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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 phase involves zooplankton-feeding juveniles and young adults. The second phase consists of accelerated growth of large, piscivorous adults. We present two modified versions of the von Bertalanffy growth equation which account for this feature and fit them to length-at-age data on Nile perch *Lates niloticus* (Centropomidae). The growth parameters estimated for the new equations allow one to make preliminary estimates of the energy gains in Nile perch associated with transition from zooplanktivory to piscivory.

Résumé. On peut parfois distinguer deux phases de croissance parmi les espèces de poisson qui vivent longtemps. La première phase comprend les poissons juvéniles et adultes jeunes qui se nourrissent de zooplankton. La seconde phase consiste en la croissance accélérée des grands poissons piscivores. On présente deux formes modifiées de l'équation de croissance de von Bertalanffy qui prennent ce phénomène en considération. On applique ces modèles aux données de longeur et d'âge de la perche du Nil *Lates niloticus* (Centropomidae). Les paramètres de croissance estimés à partir des nouvelles équations permettent de faire des estimations préliminaires sur les gains d'énergie de la perche du Nil associés à la transition du regime de zooplankton à celui de poisson.

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. This function has the form:

$$L_t = L_\infty(1 - e^{-K(t-t_o)}) \qquad (1)$$

where L_∞ is the asymptotic length, i.e. the mean length the fish would reach if they were to grow indefinitely; K is a growth coefficient with dimension time^{-1}; t_o is a location parameter indicating where 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 providing a good description of the growth patterns of fish, has three major problems which 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 that an isometrically growing surface limits growth, which is implicit in the model, is not realistic. This is especially so for some fast-growing fishes capable of reaching large sizes (such as tunas). As a result, there is a tendency for estimates of asymptotic sizes to be too large when estimated using 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, but which become piscivorous as larger adults, are not reproduced by equation (1).

Emphasis is given here to item (3) which, to our knowledge, has not been tackled previously. Items (1) and (2) are discussed in 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 allometric growth of surfaces, are straightforward.

Two New Models for Biphasic Growth

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

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

the growth curve then becomes (Figure 1b)

$$L_t = L_\infty A\,(1 - e^{-K(t-t_o)}) \ . \qquad (2)$$

The factor A 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 second obvious variant of the von Bertalanffy curve is where the value of K changes as age increases. This leads to (Figure 1c)

$$L_t = L_\infty (1 - e^{-K A (t-t_0)}) \qquad (3)$$

with A as defined previously.

We fitted these functions by using the Gauss-Newton method for nonlinear regression (Neter et al. 1985). A derivative-free alternative is the Nelder-Mead (1965) simplex search (see Schnute [1983] or Press et al. [1987]). A linearized form of equation (3) is given in Appendix 1 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.

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 studies are conducted in several years, and if a dip in the growth curve appears in each curve at the same age, then this is supportive of true biphasic growth. In longitudinal growth studies, e.g. 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 individual 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 as homogeneous a group of fish 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: a Look at Nile Perch Growth

Nile perch Lates niloticus (Centropomidae) is a large freshwater fish which 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. They stem 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 and Table 2). Equation (2) gave a better fit than equation (3) in all three cases.

Unfortunately, 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 the biphasic model even if the results are somewhat speculative.

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

Lake Nasser	$W = 0.0332\, L^{2.91}$	(Moreau 1982)
Northern Lake Chad	$W = 0.0463\, L^{2.85}$	(Hopson 1972)
Southern Lake Chad	$W = 0.0404\, L^{2.81}$	(Loubens 1974)

where 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. is a "routine metabolism". 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):

$$M_r = \left(\frac{W_\infty \text{ small}}{W_\infty \text{ large}}\right)^{(1-d)} \tag{5}$$

where d is the power of body weight with which the gill surface area (and the metabolism) of Nile perch is assumped 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, $\bar{M}_r = 0.83$, 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, "dilute" prey requiring a large amount of water to be searched or filtered for a sufficient daily ration to be obtained. Large, piscivorous Nile perch, on the other hand, stalk their prey. This is a mode of feeding which 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 $\bar{M}_r$, 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:

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

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 comprise 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) which 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 periods as the length-at-age data. We thus consider the hypothesis that $L_{0.5} = L_{th}$ is still open for testing when better data become available.

