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New Functions for the Analysis of Two-Phase Growth of Juvenile and Adult Fishes, with Application to Nile Perch

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Abstract.—Two phases of growth can sometimes be distinguished in long-lived fish species. The first involves the growth of zooplankton-feeding juveniles and young adults. The second consists of accelerated growth of large, piscivorous adults. We present modified versions of the von Bertalanffy growth equation that account for this feature and fit them to length-at-age data on Nile perch *Lates niloticus* (Centropomidae) from Lake Chad (north and south) in north-central Africa, and from Lake Nasser in Egypt. The growth parameters estimated for the new equations allow one to make preliminary estimates of the energy gains by Nile perch associated with transition from zooplanktivory to piscivory.

The equation most commonly used in fishery biology to describe length-at-age relationships of juvenile and adult fishes is the von Bertalanffy growth function, of the form

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

L_∞ is the asymptotic length, the mean length the fish would reach if they were to grow indefinitely; K is a growth coefficient with dimension time^{-1}; t_0 is a location parameter indicating the time at which the growth curve crosses the time axis; and L_t is the predicted length at age t.

This equation, although easy to fit and generally a good descriptor of the growth patterns of fish, has three major problems that have led authors to seek alternatives.

(1) Seasonal growth oscillations, which occur in many fishes (see Longhurst and Pauly 1987), are not considered.

(2) The assumption implicit in the model, that an isometrically growing surface limits growth, is not realistic. This is especially so for some fast-growing fishes capable of reaching large sizes (such as tunas). As a result, estimates of asymptotic sizes tend to be too large when estimated by the von Bertalanffy growth function (Pauly 1981).

(3) Two-phase growth patterns, which may occur in fishes that feed on zooplankton as juveniles and young adults and on fish as larger adults, are not reproduced by equation (1).

Here we emphasize item (3), which, to our knowledge, has not been addressed previously. Items (1) and (2) were discussed by Pauly and Gaschütz (1979), Pauly (1981, 1984), Longhurst and Pauly (1987), Somers (1988), and Soriano and Jarre (1988). Modifications of a biphasic growth curve to account for seasonality of growth and for allometric growth of surfaces are straightforward.

Three New Models for Biphasic Growth

The first variant of the von Bertalanffy curve that we propose to model biphasic growth relies on a factor A_t (Figure 1a), which modifies L_∞ as age increases. This factor is defined as

$$A_t = 1 - \frac{h}{(t - t_h)^2 + 1}.$$

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The growth curve then becomes (Figure 1b)

$$L_t = L_\infty A_t[1 - e^{-K(t-t_0)}]. \qquad (2)$$

The factor A_t introduces two new parameters: t_h, the age at which the transition between the two growth phases occurs; and h, which determines the magnitude of the maximum difference between equations (1) and (2). The factor A_t was not derived from theoretical principles. Rather, it was developed empirically to describe observed growth patterns.

The second obvious variant of the von Bertalanffy curve modifies the value of K as age increases. This leads to (Figure 1c)

$$L_t = L_\infty[1 - e^{-KA_t(t-t_0)}], \qquad (3)$$

with A_t as defined previously.

We fitted these functions by using the Gauss–Newton method for nonlinear regression (see Neter et al. 1985). A derivative-free alternative is the Nelder and Mead (1965) simplex search (see Schnute 1983 or Press et al. 1987). A linearized form of equation (3) is given in the Appendix for use when only a calculator is available for performing the computations. With both biphasic models, we sometimes found it necessary to constrain the values of the fitted parameters to prevent a phase of negative growth from being generated. A computer program for fitting equations (2) and (3) to data, which incorporates these constraints and which outputs standard errors for all parameters estimated, is available from the first author's institution.

