Growth with seasonally varying temperatures: an expansion of the von Bertalanffy growth model

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The von Bertalanffy growth function has limitations for describing the growth of fishes in seasonal climates. In the present work, a new equation is proposed where the growth parameter *k* is substituted by a function related to monthly water temperatures. The computer program GROWTH5 was developed to fit and simulate the growth for seasonally varying temperatures. Examples for natural populations of *Barbatula barbatula* and *Cottus gobio* are presented.

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INTRODUCTION

Growth, as proposed by von Bertalanffy (1938), is the result of the antagonistic effects of anabolism and catabolism. Although von Bertalanffy related anabolism exclusively to the surface area and catabolism with animal weight or volume, there is no doubt that metabolic constants are related to biotic and abiotic factors. As a first approximation, we can list such factors as the qualitative and quantitative aspects of food ingestion, population density, and the influence of temperature, photoperiod and rainfall through production of growth hormone, migration and gonadal maturation. Even considering animal growth as a result of several factors, it is clear that temperature has an important role over growth regulation. Several mathematical models relating temperature to growth have been proposed (for reviews, see Ricker, 1979; Ahlgren, 1987; Elliott *et al.*, 1987; Moreau, 1987; Weatherley & Gill, 1987).

THE VON BERTALANFFY GROWTH FORMULA AND TEMPERATURE

The von Bertalanffy growth formula (VBGF) (Bertalanffy, 1938) has been widely applied in fisheries biology. von Bertalanffy (1938) considered an organism as an open system where growth was a result of an equilibrium between synthesis and breakdown of organic compounds; catabolism was proportional to the weight of the organism while anabolism depended on the surface available for changing nutrients (definitions of the parameters are summarised in Table I):

$$L_t = E/k - (E/k - L_0) \cdot \exp(-k \cdot t) \tag{1}$$

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TABLE I. Parameter definitions

Symbol	Definition
a	condition factor
A	amplitude of the sine function
A_1	annual temperature amplitude
A_2	semestral temperature amplitude
A_3	quadrimestral temperature amplitude
b	weight/length isometric index
C_1, C_2, C_3	empirical constants
E	constant related to anabolism
E_{max}	maximum anabolism value
E_p	anabolism coefficient
F_1	empirical function
f_1	time factor for annual wave phase correction
f_2	time factor for semestral wave phase correction
f_3	time factor for quadrimestral wave phase correction
I	sample interval
L_∞	asymptotic length
k	constant related to catabolism (von Bertalanffy's growth coefficient)
k_{max}	maximum reaction rate or catabolism value
k_p	catabolism coefficient
k_t	average growth rate
L_{est}	estimated length
I_o	length when $t=0$
L_{obs}	observed length
L_t	length at age t
N	number of samples
t	age
t_o	time correction factor related to the size at recruitment
T_{opt}	optimum temperature
T	temperature
T_m	annual average temperature
T_{max}	upper threshold temperature
T_t	estimated average temperature at time t
W_∞	asymptotic weight
W_t	weight at age t

where L_t is the length at age t; E is a constant related to anabolism; k is a constant related to catabolism (the growth coefficient); L_0 is the length when $t=0$; and t is the age.

The asymptotic length (L_∞) may be equal to E/k. Transforming L_0 to a factor of time correction (t_0) and substituting L_∞ for E/k:

$$L_t = L_\infty(1 - \exp(-k \cdot (t - t_0))). \tag{2}$$

Taylor (1958, 1959, 1960) fitted the VBGF to growth data for cod (*Gadus callarias* L., Taylor, 1958) and two species of clams (*Siliqua patula*, Taylor, 1959; *Cardium corbis*, Taylor, 1960) at different latitudes. He used exponential regressions between the constant k and the annual average temperature at each

study site, obtaining high correlation coefficients. As a consequence of Taylor's findings, we have:

$$k = F_1(T_m) \tag{3}$$

where T_m is the annual average temperature; and F_1 is an empirical function. A function relating growth to different constant temperatures was proposed by Elliott (1975) based on 55 experiments on brown trout *Salmo trutta* L. Although this provides a description of growth for any average environmental temperature, it requires a good record of temperature. Ursin (1963) was the first to introduce a sinusoidal pattern based on the von Bertalanffy growth formulae by substituting the catabolism (E) and anabolism (k) constants by empirical catenary curves, according to Janisch (1927; in Ursin, 1963):

$$E = E_{\max}(\cosh\ E_p\ (T - T_{\mathrm{opt}}))^{-1} \tag{4}$$

$$k = k_{\max}(\cosh\ k_p\ (T - T_{\mathrm{opt}}))^{-1}$$

where $E_{\max}$ is the maximum anabolism value; E_p is an anabolism coefficient; $k_{\max}$ is the maximum catabolism value; k_p is a catabolism coefficient; T is the temperature; and T_{opt} is the optimum temperature.

