A Versatile Growth Model with Statistically Stable Parameters

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This paper presents a new comprehensive growth model which includes numerous historical models as special cases. The new model is derived from a concise biological principle which, unlike earlier theories, relates to growth *acceleration*. Properties of growth curves, such as asymptotic limits or inflection points, are shown to be incidental in this new context. Possible submodels include not only asymptotic growth (such as von Bertalanffy, Richards, Gompertz, or logistic growth) but also linear, quadratic, or exponential growth. By simple analysis of variance, the observed data can be used directly in deciding which type of model is most appropriate. The new model is cast in terms of parameters which have stable statistical estimates. From this perspective, it is shown how earlier formulations sometimes result in an endless computer search for optimal parameter estimates.

Key words: Growth, asymptotic growth, von Bertalanffy, Richards, Gompertz, logistic, length at age, weight at age, nonlinear parameter estimation

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On trouvera dans l'article qui suit un modèle de croissance général nouveau incluant plusieurs anciens modèles comme cas spéciaux. Le nouveau modèle a été dérivé d'un principe biologique concis qui, contrairement aux théories antérieures, se rapporte à l'*accélération* de la croissance. Nous démontrons que les propriétés des courbes de croissance telles que limites asymptotiques ou points d'inflexion sont fortuites dans ce contexte nouveau. Des sous-modèles possibles incluent non seulement la croissance asymptotique (croissance de von Bertalanffy, Richards, Gompertz, ou logistique), mais également une croissance linéaire, quadratique ou exponentielle.On peut utiliser les données directement, par simple analyse de variance, afin de décider quel type de modèle est le plus approprié. Le nouveau modèle est présenté en termes de paramètres statistiquement stables. De ce point de vue, nous démontrons comment les formulations antérieures nécessitent parfois une recherche interminable par ordinateur en vue de trouver les estimations de paramètres optimales.

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THE biologist who wishes to find a curve describing size-at-age data invariably faces the problem of picking an appropriate model. Judging from the available literature, there is an extensive menu of models to contemplate, associated with such names or titles as Pütter, von Bertalanffy, Richards, Gompertz, or logistic. In addition to these models which all exhibit limiting, or asymptotic, growth, there are still others which do not, such as linear or exponential growth models. Ricker (1979) reviews much of the historical literature.

Even when a model is chosen, the biologist's problems are not over. There may also be a diverse suite of methods for estimating the parameters, such as a Walford (1946) plot or the procedures by Fabens (1965) or Allen (1966) to estimate certain von Bertalanffy parameters. Some methods fail to give all the parameters, and sometimes computer methods designed to estimate all parameters fail mysteriously. For example, it may happen that a parameter estimate slips gradually towards infinity as the computer grinds on in endless pursuit.

If the parameters are actually found, at last, there still remains the problem of their interpretation and appropriateness. Consider, for example, generalized von Bertalanffy growth

(1) $Y(t) = y_\infty(1 - e^{-g(t-t_0)})^p$,

Richards growth

(2) $Y(t) = y_\infty(1 + \frac{1}{p} e^{-g(t-t_0)})^{-p}$,

Gompertz growth

(3) $Y(t) = y_\infty e^{-e^{-g(t-t_0)}}$,

logistic growth (Richards growth with $p = 1$)

(4) $Y(t) = y_\infty(1 + e^{-g(t-t_0)})^{-1}$,

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and linear growth

$$(5) \quad Y(t) = g(t - t_0),$$

where $Y(t)$ represents fish size at age t, and y_∞, g, p, and t_0 are parameters, usually with $y_\infty > 0$, $g > 0$, and $p > 0$. In (1) and (5) the parameter t_0 represents a time when the growth curve crosses the t-axis. By contrast, in (2)−(4) t_0 corresponds to an inflection point on the curve. Indeed, the curves (3) and (4) never cross the t-axis and neither does (2) if $p > 0$. Why should or shouldn't axis crossings and inflection points be important? Furthermore, if $g > 0$, then y_∞ in (1)−(4) is a theoretical limiting size. By contrast, in (5) there is no limiting size. Why should a limiting size be important or well defined? In addition, models (1) and (2) have four parameters, while (3) and (4) have three parameters, and (5) has only two. What is a reasonable number of parameters to use? The practitioner invariably faces such questions.