A third type of model to consider is a segmented regression in which the nature of the growth pattern changes abruptly at age t_h. For example, one could have two von Bertalanffy equations (with separate values of L_∞ and K) joined together at age t_h. Thus,

$$L_t = \begin{cases} L_\infty^{(1)}[1 - e^{-K^{(1)}(t-t_0)}] & \text{if } t < t_h; \\ L_{t_h} + L_\infty^{(2)}[1 - e^{-K^{(2)}(t-t_h)}] & \text{if } t > t_h. \end{cases}$$

A special case of this model occurs when the value of K is the same in the two phases. A derivative-free method, such as the Nelder–Mead simplex search, must be used to fit this model because the curve is not smooth. Alternatively, one can estimate the transition age t_h visually and then fit separate von Bertalanffy curves to the two growth phases.

An abrupt change in growth pattern is probably unrealistic for individual fish. It is even less realistic for describing average growth in a population because individual variability in growth will tend to smooth a curve constructed from data on many fish. However, as shown in the section on growth of Nile perch, it may be of interest to fit separate von Bertalanffy growth curves to each phase of growth.

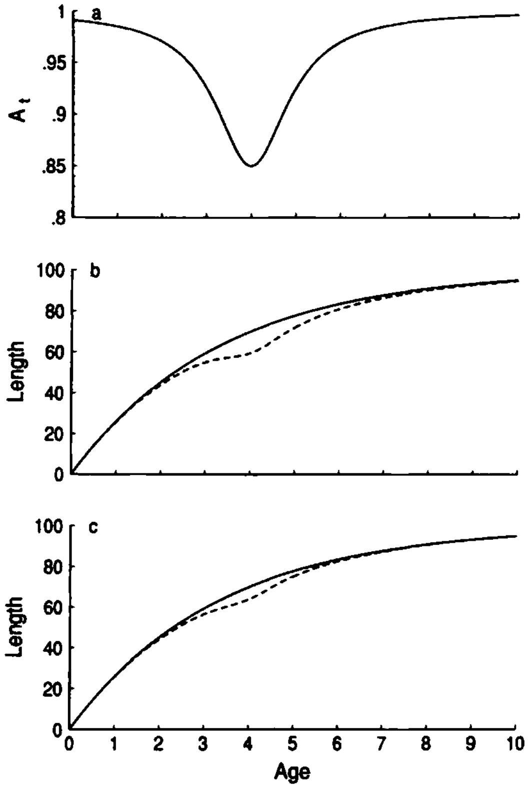

FIGURE 1.—The von Bertalanffy growth curve and its modification for biphasic growth. (**a**) The factor A_t used to modify L_∞ or K shown as a function of age. A_t is based on $t_h = 4$ and $h = 0.15$. (**b**) Ordinary von Bertalanffy growth curve (solid line) with $L_\infty = 100$, $K = 0.3$, and $t_0 = 0$, and biphasic curve (dashed line) with L_∞ modified by the factor A_t (text equation 2). (**c**) Ordinary von Bertalanffy growth curve as in (b) above (solid line), and biphasic curve (dashed line) with K modified by the factor A_t (text equation 3).

Biphasic Growth Versus Sampling Artifacts

The biphasic growth patterns seen in Figure 1 can arise as an artifact of sampling in several ways. In a cross-sectional study, where fish are sampled at only one time and the mean size at each age is determined from a single year-class, a year-class that happened to grow slowly would appear as a dip in the growth curve. This possibility can be ruled out in two ways. If cross-sectional growth

TABLE 1.—Mean standard length (cm) at age of Nile perch at three African locations.

Age (years)	Lake Chad north (Hopson 1972)	Lake Chad south (Loubens 1974)	Lake Nasser (Moreau 1982; Latif 1984)
1	17.4	20.7	21.0
2	31.6	36.3	32.8
3	42.3	45.8	46.5
4	50.2	54.0	53.9
5	56.8	61.0	58.5
6	63.8	67.7	64.5
7	70.6	74.2	66.0
8	77.0	80.6	80.0
9	83.5	86.8	89.0
10	89.3	93.0	97.7
11	94.1	99.0	111.0
12	103.0	104.8	122.0
13		110.5	127.0
14		116.0	132.0
15			136.0

studies are conducted in several years, and if a dip in the growth curve appears in each curve at the same age, true biphasic growth is supported. In longitudinal growth studies, such as when the growth history of each fish in the catch is determined by back-calculation, one has the opportunity to determine directly if the growth of each year-class slowed down in the vicinity of a given age t_h.