Other attempts have been made to describe a growth rate following a seasonal cycle, all of them including a sine function in the exponent part of the VBGF (Pitcher & Macdonald, 1973; Cloern & Nichols, 1978; Pauly & David, 1981; Akamine, 1986). For instance, Pitcher & Macdonald (1973) proposed:

$$L_t = L_\infty \cdot (1 - \exp(-k_1)) \tag{5}$$

$$k_1 = A \cdot \sin(2\pi \cdot (t - f)/52) + k(t - t_0)$$

where A is the amplitude of the sine function; and f is the starting point of the sine function. Although the association between growth parameters and ambient temperature has been proposed previously (Ursin, 1963; Pitcher & Macdonald, 1973; Pauly & David, 1981), this is not made explicit as a formal mathematical function including both k/temperature and temperature/time relationships.

GROWTH WITH SEASONALLY VARYING TEMPERATURES: A SIMULATION MODEL

The starting point for the model development is to assume seasonal temperature variation as described by a sine function, which would incorporate one or more sinusoidal components depending on the required precision:

$$
\begin{aligned}
T_t = T_m\quad &+ A_1 \cdot \cos(2\pi \cdot (t - f_1))\ \text{(annual wave)} \\
&+ A_2 \cdot \cos(4\pi \cdot (t - f_2))\ \text{(semestral wave)} \\
&+ A_3 \cdot \cos(8\pi \cdot (t - f_3))\ \text{(quadrimestral wave)}
\end{aligned}
\tag{6}
$$

where T_t is the estimated average temperature at time t; T_m is the annual average temperature; A_1 is the annual temperature amplitude; A_2 is the semestral temperature amplitude; A_3 is the quadrimestral temperature amplitude; f_1 is a time factor for annual wave phase correction; f_2 is a time factor for semestral wave phase correction; f_3 is a time factor for quadrimestral wave phase correction and t is the time. Considering growth as a historical process, that is, the length or weight of an animal at a moment t is the result of all the conditions since fertilization, it is useful to transform average monthly temperatures (T_t) into average temperatures of growth (T):

$$T = 1/(t-t_0) \cdot \int_{t_0}^{t} (T_m + A_1 \cdot \cos(2\pi \cdot (t-f_1)) + A_2 \cdot \cos(4\pi \cdot (t-f_1))$$
$$+ A_3 \cdot \cos(8\pi \cdot (t-f_3))) \mathrm{d}t. \tag{7}$$

Solving:

$$T = 1/(t - t_0) \cdot (T_1 - T_2) \tag{8}$$

$$
\begin{aligned}
T_1 = T_m \cdot t \quad &+ (A_1/2\pi) \cdot \sin(2\pi \cdot (t - f_1)) \\
&+ (A_2/4\pi) \cdot \sin(4\pi \cdot (t - f_2)) \\
&+ (A_3/8\pi) \cdot \sin(8\pi \cdot (t - f_3)) \\
T_2 = T_m \cdot t_0 \quad &+ (A_1/2\pi) \cdot \sin(2\pi \cdot (t_0 - f_1)) \\
&+ (A_2/4\pi) \cdot \sin(4\pi \cdot (t_0 - f_2)) \\
&+ (A_3/8\pi) \cdot \sin(8\pi \cdot (t_0 - f_3)).
\end{aligned}
$$

By isolating k of the VBGF, it is possible to estimate the average growth rate (k_t) until moment t:

$$k_t = (t_0 - t)^{-1} \cdot \ln((L_\infty - L_t)/L_\infty) \tag{9}$$

To relate the average growth rate (k_t) to the average temperature of growth (T), we will choose, as a first approximation, the exponential model proposed by Taylor (1960):

$$k_t = C_1 \cdot \exp(C_2 \cdot T) \tag{10}$$

where C_1 and C_2 are empirical parameters. By combining equations (8) and (10) with the VBGF, we can describe the growth with seasonally varying temperatures:

$$L_t = L_\infty \cdot (1 - \exp(-k_t(t - t_0))) \tag{11}$$

$$k_t = C_1 \cdot \exp(C_2 \cdot T)$$

$$T = 1/(t - t_0) \cdot (T_1 - T_2)$$

$$
\begin{aligned}
T_1 = T_m \cdot t \quad &+ (A_1/2\pi) \cdot \sin(2\pi \cdot (t - f_1)) \\
&+ (A_2/4\pi) \cdot \sin(4\pi \cdot (t - f_2)) \\
&+ (A_3/8\pi) \cdot \sin(8\pi \cdot (t - f_3))
\end{aligned}
$$

$$T_2 = T_m \cdot t_0 \quad + (A_1/2\pi) \cdot \sin(2\pi \cdot (t_0 - f_1))$$
$$+ (A_2/4\pi) \cdot \sin(4\pi \cdot (t_0 - f_2))$$
$$+ (A_3/8\pi) \cdot \sin(8\pi \cdot (t_0 - f_3)).$$

where all the parameters have been defined earlier (see Table I). Nevertheless, at high temperature levels, the exponential model for k/temperature function describes an ever increasing growth rate, which obviously is not observed. Considering that almost all the chemical reactions within an organism are catalysed by enzymes, the starting point for a k/temperature function should be an equation that could describe the enzyme reaction rate as a function of environmental temperature. That model should consider the probability of enzyme/substrate linking and quantify the rate of active enzymes to denatured ones.

