

Solutions of Rate-state Equation Describing Biological Growths

Purnachandra Rao Koya, Ayele Taye Goshu*

School of Mathematical and Statistical Sciences, Hawassa University

Abstract In this paper, we consider the commonly used growth models and explicitly shown that each is a solution of the rate-state ordinary differential equation $f'(t) = r_t f(t)$ which describes biological growths. We construct growth function $f(t)$ and relative growth function r_t for the models: Generalized logistic, Particular case of generalized logistic, Richards, Von Bertalanffy, Brody, Classical logistic, Gompertz, Weibull, Generalized Weibull, Monomolecular and Mitscherlich. Detailed derivations are presented considering non-mathematicians working in the fields of Biological sciences and non-availability of these derivations in literature.

Keywords Growth Models, Rate-State Equation, Gompertz, Logistic, Richards, Weibull

1. Introduction

Measuring biological growth has been important in many fields. Many researchers have contributed in developing relevant models: Brody[1] for Brody function; Bertalanffy[2] for Von Bertalanffy function, Richards[3], France & Thornley[4] for Richards function; Winsor[5] for Gompertz function; Nelder[6], Brown et al[7], Robertson[8] for Logistic function; Eberhardt & Breiwick[9], Fekedulegn et al[10], Ayala et al[11] and Nelder[6] for Generalized Logistic, Rawlings & Cure[12] and Rawlings et al[13] for Weibull function; Spillman & Lang[14] and Brody[1] for Monomolecular function.

The growth models have been widely used in many biological growth problems including: in animal sciences (France et al[15]; Brown et al[7]; Brody[1]; Robertson[8]; Winsor[5]; Ersoy et al[16]) and in forestry (Lie and Zhang[17]; Zeide[18]).

The generalized logistic function has been studied by some researchers (Eberhardt and Breiwick[9]; Fekedulegn et al[10]; Ayala et al[11]; Nelder, [6]). Eberhardt and Breiwick[9] applied the models to growth of birds and mammal populations.

The mathematical representation of the relative growth is described by the ordinary differential equation (ODE) or rate-state equation:

$$\frac{df(t)}{dt} = r_t f(t) \quad (1)$$

where $f(t)$ is representing growth function and r_t is relative rate function at time t . This ordinary differential equation

has many solutions among which some are studied here. The purpose of this paper is to explicitly show that the commonly used growth models are solutions of the rate-state equation by constructing $f(t)$ and r_t .

In the current paper, detailed derivations of $f(t)$ and r_t are presented considering non mathematicians working in the fields of Biological sciences and non availability of these derivations in the literature. All the growth functions discussed here are displayed in Table 1 together with respective relative growth rate functions, expression for B and integral constant.

2. Derivations of Growth and Relative Growth Rate Functions

In this section we consider various growth functions and construct for them the respective r_t and $f(t)$. The growth curves considered in this paper are: Generalized logistic, Particular case of the generalized logistic, Richards, Von Bertalanffy, Brody, Classical logistic, Gompertz, Weibull, Generalized Weibull, Monomolecular and Mitscherlich functions.

2.1. Generalized Logistic Function

The Generalized Logistic function as given in (Wikipedia) is expressed in its original notations as $Y(t) = \mathcal{A} + \frac{\mathcal{K} - \mathcal{A}}{1 + Qe^{-B(t-M)^\omega}}$ which we now re-express in the same notations used in this paper as

$$f(t) = A_L + (A - A_L) [1 - Be^{-k(t-\mu)}]^m \quad (2)$$

by replacing in the equation $Y(t) = f(t)$, $\mathcal{A} = A_L$, $\mathcal{K} = A$, $B = k$, $M = \mu$, $\omega = \left[-\frac{1}{m}\right]$ and $[-Q] = 1 - \left(\frac{A - A_L}{A - A_L}\right)^{\frac{1}{m}}$.

* Corresponding author:

ayeley_taye@yahoo.com (Ayele Taye Goshu)

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Detailed derivations of $f(t)$ and r_t for generalized logistic function are given here under.

Derivation of r_t

Consider, $f(t) = A_L + (A - A_L) [1 - B e^{-k(t-\mu)}]^m$ where $B = \left[1 - \left(\frac{A_\mu - A_L}{A - A_L}\right)^{\frac{1}{m}}\right]$ which can be rewritten as $\left(\frac{f(t) - A_L}{A - A_L}\right)^{\frac{1}{m}} = 1 - B e^{-k(t-\mu)}$ or $\left[1 - \left(\frac{f(t) - A_L}{A - A_L}\right)^{\frac{1}{m}}\right] = B e^{-k(t-\mu)}$. Also, on differentiating $f(t)$, we get $f'(t) = m(A - A_L) [1 - B e^{-k(t-\mu)}]^{m-1} [-B e^{-k(t-\mu)}] (-k)$

$$= mk(A - A_L) \left(\frac{f(t) - A_L}{A - A_L}\right)^{1-\frac{1}{m}} \left[1 - \left(\frac{f(t) - A_L}{A - A_L}\right)^{\frac{1}{m}}\right] = mk[f(t) - A_L] \left[\left(\frac{A - A_L}{f(t) - A_L}\right)^{\frac{1}{m}} - 1\right]$$

$$= mk \left[\left(\frac{A - A_L}{f(t) - A_L}\right)^{\frac{1}{m}} - 1\right] \left[\frac{f(t) - A_L}{f(t)}\right] f(t). \text{ On comparison of this } f'(t) \text{ with } f'(t) = r_t f(t), \text{ we get}$$

$$r_t = mk \left[\left(\frac{A - A_L}{f(t) - A_L}\right)^{\frac{1}{m}} - 1\right] \left[\frac{f(t) - A_L}{f(t)}\right] \quad (3)$$

It is the Generalized Logistic relative growth rate function.

