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Analysis of logistic growth models

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Abstract

A variety of growth curves have been developed to model both unpredated, intraspecific population dynamics and more general biological growth. Most predictive models are shown to be based on variations of the classical Verhulst logistic growth equation. We review and compare several such models and analyse properties of interest for these. We also identify and detail several associated limitations and restrictions. A generalized form of the logistic growth curve is introduced which incorporates these models as special cases. Several properties of the generalized growth are also presented. We furthermore prove that the new growth form incorporates additional growth models which are markedly different from the logistic growth and its variants, at least in their mathematical representation. Finally, we give a brief outline of how the new curve could be used for curve-fitting.

Keywords: Biological growth dynamics; Logistic growth; Generalized logistic growth; Inflection point; Incomplete beta function; Beta function; Gamma function; Mimimax; Saddle curve; Finite difference method

1. Introduction

In order to model growth of biological systems numerous models have been introduced. These variously address population dynamics, either modelled discretely or, for large populations, mostly continuously. Others model actual physical growth of some property of interest for an organism or organisms.

The simple exponential growth model can provide an adequate approximation to such growth for the initial period. However, for populations, no predation or intraspecific competition is included. The population would therefore continue to increase unhindered (or inevitably reduce to

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zero if an initial growth reduction were present). Even in the case where predation was at most negligible, the model does not accommodate growth reductions due to intraspecific competition for environmental resources such as food and habitat. For the case of growth per se, unrestricted growth is also unrealistic. For example, as plants approach maturity, the physical characteristics of interest will reach a limiting dimension.

Verhulst [1] considered that, for the population model, a stable population would consequently have a saturation level characteristic; this is typically called the carrying capacity, K, and forms a numerical upper bound on the growth size. To incorporate this limiting form he introduced the logistic growth equation which is shown later to provide an extension to the exponential model. We will see later that the Verhulst logistic growth model has formed the basis for several extended models. Each is a parameterised version of the original and provides a relaxation of the logistic curve's restrictions.

Notwithstanding this limitation the logistic growth equation has been used to model many diverse biological systems. Carlson [2] reported the growth of yeast which is modelled well by the curve [3,4]. Morgan [5] ingeniously used the equation to describe herding behaviour of African elephants. Krebs [6] also used the Verhulst logistic equation to fit to population data for Peruvian anchovies.

There have been applications of the logistic model outside the field of Biology also. Fisher and Fry [7] have successfully exploited the logistic model to describe the market penetration of many new products and technologies. In this particular application of the logistic model N represents a measure of the market already captured and $(K - N)/K$ that for the fraction of the market remaining to be captured. Marchetti and Nakicenovic [8] have given a summary of world energy usage and source substitution by employing the logistic model. Herman and Montroll [9] have shown that as basic an evolutionary process as the industrial revolution may also be modelled by logistic dynamics. Here, as the industrial revolution evolved, the fraction of the labour force in agriculture declined while the fraction in industry grew.

In this paper we introduce a generalized logistic equation and present its properties. Then we revisit several important growth models in chronological order and examine their properties. Finally, we prove that each model can be derived from the generalized logistic growth model introduced and contrast the generalized logistic form with other generalized forms.

2. Generalized logistic growth function

Here we propose a generalized logistic growth equation which incorporates all previously reported functional forms as special cases. We will adopt the term *generalized logistic equation* in our exposition, a term first used by Nelder [10] to describe the Richards equation. We believe the adopted term is an appropriate one as it connotes exactly what it purports to achieve and is clearly more general than that of Richards model.

2.1. Definition and properties of the generalized logistic function

We define the generalized logistic function thus:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN^{\alpha}\left[1 - \left(\frac{N}{K}\right)^{\beta}\right]^{\gamma}, \tag{1}$$

where α, β, γ are positive real numbers. In this paper we confine ourselves mostly to positive values for these parameters, as negative exponents do not always provide a biologically plausible model.

The three main features of the generalized logistic growth are

(i) $\lim_{t\to\infty} N(t) = K$, the population will ultimately reach its carrying capacity.
(ii) The relative growth rate, $(1/N)(\mathrm{d}N/\mathrm{d}t)$, attains its maximum value at

$$N^* = \left(1 + \frac{\beta\gamma}{\alpha - 1}\right)^{-(1/\beta)} K \tag{2}$$

provided N^* is real and greater than N_0, otherwise it declines non-linearly reaching its minimum zero value at $N = K$. The maximum relative growth rate is given by

$$\left(\frac{1}{N}\frac{\mathrm{d}N}{\mathrm{d}t}\right)_{\max} = rK^{\alpha-1}\left(\frac{\alpha - 1}{\alpha - 1 + \beta\gamma}\right)^{(\alpha-1)/\beta}\left(\frac{\beta\gamma}{\alpha - 1 + \beta\gamma}\right)^{\gamma}. \tag{3}$$

Important limit values of N^* are

$$\lim_{\alpha\to 0} N^* = 0$$
$$\lim_{\beta\to 0} N^* = \mathrm{e}^{\gamma/(1-\alpha)}$$
$$\lim_{\gamma\to 0} N^* = K.$$

(iii) The population at the inflection point (where growth rate is maximum), is given by

$$N_{\inf} = \left(1 + \frac{\beta\gamma}{\alpha}\right)^{-(1/\beta)} K > N^*. \tag{4}$$

Clearly if $N_{\inf} < N_0$, no inflection is possible as the population will have started with this initial value, N_0, and with a positive intrinsic growth per capita rate thus ensuring that $N_{\inf}$ is not achievable. The relative growth rate at $N_{\inf}$ is again given by (3) with the substitution α for $\alpha - 1$ in the bracketed expressions only. The maximum growth rate is given by

$$\left(\frac{\mathrm{d}N}{\mathrm{d}t}\right)_{\max} = \left(\frac{\mathrm{d}N}{\mathrm{d}t}\right)_{N_{\inf}} = rK^{\alpha}\left(\frac{\alpha}{\alpha + \beta\gamma}\right)^{\alpha/\beta}\left(\frac{\beta\gamma}{\alpha + \beta\gamma}\right)^{\gamma}. \tag{5}$$

Important limit values of $N_{\inf}$ are

$$\lim_{\gamma\to\infty} N_{\inf} = \lim_{\alpha\to 0} N_{\inf} = 0$$
$$\lim_{\beta\to 0} N_{\inf} = K\,\mathrm{e}^{-(\gamma/\alpha)}$$
$$\lim_{\beta\to\infty} N_{\inf} = \lim_{\alpha\to\infty} N_{\inf} = \lim_{\gamma\to 0} N_{\inf} = K.$$

The same inflection value is obtained for a multitude of generalized logistic forms when α, γ are allowed to vary provided the ratio γ/α and β remain constant.

By introducing the auxiliary variable $x = (N/K)^{\beta}$ we can transform the autonomous differential equation (1) into

$$\frac{dx}{dt} = \beta r K^{\alpha-1} x^{((\alpha-1)/\beta)+1}(1-x)^{\gamma}$$

and upon separation of variables and subsequent integration from 0 to t

$$\int_{(N_0/K)^{\beta}}^{(N(t)/K)^{\beta}} x^{((1-\alpha)/\beta)-1}(1-x)^{-\gamma}\,dx = \beta r K^{\alpha-1} t. \tag{6}$$

The integral in (6) can be evaluated, in the general case where the parameters α, β, γ can take any numerical values, by binomially expanding $(1-x)^{-\gamma}$ and subsequently integrating the resulting series term by term. When $p = (1-\alpha)/\beta > 0$, $q = 1-\gamma > 0$, the integral

$$\int_{x_0}^{x_1} x^{p-1}(1-x)^{q-1}\,dx,$$

where $x_1 = (N(t)/K)^{\beta}$, $x_0 = (N_0/K)^{\beta}$, is the difference of the two incomplete beta functions $B_{x_1}(p,q)$ and $B_{x_0}(p,q)$. The *incomplete beta function* is defined thus

$$B_{x_1}(p,q) = \int_0^{x_1} x^{p-1}(1-x)^{q-1}\,dx.$$

Hence,

$$B_{x_1}(p,q) - B_{x_0}(p,q) = \int_{x_0}^{x_1} x^{p-1}(1-x)^{q-1}\,dx = \beta r K^{\alpha-1} t. \tag{7}$$

From the restrictions $p > 0$, $q > 0$ two possible ranges of values for α, β are acceptable:

$$\alpha < 1, \quad \beta > 0, \quad \gamma < 1$$
$$\alpha > 1, \quad \beta < 0, \quad \gamma < 1.$$

The integral in (7) can be expressed as a difference of two series expansions since $0 < x_0 < 1$, $0 < x_1 < 1$ [11]:

$$\int_{x_0}^{x_1} x^{p-1}(1-x)^{q-1}\,dx = \frac{x_1^p(1-x_1)^q}{p}\left[1 + \sum_{n=0}^{\infty} \frac{B(p+1,n+1)}{B(p+q,n+1)} x_1^{n+1}\right] - \frac{x_0^p(1-x_0)^q}{p}\left[1 + \sum_{n=0}^{\infty} \frac{B(p+1,n+1)}{B(p+q,n+1)} x_0^{n+1}\right] = \beta r K^{\alpha-1} t. \tag{8}$$

Eq. (8) contains an infinite series of *beta function* terms, which in turn can be expressed in terms of the *gamma function* [11]. The logistic form (1) does not in general admit an analytic solution $N(t)$ but t as a function of N. The integrand in (6) can be binomially expanded to provide, in the general case, an expression for the time to inflection, $t_{\inf}$:

$$t_{\inf} = \frac{1}{rK^{\alpha-1}}\left[\frac{\left(1+\frac{\beta\gamma}{\alpha}\right)^{(\alpha-1)/\beta}}{1-\alpha} + \gamma\frac{\left(1+\frac{\beta\gamma}{\alpha}\right)^{(\alpha-1-\beta)/\beta}}{1-\alpha+\beta} + \frac{\gamma(\gamma+1)}{2!}\frac{\left(1+\frac{\beta\gamma}{\alpha}\right)^{(\alpha-1-2\beta)/\beta}}{1-\alpha+2\beta} + \cdots\right] - \frac{1}{r}\left[\frac{N_0^{1-\alpha}}{1-\alpha} + \gamma\frac{N_0^{1-\alpha+\beta}}{K^{\beta}(1-\alpha+\beta)} + \frac{\gamma(\gamma+1)}{2!}\frac{N_0^{1-\alpha+2\beta}}{K^{2\beta}(1-\alpha+2\beta)} + \cdots\right] \quad \alpha \neq 1 \tag{9}$$

$$t_{\text{inf}} = \frac{1}{\beta r} \ln \left[\frac{(1+\beta\gamma)^{-1}}{\left(\frac{N_0}{K}\right)^{\beta}} \right] + \frac{1}{\beta r} \left[\gamma (1+\beta\gamma)^{-1} + \frac{1}{2} \frac{\gamma(\gamma+1)}{2!} (1+\beta\gamma)^{-2} + \cdots \right]$$
$$- \frac{1}{\beta r} \left[\gamma \left(\frac{N_0}{K} \right)^{\beta} + \frac{1}{2} \frac{\gamma(\gamma+1)}{2!} \left(\frac{N_0}{K} \right)^{2\beta} + \cdots \right] \quad \alpha = 1. \tag{10}$$

Fig. 1 is a display of the population size N versus time t for the generalized logistic form (1) for the following parameter values:

(i) $r = 0.1$, $N_0 = 1$, $K = 100$, $\alpha = 1$, $\beta = 3$, $\gamma = 2$.
(ii) $r = 0.5$, $N_0 = 5$, $K = 65$, $\alpha = 1$, $\beta = 0.6$, $\gamma = 1.8$.
(iii) $r = 1$, $N_0 = 0.5$, $K = 50$, $\alpha = 0.5$, $\beta = 1.5$, $\gamma = 1$.
(iv) $r = 1$, $N_0 = 0.5$, $K = 40$, $\alpha = 3$, $\beta = 0.5$, $\gamma = 3$.
(v) $r = 0.001$, $N_0 = 10$, $K = 100$, $\alpha = 2$, $\beta = -1$, $\gamma = 2$.
(vi) $r = 0.3$, $N_0 = 0.1$, $K = 30$, $\alpha = 1.5$, $\beta = 1.5$, $\gamma = 2.5$.

Figs. 2 and 3 show the growth rates with their respective maxima for the same parameters as in Fig. 1. The inflection points are at

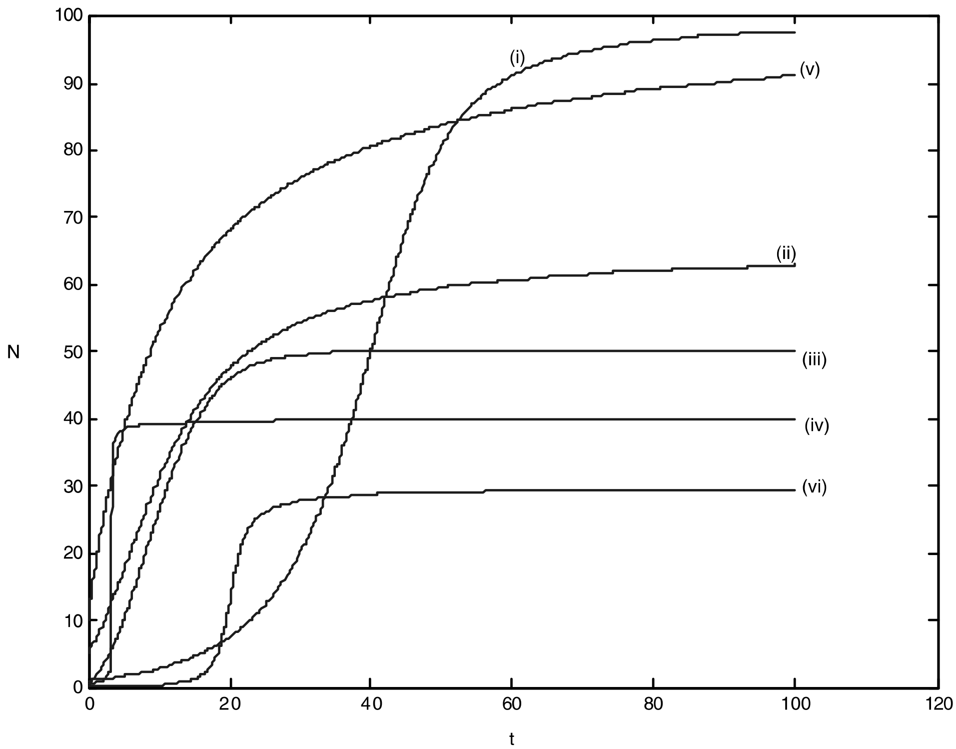

Fig. 1. The evolution of population size in time for the generalized logistic growth for the following parameter values: (i) $r = 0.1$, $N_0 = 1$, $K = 100$, $\alpha = 1$, $\beta = 3$, $\gamma = 2$; (ii) $r = 0.5$, $N_0 = 5$, $K = 65$, $\alpha = 1$, $\beta = 0.6$, $\gamma = 1.8$; (iii) $r = 1$, $N_0 = 0.5$, $K = 50$, $\alpha = 0.5$, $\beta = 1.5$, $\gamma = 1$; (iv) $r = 1$, $N_0 = 0.5$, $K = 40$, $\alpha = 3$, $\beta = 0.5$, $\gamma = 3$; (v) $r = 0.001$, $N_0 = 10$, $K = 100$, $\alpha = 2$, $\beta = -1$, $\gamma = 2$; (vi) $r = 0.3$, $N_0 = 0.1$, $K = 30$, $\alpha = 1.5$, $\beta = 1.5$, $\gamma = 2.5$.