Even in developing a theoretical enzyme model, there remain some problems. First of all, the enzyme complex of an organism does not show an equal response to environmental temperatures (Sauer & Haider, 1977; Davison & Davison, 1987). On the other hand, it could be observed within a species or individual that there is a change in concentrations of isoenzymes of the same function but with different optimum temperatures depending on the environmental temperature of acclimation (Lapkin *et al.*, 1983). Temperature influences the passive and active transport across membranes (Volmer, 1981; Houston & Mearow, 1981, 1982; Hennessey *et al.*, 1983; Paszewski & Spiewla, 1986; Hansen & Fisahn, 1987) and this is another important factor to be considered.

Faced with the problems presented here, we consider it improbable to develop a strictly theoretical model. So, it appears more adequate to use empirical models where the parameters present some ecological or physiological meaning, as in the equations proposed by Parker (1974):

$$k_t = k_{\max} \cdot ((T/T_{\mathrm{opt}}) \cdot Z^U)^{C_3} \tag{12}$$
$$Z = (T_{\max} - T)/(T_{\max} - T_{\mathrm{opt}})$$
$$U = (T_{\max} - T_{\mathrm{opt}})/T_{\mathrm{opt}}$$

where $k_{\max}$ is the maximum reaction rate; $T_{\max}$ is the upper threshold temperature; T_{opt} is the optimum temperature; T is the temperature; and C_3 is an empirical constant. In this case, considering that one of the major characteristics of the proposed model is the possibility of simulating growth, it is desirable to change the exponential function by Parker's model since the former expects an even increase in growth rate with temperature rise (see Table I for definitions).

$$L_t = L_\infty \cdot (1 - \exp(-k_t(t - t_0))) \tag{13}$$
$$k_t = k_{\max} \cdot ((T/T_{\mathrm{opt}}) \cdot Z^U)^{C_3} \quad \text{(Parker, 1974)}$$
$$Z = (T_{\max} - T)/(T_{\mathrm{opt}})$$
$$U = (T_{\max} - T_{\mathrm{opt}})/T_{\mathrm{opt}}$$
$$T = 1/(t - t_0) \cdot (T_1 - T_2)$$

$$
\begin{aligned}
T_1 = T_m \cdot t \quad &+ (A_1/2\pi) \cdot \sin(2\pi \cdot (t - f_1)) \\
&+ (A_2/4\pi) \cdot \sin(4\pi \cdot (t - f_2)) \\
&+ (A_3/8\pi) \cdot \sin(8\pi \cdot (t - f_3)) \\
T_2 = T_m \cdot t_0 \quad &+ (A_1/2\pi) \cdot \sin(2\pi \cdot (t_0 - f_1)) \\
&+ (A_2/4\pi) \cdot \sin(4\pi \cdot (t_0 - f_2)) \\
&+ (A_3/8\pi) \cdot \sin(8\pi \cdot (t_0 - f_3)).
\end{aligned}
$$

The major problem concerning the use of Parker's formulae instead of the exponential one is the impossibility of estimating optimum and upper lethal temperatures from ordinary data, making it necessary to obtain these values from the literature or specially designed experiments.

SYSTEM GROWTH5: PARAMETER ESTIMATION

For an easy adjustment of the growth model to data from natural populations, a BASIC system for PC computers was developed (GROWTH5). Copies can be obtained from the authors. The sine function for monthly average temperatures is adjusted according to Amaral (1965):

$$
T_m = 1/12 \cdot \sum_{t=1}^{12} T_t . \tag{14}
$$

$$
P_1 = 1/6 \cdot \sum_{t=1}^{12} T_t \cdot \cos((t-1) \cdot 2\pi/12)
$$

$$
P_2 = 1/6 \cdot \sum_{t=1}^{12} T_t \cdot \cos((t-1) \cdot 2\pi/6)
$$

$$
P_3 = 1/6 \cdot \sum_{t=1}^{12/I} T_t \cdot \cos((t-1) \cdot 2\pi/3)
$$

$$
Q_1 = 1/6 \cdot \sum_{t=1}^{12/I} T_t \cdot \sin((t-1) \cdot 2\pi/12)
$$

$$
Q_2 = 1/6 \cdot \sum_{t=1}^{12/I} T_t \cdot \sin((t-1) \cdot 2\pi/6)
$$

$$
Q_3 = 1/6 \cdot \sum_{t=1}^{12/I} T_t \cdot \sin((t-1) \cdot 2\pi/3)
$$

$$
\begin{aligned}
A_1 &= (P_1^2 + Q_1^2)^{1/2}/I \\
A_2 &= (P_2^2 + Q_2^2)^{1/2}/I \\
A_3 &= (P_3^2 + Q_3^2)^{1/2}/I \\
f_1 &= \arctan(Q_1/P_1) \\
f_2 &= \arctan(Q_1/P_1) \\
f_3 &= \arctan(Q_1/P_1)
\end{aligned}
$$

