth model. Few inferences are immediately available from Table 1.

TABLE 1

Comparison of Bertalanffy and Gompertz fits to growth data of Indian major carps

Fish	Catla catla (Ham.)	Cirrihinus mrigala (Ham.)	Cirrihinus mrigala (Ham.)	Labeo calbasu (Ham.)
Habitat	R. Yamuna	R. Yamuna	R. Godavari	R. Yamuna
Source of (i) Growth data	Natrajan and Jhingran (1963)	Kamal (1969)	H. Rao (MS (1972)	Gupta & Jhingran (MS 1973)
(ii) Length-weight relationship	-do-	-do-	Avon (65)	Jhingran (Personal Communication)
(iii) Bertalanffy curve parameters	-do-	-do-	H. Rao (MS 1972)	Gupta & Jhingran (MS 1973)
L/W exponent	3.282	3.221	3.083	3.375
Ages included	1-5	1-8	1-8	1-8
Gompertz parametres				
W ∞	19.512 kg	11.497 kg	13.5 kg	11.888 kg
G	7.7563	6.8866	6.3607	6.9095
g	.6691	.5788	.3193	.3058
t_r	0	.0	.0	.0
W_r	9 g	12 g	23 g	12 g
Bertalanffy parameters				
L∞	1275 mm	1060 mm	1400 mm	1028 mm
W ∞ (Cubic)	34,930 kg	14.253 kg	31.696 kg	15.870 kg
W ∞ (Allometric)	43.089 kg	15.813 kg	34.307 kg	21.654 kg
k	.28	.1906	.1220	.1496
t_0	.11	.0396	—.4622	.1856
Bhattacharya's				
δ	6.5167	3.4716	17 5383	4.8629

Fish	Catla catla (Ham.)	Cirrihinus mrigala (Ham.)	Cirrihinus mrigala (Ham.)	Labeo calbasu (Ham.)
Habitat	R. Yamuna	R. Yamuna	R. Godavari	R. Yamuna
Co-efficient of determination r^2				
(i) Gompertz	.997	.998	.9997	·999
(ii) Bertalanffy (cubic)	.987	.998	.998	.991
(iii) Bertalanffy (allometric)	.977	.998	.921	.993
Lack of fit $S(\theta)$				
(i) Gompertz	873	503	27	40
(ii) Bertalanffy (cubic)	22375	2484	113	5480
(iii) Bertalanffy (allometric)	19540	537	1431	480

N.B. : (i) 'L-W exponent' stands for n in $W=al^n$ fit.

(ii) $W\infty$ (cubic) stands for asymptotic weight as calculated by fitting a cubic, $W=al^3$, to weight-length data and using $L\infty$ value of Bertalanffy fit.

(iii) $W\infty$ (allometric) stands for the value calculated on the known allometric formula $W=al^n$ from $L\infty$.

(i)   Bhattacharya's δ provides a good indicator and establishes superiority of Gompertz whenever δ is high.

(ii) Both curves fit well as in evident from r^2 values. Yet the values for Gompertz are higher than those for Bertlanffy. Where Bhattacharya's δ is low r^2 values are more close, as in the case of mrigal of Yamuna, while the *vice versa* is also true *e.g.* mrigal of Godavari.

(iii) Lack of fit is lowest in Gompertz in all cases.

(iv) The fundamental of Bertalanffy, the cubic law, is true only for mrigal of Godavari, yet the Gompertz is far superior to Bertalanffy, probably because the anabolic rate may not be governed by surface law but by a higher power.

(v)   The $W\infty$ values of Gompertz are generally lower than that of Bertalanffy whether cubic or modified allometric. While the Gompertz estimates are much more realistic, the allometric relation estimates of Bertalanffy appear to be overestimated. Silliman (1969) also found Gompertz providing an excellent fit for a number of fishes. He also found the $W\infty$ estimates lower for Gompertz as compared to those for Bertalanffy.