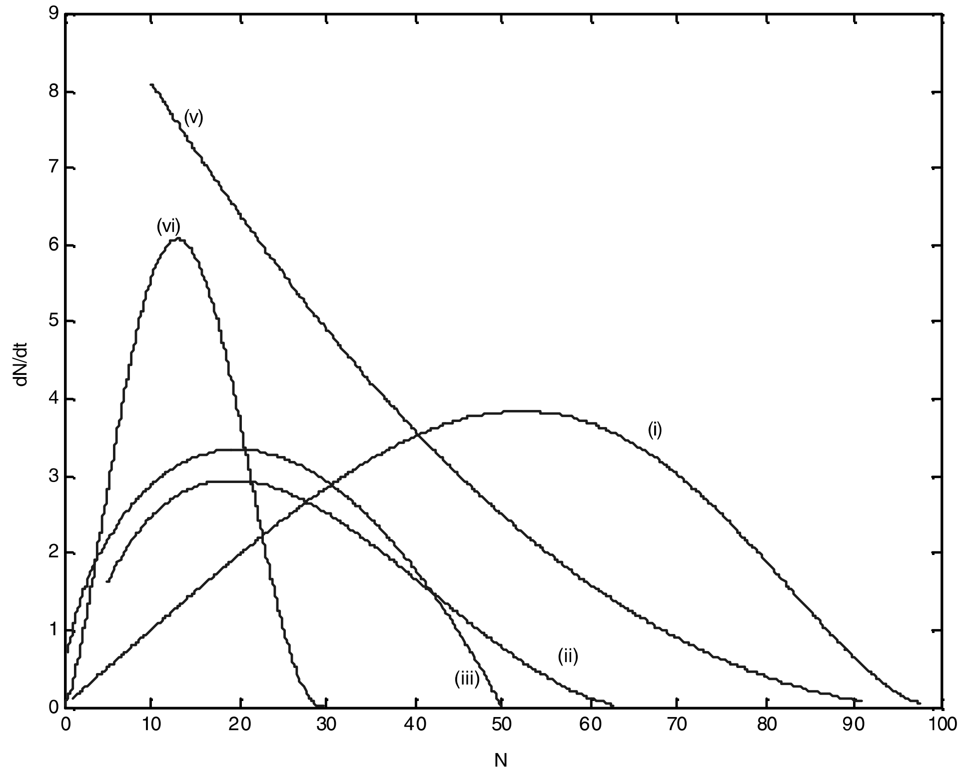

Fig. 2. Plots of the growth rate versus population size for the generalized logistic growth for the following parameter values: (i) $r = 0.1$, $N_0 = 1$, $K = 100$, $\alpha = 1$, $\beta = 3$, $\gamma = 2$; (ii) $r = 0.5$, $N_0 = 5$, $K = 65$, $\alpha = 1$, $\beta = 0.6$, $\gamma = 1.8$; (iii) $r = 1$, $N_0 = 0.5$, $K = 50$, $\alpha = 0.5$, $\beta = 1.5$, $\gamma = 1$; (v) $r = 0.001$, $N_0 = 10$, $K = 100$, $\alpha = 2$, $\beta = -1$, $\gamma = 2$; (vi) $r = 0.3$, $N_0 = 0.1$, $K = 30$, $\alpha = 1.5$, $\beta = 1.5$, $\gamma = 2.5$.

(i) $N_{\text{inf}} \approx 52.31$.
(ii) $N_{\text{inf}} \approx 19.19$.
(iii) $N_{\text{inf}} \approx 20$.
(iv) $N_{\text{inf}} \approx 17.77$.
(v) $N_{\text{inf}} = 0 < N_0 = 10$ (no inflection).
(vi) $N_{\text{inf}} \approx 13$.

Figs. 4 and 5 depict the variation of the relative growth rate versus population. In Fig. 4 cases (i)–(iii) and (v) are illustrated with no N^*. In Fig. 5 cases (iv) and (vi) are illustrated with $N^* \approx 13.06 > N_0 = 0.5$ and $N^* \approx 7.21 > N_0 = 0.1$ respectively.

3. Logistic growth curve and extensions

In this section we revisit some well known growth forms in chronological order and prove that that they can all be deduced from (1). In addition, we establish the existence of the sigmoidal

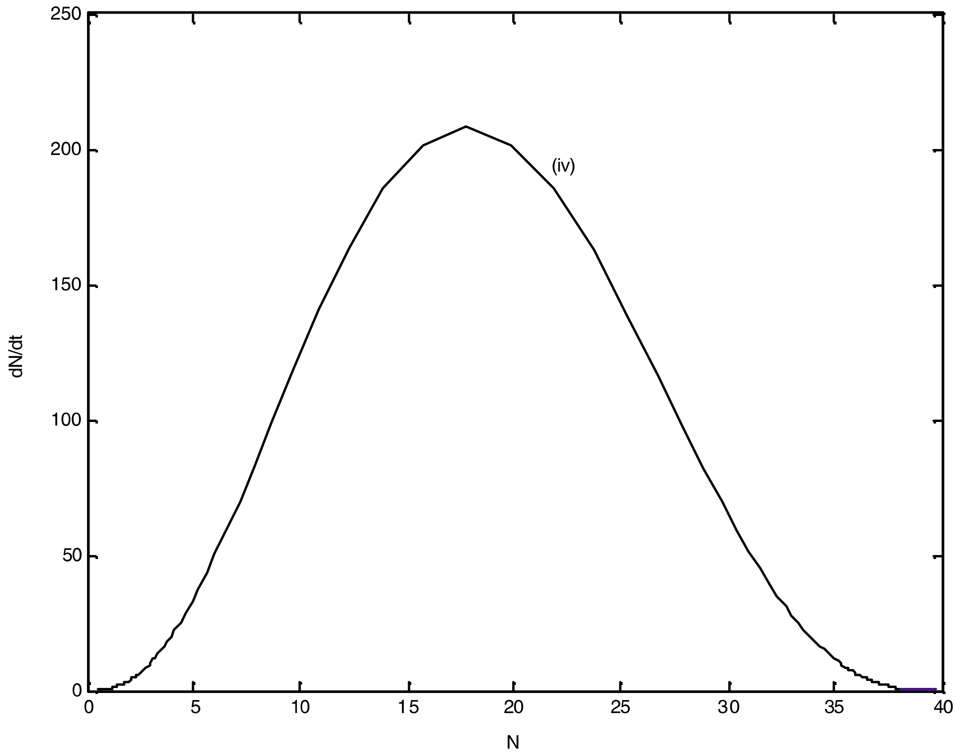

Fig. 3. Plots of the growth rate versus population size for the generalized logistic growth for the following parameter values: (iv) $r = 1$, $N_0 = 0.5$, $K = 40$, $\alpha = 3$, $\beta = 0.5$, $\gamma = 3$.

feature that characterizes most growth curves and is responsible for the existence of an inflection point, where present, and undertake an analysis of this appropriately.

Since the original work of Verhulst [1] and Pearl and Reed [12] there have been several contributions suggesting alternative functional forms, $f(N)$, for growth whilst retaining the sigmoidal and asymptotic property of the Verhulst logistic curve. In the plant sciences, Richards [13] was the first to apply a growth equation developed by Von Bertalanffy [14] to describe the growth of animals. Richards growth curve was used for fitting experimental data by Nelder [10], who introduced the term *generalized logistic equation* to describe the equation. Blumberg [15] introduced the *hyperlogistic equation* as a generalization of Richards equation. Turner et al. [16,17] suggested a further generalization of the logistic growth and termed their equation *the generic logistic equation*. In a more recent survey paper Buis [18] revisited several previous logistic growth derived functions that have been introduced and outlined some of their respective properties.

3.1. The logistic growth

The simplest realistic model of population dynamics is the one with exponential growth

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN$$

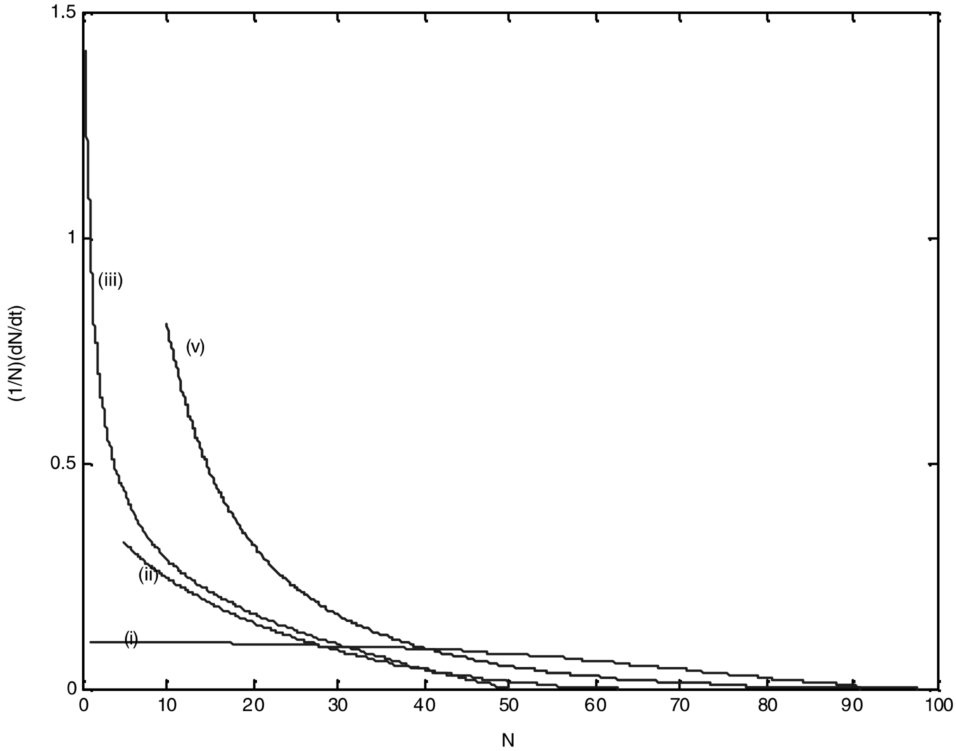

Fig. 4. Relative growth rate plot versus N for the following parameter values: (i) $r = 0.1, N_0 = 1, K = 100, \alpha = 1, \beta = 3, \gamma = 2$; (ii) $r = 0.5, N_0 = 5, K = 65, \alpha = 1, \beta = 0.6, \gamma = 1.8$; (iii) $r = 1, N_0 = 0.5, K = 50, \alpha = 0.5, \beta = 1.5, \gamma = 1$; (v) $r = 0.001, N_0 = 10, K = 100, \alpha = 2, \beta = -1, \gamma = 2$.

with solution

$$N(t) = N_0 e^{rt},$$

where r is the *intrinsic growth rate* and represents growth rate per capita. To remove unrestricted growth Verhulst [1] considered that a stable population would have a saturation level characteristic of the environment. To achieve this the exponential model was augmented by a multiplicative factor, $1 - (N/K)$, which represents the fractional deficiency of the current size from the saturation level, K

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right). \tag{11}$$

The Verhulst logistic equation is also referred to in the literature as the Verhulst–Pearl equation after Verhulst, who first introduced the curve, and Pearl [12], who used the curve to approximate population growth in the United States in 1920.

Eq. (11) has solution

$$N(t) = \frac{KN_0}{(K - N_0)e^{-rt} + N_0}, \tag{12}$$

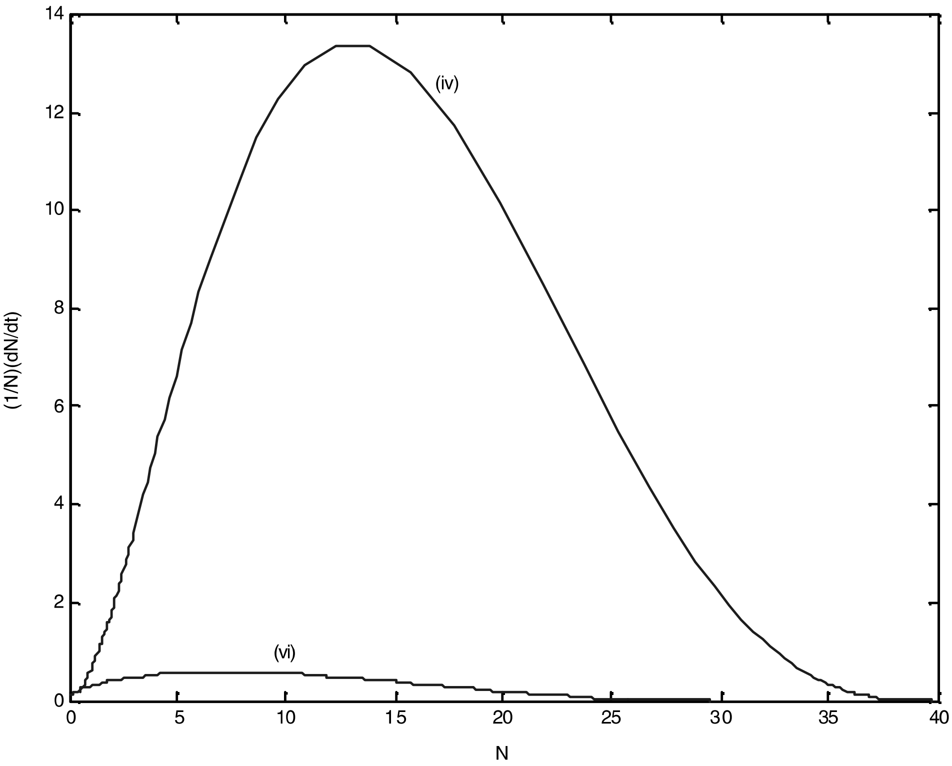

Fig. 5. Relative growth rate plot versus N for the following parameter values: (iv) $r = 1$, $N_0 = 0.5$, $K = 40$, $\alpha = 3$, $\beta = 0.5$, $\gamma = 3$; (vi) $r = 0.3$, $N_0 = 0.1$, $K = 30$, $\alpha = 1.5$, $\beta = 1.5$, $\gamma = 2.5$.

where N_0 is the population size at time $t = 0$.