Conclusions

We have presented two models for biphasic growth which 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 esturarine 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. Unfortunately, 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. Unfortunately, available data 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 as well as insights into ecological and physiological relationships.

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Appendix 1. A 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, e.g. from the largest sized fish in the catch and from the inflection point of a growth curve drawn by hand. Then equation (3)

$$L_t = L_\infty (1 - e^{-K\,A\,(t-t_o)})$$

can be expressed as

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

which has the form of a linear regression, i.e.

$$Y = b_o + b_1x_1 + b_2x_2 + b_3x_3 + \varepsilon$$

where

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

$$b_o = Kt_o$$

$$b_1 = -K \quad , \quad x_1 = t$$

$$b_2 = Kh \quad , \quad x_2 = \frac{t}{(t-t_h)^2 + 1}$$

$$b_3 = -Kht_o \quad , \quad x_3 = \frac{1}{(t-t_h)^2 + 1}$$

$$\varepsilon = \text{random error term} \sim N(0,1) \ .$$

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

$$\hat{K} = -\hat{b}_1 \quad , \quad \hat{h} = -\frac{\hat{b}_2}{\hat{b}_1} \quad , \quad \hat{t}_o = -\frac{\hat{b}_o}{\hat{b}_1}$$

where the ^ symbol indicates estimates.

Note that with four equations (defining b_o, b_1, b_2, b_3) and three unknowns (K, h, and t_o), there won't be a unique solution for the parameter estimates. Thus, estimates obtained by the linearization method should be replaced by estimates from a nonlinear regression routine whenever possible.

Table 1. Mean length at age of Nile perch at three African locations.

Age (years)	Standard length (cm)		
	Lake Chad North (Hopson 1972)	Lake Chad South (Loubens 1974)	Lake Nasser (Latif 1984; Moreau 1982)
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

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 using the Gauss-Newton method for nonlinear least squares estimation. Estimates of W_∞ were obtained by using the length-weight relationships described in the text to convert the estimates of L_∞.

equation & ages	L_∞ cm	W_∞ kg	K yr^{-1}	t_0 yr	t_h yr	h	range of ages used	residual sum of squares
			Lake Nasser					
A) Eq 1, all	—	872.0	0.001	-1.915	—	—	1-15	227.3
B) Eq1, young	75.2	9.6	0.308	-0.027	—	—	1-7	7.8
C) Eq 1, old	360.1	913.0	0.034	0.352	—	—	8-15	67.3
D) Eq 2, all	360.1	913.0	0.030	-1.223	7.119	0.154	1-15	87.6
E) Eq 3, all	372.6	1008.0	0.029	-1.264	7.129	0.171	1-15	88.2
			Northern Lake Chad					
F) Eq 1, all	168.2	102.1	0.071	-0.790	—	—	1-12	30.7
G) Eq 1, young	98.6	22.3	0.172	-0.174	—	—	1-7	4.5
H) Eq 1, old	152.2	76.9	0.102	1.186	—	—	8-12	7.6
I) Eq 2, all	152.2	76.9	0.086	-0.587	7.496	0.047	1-12	23.4
J) Eq 3, all	149.5	73.0	0.088	-0.587	6.683	0.063	1-12	25.4
			Southern Lake Chad					
K) Eq 1, all	188.3	99.7	0.062	-1.259	—	—	1-14	36.2
L) Eq 1, young	110.7	22.4	0.150	-0.473	—	—	1-8	9.5
M) Eq 1, old	171.5	76.7	0.084	0.726	—	—	9-14	1.0
N) Eq 2, all	171.5	76.7	0.074	-1.019	8.475	0.046	1-14	26.2
O) Eq 3, all	171.6	76.8	0.073	-1.053	7.671	0.054	1-14	25.5