It, therefore, emerges that the Gompertz growth curve is a better choice for describing growth data of Indian major carps.

SUMMARY

von Bertalanffy's growth curve has been compared to Gompertz growth curve as capable of describing fish growth. Both curves have been shown to be derivable from basic equation of growth. Gompertz curve is shown to be free from some restrictive conditions necessary for the validity of von Betalanffy's curve. Criteria for choosing the closer fitting curve have been given. The growth data of Indian major carps, *Catla catla* of R. Yamuna, *Cirrihinus mrigala* of R. Yamuna and R. Godavari and *Labeo calbasu* of R. Yamuna have been analysed for finding the more suitable curve. The superiority of Gompertz in all cases has been established.

A simplified yield equation when Gompertz growth model is valid has also been developed involving the use of incomplete gamma function.

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APPENDIX

The total biomass of a fishery in the exploitable phase is

$$N_t \quad W_t$$

Summation over exploitable phase

Where N_t is the population size and W_t is the weight of t year old fishes.

Under the exponential population growth model, using standard terminology (Beverton & Holt, 1957).

$$N_t = Re^{-M(t_{\rho'} - t_{\rho'})} e^{-(F+M)(t-t_{\rho'})} \qquad \ldots(i)$$

In our notation $t_{\rho'} = t_r$ of Gompertz curve. Hence equation (i) becomes

$$N_t = Re^{-M(t_r - t_{\rho})} e^{-(F+M)(t-t_r)}$$

If now Gompertz model of growth is introduced then

$$W_t = W_r e^{G - Ge^{-g(t - t_r)}}$$

Therefore,

$$N_t W_t = Re^{-M(t_r - t_{\rho})} e^{-(F+M)(t-t_r)} W_r e^{G - Ge^{-g(t-t_r)}}$$

Putting $t = t - t_r$, without loss of generality

$$N_t W_t = Re^{-M(t_r - t_{\rho}) + G} W_r e^{-(F+M)t - Ge^{gt}}$$

The rate of yield is obtained by multiplying by F, the fishing mortality rate.

$$\frac{d Y w}{d t} = F R W_r e^{-M(t_r - t_{\rho}) + Ge - (F + M)t - Ge^{-gt}} \qquad \ldots(ii)$$

Integrating this equation over the fishable life span, defined as t_r to t_λ i.e. from $t = 0$ to $t = t_\lambda - t_r = \lambda$ say, we have the yield equation as

$$Yw = FRWre^{-M(t_r - t_o) + G} \int_0^{\lambda} e^{-(F + M) t - Ge^{gt}} dt \quad ...(iii)$$

Putting $e^{-gt} = y$, equation (iii) reduces to

$$Yw = FRW_r e^{-M(t_r - t_o) + G} \frac{1}{g} \int_{e^{-g\lambda}}^{1} Y^{(M + F)/g - 1} e^{-Gv} d v$$

Putting $e^{-g\lambda} = \lambda_o$, which is necessairly <1, if $\dfrac{F + M}{g}$ $\geqslant 1$ and $G > 0$, the expression under the integral can be recognised as the gamma function. In practice $\dfrac{F + M}{g}$ will almost always be >1 and $G > 0$.

The evaluation of the integral can be done by taking recourse to the extensive tables of incomplete gamma functions published by Pearson (1922).

Barrowing the expression 'Incomplete', used by Jones (1957) for evaluating the yield equation under Bertalanffy growth model with the aid of incomplete beta functions, the expression (iv) is easily computed as a difference of two incomplete gamma integrals.

Denoting by

$IG(a, p, x,)$, the integral $\int_0^{x} x^{p - 1} e^{-ax} dx$

The expression (iv) is easily computed from the relation

$$Yw = FRW_r e^{-M(t_r - t_o) + G}$$
$$\frac{1}{g} \left[IG(G, \frac{F + M}{g}, 1) - IG(G \frac{F+M}{g}, \lambda_o) \right]$$