where I is the sample interval. Preliminary values of the asymptotic length (L_∞) are estimated by the Walford (1946) method. The growth constant k and t_0 are estimated by least squares through VBGF linearization:

$$\ln(1 - (L_t/L_\infty)) = -k \cdot t + k \cdot t_0. \tag{15}$$

The parameters of the weight/length relationship are estimated through the regression of log length on log weight. The asymptotic weight (W_∞) is obtained by the application of asymptotic size (L_∞) on the weight/length relationship. The residual variance (S^2) is calculated as follows:

$$S^2 = \sum_{t=1}^{N} (L_{\text{obs}} - L_{\text{est}})^2 / N \tag{16}$$

where N is the number of samples; L_{obs} is the observed length; and L_{est} is the estimated length. For the estimation of the k_t/temperature relationship, the values of k_t for each sample are calculated through equation (9). Since weight is frequently more sensitive to temperature than length, we can substitute L_t of equation (9) by $(W_t/a)^{1/b}$:

$$k_t = (t_0 - t)^{-1} \cdot \ln((L_\infty - (W_t/a)^{1/b})/L_\infty) \tag{17}$$

where W_t is the weight at age t; a is the condition factor; and b is the weight/length isometric index. To each value of k_t is associated a value of average temperature of growth (T) obtained through equation (8). The parameters C_1 and C_2 of the exponential k_t/temperature relationship equation (10) are computed through linear regression of log k_t on log T. Once T_{max} and T_{opt} values are available, Parker's model equation (12) for k_t/temperature relationship can be linearized:

$$\ln k_t = \ln k_{\text{max}} + C_3 \ln((T/T_{\text{opt}}) \cdot Z^U) \tag{18}$$

where Z and U are defined on equation (12). Since L_∞ estimates from seasonal data by means of Ford–Walford plots frequently lead to unreal values and C_1, C_2 and C_3 calculations are greatly affected by L_∞ and t_0, the solution of the parameters is not possible using only analytical methods. In this case it is necessary to check by means of computational routines the values of L_∞ and t_0 that minimize residual variance in the seasonal model. For each L_∞ and t_0 combination, within a biologically acceptable range, the values of C_1, C_2, C_3 and S^2 are recalculated by the program GROWTH5, being chosen as the ones that produce the best fit.

EXAMPLES AND DISCUSSION

Tables II and III present the parameter estimates of the growth curve with seasonally varying temperatures for *Cottus gobio* L. in Bere Stream and *Barbatula barbatula* (L.) in Docken's Water (data from Mann, 1971). Temperature variation, k/temperature functions, the length and weight growth

TABLE II. Growth curve parameters with seasonally varying temperatures of *Cottus gobio* at Bere stream (Mann, 1971)

Weight/length relationship	
a	0·0201
b	2·8057
r	0·9938
von Bertalanffy growth curve parameters	
L_∞ (cm)	7·1210
W_∞ (g)	4·9468
t_o (yr)	− 0·0788
k	1·5746
S^2	0·1950
Time/temperature function	
T_m (° C)	11·7083
A_1 (° C)	3·3786
A_2 (° C)	0·4936
A_3 (° C)	0·4003
f_1 (yr)	0·0980
f_2 (yr)	0·1350
f_3 (yr)	0·3398
Seasonal model with exponential k/temperature function	
C_1	0·0913
C_2	0·1937
r^2	0·9522
L_∞ (cm)	8·1000
W_∞ (g)	7·1003
t_o (yr)	− 0·2200
S^2	0·0049
Seasonal model with Parker's k/temperature function	
C_3	4·4344
k_{max}	1·4185
T_{opt} (*)	16·0000
T_{max} (*)	21·0000
r^2	0·9166
L_∞ (cm)	8·2000
W_∞ (g)	7·3494
t_o (yr)	− 0·2600
S^2	0·0070

*Arbitrary value.

curves, and standardized residuals for *C. gobio* and *B. barbatula* are presented in Figs 1–4.

Analysing the application of the program GROWTH5 on *C. gobio* and *B. barbatula* data, the first aspect to draw attention to is a result of the adjusting method used to fit the growth curve. Since we relate average growth rate (k_t) to average temperature of growth (T), there is a narrow range of temperature in the k_t/temperature relationship (Figs 1 and 3). The average temperature for growth (T) concentrates on the average annual temperature with increasing time, so that

TABLE III. Growth curve parameters with seasonally varying temperatures of *Barbatula barbatula* at Docken's Water (Mann, 1971)

Weight/length relationship

a	0·0056
b	3·2353
r	1·0000

von Bertalanffy growth curve parameters

L_∞ (cm)	11·5375
W_∞ (g)	15·3404
t_o (yr)	− 0·1271
k	0·7805
S^2	0·1628

Time/temperature function

T_m (° C)	10·1500
A_1 (° C)	6·5346
A_2 (° C)	0·3219
A_3 (° C)	0·7006
f_1 (yr)	0·0063
f_2 (yr)	0·8669
f_3 (yr)	0·3183