The three key features of the logistic growth are

(i) $\lim_{t\to\infty} N(t) = K$, the population will ultimately reach its carrying capacity.
(ii) The relative growth rate, $(1/N)(\mathrm{d}N/\mathrm{d}t)$, declines linearly (no maximum) with increasing population size and reaches its zero minimum at $N = K$.
(iii) The population at the inflection point (where growth rate is maximum), N_{inf}, is exactly half the carrying capacity, $N_{\mathrm{inf}} = K/2$, and the maximum growth rate is $(\mathrm{d}N/\mathrm{d}t)_{\max} = rK/4$.

For $r > 0$, the resulting growth curve has a sigmoidal shape and, from (12), is asymptotic to the carrying capacity. In the trivial case of no intrinsic growth rate, $r = 0$, the population remains static at the initial value of N_0. Population biologists and ecologists are interested mainly in the case where $r > 0$ and we restrict our investigations to this case in this paper. Furthermore, the population size N can assume any real positive value.

Fig. 6 depicts several logistic curves for the following parameter values:

(i) $r = 0.5$, $N_0 = 1$, $K = 50$.
(ii) $r = 0.8$, $N_0 = 10$, $K = 30$.

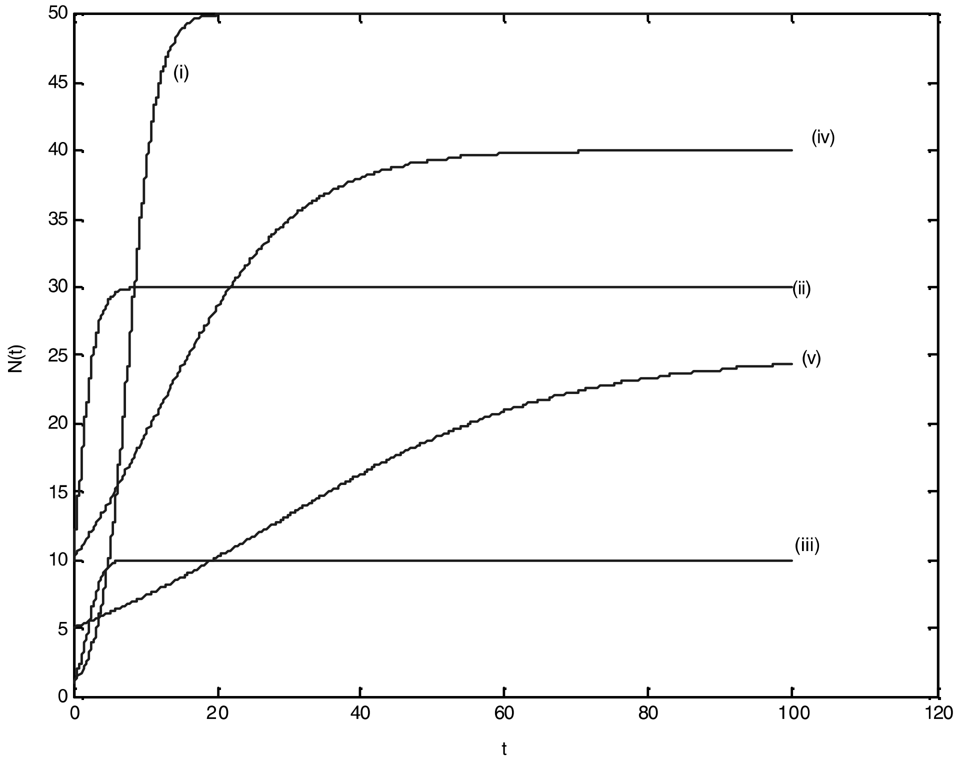

Fig. 6. Logistic growth curve $N(t)$ versus t for the following parameters: (i) $r = 0.5$, $N_0 = 1$, $K = 50$; (ii) $r = 0.8$, $N_0 = 10$, $K = 30$; (iii) $r = 1.0$, $N_0 = 1$, $K = 10$; (iv) $r = 0.1$, $N_0 = 10$, $K = 40$; (v) $r = 0.05$, $N_0 = 5$, $K = 25$.

(iii) $r = 1.0$, $N_0 = 1$, $K = 10$.
(iv) $r = 0.1$, $N_0 = 10$, $K = 40$.
(v) $r = 0.05$, $N_0 = 5$, $K = 25$.

Fig. 7 depicts the rate of growth versus size for the same parameters as in Fig. 6. The inflection values are respectively:

(i) $N_{\mathrm{inf}} = 25$.
(ii) $N_{\mathrm{inf}} = 15$.
(iii) $N_{\mathrm{inf}} = 5$.
(iv) $N_{\mathrm{inf}} = 20$.
(v) $N_{\mathrm{inf}} = 12.5$.

The inflection value, $N_{\mathrm{inf}} = K/2$, for the logistic growth can be derived immediately from (4) by setting $\alpha = \beta = \gamma = 1$, and the time to inflection from (10):

$$t_{\mathrm{inf}} = \frac{1}{r}\ln\left[\frac{K}{2N_0}\right] + \frac{1}{r}\ln 2 + \frac{1}{r}\ln\left[\frac{K - N_0}{K}\right] = \frac{1}{r}\ln\left[\frac{K - N_0}{N_0}\right]. \tag{13}$$

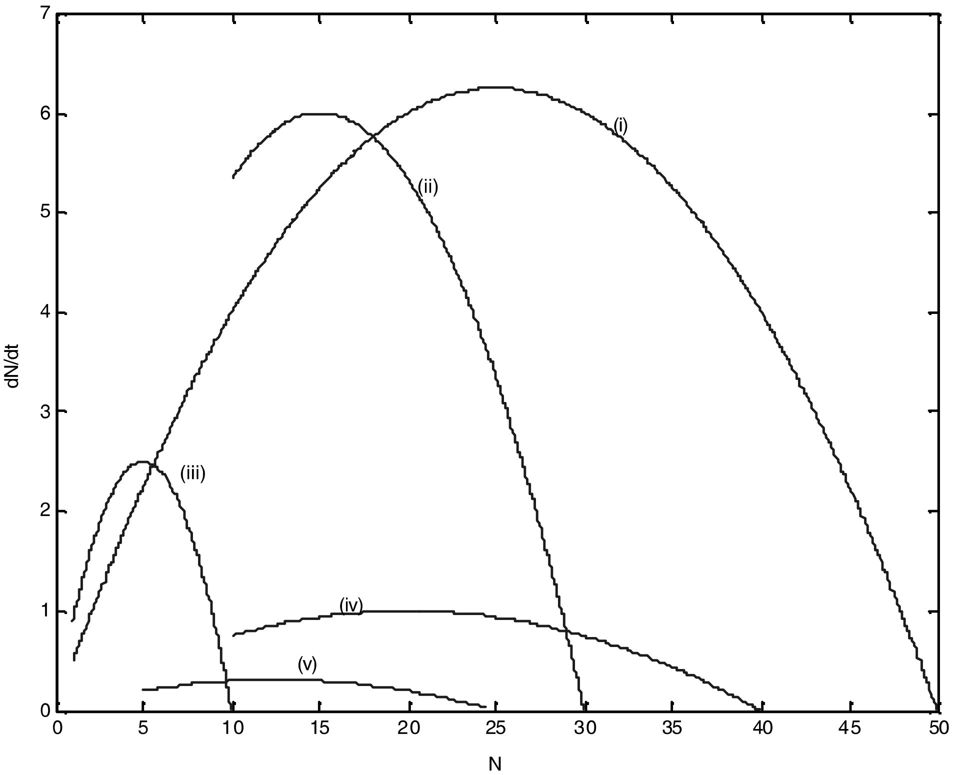

Fig. 7. Rate of logistic growth curve $\mathrm{d}N/\mathrm{d}t$ versus N for the following parameters: (i) $r = 0.5$, $N_0 = 1$, $K = 50$; (ii) $r = 0.8$, $N_0 = 10$, $K = 30$; (iii) $r = 1.0$, $N_0 = 1$, $K = 10$; (iv) $r = 0.1$, $N_0 = 10$, $K = 40$; (v) $r = 0.05$, $N_0 = 5$, $K = 25$.

3.2. Von Bertalanffy's growth equation

Von Bertalanffy [14] introduced his growth equation to model fish weight growth. Here the Verhulst logistic growth curve was modified to accommodate crude 'metabolic types' based upon physiological reasoning. He proposed the form given below which can be seen to be a special case of the Bernoulli differential equation, namely:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN^{2/3}\left[1 - \left(\frac{N}{K}\right)^{1/3}\right] \tag{14}$$

which has solution

$$N(t) = K\left[1 - \left[1 - \left(\frac{N_0}{K}\right)^{1/3}\right]\mathrm{e}^{-(rt/3K^{1/3})}\right]^3. \tag{15}$$

Here, N_{inf} is given by

$$N_{\mathrm{inf}} = \frac{8}{27}K. \tag{16}$$

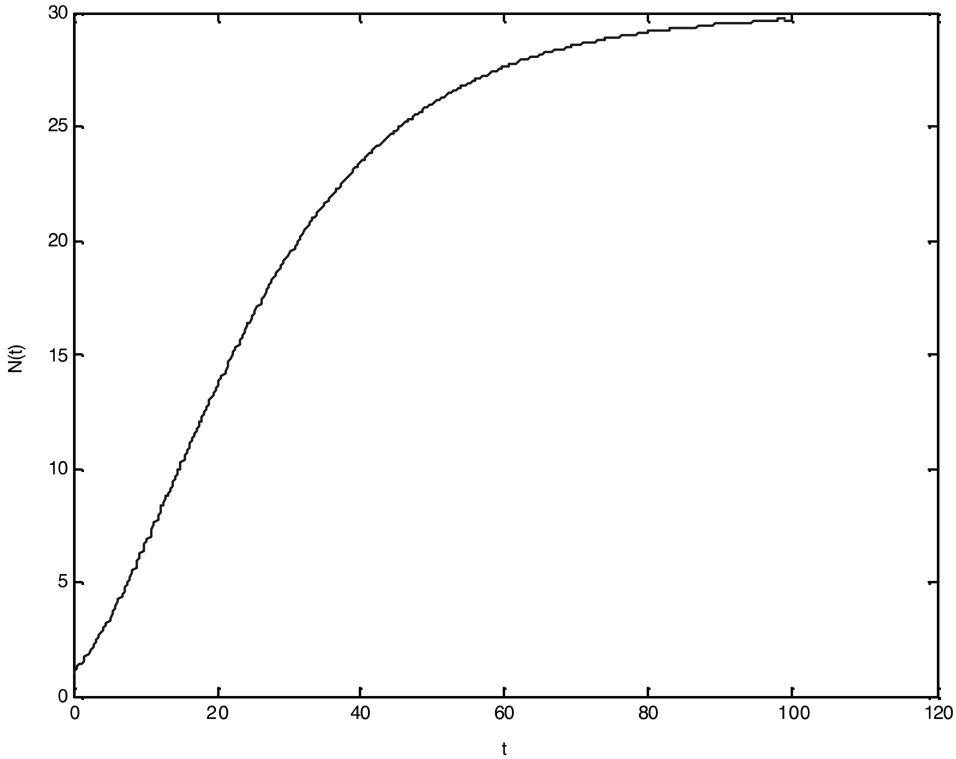

Fig. 8. Von Bertalanffy's weight curve in time t. The parameters are $r = 0.5$, $N_0 = 1$, $K = 30$.

The Bertalanffy form derives from the generalized form (1) with $\alpha = 2/3$, $\beta = 1/3$, $\gamma = 1$. The time to inflection is found from (9):

$$t_{\mathrm{inf}} = -\frac{3K^{1/3}}{r}\ln\left(\frac{1}{3}\right) + \frac{3K^{1/3}}{r}\ln\left[1 - \left(\frac{N_0}{K}\right)^{1/3}\right] = \frac{3K^{1/3}}{r}\ln\left[3\left(1 - \left(\frac{N_0}{K}\right)^{1/3}\right)\right] \tag{17}$$

and the maximum growth rate from (5):

$$\left(\frac{\mathrm{d}N}{\mathrm{d}t}\right)_{\max} = \frac{4}{27} r K^{2/3}. \tag{18}$$

Von Bertalanffy's form does not admit a real-valued N^* as the relative growth rate declines nonlinearly with increasing N.

Figs. 8 and 9 display respectively a typical Von Bertalanffy weight growth curve and its associated inflection point. The parameters are $r = 0.5$, $N_0 = 1$, $K = 30$. Inflection occurs at approximately $N_{\mathrm{inf}} \approx 8.9$ and at time $t_{\mathrm{inf}} \approx 13.23$.

3.3. Richards growth equation

Richards extended the growth equation developed by Von Bertalanffy to fit empirical plant data [13]. Richards suggestion was to use the following equation which is also a special case of the Bernoulli differential equation:

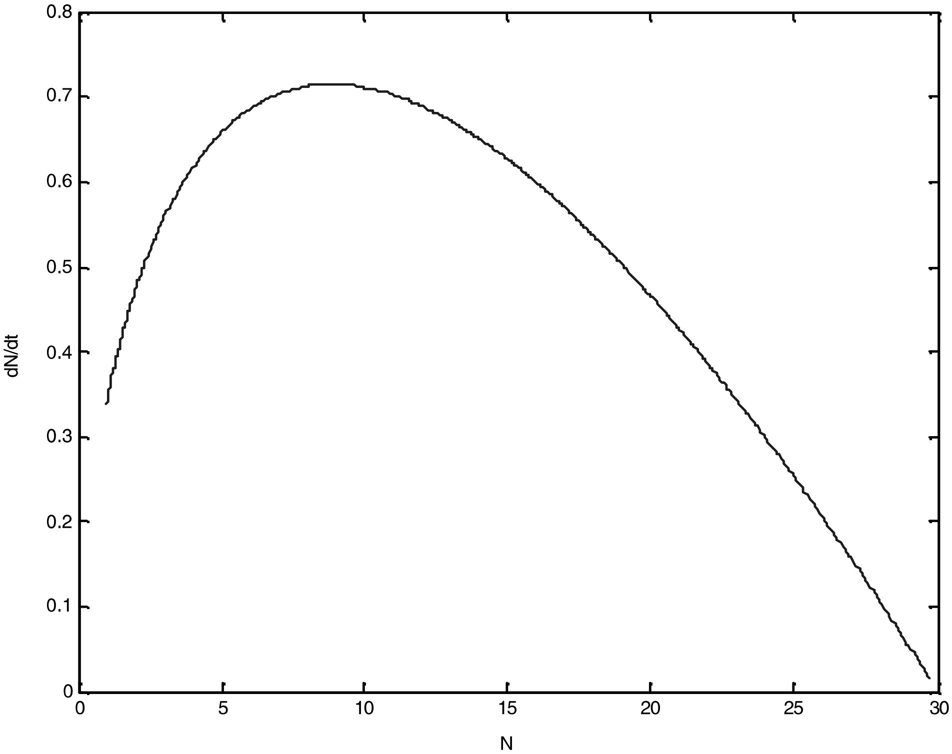

Fig. 9. Von Bertalanffy's rate of weight growth versus weight curve. The parameters are $r = 0.5$, $N_0 = 1$, $K = 30$.

$$\frac{dN}{dt} = rN\left[1 - \left(\frac{N}{K}\right)^{\beta}\right]. \tag{19}$$

This has the solution,

$$N(t) = \frac{N_0 K}{\left[N_0^{\beta} + (K^{\beta} - N_0^{\beta})e^{-\beta r t}\right]^{1/\beta}}. \tag{20}$$

Here inflection occurs at

$$N_{\mathrm{inf}} = \left(\frac{1}{1+\beta}\right)^{1/\beta} K. \tag{21}$$

Richards form is readily deduced from (1) with $\alpha = \gamma = 1$. For $\beta = 1$, (19) trivially reduces to the Verhulst logistic growth equation (11) and similarly exhibits the same inflexible inflection point value, and for $\beta = 0$ reduces to exponential growth. Dividing (19) by β produces the Gompertz growth as $\beta \to 0$, and the monomolecular or Mitscherlich growth form for $\beta = -1$ (no inflection). For $\beta < -1$, N_{inf} is undefined. The time to inflection is obtained from (10):

$$
\begin{aligned}
t_{\inf} &= \frac{1}{\beta r}\ln\left[\frac{K^{\beta}}{(1+\beta)N_0^{\beta}}\right] - \frac{1}{\beta r}\ln\left[\frac{\beta}{1+\beta}\right] + \frac{1}{\beta r}\ln\left[1-\left(\frac{N_0}{K}\right)^{\beta}\right] \\
&= \frac{1}{\beta r}\ln\left[\frac{1}{\beta}\left(\left(\frac{K}{N_0}\right)^{\beta}-1\right)\right].
\end{aligned}
\tag{22}
$$

For extreme values of β we obtain the following values for $N_{\inf}$:

$$\lim_{\beta\to 0} N_{\inf} = K\,\mathrm{e}^{-1}$$

$$\lim_{\beta\to\infty} N_{\inf} = K.$$

The maximum growth rate is found from (5):

$$\left(\frac{\mathrm{d}N}{\mathrm{d}t}\right)_{\max} = \frac{rK\beta}{(1+\beta)^{1+(1/\beta)}}. \tag{23}$$

Richards form does not admit a real-valued N^* as the relative growth rate declines non-linearly with increasing N.