Derivation of $f(t)$

Put $r_t = mk \left[\left(\frac{A - A_L}{f(t) - A_L}\right)^{\frac{1}{m}} - 1\right] \left[\frac{f(t) - A_L}{f(t)}\right]$ in $f'(t) = r_t f(t)$. Then, we get

$$f'(t) = mk \left[\left(\frac{A - A_L}{f(t) - A_L}\right)^{\frac{1}{m}} - 1\right] \left[\frac{f(t) - A_L}{f(t)}\right] f(t)$$

$$= mk \left[\left(\frac{A - A_L}{f(t) - A_L}\right)^{\frac{1}{m}} - 1\right] [f(t) - A_L]$$

$$= mk \left\{ (A - A_L)^{\frac{1}{m}} - [f(t) - A_L]^{\frac{1}{m}} \right\} [f(t) - A_L]$$

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$$\Rightarrow \left\{ \frac{\left(-\frac{1}{m}\right) [f(t) - A_L]^{\frac{1}{m}-1}}{(A - A_L)^{\frac{1}{m}} - [f(t) - A_L]^{\frac{1}{m}}} \right\} df(t) = -k dt$$

$$\Rightarrow \log \left\{ (A - A_L)^{\frac{1}{m}} - [f(t) - A_L]^{\frac{1}{m}} \right\}$$

$$= -kt + \log \left[(A - A_L)^{\frac{1}{m}} B e^{k\mu} \right]$$

$$\Rightarrow (A - A_L)^{\frac{1}{m}} - [f(t) - A_L]^{\frac{1}{m}} = B (A - A_L)^{\frac{1}{m}} e^{k\mu} e^{-kt}$$

$$\Rightarrow [f(t) - A_L]^{\frac{1}{m}} = (A - A_L)^{\frac{1}{m}} - B (A - A_L)^{\frac{1}{m}} e^{-k(t-\mu)}$$

$$= (A - A_L)^{\frac{1}{m}} [1 - B e^{-k(t-\mu)}]$$

$$\Rightarrow f(t) - A_L = (A - A_L) [1 - B e^{-k(t-\mu)}]^m \Rightarrow f(t)$$

$$= A_L - (A - A_L) [1 - B e^{-k(t-\mu)}]^m$$

It is Generalized Logistic growth function. The integral constant in this case is $\log \left[(A - A_L)^{\frac{1}{m}} B e^{k\mu} \right]$.

2.2. Particular Case of Logistic Function

A function called Particular Case of Logistic function is defined (Wikipedia) as $Y(t) = \left\{ \frac{\mathcal{K}}{[1 + Q e^{-\alpha v(t-t_0)}]^{\frac{1}{\omega}}} \right\}$ which

we now re-express with same notations used in this paper as $f(t) = A [1 - B e^{-k(t-\mu)}]^m$ (4)

by replacing in the functions and other quantities using $Y(t) = f(t)$, $\mathcal{K} = A$, $k = \alpha\omega$, $t_0 = \mu$, $\omega = -\frac{1}{m}$ and

$[-Q] = \left[1 - \left(\frac{A_\mu}{A}\right)^{\frac{1}{m}}\right]$. Note that the Generalized Logistic function with $A_L = 0$, $mk + \alpha = 0$ reduces to the Particular case of Logistic function. In the latter case, the parameter B takes the form $B = 1 - \left(\frac{A_\mu}{A}\right)^{\frac{1}{m}}$. Detailed derivations of the growth function $f(t)$ and the relative growth rate function r_t are given here under.

Derivation of r_t

Consider $f(t) = A [1 - B e^{-k(t-\mu)}]^m$ where $B = \left[1 - \left(\frac{A_\mu}{A}\right)^{\frac{1}{m}}\right]$. It can be rewritten as $f(t) A^{1/m} = 1 - B e^{-k(t-\mu)}$ or equivalently $1 - \left(\frac{f(t)}{A}\right)^{\frac{1}{m}} = B e^{-k(t-\mu)}$. Also, on differentiating $f(t)$, we get $f'(t) = m A [1 - B e^{-k(t-\mu)}]^{m-1} [-B e^{-k(t-\mu)}] (-k)$

$$= m k A \left(\frac{f(t)}{A}\right)^{1-\frac{1}{m}} \left[1 - \left(\frac{f(t)}{A}\right)^{\frac{1}{m}}\right] = m k \left[\left(\frac{A}{f(t)}\right)^{\frac{1}{m}} - 1\right] f(t).$$

On comparison of this $f'(t)$ with $f'(t) = r_t f(t)$, we get

$$r_t = m k \left[\left(\frac{A}{f(t)}\right)^{\frac{1}{m}} - 1\right] \quad (5)$$

It is the relative growth rate function of Particular case of the generalized Logistic.