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

Range of stanard length (cm)	Fraction of fishes in the diet	Area	References
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 Nile River	Lauzanne (1976) Hashem & Hussein (1973)
45 - 55	0.80	Lake Victoria & Lake 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 & Hussein (1973)

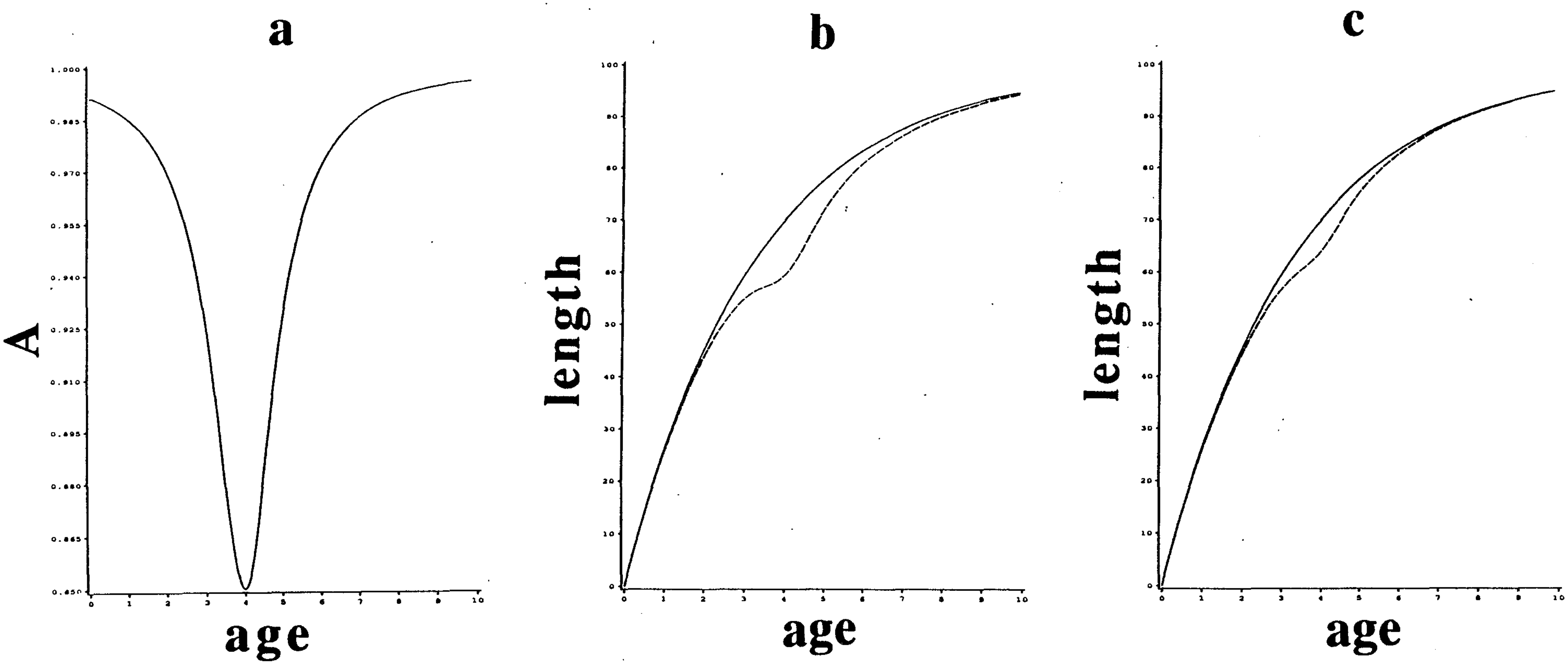

FIGURE 1. von Bertalanffy growth curve and its modification for biphasic growth. (a) the factor "A" used to modify L_∞ or K shown as a function of age. "A" is based on $t_h = 4$ and h = 0.85; (b) ordinary von Bertalanffy growth curve (solid line) with $L_{oo} = 100$, K = 0.3, and to = 0, and biphasic curve (dashed line) with L_∞ modified by the factor "A" (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" (text equation 3).