Apparent biphasic growth can also be seen if fish change habitats upon reaching a certain size and if sampling is heavy in the area inhabited by the younger fish. For example, if fish leave estuarine areas upon reaching a certain size at, say, age 4 to 5, then only the smallest of the 5 year olds will remain to be sampled in the estuaries and hence the estimated size at age 5 will be too small. By back-calculating growth histories of in-

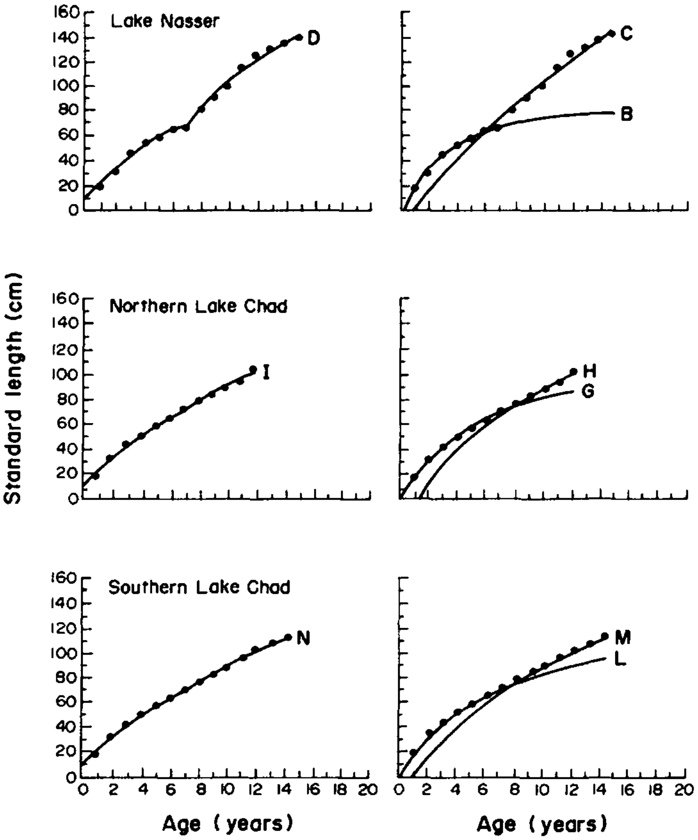

FIGURE 2.—Mean lengths at age of Nile perch from three African locations (from Table 1). Fitted growth curves in the panels to the left are biphasic growth models described by text equation (2). Curves in the panels to the right are ordinary von Bertalanffy growth curves (equation 1) fitted separately to young and old fishes. Upper case letters refer to regression statistics (parameter sets) in Table 2.

TABLE 2.—Growth parameters estimated from data in Table 1 for Nile perch from Lake Nasser, northern Lake Chad, and southern Lake Chad. Equation (1) is the ordinary von Bertalanffy growth curve, equation (2) is the biphasic growth equation in which L_∞ is modified in the vicinity of age t_h, and equation (3) is the biphasic curve in which K is modified. Curves were fitted by the Gauss–Newton method for nonlinear least-squares estimation. Estimates of W_∞ (asymptotic weight) were obtained by the length–weight relationships described in the text to convert the estimates of L_∞.