Derivation of $f(t)$

Put $r_t = m k \left[\left(\frac{A}{f(t)}\right)^{\frac{1}{m}} - 1\right]$ in $f'(t) = r_t f(t)$. Then, we

$$\text{get } f'(t) = m k \left[\left(\frac{A}{f(t)}\right)^{\frac{1}{m}} - 1\right] f(t)$$

$$\Rightarrow \left\{ \frac{\left(-\frac{1}{m}\right) [f(t)]^{\frac{1}{m}-1}}{A^{\frac{1}{m}} - [f(t)]^{\frac{1}{m}}} \right\} df(t) = -k dt$$

$$\Rightarrow \log \left\{ A^{\frac{1}{m}} - [f(t)]^{\frac{1}{m}} \right\}$$

$$= -kt + \log \left[A^{\frac{1}{m}} B e^{k\mu} \right]$$

$$\Rightarrow A^{\frac{1}{m}} - [f(t)]^{\frac{1}{m}} = B A^{\frac{1}{m}} e^{k\mu} e^{-kt} \Rightarrow [f(t)]^{\frac{1}{m}}$$

$$= A^{\frac{1}{m}} - B A^{\frac{1}{m}} e^{-k(t-\mu)}$$

$$= A^{\frac{1}{m}} [1 - B e^{-k(t-\mu)}]$$

$\Rightarrow f(t) = A [1 - B e^{-k(t-\mu)}]^m$. It is the growth function of Particular case of Generalized

Logistic. The integral constant in this case is given by $\log \left[A^{\frac{1}{m}} B e^{k\mu} \right]$.

2.3. Richards Function

The Richards function is defined as in the usual notations (Richards, 1959) as

$$f(t) = A(1 - B e^{-kt})^m \quad (6)$$

where $B = 1 - \left(\frac{A_0}{A}\right)^{\frac{1}{m}}$. The Richards function $f(t)$ can be directly derived from the ODE or rate-state equation (1) with relative rate function $r_t = mk \left[\left(\frac{A}{f(t)}\right)^{\frac{1}{m}} - 1 \right]$.

Derivation of r_t

Consider $f(t) = A(1 - B e^{-kt})^m$ which can be rewritten as $\left(\frac{f(t)}{A}\right)^{\frac{1}{m}} = [1 - B e^{-kt}]$ or equivalently we can write $\left[1 - \left(\frac{f(t)}{A}\right)^{\frac{1}{m}}\right] = B e^{-kt}$. Also on differentiating $f(t)$, we get $f'(t) = mA(1 - B e^{-kt})^{m-1} B k e^{-kt} = mABk e^{-kt} (1 - B e^{-kt})^{m-1}$.

On substituting all these in $f'(t) = r_t f(t)$ and simplifying, we get

$$\begin{aligned} mABk e^{-kt} (1 - B e^{-kt})^{m-1} &= r_t A (1 - B e^{-kt})^m \\ \Rightarrow mBk e^{-kt} &= r_t (1 - B e^{-kt}) \\ \Rightarrow \end{aligned}$$

$$r_t = \frac{mBk e^{-kt}}{1 - B e^{-kt}} = mk \left(\frac{B e^{-kt}}{1 - B e^{-kt}} \right) = mk \left(\frac{1 - \left(\frac{f(t)}{A}\right)^{\frac{1}{m}}}{\left(\frac{f(t)}{A}\right)^{\frac{1}{m}}} \right).$$

Hence

$$r_t = mk \left(\frac{\frac{1}{A^{\frac{1}{m}} - f^{\frac{1}{m}}(t)}}{\frac{1}{f^{\frac{1}{m}}(t)}} \right) \quad (7)$$

This is the required Richards expression for the relative growth rate function.

Derivation of $f(t)$

Put $r_t = mk \left(\frac{\frac{1}{A^{\frac{1}{m}} - f^{\frac{1}{m}}(t)}}{\frac{1}{f^{\frac{1}{m}}(t)}} \right)$ in $f'(t) = r_t f(t)$. Then, we get

$$\begin{aligned} \frac{df(t)}{dt} &= mk \left(\frac{\frac{1}{A^{\frac{1}{m}} - f^{\frac{1}{m}}(t)}}{\frac{1}{f^{\frac{1}{m}}(t)}} \right) f(t) = mk \left(\frac{1}{A^{\frac{1}{m}} - f^{\frac{1}{m}}(t)} \right) f^{1-\frac{1}{m}}(t) \\ \Rightarrow \left[\frac{\left(-\frac{1}{m}\right) f^{\frac{1}{m}-1}(t)}{A^{\frac{1}{m}} - f^{\frac{1}{m}}(t)} \right] df(t) &= -k dt \Rightarrow \log \left[A^{\frac{1}{m}} - f^{\frac{1}{m}}(t) \right] = -kt + \log \left(A^{\frac{1}{m}} B \right) \\ \Rightarrow A^{\frac{1}{m}} - f^{\frac{1}{m}}(t) &= A^{\frac{1}{m}} B e^{-kt} \Rightarrow f^{\frac{1}{m}}(t) = A^{\frac{1}{m}} - A^{\frac{1}{m}} B e^{-kt} = A^{\frac{1}{m}} (1 - B e^{-kt}) \\ \Rightarrow f(t) &= A (1 - B e^{-kt})^m. \text{ This is the required Richards expression for the growth function.} \end{aligned}$$