This paper presents a new comprehensive model which includes (1)−(5) as special cases and many other models as well. The model is motivated by a concise biological principle, and the four (or fewer) parameters in the model almost always have stable statistical estimates. In addition, the parameters have reasonable biological interpretations, and submodels correspond simply to limiting parameter values. These parametric properties allow direct use of the data in selecting an appropriate model systematically. The apparent problem of comparing parameters in models (1)−(5) disappears. Axis crossings, inflection points, and asymptotic size no longer play an essential or dominant role, although they can be identified easily if they occur. Finally, an example is given which illustrates how a data set can suggest Gompertz growth (3) as a limiting version of von Bertalanffy growth (1).

Throughout this paper, the model is formulated in the language of fish growth. Obviously, it need not be restricted to fish; it could apply to a life stanza for any organism. In addition, it might be used to describe the growth of a whole population. Such analogies are hardly new. For example, Schaefer (1954) used logistic growth as a model for tuna populations. Later, Pella and Tomlinson (1969) generalized this approach by employing, essentially, Richards growth. Still other applications are possible for the model here. It might, for instance, describe the total mortality of a cohort as a function of time or the mortality resulting from the sudden presence of toxic material. Each new application may require a shift in language, but the mathematics remains the same.

Model Assumptions

As in equations (1)−(5), let $Y(t)$ denote the size of a fish at age t. Here "size" can refer to standard length, hypural length, fork length, live weight, eviscerated weight, volume (measured by water displacement), or whatever standard measure of fish dimension the biologist seeks to describe. The rate of growth is then the derivative dY/dt, and

$$(6) \quad Z = \frac{1}{Y}\frac{dY}{dt}$$

represents the relative growth rate, that is, the rate of growth in relation to size. Equivalently, Z represents the logarithmic growth rate:

$$Z = \frac{d}{dt}(\log Y).$$

Just as one might study how the size $Y(t)$ of a fish develops in relation to age, so one might also examine the development of the relative growth rate $Z(t)$. In particular, one might consider the seemingly abstract question: What is the relative growth rate of the relative growth rate, that is,

$$\frac{1}{Z}\frac{dZ}{dt} = ?$$

Perhaps the simplest possible assumption is that this quantity is a linear function of the relative growth rate:

$$(7) \quad \frac{1}{Z}\frac{dZ}{dt} = -(a + bZ),$$

where a and b are constants. For convenience, (7) is written with a minus sign on the right-hand side because the growth rate typically decreases. However, a and b should be considered unrestricted; either parameter can be positive, negative, or zero.

Conceptually, (7) represents a simple but significant departure from previous descriptions of the nature of growth. Traditionally, writers have focused on the growth *rate* dY/dt. [See Ricker's (1979) review or Fletcher (1973).] By contrast, (7) focuses on a rate of a rate, that is, *acceleration* in growth d^2Y/dt^2. A short calculation (given in Appendix B) shows that (6) and (7) together imply

$$(8) \quad \frac{d^2Y}{dt^2} = \frac{dY}{dt}[-a + (1 - b)Z].$$

Thus a fish whose growth conforms to (7) experiences growth acceleration which is proportional to the growth rate and to a linear function of the relative growth rate. Depending on the constants a and b, the animal's growth may be accelerated, decelerated, or both. In particular, the model includes possible S-shaped growth curves with a juvenile period of accelerated development followed later by decelerated growth during which the animal approaches a final limiting size.

For such S-curves, the parameters a and b have a rather simple significance. Associated with the S, there are two heights: that of the bottom arc and that of the full S. These correspond to the size when growth acceleration ends and to the final limiting size. There is also a width associated with the bottom arc of the S. This is the time spent during the accelerated growth phase. The dimensionless parameter b relates to the ratio of the two heights, or sizes, just mentioned. The parameter a has units time^{-1}. Its reciprocal $\frac{1}{a}$ relates to the width, or time, described above. The precise mathematical relationships among a, b, and S-curve characteristics are given later.