Parameter set	Equation	Range of ages used	L_∞ (cm)	W_∞ (kg)	K (year^{-1})	t_0 (year)	t_h (years)	h	Residual sum of squares
				Lake Nasser					
A	(1)	1–15		872.0	0.001	−1.915			227.3
B	(1)	1–7	75.2	9.6	0.308	−0.027			7.8
C	(1)	8–15	360.1	913.0	0.034	0.352			67.3
D	(2)	1–15	360.1	913.0	0.030	−1.223	7.119	0.154	87.6
E	(3)	1–15	372.6	1,008.0	0.029	−1.264	7.129	0.171	88.2
				Northern Lake Chad					
F	(1)	1–12	168.2	102.1	0.071	−0.790			30.7
G	(1)	1–7	98.6	22.3	0.172	−0.174			4.5
H	(1)	8–12	152.2	76.9	0.102	1.186			7.6
I	(2)	1–12	152.2	76.9	0.086	−0.587	7.496	0.047	23.4
J	(3)	1–12	149.5	73.0	0.088	−0.587	6.683	0.063	25.4
				Southern Lake Chad					
K	(1)	1–14	188.3	99.7	0.062	−1.259			36.2
L	(1)	1–8	110.7	22.4	0.150	−0.473			9.5
M	(1)	9–14	171.5	76.7	0.084	0.726			1.0
N	(2)	1–14	171.5	76.7	0.074	−1.019	8.475	0.046	26.2
O	(3)	1–14	171.6	76.8	0.073	−1.053	7.671	0.054	28.5

dividual fish, one can determine if the observed biphasic pattern is real.

Finally, if two groups of fish have different growth rates, and they have different mortality rates or mingle at certain ages, then apparent biphasic growth may be observed. This problem can be minimized by studying the growth of fish from a group that is as homogeneous as possible. Thus, studies can be conducted separately for each sex, location, and time of the year. Also, back-calculation can be used to examine individual growth patterns as described above.

Bioenergetic Implications: Growth of Nile Perch

Nile perch *Lates niloticus* (Centropomidae) is a large freshwater fish that attains sizes of 200 cm and is commonly found in inland waters of Africa. Lowe-McConnell (1975) noted its biphasic growth and attributed this to a change of diet. Table 1 summarizes the length-at-age data extracted from the literature for illustrative purposes. The data were collected from two areas of Lake Chad (north and south) in north-central Africa and from Lake Nasser in Egypt.

For all three sets of length-at-age data, the ordinary von Bertalanffy growth equation (not modified for biphasic growth) gave the worst fit (Figure 2; Table 2). Equation (2) gave a better fit than equation (3) in all three cases.

The available data do not allow a rigorous validation of the biphasic growth pattern in Nile perch. For now, it is of interest to explore the possible uses of a biphasic model even if the results are somewhat speculative.

For each geographic location, we fit the ordinary von Bertalanffy curve (equation 1) separately to the two growth phases defined by values of t_h estimated visually (Figure 2). The two estimates of asymptotic length were converted to estimates of asymptotic weight (W_∞) by the following length–weight relationships:

Lake Nasser (Moreau 1982):

$$W = 0.0332L^{2.91};$$

northern Lake Chad (Hopson 1972):

$$W = 0.0463L^{2.85};$$

southern Lake Chad (Loubens 1974):

$$W = 0.0404L^{2.81};$$

L is the standard length (cm), and W is live weight (kg).

Metabolism of fish of mass W_∞ is, by definition, just sufficient to sustain life (i.e., "routine metab-

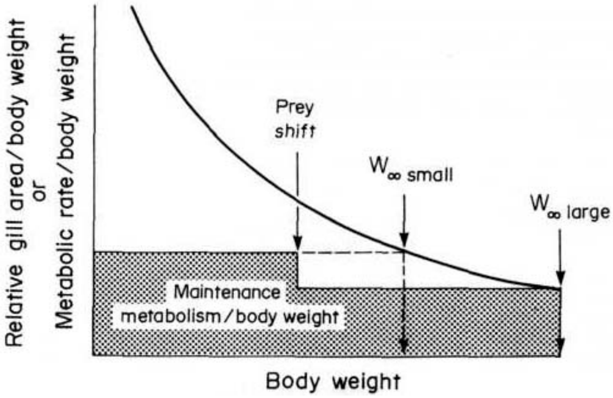

FIGURE 3.—Schematic representation of the increase of the scope for growth following shift to a prey that can be captured with less energy outlay. W_∞ is, by definition, the body weight where metabolism is just sufficient to life (maintenance metabolism). Thus, lowering energy expenditures for food enables organisms to reach a larger size.