Interpretation of B: Here $\log \left(A^{\frac{1}{m}} B \right)$ is the integral constant. Put $f(t) = A_0$ for $t = 0$, since A_0 is the initial weight of an organism. Hence we get,

$$\begin{aligned} A_0 &= A (1 - B)^m \Rightarrow \left(\frac{A_0}{A} \right)^{\frac{1}{m}} = 1 - B \Rightarrow \\ B &= 1 - \left(\frac{A_0}{A} \right)^{\frac{1}{m}} = \frac{A^{\frac{1}{m}} - A_0^{\frac{1}{m}}}{A^{\frac{1}{m}}}. \end{aligned}$$

2.4. Von Bertalanffy Function

The Von Bertalanffy function is defined (Bertalanffy, 1957) as

$$f(t) = A(1 - B e^{-kt})^3 \quad (8)$$

where $B = 1 - \left(\frac{A_0}{A}\right)^{\frac{1}{3}}$. The Von Bertalanffy function is a special case of Richards function with $m = 3$. The Von Bertalanffy function can be derived from ODE (1) given relative rate function.

Derivation of r_t

Consider $f(t) = A(1 - B e^{-kt})^3$ which can be rewritten as $\left(\frac{f(t)}{A}\right)^{\frac{1}{3}} = [1 - B e^{-kt}]$ or equivalently rewritten as $\left[1 - \left(\frac{f(t)}{A}\right)^{\frac{1}{3}}\right] = B e^{-kt}$. Also, on differentiating $f(t)$, we get $f'(t) = 3A(1 - B e^{-kt})^2 (B k e^{-kt}) = 3ABk (e^{-kt})^2 (1 - B e^{-kt})^2$. On substituting all the above in $f'(t) = r_t f(t)$ and simplifying, we get

$$\begin{aligned} 3ABk (e^{-kt})^2 (1 - B e^{-kt})^2 &= r_t A (1 - B e^{-kt})^3 \Rightarrow \\ 3Bk e^{-kt} &= r_t (1 - B e^{-kt}) \\ \Rightarrow r_t &= \frac{3Bk e^{-kt}}{1 - B e^{-kt}} = 3k \left(\frac{B e^{-kt}}{1 - B e^{-kt}} \right) = 3k \left(\frac{1 - \left(\frac{f(t)}{A}\right)^{\frac{1}{3}}}{\left(\frac{f(t)}{A}\right)^{\frac{1}{3}}} \right) = \\ 3k \left(\frac{\frac{1}{A^{\frac{1}{3}} - f^{\frac{1}{3}}(t)}}{\frac{1}{f^{\frac{1}{3}}(t)}} \right). \text{ Hence} \end{aligned}$$

$$r_t = 3k \left(\frac{\frac{1}{A^{\frac{1}{3}} - f^{\frac{1}{3}}(t)}}{\frac{1}{f^{\frac{1}{3}}(t)}} \right) \quad (9)$$

This r_t is the required Von Bertalanffy expression for the relative growth rate function.

Derivation of $f(t)$

$$\begin{aligned} \text{Put } r_t &= 3k \left(\frac{\frac{1}{A^{\frac{1}{3}} - f^{\frac{1}{3}}(t)}}{\frac{1}{f^{\frac{1}{3}}(t)}} \right) \text{ in } f'(t) = r_t f(t). \text{ Then, we get} \\ \frac{df(t)}{dt} &= 3k \left(\frac{\frac{1}{A^{\frac{1}{3}} - f^{\frac{1}{3}}(t)}}{\frac{1}{f^{\frac{1}{3}}(t)}} \right) f(t) = 3k \left(A^{\frac{1}{3}} - f^{\frac{1}{3}}(t) \right) f^{\frac{2}{3}}(t) \\ \Rightarrow \left[\frac{\left(-\frac{1}{3}\right) f^{-\frac{2}{3}}(t)}{A^{\frac{1}{3}} - f^{\frac{1}{3}}(t)} \right] df(t) &= -k dt \Rightarrow \log \left[A^{\frac{1}{3}} - f^{\frac{1}{3}}(t) \right] = -kt + \log \left(A^{\frac{1}{3}} B \right) \\ \Rightarrow A^{\frac{1}{3}} - f^{\frac{1}{3}}(t) &= A^{\frac{1}{3}} B e^{-kt} \Rightarrow f^{\frac{1}{3}}(t) = A^{\frac{1}{3}} - A^{\frac{1}{3}} B e^{-kt} = A^{\frac{1}{3}} (1 - B e^{-kt}) \\ \Rightarrow f(t) &= A (1 - B e^{-kt})^3. \text{ This is the required Von Bertalanffy expression for the growth function.} \end{aligned}$$

Interpretation of B: Here $\log \left(A^{\frac{1}{3}} B \right)$ is the integral constant. Put $f(t) = A_0$ when $t = 0$, since A_0 is the initial weight of an organism. Thus, we get

$$A_0 = A(1-B)^3 \Rightarrow \left(\frac{A_0}{A}\right)^{\frac{1}{3}} = 1-B \Rightarrow B = 1 - \left(\frac{A_0}{A}\right)^{\frac{1}{3}} = \frac{1}{A^{\frac{1}{3}}} - \frac{1}{A_0^{\frac{1}{3}}}.$$

2.5. Brody Function

Brody is defined (Brody, 1945) as

$$f(t) = A(1 - Be^{-kt}) \quad (10)$$

where $B = 1 - \frac{A_0}{A}$. It is a special case of Richards function with $m = 1$. It can also be derived from ODE (1) with given rate function.