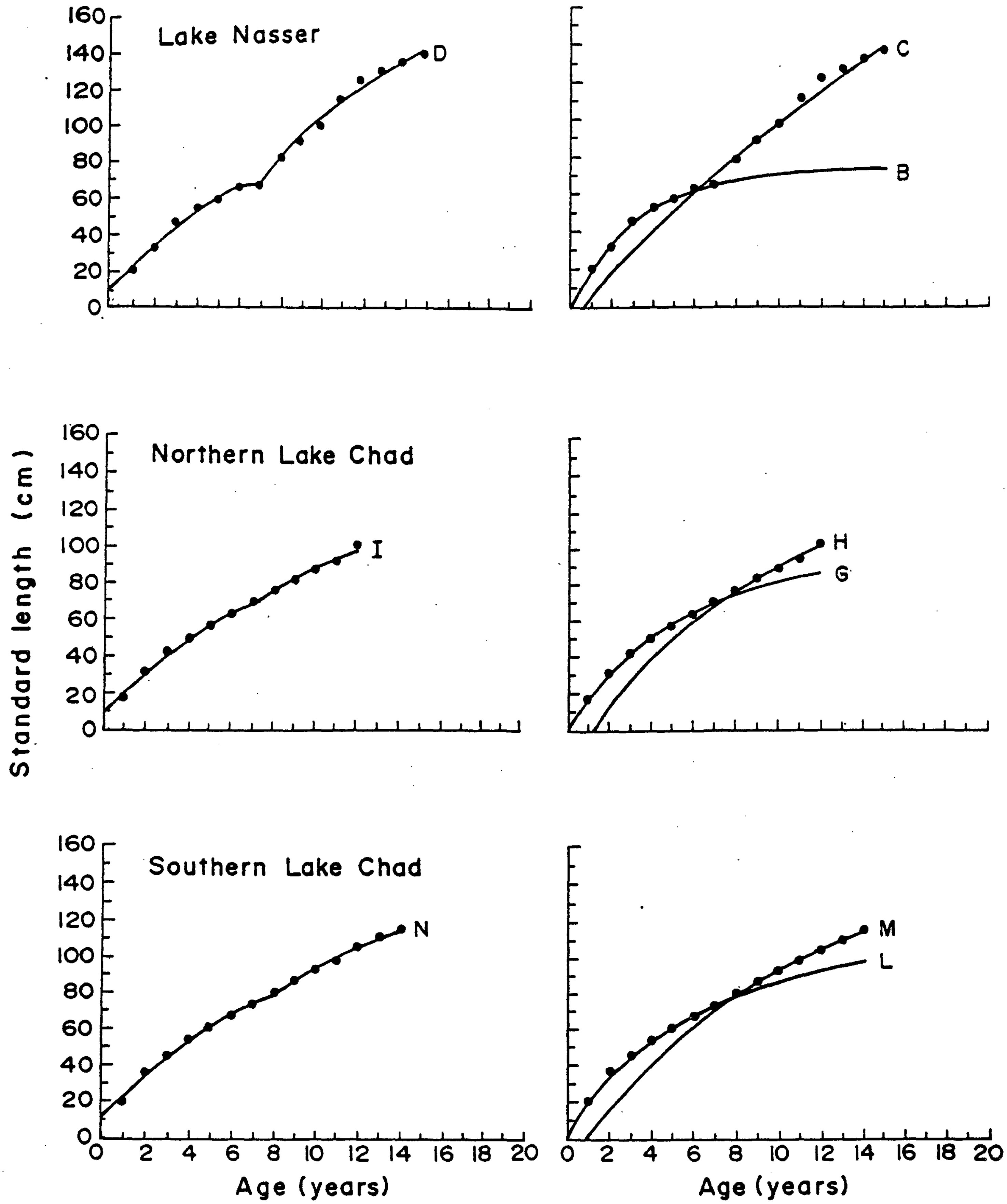

FIGURE 2. Mean length at age data of Nile perch from three African locations (from Table 1). Fitted growth curves in the panels to the left are biphasic growth models described by text equation (2). Curves in the panels to the right are ordinary von Bertalanffy growth curves (equation 1) fitted separately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