Model Equations

I do not wish to propose (7) as a new esoteric principle which somehow underlies the true subtleties of biological growth. Certainly the equation affords grounds for lengthy philosophical speculation, but the history of this problem suggests that such speculations have little practical value. The main purpose of (7) here is to provide a simple foundation for constructing a unified approach to a menu of growth models including (1)−(5) cited earlier. To achieve this goal, it is necessary first to incorporate (7) into a formal mathematical problem. Begin by rewriting (6) and (7), respectively, as follows:

$$(9)\quad \frac{dY}{dt} = YZ,$$

$$(10)\quad \frac{dZ}{dt} = -Z(a + bZ).$$

Equations (9) and (10) together comprise a pair of differential equations for the two functions $Y(t)$ and $Z(t)$. They can be solved if suitable end conditions are specified. For example, it is enough to require that the size take two specific values at two particular times, that is,

$$(11)\quad Y(\tau_1) = y_1,$$

$$(12)\quad Y(\tau_2) = y_2.$$

It is also enough to specify both Y and Z at one particular time, that is,

$$(13)\quad Y(\tau_1) = y_1,$$

$$(14)\quad Z(\tau_1) = z_1.$$

The formal development of the previous paragraph can be stated informally in the language of biology. Let τ_1 and τ_2 be two particular ages in the life of a fish. For example, τ_1 might be the age of a young fish and τ_2 the age of an old fish. Then, given the growth law (7), the fish's entire growth curve $Y(t)$ is determined from its sizes y_1 and y_2 at ages τ_1 and τ_2. The resulting curve depends on the four parameters in (9)−(12), namely a, b, y_1, and y_2. The two times τ_1 and τ_2 are regarded as chosen and fixed by the biologist. Similarly, given the growth law (7), the fish's entire growth curve $Y(t)$ is determined by its size y_1 and relative growth rate z_1 at a particular time τ_1. In this case the curve $Y(t)$ depends on the four parameters in (9)−(10) and (13)−(14), namely a, b, y_1, and z_1.

Mathematically, (9)−(12) is a *two-point boundary value problem*. For convenience, call it Problem (I). Also, (9)−(10) and (13)−(14) is an *initial value problem*. Call it Problem (II). The solutions to both Problems (I) and (II) for both Y and Z are obtained in Appendix A. It turns out that the solution to (II) involves formulas which look a bit more compact than the solution to (I). However, for reasons which will be made clear in the statistical analysis later, the main emphasis in this paper is on the solution $Y(t)$ to Problem (I). The form of the solution depends on whether or not the parameters a and b are zero. Explicitly, the solution in the four possible cases turns out to be:

Case 1: $a \neq 0,\ b \neq 0$

$$(15)\quad Y(t) = \left[y_1^{\,b} + (y_2^{\,b} - y_1^{\,b})\,\frac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}}\right]^{1/b},$$

Case 2: $a \neq 0,\ b = 0$

$$(16)\quad Y(t) = y_1 \exp\left[\log\,(y_2/y_1)\frac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}}\right],$$

Case 3: $a = 0,\ b \neq 0$

$$(17)\quad Y(t) = \left[y_1^{\,b} + (y_2^{\,b} - y_1^{\,b})\frac{t - \tau_1}{\tau_2 - \tau_1}\right]^{1/b},$$

Case 4: $a = 0,\ b = 0$

$$(18)\quad Y(t) = y_1 \exp\left[\log\,(y_2/y_1)\frac{t - \tau_1}{\tau_2 - \tau_1}\right].$$

It is assumed throughout this paper that $y_2 > y_1 > 0$ and $\tau_2 > \tau_1$. Thus, the model describes growth, as opposed to shrinkage, in fish size.

There are four basic facts to realize about equations (15)−(18). First, they result from solving Problem (I), that is, equations (9)−(12). In fact, it is reasonably easy to see at once that (11) and (12) are satisfied. Simply substitute $t = \tau_1$ or $t = \tau_2$ in the right-hand side of any equation (15)−(18) and note that the expression collapses to y_1 or y_2. Second, even if the formulas (15)−(18) look a bit complicated and unfamiliar, they determine a growth curve $Y(t)$ from the four parameters a, b, y_1, and y_2. (Remember that τ_1 and τ_2 are ages fixed by the biologist for the species in question; typically τ_1 and τ_2 are young and old ages for a fish.) Third, although (15)−(18) look like four distinct formulas for $Y(t)$, in a numerical sense they are all one formula. If, for example, b is allowed to approach 0 in (15), then the limiting value of $Y(t)$ is given by (16). Indeed, (15) is undefined when $b = 0$. Fourth, the formulas (15)−(18) incorporate all the models (1)−(5) and many others as well. Table 1 lists a number of special cases.