Derivation of r_t

Consider $f(t) = A(1 - Be^{-kt})$ which can be rewritten as $\left[\frac{f(t)}{A}\right] = [1 - Be^{-kt}]$ or equivalently we can write it as $\left[1 - \frac{f(t)}{A}\right] = [Be^{-kt}]$. Also, on differentiating $f(t)$, we get $f'(t) = ABk \exp(-kt)$. On substituting all these in $f'(t) = r_t f(t)$ and simplifying, we get $[ABk \exp(-kt)] = r_t A(1 - Be^{-kt}) \Rightarrow r_t = \frac{Bk e^{-kt}}{1 - Be^{-kt}} = k \left(\frac{Be^{-kt}}{1 - Be^{-kt}}\right) = k \left[\frac{1 - \left(\frac{f(t)}{A}\right)}{\left(\frac{f(t)}{A}\right)}\right] = k \left[\frac{A - f(t)}{f(t)}\right]$. That is,

$$r_t = k \left[\frac{A}{f(t)} - 1\right] \quad (11)$$

This is the required Gompertz expression for the relative growth rate function.

Derivation of $f(t)$

Put $r_t = k \left(\frac{A - f(t)}{f(t)}\right)$ in $f'(t) = r_t f(t)$. Then, we get $\frac{df(t)}{dt} = k \left(\frac{A - f(t)}{f(t)}\right) f(t) = k[A - f(t)] \Rightarrow \frac{1}{A - f(t)} df(t) = k dt \Rightarrow \frac{(-1)}{A - f(t)} df(t) = -k dt \Rightarrow \log[A - f(t)] = -kt + \log AB$
 $\Rightarrow A - f(t) = AB e^{-kt} \Rightarrow f(t) = A - AB e^{-kt} = A(1 - Be^{-kt})$. This is the required Gompertz expression for the growth function.

Interpretation of B: Here $\log(AB)$ is the integral constant. Put $f(t) = A_0$ when $t = 0$, since A_0 is the initial weight of an organism. Thus, we get $A_0 = A(1 - B)$ or equivalently $B = \left[1 - \frac{A_0}{A}\right] = \left[\frac{A - A_0}{A}\right]$. Thus, B can be interpreted as the net amount of growth, resulted during the whole life period, per one unit of final (fruit) quantity.

2.6. Classical Logistic Function

The classical Logistic function [6] is defined as

$$f(t) = \frac{A}{1 + Be^{-kt}} \quad (12)$$

where $B = \left(\frac{A}{A_0} - 1\right)$. The Logistic function is a special case of (i) Richards function (5) with $m = -1$ (ii) Particular case of logistic function (4) with $\mu = 0$, $m = -1$ (ii) Generalized logistic function (3) with $\mu = 0$, $A_L = 0$, $m = -1$, $\alpha = k$. The Logistic function can be derived from the ODE (1). Detailed derivations are given below.

Derivation of r_t

Consider, $f(t) = \left[\frac{A}{1 + Be^{-kt}}\right]$ which can be rewritten as $[1 + Be^{-kt}] = \frac{A}{f(t)}$ or $Be^{-kt} = \frac{A}{f(t)} - 1$. Also, differentiating $f(t)$, we get $f'(t) = \left[\frac{ABk e^{-kt}}{(1 - Be^{-kt})^2}\right]$. On substituting all these in $f'(t) = r_t f(t)$ and after simplification we get $\left[\frac{ABk e^{-kt}}{(1 - Be^{-kt})^2}\right] = r_t \left(\frac{A}{1 + Be^{-kt}}\right)$
 $\Rightarrow r_t = \frac{Bk e^{-kt}}{1 + Be^{-kt}} = k \left(\frac{Be^{-kt}}{1 + Be^{-kt}}\right) = k \left[\frac{\left(\frac{A}{f(t)} - 1\right)}{\left(\frac{A}{f(t)}\right)}\right] = k \left[\frac{A - f(t)}{A}\right]$. That is,

$$r_t = k \left[1 - \frac{f(t)}{A}\right] \quad (13)$$

This is the required Logistic expression for the relative growth rate function.

Derivation of $f(t)$

Putting $r_t = k \left(\frac{A - f(t)}{A}\right)$ in $f'(t) = r_t f(t)$ we get $\frac{df(t)}{dt} = \left[k \left(\frac{A - f(t)}{A}\right) f(t)\right]$ or equivalently $\left[\frac{-A}{(A - f(t)) f(t)}\right] df(t) = [-k dt]$. Using partial fractions, it reduces to $\left[\frac{(-1)}{A - f(t)} - \frac{1}{f(t)}\right] df(t) = -k dt \Rightarrow \log \left[\frac{A - f(t)}{f(t)}\right] = -kt + \log B$
 $\Rightarrow \frac{A - f(t)}{f(t)} = B e^{-kt}$
 $\Rightarrow \frac{A}{f(t)} - 1 = B e^{-kt} \Rightarrow \frac{A}{f(t)} = 1 + B e^{-kt}$. This is the required Logistic expression for the growth function.

Interpretation of B: Here $\log B$ is the integral constant. Put $f(t) = A_0$ when $t = 0$, since A_0 is the initial weight of an organism. Thus, we get $A_0 = \left(\frac{A}{1 + B}\right)$ or $B = \left(\frac{A - A_0}{A_0}\right)$. Therefore, B is interpreted as the 'Net amount of growth', resulted during the life period per one unit of initial (seed) quantity.