Seasonal model with exponential k/temperature function

C_1	0·2149
C_2	0·0953
r^2	0·9758
L_∞ (cm)	13·8000
W_∞ (g)	27·3801
t_o (yr)	− 0·0900
S^2	0·0140

Seasonal model with Parker's k/temperature function

C_3	1·5161
k_{max}	0·8960
T_{opt} (*)	19·0000
T_{max} (*)	24·0000
r^2	0·9795
L_∞ (cm)	14·3000
W_∞ (g)	30·7214
t_o (yr)	− 0·1100
S^2	0·0099

*Arbitrary value.

almost all temperature variation is determined by the first months of growth. Despite this methodological problem, a high coefficient of determination (r^2) was observed for the k_t/temperature function (Tables II and III).

A residual analysis (Chatterjee & Price, 1977) should be used to detect data patterns not predicted by the proposed model by means of plotting standardized deviations against a dependent or/and independent variable. The introduction of a temperature component had reduced most of the seasonal residuals (Figs 2, 4).
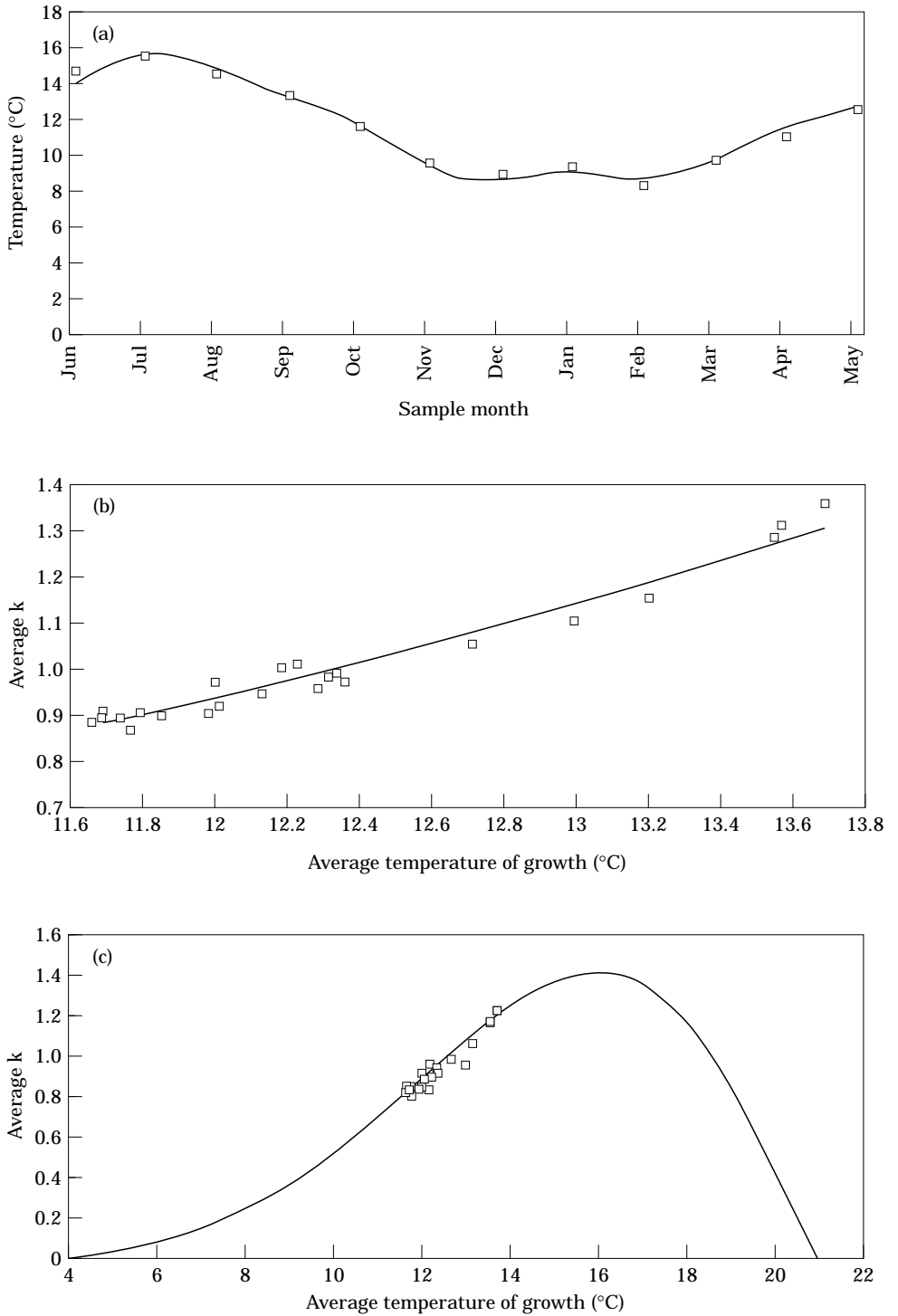
FIG. 1. (a) Monthly average water temperatures in Bere stream; (b) exponential *k*/temperature; (c) and Parker's *k*/temperature function for *Cottus gobio*.
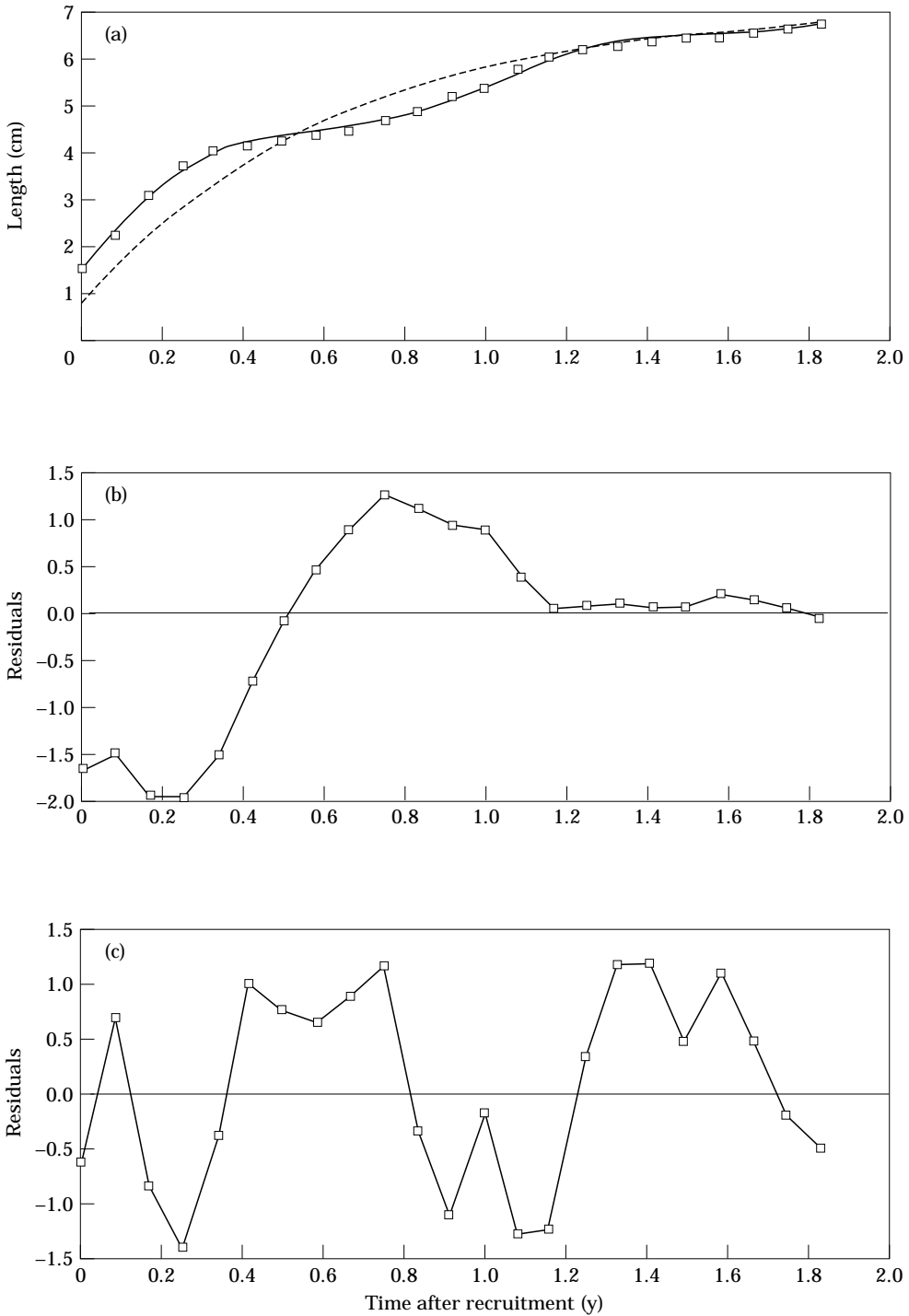
FIG. 2. Length–growth curve and standardized residual distribution of *Cottus gobio* in Bere stream. (a) Bertalanffy and seasonal