To see how the formulas (15)−(18) do indeed translate to models like (1)−(5), it is necessary to do a little algebraic tinkering in each case. For example, it turns out that equations (1) and (15) both have the general form

$$Y(t) = (\alpha + \beta e^{\gamma t})^{\delta}$$

for constants α, β, γ, δ. Consequently, (1) and (15) represent the same curve with different sets of four parameters. In particular, (1) uses y_∞, g, t_0, and p, while (15) uses a, b, y_1, and y_2. Each of these parameter sets can easily be transformed to the other. For example, in this case $g = a$ and $p = 1/b$. Expressions for y_∞ and t_0 are given in the next section. Incidentally, the von Bertalanffy growth law (1) with $p = 1$ was rewritten parametrically in a form very similar to (15) with $b = 1$ by Schnute and Fournier (1980). They used this form to obtain statistically stable estimates for mean length at age from length−frequency data.

In spite of the similarities, there is a very important difference between (15)−(18) and a list of models like (1)−(5). As stated above, (15)−(18) really constitute a single equation

TABLE 1. Special cases of the general model (15)−(18). For a historical review of model origins, see Ricker (1979). It is assumed in (15)−(18) that $\tau_2 > \tau_1$ and $y_2 > y_1 > 0$.

Choice of a,b	Model title(s)	Equation
$a>0,\ b>0$	Generalized von Bertalanffy	(1)
$a>0,\ b=1$	Pütter No. 1 Specialized von Bertalanffy	(1) with $p=1$
$a>0,\ b=\frac{1}{3}$	Putter No. 2	(1) with $p=3$
$a>0,\ b=0$	Gompertz	(3)
$a>0,\ b<0$	Richards	(2)
$a>0,\ b=-1$	Logistic	(4)
$a=0,\ b=1$	Linear	(5)
$a=0,\ b=\frac{1}{2}$	Quadratic	(19)
$a=0,\ b=0$	tth power	(20)
$a<0,\ b=1$	Exponential	(21)

expressed in several limiting forms. By contrast, (1)−(5) are separate equations, and it is impossible on the surface to see how they relate continuously to each other. For example, (1) *always* crosses the t-axis at $t = t_0$, while (3) *never* crosses that axis. It simply isn't clear how to manipulate the four parameters in (1) to obtain (3) as a limiting three-parameter model. This difficulty has practical consequences, illustrated numerically later.

Another new feature in the system (15)−(18) is that it includes more models than those considered relevant historically. Authors have primarily focused on models in which growth is asymptotic, that is, models which imply a limiting animal size. Yet the attitude toward such models is, at best, hesitant. Ricker (1979) includes a section titled "Asymptotic growth: is it real?" Knight (1968) writes about "Asymptotic growth: an example of nonsense disguised as mathematics." Equations (15)−(18) allow this whole debate to be resolved simply, because they include non-asymptotic models. This gives the actual size-at-age data the freedom to select the most appropriate model, asymptotic or not. The parameter estimates summarize the data's choice. For example, when $a = 0$ and $b = \frac{1}{2}$, the model takes the form

$$(19)\quad Y(t) = (\alpha + \beta t)^2$$

with $\beta > 0$, that is, quadratic growth. If $a = 0$ and $b = 0$, the model becomes essentially

$$(20)\quad Y(t) = \alpha\beta^t$$

with $\alpha > 0$ and $\beta > 0$, that is, t-th power growth. As a final example, if $a < 0$ and $b = 1$, the model reduces to the exponential growth equation

$$(21)\quad Y(t) = \alpha + \beta e^{\gamma t}$$

with $\beta > 0$ and $\gamma > 0$.