2.7. Gompertz Function

The Gompertz function (Winsor, 1932) is defined as

$$f(t) = Ae^{-B \exp(-kt)} \quad (14)$$

where $B = \log \left(\frac{A}{A_0}\right)$. It can be shown that Gompertz function a special case of (i) Richards function with $m \rightarrow \infty$ (ii) Particular case of logistic function with $m \rightarrow -\infty$ and (iii) Generalized logistic function with $\mu = 0$, $A_L = 0$, $m \rightarrow -\infty$, $\alpha \rightarrow \infty$. The Gompertz function can be derived from the ODE (1) with given rate function. Detailed derivations are given below.

Derivation of r_t

Consider $f(t) = Ae^{-B \exp(-kt)}$, $B = \log \left(\frac{A}{A_0}\right)$ and can be rewritten as $\left[\frac{f(t)}{A}\right] = e^{-B \exp(-kt)} \Rightarrow \frac{A}{f(t)} = e^{B \exp(-kt)} \Rightarrow \log \left(\frac{A}{f(t)}\right) = [B \exp(-kt)]$. Also, on differentiating $f(t)$, we get $f'(t) = Bk \exp(-kt) e^{-B \exp(-kt)}$. On substituting all these in $f'(t) = r_t f(t)$ and after simplification we get

$$[Bk \exp(-kt) e^{-B \exp(-kt)}] = [r_t e^{-B \exp(-kt)}] \Rightarrow r_t = [Bk \exp(-kt)] = [k(B \exp(-kt))] = \left[k \log \left(\frac{A}{f(t)} \right) \right]. \text{ Thus}$$

$$r_t = k \log \left(\frac{A}{f(t)} \right) \quad (15)$$

This is the required Gompertz expression for the relative growth rate function.

Derivation of $f(t)$

Put $r_t = k \log \left(\frac{A}{f(t)} \right)$ in $f'(t) = r_t f(t)$. Then, we get

$$\frac{df(t)}{dt} = k \log \left(\frac{A}{f(t)} \right) f(t) \Rightarrow \frac{1}{f(t) \log \left(\frac{A}{f(t)} \right)} df(t) = k dt$$

$$\Rightarrow \frac{\left(-\frac{A}{f^2(t)} \right) df(t)}{\left(\frac{A}{f(t)} \right) \log \left(\frac{A}{f(t)} \right)} = -k dt$$

$$\Rightarrow \log \left(\log \left(\frac{A}{f(t)} \right) \right) = -kt + \log B \Rightarrow \log \left(\frac{A}{f(t)} \right) = B \exp(-kt) \Rightarrow \left(\frac{A}{f(t)} \right) = e^{-B \exp(-kt)} \Rightarrow f(t) = A e^{-B \exp(-kt)}.$$

This is the required Gompertz expression for the growth function.

Interpretation of B: Here $\log B$ is the integral constant. Put $f(t) = A_0$ when $t = 0$, since A_0 is the initial weight of an organism. Thus, we get $A_0 = A e^{-B}$ or equivalently $B = \log \left(\frac{A}{A_0} \right)$. Thus, B can be interpreted as the logarithm of the total amount of growth, resulted during the whole life period, per one unit of initial (seed) quantity.

2.8. Weibull Function

The Weibull growth model [13] is given as

$$f(t) = 1 - e^{-\left(\frac{t-\mu}{\delta}\right)^\nu} \quad (16)$$

and this function can be derived from the ODE (1) with rate function. Detailed derivations of this function $f(t)$ and relative growth rate r_t are given below.

Derivation of r_t

Consider $f(t) = \left[1 - e^{-\left(\frac{t-\mu}{\delta}\right)^\nu} \right]$ and can be rewritten as $[1 - f(t)] = \left[e^{-\left(\frac{t-\mu}{\delta}\right)^\nu} \right]$. Also, on differentiating $f(t)$, we

get

$$f'(t) = - \left[e^{-\left(\frac{t-\mu}{\delta}\right)^\nu} \left(-\nu \left(\frac{t-\mu}{\delta} \right)^{\nu-1} \left(\frac{1}{\delta} \right) \right) \right] = \left[\left(\frac{\nu}{\delta} \right) \left(\frac{t-\mu}{\delta} \right)^{\nu-1} e^{-\left(\frac{t-\mu}{\delta}\right)^\nu} \right] = \left\{ \frac{\nu}{\delta} \left(\frac{t-\mu}{\delta} \right)^{\nu-1} [1 - f(t)] \right\} = \left\{ \frac{\nu}{\delta} \left(\frac{t-\mu}{\delta} \right)^{\nu-1} \left[\frac{1-f(t)}{f(t)} \right] f(t) \right\}.$$

On comparing this with $f'(t) = r_t f(t)$ we get, $r_t = \frac{\nu}{\delta} \left(\frac{t-\mu}{\delta} \right)^{\nu-1} \left[\frac{1-f(t)}{f(t)} \right]$. Thus

$$r_t = \left(\frac{\nu}{\delta} \right) \left(\frac{t-\mu}{\delta} \right)^{\nu-1} \left[\frac{1}{f(t)} - 1 \right] \quad (17)$$

This is the required relative growth rate function for Weibull.