Fig. 10 illustrates five different Richards growth curves with:

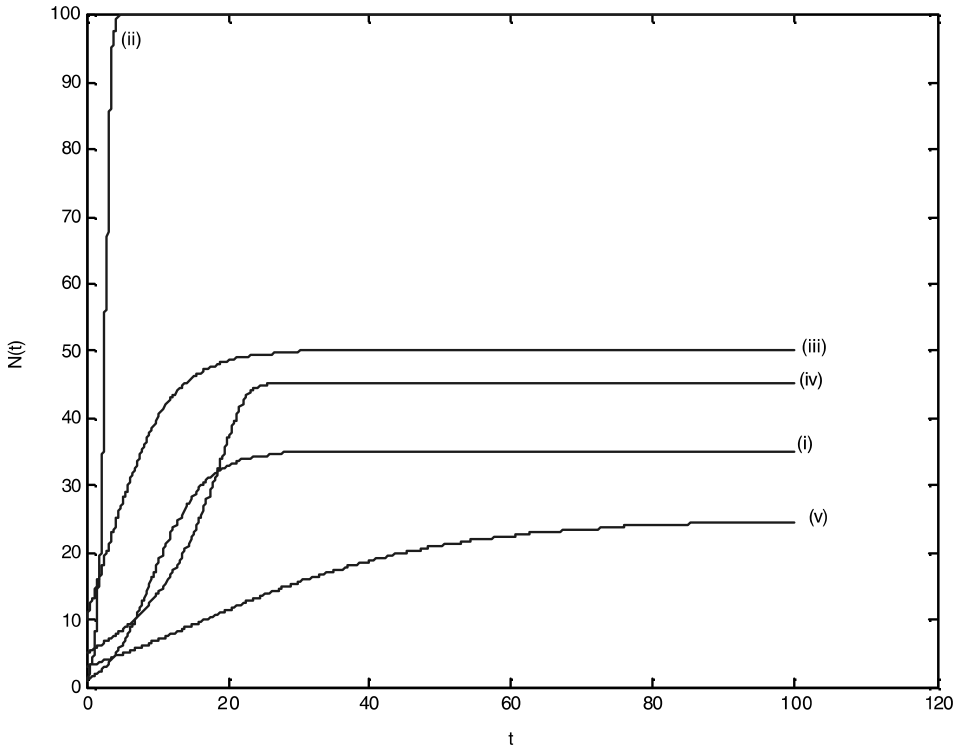

Fig. 10. Richards's curve for the following parameters: (i) $r = 0.5$, $\beta = 0.5$, $N_0 = 1$, $K = 35$; (ii) $r = 1.5$, $\beta = 2.0$, $N_0 = 1$, $K = 100$; (iii) $r = 2.0$, $\beta = 0.1$, $N_0 = 10$, $K = 50$; (iv) $r = 0.1$, $\beta = 10$, $N_0 = 5$, $K = 45$; (v) $r = 5$, $\beta = 0.01$, $N_0 = 3$, $K = 25$.

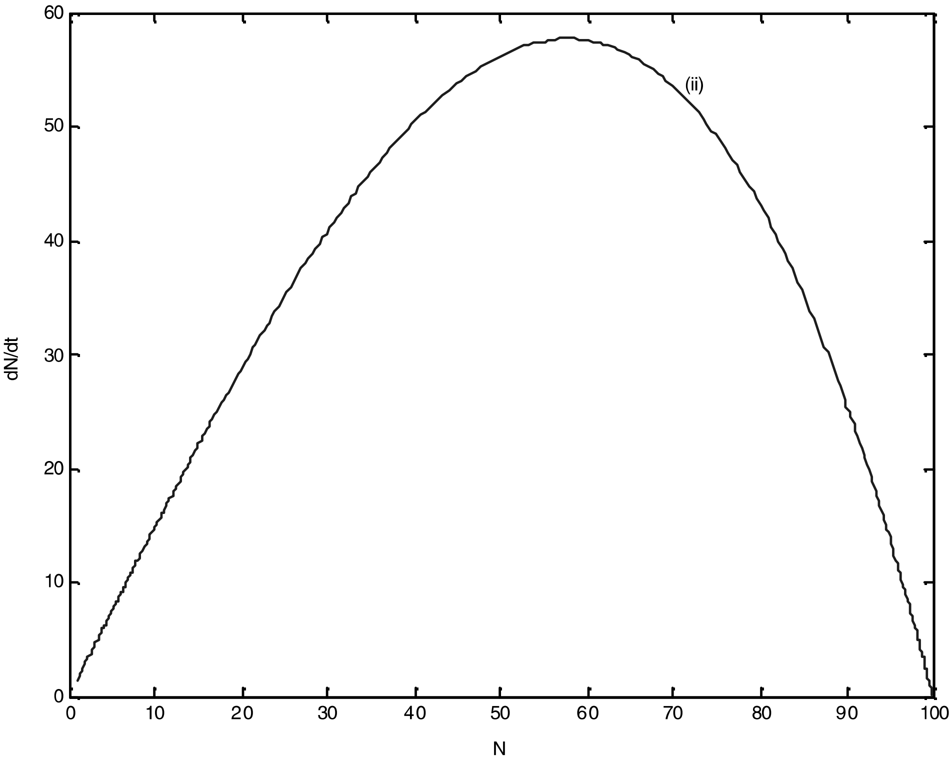

Fig. 11. Richards's rate of growth versus size for case (ii) $r = 1.5$, $\beta = 2.0$, $N_0 = 1$, $K = 100$.

(i) $r = 0.5$, $\beta = 0.5$, $N_0 = 1$, $K = 35$.
(ii) $r = 1.5$, $\beta = 2.0$, $N_0 = 1$, $K = 100$.
(iii) $r = 2.0$, $\beta = 0.1$, $N_0 = 10$, $K = 50$.
(iv) $r = 0.1$, $\beta = 10$, $N_0 = 5$, $K = 45$.
(v) $r = 5$, $\beta = 0.01$, $N_0 = 3$, $K = 25$.

Fig. 11 displays the variation of the weight growth rate for case (ii) and Fig. 12 for cases (i), (iii), (iv), (v). Inflection occurs at

(i) $N_{\text{inf}} \approx 15.55$.
(ii) $N_{\text{inf}} \approx 57.73$.
(iii) $N_{\text{inf}} \approx 19.28$.
(iv) $N_{\text{inf}} \approx 35.40$.
(v) $N_{\text{inf}} \approx 9.24$ (near the limit of $K/e \approx 9.225$).

3.4. Smith's equation

Smith [19] reported that the Verhulst logistic growth equation did not fit experimental data satisfactorily due to problems associated with time lags. Time lags in the effects of density upon

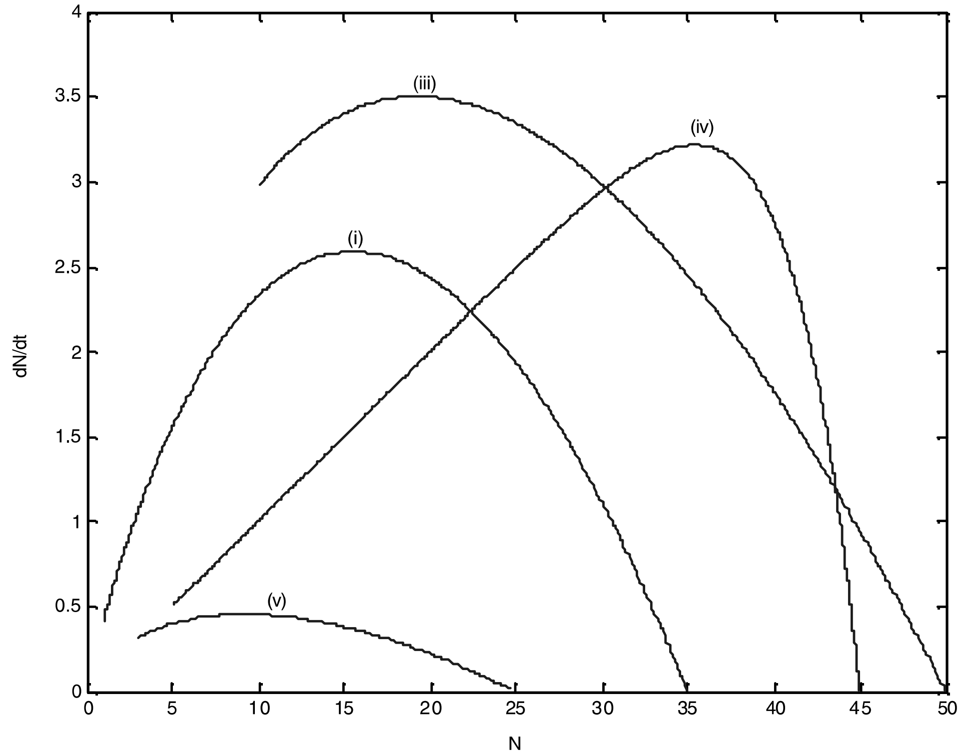

Fig. 12. Richards's rate of growth versus size for cases: (i) $r = 0.5$, $\beta = 0.5$, $N_0 = 1$, $K = 35$; (iii) $r = 2.0$, $\beta = 0.1$, $N_0 = 10$, $K = 50$; (iv) $r = 0.1$, $\beta = 10$, $N_0 = 5$, $K = 45$; (v) $r = 5$, $\beta = 0.01$, $N_0 = 3$, $K = 25$.

natality and mortality distort the shape of the population growth curve. According to Smith, the major problem in applying the logistic to data concerns an accurate portrayal of the portion of the limiting factor as yet unutilized, that is, $1 - (N/K)$. He then argued that for a food-limited population the term $1 - (N/K)$ should be replaced with a term representing the proportion of the rate of food supply currently unutilized by the population. If F is the rate at which a population of size N uses food and T is the corresponding rate at saturation level, then

$$\frac{1}{N}\frac{\mathrm{d}N}{\mathrm{d}t} = r\left(1 - \frac{F}{T}\right),$$

where $(F/T) > (N/K)$, since a growing population will use food faster than a saturated population. F must depend on N and $\mathrm{d}N/\mathrm{d}t$, and the simplest relationship will be linear

$$F = aN + b\frac{\mathrm{d}N}{\mathrm{d}t}, \quad a > 0, \;\; b > 0.$$

At saturation $F = T$, $N = K$, $\mathrm{d}N/\mathrm{d}t = 0$, hence $T = aK$, and as a result the modified growth equation is now

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\left(\frac{1 - \frac{N}{K}}{1 + c\frac{N}{K}}\right), \tag{24}$$

where $c = rb/a$. Differential equation (24) is the Verhulst logistic growth scaled by the 'delaying' factor $(1 + c(N/K))^{-1}$ and does not admit an analytical solution for N as a function of t, but rather the other way round

$$t = \frac{1}{r}\ln\left[\frac{(K - N_0)^{1+c}}{N_0}\right] + \frac{1}{r}\ln\left[\frac{N}{(K - N)^{1+c}}\right]. \tag{25}$$

The inflection value for Smith's equation is

$$N_{\text{inf}} = \frac{K}{1 + \sqrt{1 + c}}. \tag{26}$$

For $c = 0$ Smith's form reduces to the Verhulst logistic growth form with $N_{\text{inf}} = K/2$, whereas for $c > 0$, $N_{\text{inf}} < K/2$ and for $c < 0$, $N_{\text{inf}} > K/2$. For $c = -1$, the growth is exponential, $\mathrm{d}N/\mathrm{d}t = rN$, and there is no inflection point.

The maximum growth rate, when $c \neq -1$, is given by

$$\left(\frac{\mathrm{d}N}{\mathrm{d}t}\right)_{\max} = \frac{rK}{(1 + \sqrt{c + 1})^2}. \tag{27}$$

The relative growth rate, $(1/N)(\mathrm{d}N/\mathrm{d}t)$, decreases non-linearly with increasing N for $c > -1$, with the rate of decrease being regulated by the parameter c.

Smith in his paper gave values $r = 0.44$, $c = 3.46$, $N_0 = 1.875$, $K = 15$. The inflection point for this set of values is at $N_{\text{inf}} \approx 4.82$, the maximum growth rate is $(\mathrm{d}N/\mathrm{d}t)_{\max} \approx 0.68$, and the time to inflection is $t_{\text{inf}} \approx 4.72$.