olism"). The pairs of W_∞ values, for each stock, allow us to estimate the fraction, M_r, expressing the maintenance metabolism of the larger fishes as a fraction of the maintenance metabolism of the smaller fishes (see Figure 3):

$$M_r = \left(\frac{W_\infty \text{ small}}{W_\infty \text{ large}}\right)^{(1-d)}; \quad (4)$$

d is the power of body weight to which the gill surface area (and the metabolism) of Nile perch is assumed to be proportional. Here we set $d = 0.85$, based on equation (26) in Pauly (1981).

The three estimates of M_r derived from Table 2 are 0.51 for Lake Nasser, 0.83 for northern Lake Chad, and 0.83 for southern Lake Chad. Only the mean of the two values from Lake Chad, i.e., $\overline{M}_r = 0.83$, will be used in the subsequent discussion because asymptotic size could not be estimated precisely for Lake Nasser Nile perch.

Small Nile perch feed predominantly on zooplankton and benthic invertebrates; these are "dilute" prey requiring the fish to search or filter a large amount of water to obtain a sufficient daily ration. Large, piscivorous Nile perch, on the other hand, stalk their prey. This is a mode of feeding that is very energy-efficient and whose correlates are relatively low metabolic rates and gill areas (Hughes and Morgan 1973; De Jager et al. 1977). We feel, therefore, that the value of $\overline{M}_r$, corresponding to the decline in metabolic rate of 100 − 83 = 17% associated with the transition from zooplanktivory and benthivory to piscivory, is of the right order.

Proportion of Fish in the Diet

The proportion, P_L, of fish in the diet of Nile perch increases as a function of standard length, L (Table 3). We used the method of least squares to fit these data with a logistic curve of the form

TABLE 3.—Fraction of the diet of Nile perch consisting of fishes in various African water bodies.

Range of standard length (cm)	Fraction of fishes in the diet	Area	Reference
5–15	0.00	Niger River	Daget (1964)
15–25	0.20	Niger River	Daget (1964)
25–35	0.25	Lake Kainji	Turner (1970)
35–45	0.60	Lake Chad	Lauzanne (1976)
		Nile River	Hashem and Hussein (1973)
45–55	0.80	Lakes Victoria and Kioga	Gee (1969)
55–65	1.00	Lake Chad	Lauzanne (1976); Loubens (1974)
65–75	1.00	Lake Victoria	Gee (1969)
75–85	1.00	Lake Kioga	Gee (1969)
85–95	1.00	Lake Kainji	Turner (1970)
>95	1.00	Nile River	Hashem and Hussein (1973)

$$P_L = \frac{1}{1 + e^{-g(L - L_{0.5})}} \qquad (5)$$

by applying the logit transformation to the P_L values and regressing the logits on length. Here, g is an empirically estimated rate coefficient (cm^{-1}) and $L_{0.5}$ is the length at which fish make up half of the diet of Nile perch.

One would imagine that the shift in growth pattern would occur at about the time the shift in diet occurs. There is a discrepancy between our estimates of length at age t_h (70–80 cm standard length; see Figure 2) and the estimate of $L_{0.5}$ (38 cm) that was derived from the food habits data in Table 3 (see Figure 4). This is probably due to the heterogeneity of the assembled data, which do not refer to the same sampling sites and time periods as the length-at-age data. The hypothesis that the transition in diet occurs at about the same size as the transition in growth pattern, therefore, is still open for testing when better data become available.