Model Parameters

The model (15)−(18) may or may not define a curve which crosses the y-axis, has an inflection point, or exhibits asymptotic behavior. If a particular curve has these properties, then parameters can be associated with them. Table 2 lists notation for such parameters, along with others pertinent to the model. As formulated here, the model is cast in terms of two specified parameters, τ_1 and τ_2, and four free parameters, a, b, y_1, and y_2. The remaining parameters in Table 2, if they exist, can be expressed in terms of these quantities. (See Appendix B for the required mathematical derivations.) For example, the relative growth rates z_1 and z_2 at times τ_1 and τ_2, turn out to be

$$(22)\quad z_1 = \frac{de^{-a\tau_1}}{cy_1^{\ b}},$$

$$(23)\quad z_2 = \frac{de^{-a\tau_2}}{cy_2^{\ b}}$$

where

$$c = \begin{cases} (e^{-a\tau_2} - e^{-a\tau_1})/a, & a \neq 0, \\ \tau_2 - \tau_1, & a = 0, \end{cases}$$

$$d = \begin{cases} (y_2^{\ b} - y_1^{\ b})/b, & b \neq 0, \\ \log\,(y_2/y_1), & b = 0. \end{cases}$$

The parameters c and d are introduced in (22) and (23) to simplify the treatment of the four cases resulting from whether or not a or b or both are 0.

If $b = 0$, then it can be shown (Appendix B) that there is no age τ_0 corresponding to a projected size 0. Similarly, if $a = 0$, then the growth curve is not asymptotic and has no inflection point. When they exist, the parameters appropriate to size 0, asymtotic size, and inflected growth are (Appendix B):

$$(24)\quad \tau_0 = \begin{cases} \tau_1 + \tau_2 - \dfrac{1}{a}\log\left[\dfrac{e^{a\tau_2}y_2^{\ b} - e^{a\tau_1}y_1^{\ b}}{y_2^{\ b} - y_1^{\ b}}\right]; & a \neq 0,\ b \neq 0; \\ \tau_1 + \tau_2 - \dfrac{\tau_2 y_2^{\ b} - \tau_1 y_1^{\ b}}{y_2^{\ b} - y_1^{\ b}}; & a = 0,\ b \neq 0; \end{cases}$$

$$(25)\quad y_\infty = \begin{cases} \left[\dfrac{e^{a\tau_2}y_2^{\ b} - e^{a\tau_1}y_1^{\ b}}{e^{a\tau_2} - e^{a\tau_1}}\right]^{1/b}; & a \neq 0,\ b \neq 0; \\ \exp\left(\dfrac{e^{a\tau_2}\log y_2 - e^{a\tau_1}\log y_1}{e^{a\tau_2} - e^{a\tau_1}}\right); & a \neq 0,\ b = 0; \end{cases}$$

$$(26)\quad \tau^* = \begin{cases} \tau_1 + \tau_2 - \dfrac{1}{a}\log\left[\dfrac{b(e^{a\tau_2}y_2^{\ b} - e^{a\tau_1}y_1^{\ b})}{y_2^{\ b} - y_1^{\ b}}\right]; & a \neq 0,\ b \neq 0; \\ \tau_1 + \tau_2 - \dfrac{1}{a}\log\left[\dfrac{e^{a\tau_2} - e^{a\tau_1}}{\log\,(y_2/y_1)}\right]; & a \neq 0,\ b = 0; \end{cases}$$

$$(27)\quad y^* = \begin{cases} \left[\dfrac{(1-b)\,(e^{a\tau_2}y_2^{\ b} - e^{a\tau_1}y_1^{\ b})}{e^{a\tau_2} - e^{a\tau_1}}\right]^{1/b}; & a \neq 0, b \neq 0; \\ \exp\left(\dfrac{(e^{a\tau_2}\log y_2 - e^{a\tau_1}\log y_1)}{e^{a\tau_2} - e^{a\tau_1}} - 1\right); & a \neq 0,\ b = 0; \end{cases}$$

TABLE 2. A list of possible parameters associated with the model (15)−(18). The final five parameters may not always exist. When τ_0 and y_∞ exist, they may not have the significance shown here.