Smith's form (24) does not derive immediately from the generalized form (1) but rather as an approximation to (1) by judicious selection of the values of the parameters α, β, γ. We shall see that only two of the parameters needs to be determined numerically with the other one retaining the unit value. When the appropriate parameter has been determined the rate of growth per capita, r', will be determined for the generalized logistic growth using the original data provided by Smith. We start by comparing the formulae (4) and (26) for the inflection value

$$\frac{1}{1 + \sqrt{c + 1}} = \left(\frac{\alpha}{\alpha + \beta\gamma}\right)^{1/\beta}.$$

If we now set $\beta = 1$, then we have

$$\alpha = \frac{\gamma}{\sqrt{c + 1}}. \tag{28}$$

Next let $f(r', \alpha, N)$ and $g(r, c, N)$ denote the functional forms (1) and (24) respectively, and $h(r', \alpha, N) = |f(r', \alpha, N) - g(r, c, N)|$. r' is the intrinsic growth parameter for the generalized logistic form (1). Then determine $\hat{r}'$ and $\hat{\alpha}$, such that

$$\hat{h}(\hat{r}', \hat{\alpha}) = \min_{\alpha, r'} \max_{N} h(r', \alpha, N).$$

Specifically, first the maximum (worst) deviation, $\hat{h}(\hat{N}(r', \alpha))$, is identified in the range $[N_0, K]$ and subsequently the minimization of $\hat{h}(\hat{N}(r', \alpha))$ with respect to α, r' yields those $\hat{\alpha}$, $\hat{r}'$ that produce the least deviation. For the purpose of visualization we plot $h(r', \alpha, N)$ as a surface with respect to N, α

and allow r' to be dependent parameter. Since we want the generalized logistic curve to start at an initial growth rate identical to Smith's growth rate, r' will be determined according to the formula

$$r' = \frac{0.44 \times 1.875\left(1 - \frac{1.875}{15}\right)}{\left(1 + 3.46\frac{1.875}{15}\right)1.875^{\alpha}\left(1 - \frac{1.875}{15}\right)^{\gamma}},$$

where $\gamma = \alpha\sqrt{4.46}$. If α varies in the range $[0.1, 1.0]$ for example, then r' can take values in the range $[0.35, 0.48]$. Fig. 13 displays two surfaces for two values of r': (i) $r' = 0.4$, (ii) $r' = 0.5$.

From the surface plots of Fig. 13 it is seen that $\hat{r}' = 0.4$ results in a smaller $h(N, \alpha)$, and for $\hat{\alpha} \approx 0.45$, $h(r', \alpha, N)$ attains its minimax values, $\hat{h}(\hat{r}', \hat{\alpha})$, along the saddle curve. Since r', in this case, can take values in a narrow range more refined simulations allow to obtain the more accurate values $\hat{r}' = 0.413$, $\hat{\alpha} = 0.473$. As a result $\hat{\gamma} = 0.473\sqrt{4.46} \approx 1.0$. The time to inflection for the generalized logistic is derived from (9), $t_{\mathrm{inf}} \approx 5.20$ (compared with $t_{\mathrm{inf}} \approx 4.72$ for the equivalent Smith curve) after some rounding off. We now have the generalized logistic form

$$\frac{dN}{dt} = 0.413N^{0.473}\left(1 - \frac{N}{15}\right), \quad N_0 = 1.875,$$

which fits the Smith curve very closely as illustrated in the Fig. 14:

Very close fits are also depicted in Fig. 15 for three different cases with $r = 0.44$, $N_0 = 1.875$, $K = 15$ for Smith's curve and the following values for the parameter c and the generalized logistic growth parameters α and r' (α is calculated readily from (28)):

(i) $c = 1$, $r' \approx 0.473$, $\alpha \approx 0.706$.
(ii) $c = 5$, $r' \approx 0.39$, $\alpha \approx 0.41$.
(iii) $c = -0.5$, $r' \approx 0.36$, $\alpha \approx 1.414$.

As a general rule, a range of values of α can be obtained by utilizing the fact that Smith's form does not allow for a positive N^*, the population size at which the relative growth rate is maximum, since the relative growth rate declines non-linearly with rising N when $c > -1$. From (2) we observe that for this to occur we must have

$$\alpha < 1$$
$$\beta\gamma > 1 - \alpha.$$

Setting $\beta = 1$ and $\gamma = \alpha\sqrt{c+1}$ from (28) we arrive at the following range:

$$\frac{\sqrt{c+1} - 1}{c} = \frac{N_{\mathrm{inf}}}{K} < \alpha < 1. \tag{29}$$

For $c = 3.46$ the range is $0.32 < \alpha < 1$, for $c = 1$ the range is $0.414 < \alpha < 1$, and for $c = 5$ the range is $0.29 < \alpha < 1$ (the latter two cases are confirmed by Fig. 15).

3.5. Blumberg's equation

Blumberg [15] introduced another growth equation based on a modification of the Verhulst logistic growth equation to model population dynamics or organ size evolution. Blumberg observed that the major limitation of the logistic curve was the inflexibility of the inflection point. He

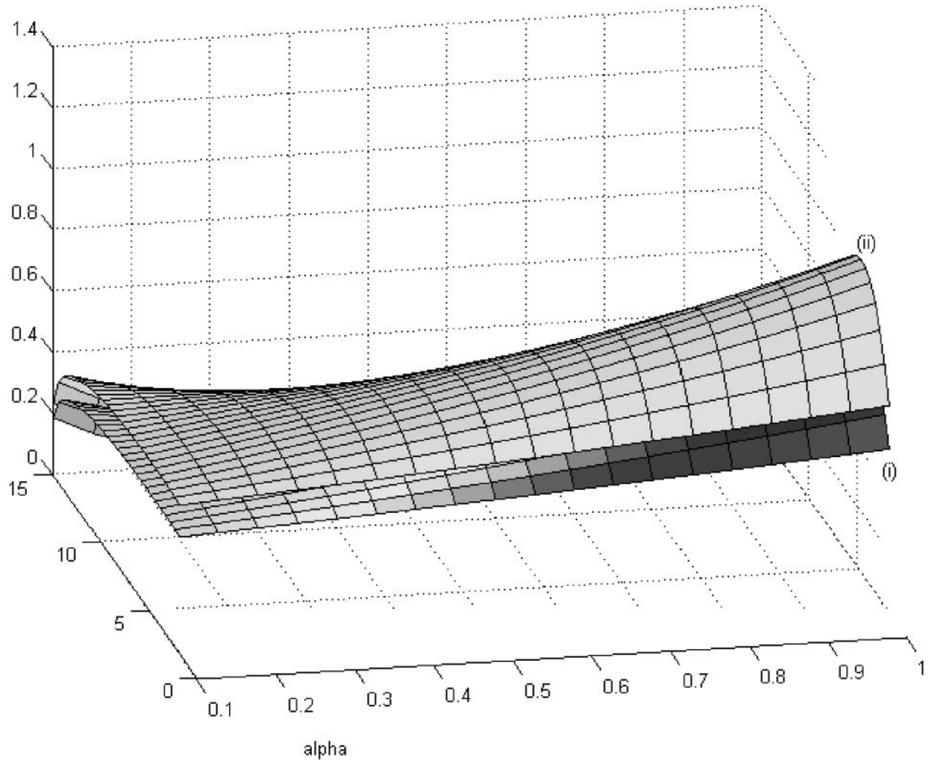

Fig. 13. Surface plots of $h(r', \alpha, N)$ against α, N for (i) $r' = 0.4$, (ii) $r' = 0.5$.

further observed that attempts to modify the constant intrinsic growth rate term, r, treating this as a time-dependent polynomial to overcome this limitation, often leads to under estimation of future values (see also [20]). Blumberg therefore introduced what he called the hyperlogistic function, accordingly,

$$\frac{dN}{dt} = rN^{\alpha}\left(1 - \frac{N}{K}\right)^{\gamma}. \tag{30}$$

Eq. (30) can be re-formulated as the integral equation

$$\int_{N_0/K}^{N(t)/K} x^{-\alpha}(1-x)^{-\gamma}\,dx = rK^{\alpha-1}t.$$

This does not always afford a closed form analytical solution (for $\alpha < 1$, $\gamma < 1$ it is again the incomplete beta function and can be expressed as in (8)). Blumberg therefore catalogued analytic expressions (when an explicit integration can be carried out) of the growth function $N(t)$ for various values of the parameters α and γ.

The population at the inflection point, N_{inf}, is given by

$$N_{\text{inf}} = \frac{\alpha}{\alpha + \gamma}K. \tag{31}$$

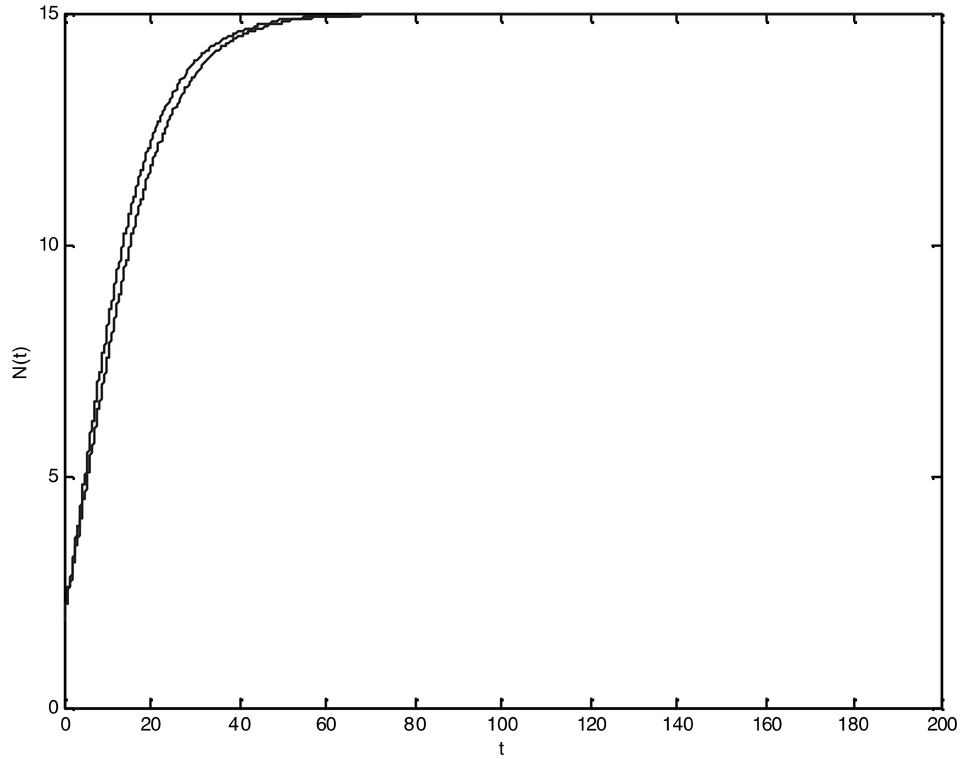

Fig. 14. Close fit of the generalized logistic $(\mathrm{d}N/\mathrm{d}t) = 0.413N^{0.473}(1-(N/15))$ with $N_0 = 1.875$, and Smith's curve $(\mathrm{d}N/\mathrm{d}t) = 0.44(N(1-(N/15))/(1+3.46(N/15)))$ with $N_0 = 1.875$.

This also coincides with that of the Verhulst logistic equation when $\alpha = \gamma$. For $\alpha \gg \gamma$ the inflection occurs very near the carrying capacity, and for $\alpha \ll \gamma$, N_{inf} approaches 0 and inflection occurs only if $N_0 < N_{\mathrm{inf}}$.

Eq. (30) is obtained from (1) by setting $\beta = 1$. The time to inflection is calculated from (9) when $\alpha \neq 1$:

$$\begin{aligned} t_{\mathrm{inf}} = {} & \frac{1}{rK^{\alpha-1}}\left[\frac{\left(1+\frac{\gamma}{\alpha}\right)^{\alpha-1}}{1-\alpha} + \gamma\frac{\left(1+\frac{\gamma}{\alpha}\right)^{\alpha-2}}{2-\alpha} + \frac{\gamma(\gamma+1)}{2!}\frac{\left(1+\frac{\gamma}{\alpha}\right)^{\alpha-3}}{3-\alpha} + \cdots\right] \\ & - \frac{1}{r}\left[\frac{N_0^{1-\alpha}}{1-\alpha} + \gamma\frac{N_0^{2-\alpha}}{K(2-\alpha)} + \frac{\gamma(\gamma+1)}{2!}\frac{N_0^{3-\alpha}}{K^2(3-\alpha)} + \cdots\right] \end{aligned} \tag{32}$$

and from (10) when $\alpha = 1$:

$$\begin{aligned} t_{\mathrm{inf}} = {} & \frac{1}{r}\ln\left[\frac{K}{N_0(1+\gamma)}\right] + \frac{1}{r}\left[\frac{\gamma}{1+\gamma} + \frac{1}{2}\frac{\gamma(\gamma+1)}{2!(1+\gamma)^2} + \cdots\right] \\ & - \frac{1}{r}\left[\gamma\frac{N_0}{K} + \frac{1}{2}\frac{\gamma(\gamma+1)}{2!}\left(\frac{N_0}{K}\right)^2 + \cdots\right]. \end{aligned} \tag{33}$$

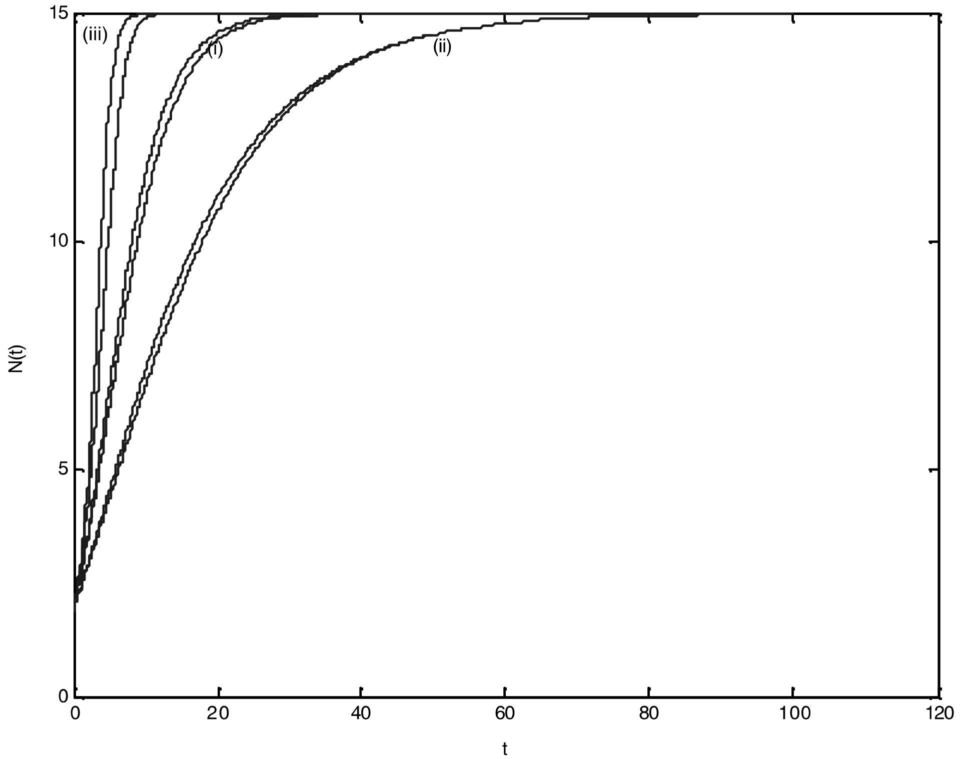

Fig. 15. Three close fits of the Smith curve and generalized logistic for $N_0 = 1.875$: (i) $dN/dt = 0.44(N(1-(N/15))/(1+(N/15)))$ and $dN/dt = 0.473N^{0.706}(1-(N/15))$; (ii) $dN/dt = 0.44(N(1-(N/15))/(1+5(N/15)))$ and $dN/dt = 0.39N^{0.41}(1-(N/15))$; (iii) $dN/dt = 0.44(N(1-(N/15))/(1-0.5(N/15)))$ and $dN/dt = 0.36N^{1.414}(1-(N/15))$.