Derivation of $f(t)$

Put $r_t = \frac{\nu}{\delta} \left(\frac{t-\mu}{\delta} \right)^{\nu-1} \left[\frac{1-f(t)}{f(t)} \right]$ in $f'(t) = r_t f(t)$. Then, we get

$$\frac{df(t)}{dt} = \frac{\nu}{\delta} \left(\frac{t-\mu}{\delta} \right)^{\nu-1} \left[\frac{1-f(t)}{f(t)} \right] f(t) \text{ or equivalently it can be written as}$$

$$\frac{df(t)}{dt} = \frac{\nu}{\delta} \left(\frac{t-\mu}{\delta} \right)^{\nu-1} [1 - f(t)] \Rightarrow \frac{df(t)}{1-f(t)} = \frac{\nu}{\delta} \left(\frac{t-\mu}{\delta} \right)^{\nu-1} dt$$

$$\Rightarrow \frac{(-1)df(t)}{1-f(t)} = - \left[\frac{\nu}{\delta} \left(\frac{t-\mu}{\delta} \right)^{\nu-1} \right] dt \Rightarrow \log[1 - f(t)] = - \left(\frac{t-\mu}{\delta} \right)^\nu \Rightarrow 1 - f(t) = e^{-\left(\frac{t-\mu}{\delta}\right)^\nu} \Rightarrow f(t) = 1 - e^{-\left(\frac{t-\mu}{\delta}\right)^\nu}.$$

This is the Weibull growth function. Note that here the integral constant is taken to be zero.

2.9. Generalized Weibull Function

The Weibull function is generalized and named here as Generalized Weibull function and is defined as

$$f(t) = A \left[1 - B e^{-k \left(\frac{t-\mu}{\delta} \right)^\nu} \right] \quad (18)$$

where $B = 1 - \frac{A_\mu}{A}$, with the same notations used in this paper. Note that the Weibull a special case of Generalized Weibull function with $A = 1, B = 1, k = 1$. Generalized Weibull function can be derived from the ODE (1) with given rate function. Detailed derivations are given below.

Derivation of r_t

Consider $f(t) = A \left[1 - B e^{-k \left(\frac{t-\mu}{\delta} \right)^\nu} \right]$ which can be rewritten as $1 - \frac{f(t)}{A} = B e^{-k \left(\frac{t-\mu}{\delta} \right)^\nu}$. Also, on differentiating $f(t)$ with respect to t , we get $f'(t) = A \left[-B e^{-k \left(\frac{t-\mu}{\delta} \right)^\nu} \right] \left[-k \nu \left(\frac{t-\mu}{\delta} \right)^{\nu-1} \right] \left(\frac{1}{\delta} \right) = \left(\frac{A k \nu}{\delta} \right) \left(\frac{t-\mu}{\delta} \right)^{\nu-1} \left[1 - \frac{f(t)}{A} \right] = \left(\frac{k \nu}{\delta} \right) \left(\frac{t-\mu}{\delta} \right)^{\nu-1} \left[\frac{A}{f(t)} - 1 \right] f(t)$. On comparison of this with $f'(t) = r_t f(t)$ we get

$$r_t = \left(\frac{k \nu}{\delta} \right) \left(\frac{t-\mu}{\delta} \right)^{\nu-1} \left[\frac{A}{f(t)} - 1 \right] \quad (19)$$

This is the required relative growth rate function for Weibull.

Derivation of $f(t)$

Put $r_t = \left(\frac{k \nu}{\delta} \right) \left(\frac{t-\mu}{\delta} \right)^{\nu-1} \left[\frac{A}{f(t)} - 1 \right]$ in $f'(t) = r_t f(t)$ to get

$$\frac{df(t)}{dt} = \left(\frac{k \nu}{\delta} \right) \left(\frac{t-\mu}{\delta} \right)^{\nu-1} \left[\frac{A}{f(t)} - 1 \right] f(t) = \left(\frac{k \nu}{\delta} \right) \left(\frac{t-\mu}{\delta} \right)^{\nu-1} [A - f(t)]$$

$$\Rightarrow \frac{(-1)df(t)}{A-f(t)} = (-k) \left(\frac{\nu}{\delta} \right) \left(\frac{t-\mu}{\delta} \right)^{\nu-1} dt \Rightarrow \log[A - f(t)] = -k \left(\frac{t-\mu}{\delta} \right)^\nu + \log(AB) A - f(t) = AB e^{-k \left(\frac{t-\mu}{\delta} \right)^\nu}$$

$$\Rightarrow f(t) = A - AB e^{-k \left(\frac{t-\mu}{\delta} \right)^\nu} = A \left[1 - B e^{-k \left(\frac{t-\mu}{\delta} \right)^\nu} \right].$$

This is the Generalized Weibull growth function. Note that here the integral constant is taken to be $\log(AB)$.