growth curves; (b) residuals, Bertalanffy model; (c) residuals, seasonal model. □, Observed, – – –, Bertalanffy; ——, seasonal.
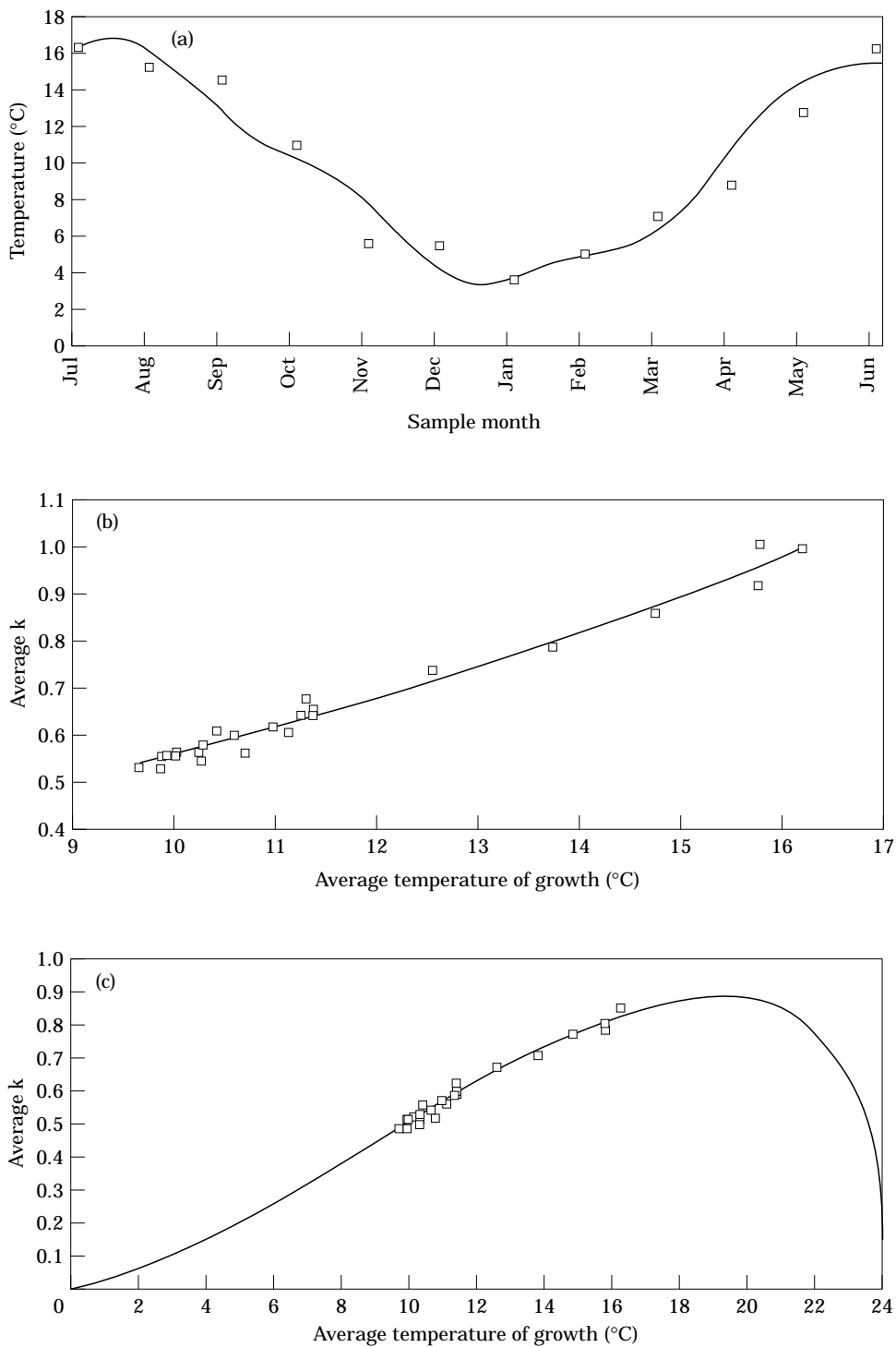
Fig. 3. (a) Monthly average water temperatures at Docken's Water; (b) exponential *k*/temperature; (c) Parker's *k*/temperature model for *Barbatula Barbatula*.
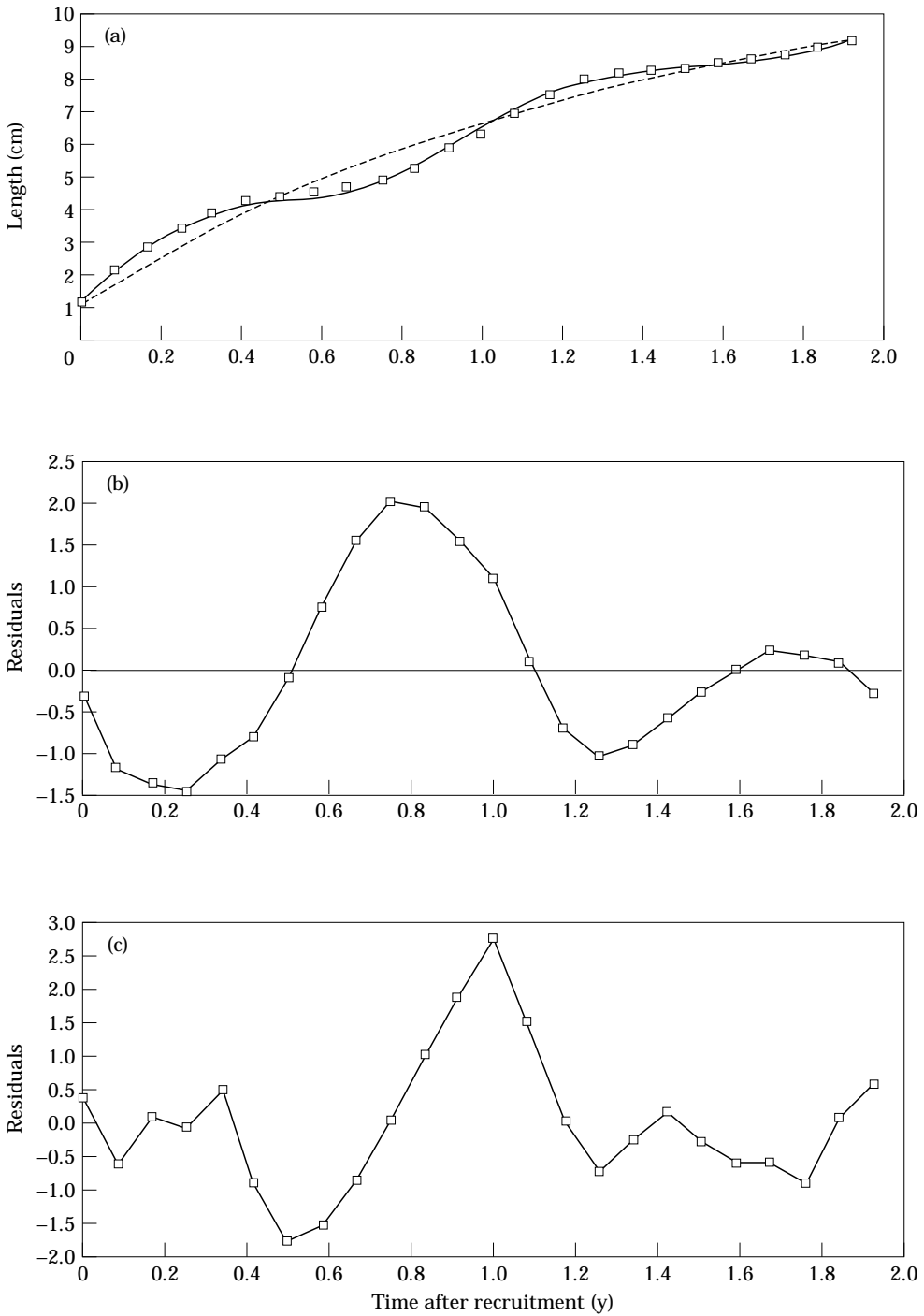
FIG. 4. Length–growth curve and standardized residual distribution of *Barbatula barbata* at Docken's Water. (a) Bertalanffy and seasonal growth curves; (b) residuals, Bertalanffy model; (c) residuals, seasonal model. □, Observed, – – –, Bertalanffy; ——, seasonal.