The maximum growth rate is again determined from (5):

$$\left(\frac{dN}{dt}\right)_{\max} = rK^{\alpha}\frac{\alpha^{\alpha}\gamma^{\gamma}}{(\alpha+\gamma)^{\alpha+\gamma}} \tag{34}$$

The relative growth rate attains its maximum value of

$$\left(\frac{1}{N}\frac{dN}{dt}\right)_{\max} = rK^{\alpha-1}\left(\frac{\alpha-1}{\alpha-1+\gamma}\right)^{\alpha-1}\left(\frac{\gamma}{\alpha-1+\gamma}\right)^{\gamma} \tag{35}$$

at

$$N^* = \frac{\alpha-1}{\alpha-1+\gamma}K \tag{36}$$

provided $\alpha > 1$ and $N^* > N_0$, otherwise it declines non-linearly with increasing N.

Figs. 16 and 17 exhibit respectively the population size as a function of time and the growth rate variation with population size for several values of the parameters α and γ. The parameter values are

(i) $r = 1$, $N_0 = 10$, $K = 40$, $\alpha = 0.5$, $\beta = 1$, $\gamma = 2.5$.
(ii) $r = 5$, $N_0 = 0.5$, $K = 20$, $\alpha = 1.5$, $\beta = 1$, $\gamma = 3.5$.

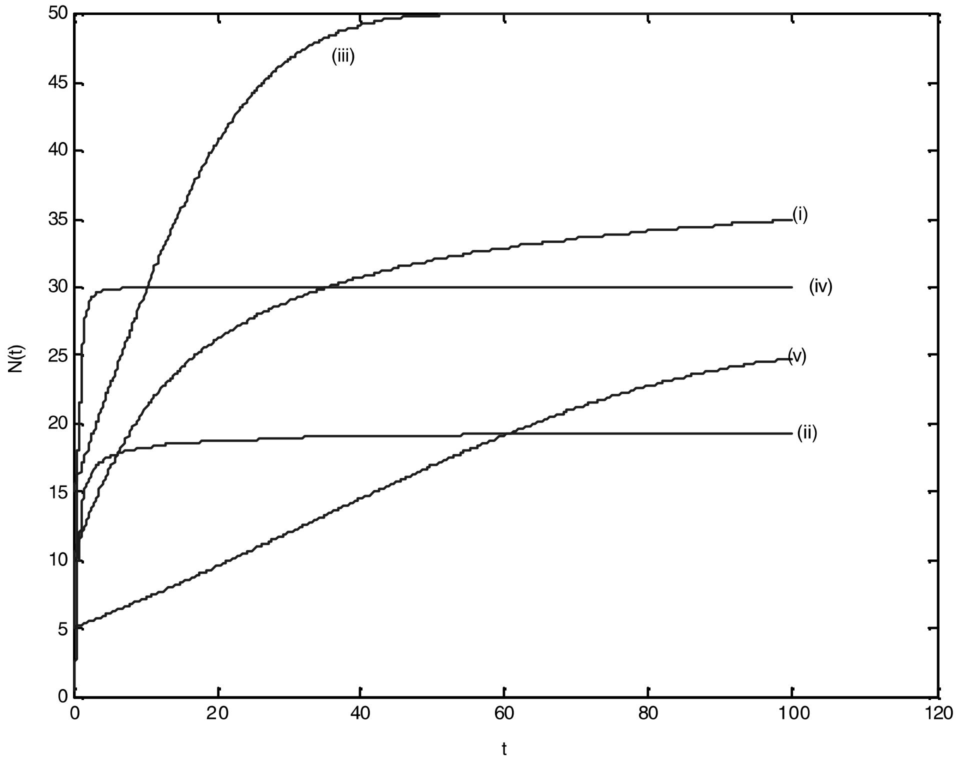

Fig. 16. Blumberg growth for parameters: (i) $r = 1$, $N_0 = 10$, $K = 40$, $\alpha = 0.5$, $\beta = 1$, $\gamma = 2.5$; (ii) $r = 5$, $N_0 = 0.5$, $K = 20$, $\alpha = 1.5$, $\beta = 1$, $\gamma = 3.5$; (iii) $r = 0.5$, $N_0 = 15$, $K = 50$, $\alpha = 0.5$, $\beta = 1$, $\gamma = 0.8$; (iv) $r = 1$, $N_0 = 5$, $K = 30$, $\alpha = 1.5$, $\beta = 1$, $\gamma = 1.5$; (v) $r = 0.1$, $N_0 = 5$, $K = 25$, $\alpha = 0.5$, $\beta = 1$, $\gamma = 0.5$.

(iii) $r = 0.5$, $N_0 = 15$, $K = 50$, $\alpha = 0.5$, $\beta = 1$, $\gamma = 0.8$.
(iv) $r = 1$, $N_0 = 5$, $K = 30$, $\alpha = 1.5$, $\beta = 1$, $\gamma = 1.5$.
(v) $r = 0.1$, $N_0 = 5$, $K = 25$, $\alpha = 0.5$, $\beta = 1$, $\gamma = 0.5$.

Inflection occurs at

(i) $N_{\text{inf}} = 6.66 < N_0 = 10$ (no inflection).
(ii) $N_{\text{inf}} = 6$.
(iii) $N_{\text{inf}} \approx 19.23$.
(iv) $N_{\text{inf}} = 15$.
(v) $N_{\text{inf}} = 12.5$.

A growth form that is of the Blumberg type is the *hyperbolic form* for regenerative growth [21]. This is represented by the sigmoid curve

$$N(t) = \frac{K(t+a)^n}{b + (t+a)^n}, \tag{37}$$

where $N(t)$ is the weight or amount, K is the final value, and a, b, n are positive parameters in the equation. Eq. (37) has differential form

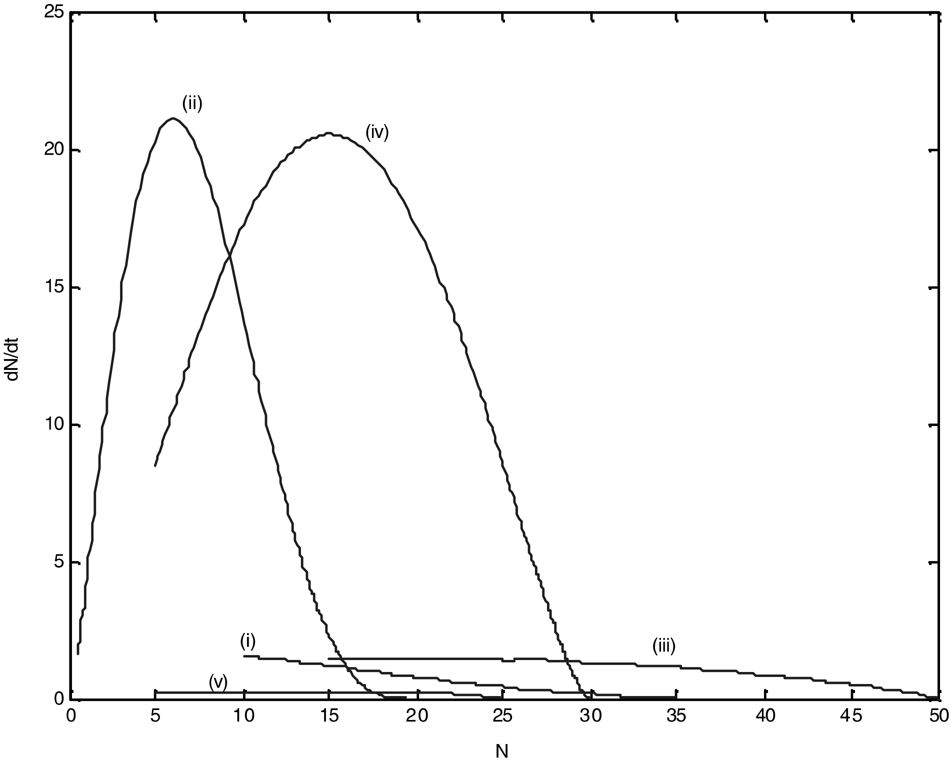

Fig. 17. Rate of growth versus size for Blumberg curve for parameters: (i) $r = 1$, $N_0 = 10$, $K = 40$, $\alpha = 0.5$, $\beta = 1$, $\gamma = 2.5$; (ii) $r = 5$, $N_0 = 0.5$, $K = 20$, $\alpha = 1.5$, $\beta = 1$, $\gamma = 3.5$; (iii) $r = 0.5$, $N_0 = 15$, $K = 50$, $\alpha = 0.5$, $\beta = 1$, $\gamma = 0.8$; (iv) $r = 1$, $N_0 = 5$, $K = 30$, $\alpha = 1.5$, $\beta = 1$, $\gamma = 1.5$; (v) $r = 0.1$, $N_0 = 5$, $K = 25$, $\alpha = 0.5$, $\beta = 1$, $\gamma = 0.5$.

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN^{1-(1/n)}\left(1 - \frac{N}{K}\right)^{1+(1/n)}, \tag{38}$$

where $r = n(K/b)^{1/n}$.

Eq. (37) derives from (1) with $\alpha = 1 - (1/n)$, $\beta = 1$, $\gamma = 1 + (1/n)$. The inflection value is identified by (4):

$$N_{\mathrm{inf}} = \frac{(n-1)}{2n}K \tag{39}$$

when $n > 1$, and the time to inflection from (9):

$$t_{\mathrm{inf}} = b^{1/n}\left[\left(\frac{n-1}{n+1}\right)^{1/n} - \left(\frac{N_0}{K - N_0}\right)^{1/n}\right], \tag{40}$$

where $N_0 = Ka^n/(b + a^n)$.

The relative growth rate declines non-linearly with increasing N since $N^* = -n < 0$ is undefined.

3.6. Generic growth function

Turner et al. [17] proposed a modified Verhulst logistic equation which they termed the generic growth function. This has the form

$$\frac{dN}{dt} = rN^{1+\beta(1-\gamma)}\left[1-\left(\frac{N}{K}\right)^{\beta}\right]^{\gamma}, \tag{41}$$

where β, γ are positive exponents and $\gamma < 1 + 1/\beta$. The solution to (41) has the following precise analytical form (only made possible by the judicious selection of the parameters):

$$N(t) = \frac{K}{\left[1+\left[(\gamma-1)\beta r K^{\beta(1-\gamma)} t + \left[\left(\frac{K}{N_0}\right)^{\beta}-1\right]^{1-\gamma}\right]^{1/(1-\gamma)}\right]^{1/\beta}}. \tag{42}$$

The population at the inflection point, N_{inf}, is given by

$$N_{\mathrm{inf}} = \left(1-\frac{\beta\gamma}{1+\beta}\right)^{1/\beta} K \tag{43}$$

and the population at the maximum relative growth rate by

$$N^* = (1-\gamma)^{1/\beta}. \tag{44}$$

The existence of both N_{inf} and N^* is ensured by the condition $\gamma < 1$. For $\beta = \gamma = 1$ the functional form for N_{inf} correctly reduces to that for the Verhulst logistic equation (11). For $\alpha = \gamma = 1$ it reduces to Richards equation (19) and for $\alpha = 2 - \gamma$, $\beta = 1$ ($\gamma < 2$) it reduces to Blumberg's form (29). Von Bertalanffy's form (14) cannot be derived from (41) however, because the values $\alpha = 2/3$, $\beta = 1/3$, $\gamma = 1$ violate the condition $\alpha = 1 + \beta(1-\gamma)$ stipulated by Turner et al.

The maximum growth rate is given by

$$\left(\frac{dN}{dt}\right)_{\max} = rK^{1+\beta(1-\gamma)}\frac{(1+\beta-\beta\gamma)^{(1-\gamma)+(1/\beta)}(\beta\gamma)^{\gamma}}{(1+\beta)^{1+(1/\beta)}} \tag{45}$$

and the maximum relative growth rate by

$$\left(\frac{1}{N}\frac{dN}{dt}\right)_{\max} = rK^{\beta(1-\gamma)}(1-\gamma)^{1-\gamma}\gamma^{\gamma}. \tag{46}$$

For extreme values of β and γ we obtain the following limits for N_{inf}:

$$\lim_{\beta\to 0} N_{\mathrm{inf}} = K\,e^{-\gamma}, \quad 0 < \gamma < \infty$$

$$\lim_{\beta\to\infty} N_{\mathrm{inf}} = K, \quad 0 < \gamma < 1$$

$$\lim_{\gamma\to 0} N_{\mathrm{inf}} = K, \quad 0 < \beta < \infty$$

$$\lim_{\gamma\to\infty} N_{\mathrm{inf}} = 0, \quad \beta \to 0.$$

The time to inflection is obtained from the formula in (9):

$$t_{\text{inf}} = \frac{1}{\beta(\gamma-1)rK^{\beta(1-\gamma)}}\left[\left(\frac{\beta\gamma}{1+\beta-\beta\gamma}\right)^{1-\gamma} - \left(\left(\frac{K}{N_0}\right)^{\beta} - 1\right)^{1-\gamma}\right]. \tag{47}$$

Fig. 18 displays several generic growth curves evolving in time t and Fig. 19 presents the growth rate versus time evolution for the following parameters:

(i) $r = 8$, $N_0 = 20$, $K = 50$, $\alpha = 0.6$, $\beta = 0.1$, $\gamma = 2$.
(ii) $r = 0.5$, $N_0 = 3$, $K = 30$, $\alpha = 1.05$, $\beta = 0.5$, $\gamma = 0.9$.
(iii) $r = 2.5$, $N_0 = 1$, $K = 10$, $\alpha = 2/3$, $\beta = 1/3$, $\gamma = 2$.
(iv) $r = 0.1$, $N_0 = 10$, $K = 20$, $\alpha = 1$, $\beta = 2$, $\gamma = 1$.

The inflection values are at

(i) $N_{\text{inf}} \approx 5.50 < N_0 = 20$ (no inflection).
(ii) $N_{\text{inf}} = 14.7$.