Table 1. List of Growth Functions with their Respective Relative Growth Rate Functions, Expressions for Parameter B and Integral Constants

Model name	Relative growth rate function r_t	Growth function $f(t)$	Expression for B	Integral constant
Generalized Logistic	$r_t = mk \left[\left(\frac{A-A_L}{f(t)-A_L} \right)^{\frac{1}{m}} - 1 \right]$ $\left[1 - \frac{A_L}{f(t)} \right]$	$f(t) = A_L + (A - A_L) \cdot [1 - B e^{-k(t-\mu)}]^m$ $m < 0$	$B = 1 - \left(\frac{A_\mu - A_L}{A - A_L} \right)^{\frac{1}{m}}$	$\log[(A - A_L)^{\frac{1}{m}} B e^{k\mu}]$
Particular Case of Logistic	$r_t = mk \left[\left(\frac{A}{f(t)} \right)^{\frac{1}{m}} - 1 \right]$	$f(t) = A [1 - B e^{-k(t-\mu)}]^m$ $m < 0$	$B = 1 - \left(\frac{A_\mu}{A} \right)^{\frac{1}{m}}$	$\log \left(A^{\frac{1}{m}} B e^{k\mu} \right)$
Richards	$r_t = mk \left[\left(\frac{A}{f(t)} \right)^{\frac{1}{m}} - 1 \right]$	$f(t) = A (1 - B e^{-kt})^m$	$B = 1 - \left(\frac{A_0}{A} \right)^{\frac{1}{m}}$	$\log \left(A^{\frac{1}{m}} B \right)$
Von Bertalanffy	$r_t = 3k \left[\left(\frac{A}{f(t)} \right)^{\frac{1}{3}} - 1 \right]$	$f(t) = A (1 - B e^{-kt})^3$	$B = 1 - \left(\frac{A_0}{A} \right)^{\frac{1}{3}}$	$\log \left(A^{\frac{1}{3}} B \right)$
Brody	$r_t = k \left(\frac{A}{f(t)} - 1 \right)$	$f(t) = A (1 - B e^{-kt})$	$B = 1 - \frac{A_0}{A}$	$\log(AB)$
Logistic	$r_t = k \left(\frac{A-f(t)}{A} \right)$	$f(t) = \frac{A}{1 + B e^{-kt}}$	$B = \frac{A}{A_0} - 1$	$\log B$
Gompertz	$r_t = k \log \left(\frac{A}{f(t)} \right)$	$f(t) = A e^{-B \exp(-kt)}$	$B = \log \left(\frac{A}{A_0} \right)$	$\log B$
Generalized Weibull	$r_t = \frac{k\nu}{\delta} \left(\frac{t-\mu}{\delta} \right)^{\nu-1} \left[\frac{A}{f(t)} - 1 \right]$	$f(t) = A \left[1 - B e^{-k \left(\frac{t-\mu}{\delta} \right)^\nu} \right]$	$B = 1 - \frac{A_\mu}{A}$	Zero
Weibull	$r_t = \frac{\nu}{\delta} \left(\frac{t-\mu}{\delta} \right)^{\nu-1} \left[\frac{1}{f(t)} - 1 \right]$	$f(t) = 1 - e^{-\left(\frac{t-\mu}{\delta} \right)^\nu}$	$B = 1$	Zero
Monomolecular	$r_t = k \left(\frac{A}{f(t)} - 1 \right)$	$f(t) = A (1 - B e^{-kt})$	$B = 1 - \frac{A_0}{A}$	$\log(A - A_0)$
Mitscherlich	$r_t = k \left(\frac{A}{f(t)} - 1 \right)$	$f(t) = A (1 - B e^{-kt})$	$B = e^{-kq}$ q is a constant	$\log(AB)$

2.10. Monomolecular and Mitscherlich Functions

The Monomolecular growth function is defined[15], in its original notations, as $w = w_f - (w_f - w_0)e^{-\lambda t} = w_f \left[1 - \left(1 - \frac{w_0}{w_f} \right) e^{-\lambda t} \right]$ where w is the growth function at time t , w_f is the final (mature) value, $w = w_0$ At $t = 0$ is the initial value and λ is the growth rate. This function can be expressed as Brody function $f(t) = A (1 - B e^{-kt})$ by considering the parametric transformation $w = f(t)$, $w_f = A$, $w_0 = A_0$, $B = 1 - \frac{w_0}{w}$, $\lambda = k$. Derivations of $f(t)$ and r_t follow same as equations (10) and (11).

Mitscherlich growth function[20] is defined, in its original notations, as $y = \alpha \left[1 - e^{-\beta(t+q)} \right]$ where y is the growth function, α is the final (mature) growth, q is a constant and β is rate of growth. The Mitscherlich function can be expressed as Brody $f(t) = A (1 - B e^{-kt})$ by considering the parametric transformation as $y = f(t)$, $\alpha = A$, $\beta =$

k , $B = e^{-kq}$. It can be derived from the ODE (1) that the rate function as $r_t = \beta \left(\frac{\alpha-y}{y} \right)$ or $r_t = k \left(\frac{A}{f(t)} - 1 \right)$. Not that the integral constant here reduces to $\log(AB) = -\beta\delta + \log \alpha$. Similarly, derivations of $f(t)$ and r_t follow same as equations (10) and (11).

3. Conclusions

In this paper, the commonly used biological growth models are considered and explicitly shown that each is a solution of the rate-state ordinary differential equation $f'(t) = r_t f(t)$. The formula for r_t and $f(t)$ are constructed as solutions of the rate-state equation describing the growth models for each of the functions: generalized logistic, the particular case of the generalized logistic, Richards, von Bertalanffy, Brody, classical logistic, Gompertz, Weibull, generalized Weibull, monomolecular and Mitscherlich.

Detailed derivations are presented considering non-mathematicians in applied fields such as Biological sciences. All the growth functions discussed are displayed in Table 1 together with respective relative growth rate functions, expression for parameter B and integral constant. We note that there is a restriction on the acceptable values of B in each of the models. Further, the rate-state equation is capable of generating still more general and useful solutions. We will explore the possibility of constructing such models, relationships among the models and their inflection points.

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