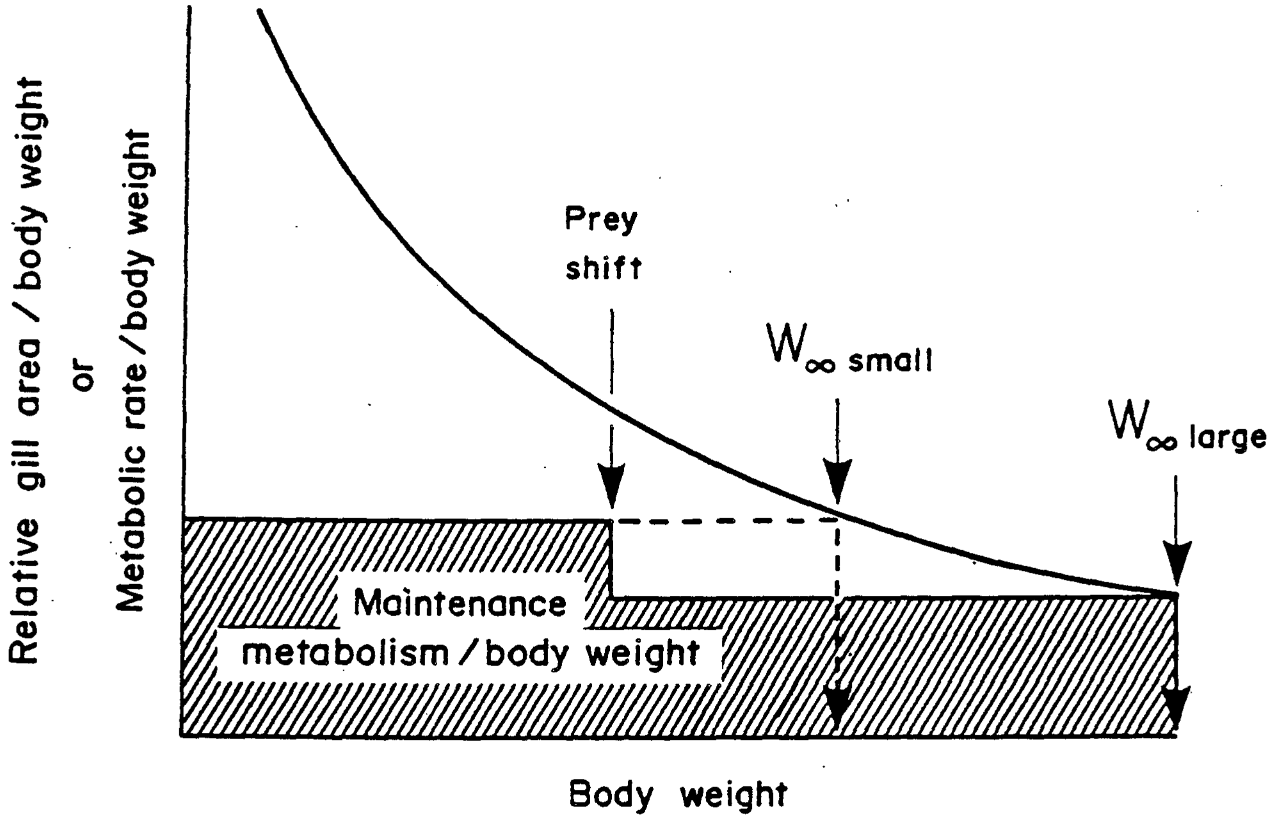

FIGURE 3. Schematic representation of the increase of the scope for growth following shift to a prey that can be captured with less energy outlay. W_∞ is, by definition, the body weight where metabolism is just sufficient to sustain life, i.e. is equal to maintenance metabolism. Thus, lowering energy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