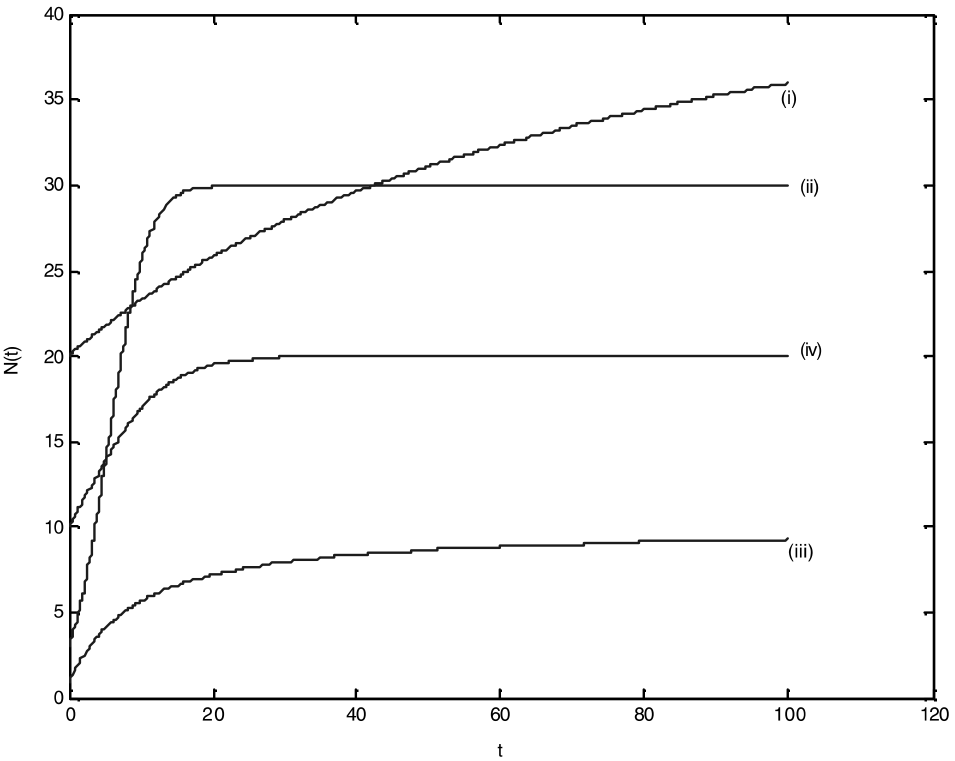

Fig. 18. Generic growth curves for the following parameters: (i) $r = 8$, $N_0 = 20$, $K = 50$, $\alpha = 0.6$, $\beta = 0.1$, $\gamma = 2$; (ii) $r = 0.5$, $N_0 = 3$, $K = 30$, $\alpha = 1.05$, $\beta = 0.5$, $\gamma = 0.9$; (iii) $r = 2.5$, $N_0 = 1$, $K = 10$, $\alpha = \frac{2}{3}$, $\beta = \frac{1}{3}$, $\gamma = 2$; (iv) $r = 0.1$, $N_0 = 10$, $K = 20$, $\alpha = 1$, $\beta = 2$, $\gamma = 1$.

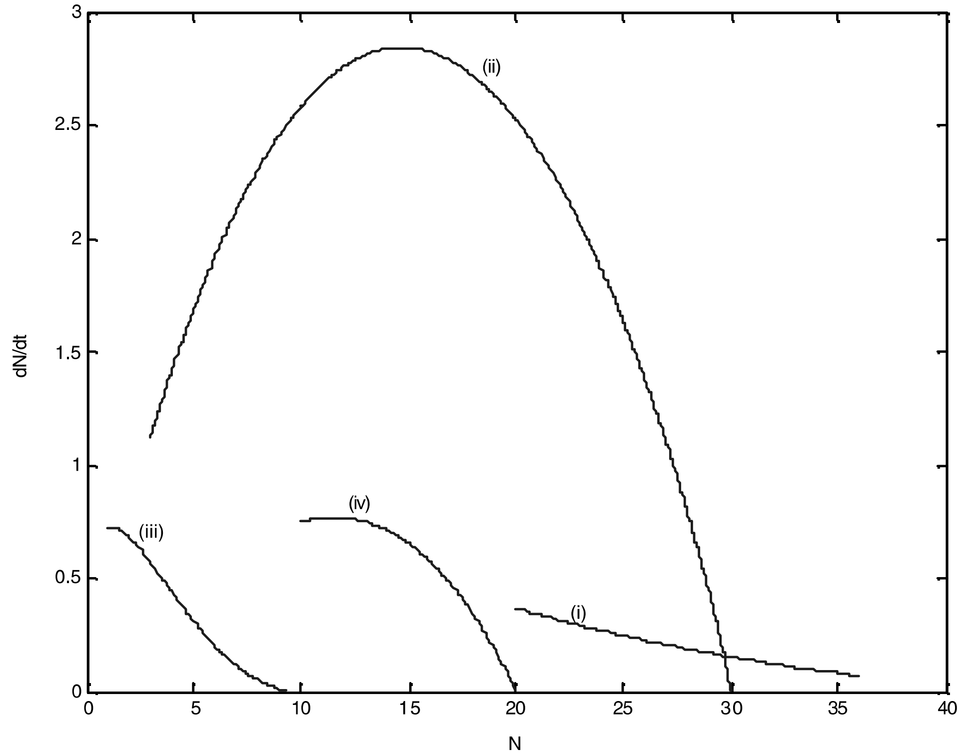

Fig. 19. Generic growth rate curves for the following parameters: (i) $r = 8$, $N_0 = 20$, $K = 50$, $\alpha = 0.6$, $\beta = 0.1$, $\gamma = 2$; (ii) $r = 0.5$, $N_0 = 3$, $K = 30$, $\alpha = 1.05$, $\beta = 0.5$, $\gamma = 0.9$; (iii) $r = 2.5$, $N_0 = 1$, $K = 10$, $\alpha = \frac{2}{3}$, $\beta = \frac{1}{3}$, $\gamma = 2$. (iv) $r = 0.1$, $N_0 = 10$, $K = 20$, $\alpha = 1$, $\beta = 2$, $\gamma = 1$.

(iii) $N_{\text{inf}} = 1.25$ (near $N_0 = 1$).
(iv) $N_{\text{inf}} \approx 11.547$ (near $N_0 = 10$).

3.7. Schnute's equation

Schnute [22] in his 1981 paper suggested the use of the relative growth rate of the relative growth rate as the quantity of interest. If $Z = (1/N)(\mathrm{d}N/\mathrm{d}t)$ is the relative growth rate, $(1/Z)(\mathrm{d}Z/\mathrm{d}t)$ is the relative growth rate of the relative growth rate. Schnute's assumption was to assume that $(1/Z)(\mathrm{d}Z/\mathrm{d}t)$ is a linear function of Z:

$$\frac{1}{Z}\frac{\mathrm{d}Z}{\mathrm{d}t} = -(a + bZ), \tag{48}$$

where a, b are positive, negative, or zero constants, and the minus sign on the right hand side indicates that the growth rate typically decreases. For appropriate values of a, b some growth models can be derived from (48).

In contrast, for the generalized logistic (1) $(1/Z)(\mathrm{d}Z/\mathrm{d}t)$ has the following form:

$$\frac{1}{Z}\frac{\mathrm{d}Z}{\mathrm{d}t} = Z\left[(\alpha+\beta\gamma-1) - \beta\gamma r^{1/\gamma} N^{(\alpha-1)/\gamma} Z^{-(1/\gamma)}\right]. \tag{49}$$

Clearly (49) is not a linear function of Z, but rather of the form

$$\frac{1}{Z}\frac{\mathrm{d}Z}{\mathrm{d}t} = aZ + b(N)Z^c,$$

where $a = \alpha + \beta\gamma - 1$ is a constant, b a function of N, and c a constant. From (49) with $\alpha = \beta = \gamma = 1$ we get the Verhulst logistic growth form

$$\frac{1}{Z}\frac{\mathrm{d}Z}{\mathrm{d}t} = Z\left(1 - \frac{r}{Z}\right) = Z - r.$$

For $\alpha = \gamma = 1$ we get Richards growth form

$$\frac{1}{Z}\frac{\mathrm{d}Z}{\mathrm{d}t} = Z\left(\beta - \frac{\beta r}{Z}\right) = \beta(Z - r).$$

From the above by dividing by β and letting $\beta \to 0$ we get Gompertz growth

$$\frac{1}{Z}\frac{\mathrm{d}Z}{\mathrm{d}t} = \lim_{\beta\to 0}(Z - r) = -r.$$

For $\gamma = 0$, $\alpha = 0$ we get linear growth

$$\frac{1}{Z}\frac{\mathrm{d}Z}{\mathrm{d}t} = -Z.$$

For $\gamma = 0$, $\alpha = 1$ we get exponential growth

$$\frac{1}{Z}\frac{\mathrm{d}Z}{\mathrm{d}t} = 0.$$

And for $\gamma = 0$, $\alpha = 1/2$ we get quadratic growth

$$\frac{1}{Z}\frac{\mathrm{d}Z}{\mathrm{d}t} = -\frac{Z}{2}.$$

Another growth forms that admits Schnute's description (48) is the generalized von Bertalanffy form, which is a special case of (1) with $\beta = 1 - \alpha$, $\gamma = 1$:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN^{\alpha}\left[1 - \left(\frac{N}{K}\right)^{1-\alpha}\right].$$

The generalized von Bertalanffy form also follows from (49)

$$\frac{1}{Z}\frac{\mathrm{d}Z}{\mathrm{d}t} = (\alpha - 1)rK^{\alpha-1} + (\alpha - 1)Z.$$

A form that cannot be expressed according to the formula prescribed by (48) is Smith's form (24), whose relative growth rate of the relative growth rate is given by the Verhulst logistic growth form scaled by the factor $(1 + c(N/K))^{-1}$ (see Section 3.4):

$$\frac{1}{Z}\frac{\mathrm{d}Z}{\mathrm{d}t} = \frac{Z - r}{1 + c\frac{N}{K}}.$$

For $c = 0$ Smith's form reduces to the Verhulst logistic growth form as expected.

Zeide [23] questioned Schnute's linear assumption, as being perhaps suitable for fish growth (Schnute's area of research) but not for example, tree growth. Zeide's research indicates that a power law, $(1/Z)(\mathrm{d}Z/\mathrm{d}t) = aZ^b$, appears to be more appropriate. In fact, (49) makes evident the fact that Schnute's linear law fails to predict any growth model for which $\gamma \neq 1$, except of course when $\gamma = 0$ in which case parameter β is of no significance. For $\gamma = 1$ (49) is rewritten as follows:

$$\frac{1}{Z}\frac{\mathrm{d}Z}{\mathrm{d}t} = -\beta r N^{\alpha-1} + Z(\alpha+\beta-1) = -\frac{\beta r}{K^\beta}N^{\alpha+\beta-1} + (\alpha-1)Z.$$

Now if $\alpha = 1$ Richard's form follows, if $\alpha = \beta = 1$ the logistic form follows, and if $\alpha + \beta = 1$ the generalized von Bertalanffy form follows. If $\alpha + \beta \neq 1$ however, the above form remains non-linear in Z.

3.8. Birch's generalization of Richards equation

In a recent publication Birch [24] reintroduced Smith's equation (24) as a generalization of Richards equation (19). Birch cited the advantages of his curve over Richards as (i) simulating exponential growth at low values of N, and (ii) having flexible inflection point values. From Eq. (26) for the inflection point, it can be seen that N_{inf} can assume any value for $-1 < c < \infty$. From (4) and for $\alpha = \beta = 1$ we see that the inflection value for the generalized logistic is $N_{\mathrm{inf}} = K/(1+\gamma)$ and can also assume any value for any positive γ (similarly, for $\beta = \gamma = 1$ the inflection value $N_{\mathrm{inf}} = (\alpha/(\alpha+1))K$ also can take any value for $\alpha > 0$). Furthermore for small N, (1) also simulates exponential growth. Fig. 20 illustrates exponential growth at low values of N. The initial growth rate is $(\mathrm{d}N/\mathrm{d}t)_{N_0} \approx 0.05$ (nearly zero lower asymptote) in all cases, and the inflection values are respectively:

(i) $N_{\mathrm{inf}} \approx 33.33$.
(ii) $N_{\mathrm{inf}} \approx 26.31$.
(iii) $N_{\mathrm{inf}} = 20$.
(iv) $N_{\mathrm{inf}} \approx 16.66$.

3.9. Exponential polynomial growth

In this section we derive exponential polynomial growth from a limiting case of the generalized logistic form. Consider again (1) with $\alpha = 1$ and divide the right hand side by β^γ, then take the limit as $\beta \to 0$:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \lim_{\beta\to 0}\frac{rN}{K^{\beta\gamma}}\left(\frac{K^\beta - N^\beta}{\beta}\right)^\gamma = rN\left[\ln\left(\frac{K}{N}\right)\right]^\gamma. \tag{50}$$

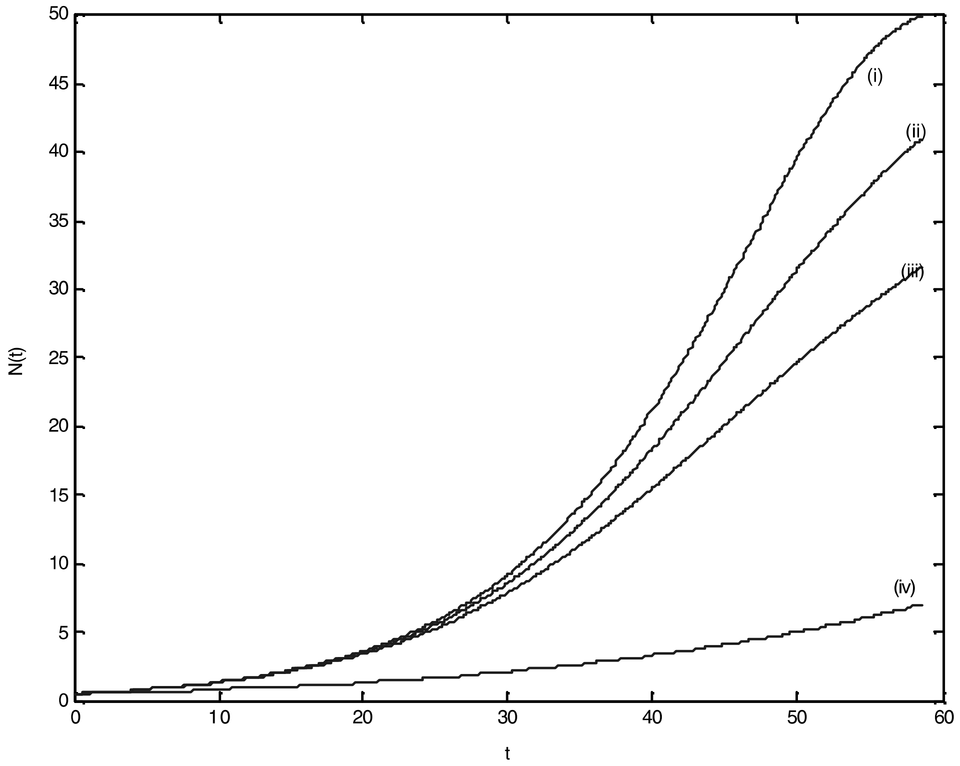

Fig. 20. Generalized logistic curves with exponential growth for small N: (i) $N_0 = 0.5$, $K = 50$, $\gamma = 0.5$, $r = 0.1$; (ii) $N_0 = 0.5$, $K = 50$, $\gamma = 0.9$, $r = 0.1$; (iii) $N_0 = 0.5$, $K = 50$, $\gamma = 1.5$, $r = 0.1$; (iv) $N_0 = 0.5$, $K = 50$, $\gamma = 2.0$, $r = 0.05$.