Nevertheless some seasonal patterns still remain, indicating that temperature is not the unique ecological factor determining seasonal growth.

A literature analysis clearly shows the existence of two major factors acting over seasonal growth: photoperiod and temperature (Hogman, 1968; Villarreal *et al.*, 1981; Thorpe, 1987; Weatherley & Gill, 1987). However, considering that the average monthly temperatures and the seasonal photoperiod variation follow both sine curves distant only by a small phase difference, it is difficult to identify the separate influence of each of these factors on the growth rate. Either of these factors chosen ' *a priori* ' will present a strong correlation coefficient due to collinearity effects. If it is not possible to isolate the individual effect of each variable, why choose temperature as the major factor acting over growth rate oscillation? First of all we have to consider two important aspects: (1) although photoperiod and temperature oscillate seasonally with small phase differences, photoperiod presents an absolute regularity while temperature shows large variations; (2) the photoperiod cycle anticipates the temperature cycle with a small time gap.

This evidence corroborates the idea that photoperiod acts as an early sign for temperature increase (Villarreal *et al.*, 1988), because: (1) growth processes depend on protein synthesis; (2) the metabolic processes depend not only on the chemical kinetics (temperature) but also on enzyme concentrations; (3) growth hormone acts on protein and RNA synthesis; and (4) there should be a physiological advantage to start synthesizing enzymes just before average temperature increases. In this case, photoperiod plays its role in synchronizing enzyme synthesis with favourable temperatures, but it is the temperature that governs the reaction rate.

Considering this proposal, how is it possible to account for seasonal growth rates that are not explained by temperature oscillation? First, it should be considered that the seasonally varying temperatures do not follow exactly the same pattern each year. The influence of seasonal rainfall over food availability and the energy cost for migration and reproduction should not be forgotten (Moreau, 1987).

Finally, comparing the model for seasonal growth presented here with previous ones (Ursin, 1963; Pitcher & Macdonald, 1973; Pauly & David, 1981; Akamine, 1986), three advantages should be mentioned. (1) Although the model should be considered an empirical function, most of the equation parameters have a biological meaning. (2) The final function is a result of the composition of more simple equations, each one related to a specific aspect of the phenomena. (3) Since the model incorporates real temperature variations, it makes possible the simulation of growth for different temperature regimes.

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