Conclusions

We have presented models for biphasic growth that are potentially of wide applicability. We examined available data on Nile perch. Casey et al. (1985) described a biphasic growth pattern for sandbar sharks *Carcharhinus plumbeus* (Carcharhinidae), which spend the first six to eight summers in estuarine areas and then switch to an offshore habitat. They reported that the biphasic pattern could be seen in the back-calculated growth histories of individual fish but presented data for only one fish. Their raw data are not available for examination.

Apparent biphasic growth patterns can arise as artifacts of sampling. Several methods are available for evaluating these possibilities, but data available in the literature were not collected with biphasic growth studies in mind, and thus appear unsuited for rigorously testing the validity of our models. It remains for future studies to establish how widespread biphasic growth may be. It can be seen from our example that when biphasic models are appropriate, they can provide a more accurate description of growth than uniphasic models, as well as insights into ecological and physiological relationships.

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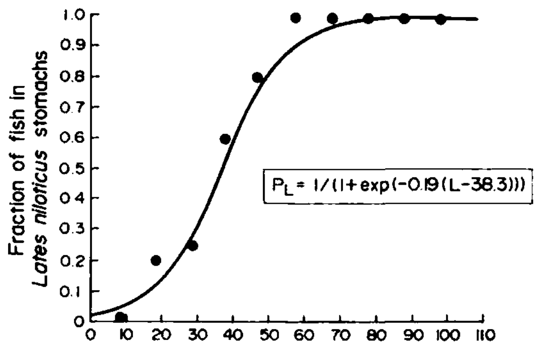

FIGURE 4.—Observed proportion of fish in Nile perch stomachs from various African water bodies (see Table 3) versus standard length of the Nile perch. The logistic curve was fitted by ordinary least squares after the logit transformation was applied to the proportions.

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Appendix: Linearized Form of a Biphasic Growth Model

It sometimes happens that advanced computer facilities are not available when data need to be analyzed. Also, most computer minimization routines require initial or trial values for the parameters. For these situations, the biphasic growth model represented by text equation (3) can be linearized and fitted by a multiple linear regression on a programmable calculator. It is necessary to assume that the parameters L_∞ and t_h are known at least approximately—for example, from the largest sized fish in the catch and from the inflection point of a growth curve drawn by hand. Then equation (3),

$$L_t = L_\infty[1 - e^{-KA_t(t-t_0)}],$$

can be expressed as

$$\log_e\left(1 - \frac{L_t}{L_\infty}\right) = -K(t - t_0)\left[1 - \frac{h}{(t - t_h)^2 + 1}\right],$$

which has the form of a linear regression,

$$Y = b_0 + b_1x_1 + b_2x_2 + b_3x_3 + \epsilon;$$

$$Y = \log_e\left(1 - \frac{L_t}{L_\infty}\right);$$

$$b_0 = Kt_0;$$

$$b_1 = -K;$$

$$b_2 = Kh;$$

$$b_3 = -Kht_0;$$

$$x_1 = t;$$

$$x_2 = \frac{t}{(t - t_h)^2 + 1};$$

$$x_3 = \frac{1}{(t - t_h)^2 + 1};$$

ϵ = random error term, $\sim N(0, \sigma^2)$.

Consequently, parameter estimates (^) for the growth model can be obtained as

$$\hat{K} = -\hat{b}_1,$$

$$\hat{h} = -\frac{\hat{b}_2}{\hat{b}_1},$$

and

$$\hat{t}_0 = -\frac{\hat{b}_0}{\hat{b}_1}.$$

Note that with four equations (defining b_0, b_1, b_2, and b_3) and three unknowns (K, h, and t_0), several inconsistent sets of parameter estimates may be possible. Thus, estimates obtained by the linearization method should be replaced by estimates from a nonlinear regression routine whenever possible.