Turner et al. [17] name (50) as the *hyper-Gompertz*, or simply *generalized Gompertz function*. For $\gamma = 1$, (50) becomes the well known Gompertz growth function with solution:

$$N(t) = K\left(\frac{N_0}{K}\right)^{e^{-rt}}. \tag{51}$$

The solution to (50) for $\gamma \neq 1$ is

$$N(t) = K\exp\left[-\left\{(\gamma-1)rt + \left[\ln\left(\frac{K}{N_0}\right)\right]^{1-\gamma}\right\}^{1/(1-\gamma)}\right]. \tag{52}$$

For positive integer values of $1/(1-\gamma)$, (52) represents general exponential polynomial growth of the form

$$N(t) = \exp(a_0 + a_1 t + a_2 t^2 + a_3 t^3 + \cdots).$$

For $\gamma = 1/2$, (52) becomes the second order exponential polynomial

$$N(t) = K\exp\left[-\left\{\left(-\frac{rt}{2}\right) + \left[\ln\left(\frac{K}{N_0}\right)\right]^{1/2}\right\}^2\right] = \exp\left[a_0 + a_1 t + a_2 t^2\right],$$

where

$$a_0 = \ln N_0$$

$$a_1 = r\sqrt{\ln\left(\frac{K}{N_0}\right)} > 0$$

$$a_2 = -\frac{r^2}{4} < 0.$$

The point of inflection is determined from (4) with $\alpha = 1$ and $\beta \to 0$:

$$N_{\text{inf}} = K\,\mathrm{e}^{-\gamma}.$$

The time to inflection is given by

$$t_{\text{inf}} = \frac{2\sqrt{\ln\left(\frac{K}{N_0}\right)} - \sqrt{2}}{r}.$$

Heinen [25] analyses the second order exponential polynomial growth by assuming the form $N(t) = \mathrm{e}^{a+bt+ct^2}$ from the outset, and subsequently arriving at the functional form (50).

4. Discussion

In this paper we have introduced a growth curve (1) which can be seen to encompass several well known growth forms as special cases. Specifically, we have shown that (1) includes the following (the first three entries in the table follow trivially from (1) and have only received a brief mention):

Exponential growth	$\alpha = 1$	$\beta = 1$	$\gamma = 1$
Mitscherlich or monomolecular growth	$\alpha = 0$	$\beta = 1$	$\gamma = 1$
Power growth	$\alpha > 1$		$\gamma = 0$
Generalized von Bertalanffy growth	α	$\beta = 1 - \alpha$	$\gamma = 1$
Specialized von Bertalanffy growth	$\alpha = \frac{2}{3}$	$\beta = \frac{1}{3}$	$\gamma = 1$
Richards growth	$\alpha = 1$	$\beta \geqslant -1$	$\gamma = 1$
Smith's growth	$\alpha = 0.473$	$\beta = 1$	$\gamma = 1$
Blumberg's growth	α	$\beta = 1$	γ
Hyperbolic growth	$\alpha = 1 - \frac{1}{n}$	$\beta = 1$	$\gamma = 1 + \frac{1}{n}$
Generic growth	$\alpha = 1 + \beta(1 - \gamma)$	β	γ
Generalized Gompertz growth	$\alpha = 1$	$\beta \to 0$	γ
Gompertz growth	$\alpha = 1$	$\beta \to 0$	$\gamma = 1$
Second order exponential polynomial	$\alpha = 1$	$\beta \to 0$	$\gamma = \frac{1}{2}$

For the growth form introduced we have derived formulae for (i) the maximum relative growth rate, $((1/N)(\mathrm{d}N/\mathrm{d}t))_{\max}$ and where it occurs, N^* (ii) the inflection value, N_{inf}, and (iii) the time to inflection, t_{inf}. We have also shown that these formulae predict the requisite values for the derived growth models. All models considered in this paper follow naturally from (1) with the exception of Smith's form (24) (and consequently Birch's generalization) and Schnute's form (48) which is a linear differential equation with the relative growth rate, Z, as the dependent variable. Smith's form was derived by utilizing the original data furnished by Smith to assign appropriate numerical values to the parameters r, α, γ, which when substituted in (1) produce an excellent fit to (24). Birch's generalization of Richards form (19) is actually a restatement of Smith's and was reintroduced to remedy the absence of zero lower asymptote and inflexibility of the inflection value inherent in Richards form. The generalized form (1) is also capable of producing a near zero lower asymptote whilst at the same time exhibiting a flexibility in its inflection value through the presence of only one parameter, α or γ ($\beta = 1$).

Schnute's form (48) includes all the non-sigmoid growth forms for which $\gamma = 0$, and all the basic sigmoid growth forms for which $\gamma = 1$ and α, β are restricted to take specific values, but fails to include anything else. As already stated previously in the text, Zeide [23] found Schnute's linear assumption unjustified and inapplicable to tree growth.

In the same paper [23] Zeide states several not so well known growth models which seem to fit the generalized form (1) and for which $\gamma \neq 1$. For example, *Hossfeld's form*

$$N(t) = \frac{t^c}{b + \frac{t^c}{a}}, \quad \frac{\mathrm{d}N}{\mathrm{d}t} = \frac{bct^{c-1}}{\left(b + \frac{t^c}{a}\right)^2}$$

can be expressed as a generalized form (1):

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \left(cb^{-(1/c)}\right)N^{1-(1/c)}\left(1 - \frac{N}{a}\right)^{1+(1/c)},$$

where

$$\begin{aligned}
r &= cb^{-(1/c)} \\
K &= a \\
\alpha &= 1 - \frac{1}{c} \\
\beta &= 1 \\
\gamma &= 1 + \frac{1}{c}.
\end{aligned}$$

Also *Levakovic's form*

$$N(t) = a\left(\frac{t^d}{b + t^d}\right)^c, \quad \frac{\mathrm{d}N}{\mathrm{d}t} = bcd\frac{N}{t(b + t^d)}$$

can be expressed as a generalized form (1):

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \left(cda^{1/cd}b^{-(1/d)}\right)N^{1-(1/cd)}\left[1 - \left(\frac{N}{a}\right)^{1/c}\right]^{(1/d)+1},$$

where

$$r = cda^{1/cd}b^{-(1/d)}$$
$$K = a$$
$$\alpha = 1 - \frac{1}{cd}$$
$$\beta = \frac{1}{c}$$
$$\gamma = \frac{1}{d} + 1.$$

Finally, in the same reference [23] *Korf's form*

$$\frac{dN}{dt} = a\exp\left(-bt^{-c}\right), \quad \frac{dN}{dt} = bcNt^{-(c+1)}$$

is a generalized Gompertz function of the form given in (50):

$$\frac{dN}{dt} = (cb^{-(1/c)})N\left[\ln\left(\frac{K}{a}\right)\right]^{1+(1/c)},$$

where

$$r = cb^{-(1/c)}$$
$$a = K$$
$$\gamma = 1 + \frac{1}{c}.$$

Heinen [25] presented a very comprehensive review of the key properties of the exponential, monomolecular, logistic, Gompertz, Richards, and second order exponential polynomial. In his study Heinen concluded that there is one model that fits all the aforementioned models except the second order exponential polynomial. His generalization has the following form:

$$Y(N(t)) = A(K) + B(N_0, K)C(r)^t, \tag{53}$$

where $C(r) = e^r$ for exponential growth and $C(r) = e^{-r}$ for all the rest.

The main disadvantage with Heinen's generalization format is that the functions $Y(N(t))$, $A(K)$, $B(N_0, K)$ do not have a fixed mathematical form but rather are adjusted accordingly each time a new model is added to the list. If another form were to be included Heinen's format would have to be augmented. Like Schnute's model Heinen's one model fits all approach works well for growth models with $\gamma = 0$ or $\gamma = 1$, and either α or β are present but never both. The reason that the second order exponential polynomial does not fit into Heinen's scheme is simply because $\gamma = 1/2$.

In a series of papers [26,27] Savageau argued that changes among the component parts of a complex system occur much faster than the growth rate of the system as a whole. Mathematically, the system's temporal behaviour is governed by the slowest phenomena; all other phenomena are assumed to have reached a steady state much faster. When there is a single, temporally dominant process, $N_1(t)$, the basic growth equation has the general form

$$\frac{dN_1}{dt} = a_1 N_1^{g_1} - b_1 N_1^{h_1}. \tag{54}$$

From the above equation Savageau derived the linear, exponential, monomolecular, logistic, and von Bertalanffy growth forms by relating the parameters a_1, b_1, g_1, h_1 to the parameters of these curves. In fact Savageau's general form is comparable to (1) with $\gamma = 1$:

$$\frac{dN}{dt} = rN^{\alpha}\left[1 - \left(\frac{N}{K}\right)^{\beta}\right] = rN^{\alpha} - \frac{r}{K^{\beta}}N^{\alpha+\beta}, \tag{55}$$

where $r = a_1$, $r/K^{\beta} = b_1$, $\alpha = g_1$, $\alpha + \beta = h_1$.

In the same papers Savageau went on to relate the Gompertz growth equation (51) and the hyperbolic growth equation (37) among others by making the basic assumption of two temporally dominant processes, $N_1(t)$ and $N_2(t)$. Zeide [23] states that the subtractive operation in Savageau's general growth equations has some merit but multiplication is a viable alternative underlying the majority of biological phenomena. But as we have shown above subtraction can be expressed as a multiplication, so the equivalence of the two approaches is assured, at least in the presence of a single temporally dominant process. It is for instance, with the Gompertz and hyperbolic growth that two temporally dominant processes are introduced. The Gompertz differential form has a logarithmic term, $\ln(K/N)$, and the hyperbolic growth has an exponent, γ. The difficulty in Savageau's general growth equations subsuming these two forms as single processes rests in their mathematical form which reads thus:

$$\frac{dN_i}{dt} = a_i \prod_{j=1}^{k} N_j^{g_{ij}} - b_i \prod_{j=1}^{k} N_j^{h_{ij}}, \quad i = 1, 2, \ldots, k, \tag{56}$$

where k is the number of temporally dominant processes. The above equations can only be factored into two multiplicative terms thus

$$\frac{dN_i}{dt} = a_i \prod_{j=1}^{k} N_j^{g_{ij}} \left(1 - \frac{b_i}{a_i} \prod_{j=1}^{k} \frac{N_j^{h_{ij}}}{N_j^{g_{ij}}}\right), \quad i = 1, 2, \ldots, k.$$

The multiplicative form above cannot produce the Gompertz and hyperbolic growth forms for $i = 1$, unless it is expanded to include more terms:

$$\frac{dN_1}{dt} = a_1 N_1^{g_1} - a_2 N_1^{g_2} - a_3 N_1^{g_3} - \cdots$$

The expanded form can be contracted into two multiplicative terms when the parameters assume particular values. In fact this form is similar to the generalized logistic form (1) upon binomial expansion:

$$\frac{dN}{dt} = rN^{\alpha} - \frac{r\gamma}{K^{\beta}}N^{\alpha+\beta} + \frac{r\gamma(\gamma-1)}{2K^{2\beta}}N^{\alpha+2\beta} - \cdots$$

Perhaps the only disadvantage of the generalized logistic growth (1) is that it cannot be integrated to give an analytic solution for $N(t)$. However, Birch [24] acknowledges in his paper that almost all applications of growth equations are numeric, so this is a minor problem. Nevertheless, the lack of an analytic solution makes the task of curve-fitting real data extremely hard. Curve-fitting of some sigmoidal growth models is extensively dealt with in Ratkowsky [28] but all the models considered have analytic solutions. The availability of t as a function of N is not of much practical use as the functional form is exceedingly complex. It seems more preferable to adopt the differential equation (1) itself as a preliminary framework for data analysis. Using the finite difference method we approximate the derivative $\mathrm{d}N/\mathrm{d}t$ by $\Delta N/\Delta t$ and taking logarithms:

$$\ln\left(\frac{\Delta N}{\Delta t}\right) \approx \ln r + \alpha \ln N + \gamma \ln\left[1 - \left(\frac{N}{K}\right)^{\beta}\right]. \tag{57}$$

For small N/K, we get

$$\ln\left(\frac{\Delta N}{\Delta t}\right) \approx \ln r + \alpha \ln N. \tag{58}$$

The above is a linear regression model in the parameters α and r which can be estimated by least squares computations. For non-negligible N/K, we have the more precise relation

$$\ln\left(\frac{\Delta N}{\Delta t}\right) \approx \ln r + \alpha \ln N - \gamma\left[\left(\frac{N}{K}\right)^{\beta} + \frac{1}{2}\left(\frac{N}{K}\right)^{2\beta} + \frac{1}{3}\left(\frac{N}{K}\right)^{3\beta} + \cdots\right]. \tag{59}$$

The above is a non-linear regression model in the parameters β, γ, K which must be estimated by using the Gauss–Newton algorithm for example.

It must be stressed that the preceding, rather sketchy procedure is simply a quick way to obtain initial parameter estimates and not a detailed outline of how to carry out curve-fitting of (1).

When the magnitudes of the parameters have been established the inflection value, the time to inflection, and the value of N at which the relative growth rate reaches its maximum value (this is possible only if $\alpha > 1$) can be determined and contrasted with any real data that may be available. Although the same inflection value can theoretically arise from the constancy of the ratio γ/α for example, the time to inflection will be distinctly different for any number of growth curves which share this property. Hence no confusion should result as to which parameter values to choose from. When $\alpha < 1$, $\beta > 0$ (a positive β is a certainty for sigmoid growth curves), and $\gamma < 1$, the solution to (1) involves the incomplete beta function which has been extensively tabulated by Pearson [29]. The tables could serve as a verification tool for the initial parameter estimates as follows: from (7) we have

$$\frac{1}{\beta r K^{\alpha-1}}\left[B_{x_1}(p,q) - B_{x_0}(p,q)\right] = t, \tag{60}$$

where t is the time taken for the population to reach a given size $N(t)$ from the initial size $N_0 = N(0)$ (or any other size for that matter), and $B_{x_1}(p,q)$, $B_{x_0}(p,q)$ are found in the tables. Then the left hand side of (60) can be compared with the table readings. Eq. (8) can be used for exactly the same purpose with beta function tables used instead.

Our purpose in this paper was to present a growth form (1) which could embrace many key growth forms. We have shown that several sigmoidal growth models and a few basic non-sigmoidal ones are subsumed by (1). We have also identified a class of generalized models, (1) with $\alpha > 1$, for which the rise in growth rate outpaces the rise in the population itself, a property not shared by more conventional growth models. Undoubtedly, the literature is replete with growth models that also need to considered [23]. Preliminary investigations, not presented here, have shown that the Weibull distribution [30] can also be alternatively represented as a generalized logistic curve (1). Finally, detailed curve-fitting of real data has to be undertaken if the generalized logistic form is to be adopted as a viable modelling tool.

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