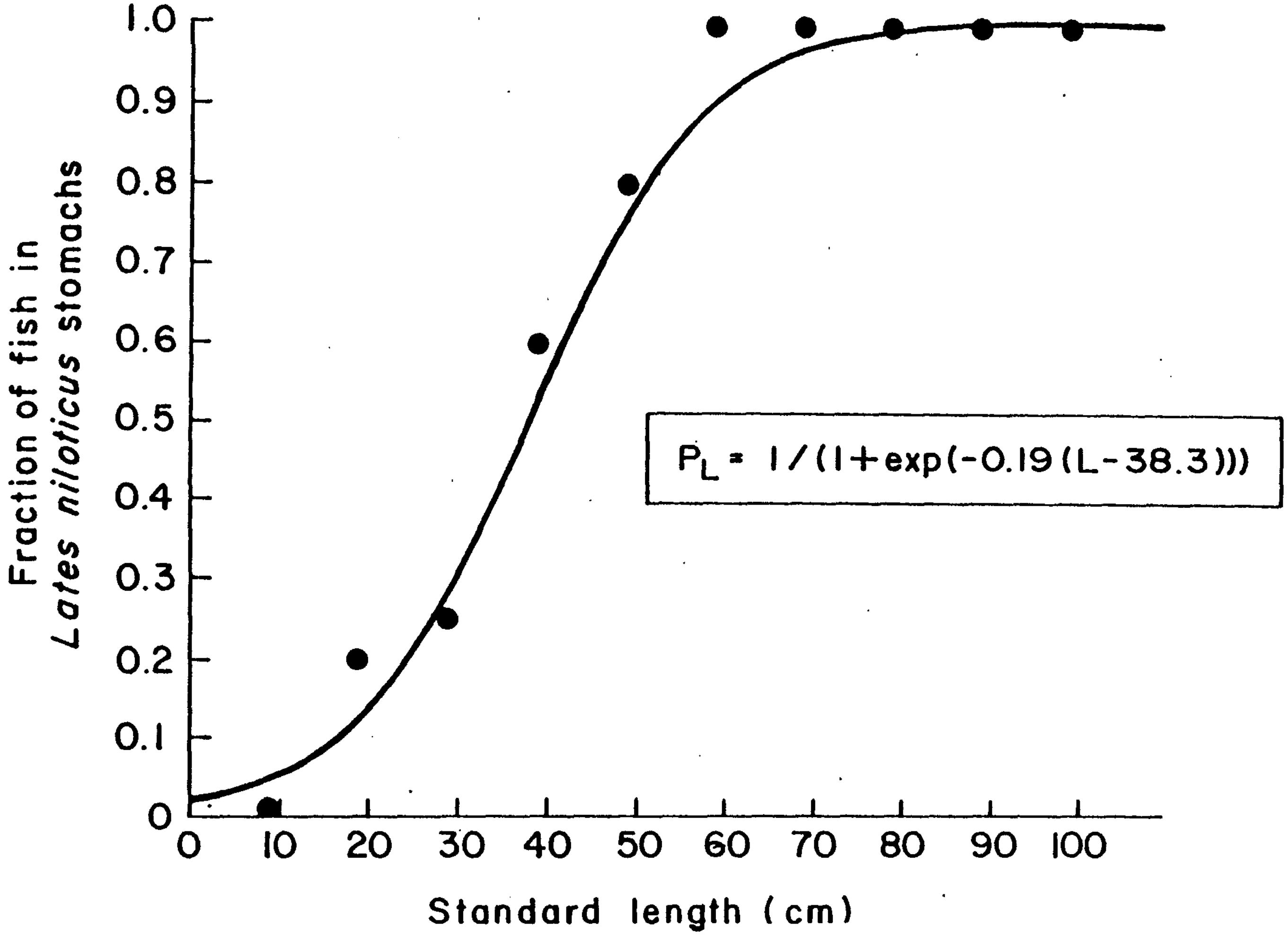

FIGURE 4. Observed proportion of fish in Nile perch stomachs from various African water bodies (see Table 2) versus standard length of the perch. The logistic curve was fitted by ordinary least squares after applying the logit transformation to the proportions.