Parameter	Defining equation	Units	Description
τ_1	—	Time	First specified age
τ_2	—	Time	Second specified age
a	See (7)	Time^{-1}	Constant relative rate of relative growth rate
b	See (7)	Dimensionless	Incremental relative rate of relative growth rate
y_1	$y_1=Y(\tau_1)$	Size	Size at age τ_1
y_2	$y_2=Y(\tau_2)$	Size	Size at age τ_2
z_1	$z_1=Z(\tau_1)$	Time^{-1}	Relative growth rate at age τ_1
z_2	$z_2=Z(\tau_2)$	Time^{-1}	Relative growth rate at age τ_2
τ_0	$Y(\tau_0)=0$	Time	Age of theoretical zero size
τ^*	$\frac{d^2Y}{dt^2}(\tau^*)=0$	Time	Age of growth inflection
y^*	$y^*=Y(\tau^*)$	Size	Size at age of inflection
z^*	$z^*=Z(\tau^*)$	Time^{-1}	Relative growth rate at age of inflection
y_∞	$y_\infty=\lim_{t\to\infty}Y(t)$	Size	Asymptotic size

$$(28)\quad z^* = \frac{a}{1-b}.$$

As in earlier equations, the expression pairs (24)−(27) each comprise one continuous numerical result; that is, the second formula simply gives the limiting form of the first when one parameter vanishes. Even if $a \neq 0$ and $b \neq 0$, it may still happen that some of the parameters (24)−(27) fail to exist. For example, if the argument of the logarithm, i.e. the expression in brackets, is negative in (24), then τ_0 is undefined. It may also happen that τ_0 and y_∞ do not have their usual significance related to size 0 and asymptotic size. All such difficulties are put into complete perspective in the next section.

Equations (22)−(28), although perhaps slightly complex, achieve the main purpose of this section: to express the last seven parameters of Table 2 in terms of the first six. The final equation (28) stands out in this list because of its simple form. Notice that the relative growth rate z^* at an inflection point depends *only* on a and b, not on τ_1, τ_2, y_1, or y_2. In essence z^* is determined by the differential equation (7) alone, regardless of the boundary conditions. Two other interesting parameters also have this property, namely, (i) the time interval $\tau^* - \tau_0$ between the projected age at size 0 and the age of growth inflection and (ii) the fraction y^*/y_∞ of asymptotic size achieved by the age of growth inflection. Explicity, in terms of a and b, these parameters are (Appendix B):

$$(29)\quad \tau^* - \tau_0 = \frac{1}{a}\log\left(\frac{1}{b}\right),$$

$$(30)\quad y^*/y_\infty = (1-b)^{1/b}.$$

Equations (29) and (30) give full mathematical expression to the earlier discussion of S-curve characteristics. Notice that b determines the ratio y^*/y_∞, which is just the ratio of heights of the lower S-arc and the full S. Similarly, once b is fixed, then $\frac{1}{a}$ determines the width $\tau^* - \tau_0$ of the lower S-arc.

As suggested in the previous section, the formulas (24)−(26) lead to a simple practical result. Suppose that, given two specified ages τ_1 and τ_2, the four parameters a, b, y_1, and y_2 are found appropriate to a growth model (15)−(18). Then, provided they exist, the traditional parameters τ_0, y_∞, and τ^* can be found at once from (24)−(26). The curve can then be expressed equivalently in either von Bertalanffy form

$$(31)\quad Y(t) = y_\infty(1 - e^{-a(t-\tau_0)})^{1/b},$$

or Richards form

$$(32)\quad Y(t) = y_\infty(1 - b\,e^{-a(t-\tau^*)})^{1/b},$$

where (31) and (32) are counterparts to (1) and (2), respectively, in the notation of Table 2. Consequently, in some cases, alternative sets of four parameters, such as (y_∞, τ_0, a, b) or (y_∞, τ^*, a, b), can also be used to describe the curve. There is, nevertheless, a compelling reason to focus primarily on (y_1, y_2, a, b). These parameters exist for any curve in the family, while other parameters, such as y_∞, τ_0, and τ^*, may not.

Historically, it is possible to see how first-order differential equations gave a limited view of available growth curves. Both (31) and (32) satisfy

$$(33)\quad \frac{dY}{dt} = \frac{a}{b}\left[\left(\frac{y_\infty}{Y}\right)^b - 1\right]Y.$$

This first-order three-parameter differential equation (proved in Appendix B) makes it seem as if y_∞ needs to be a model parameter. By contrast, the second-order two-parameter dif-

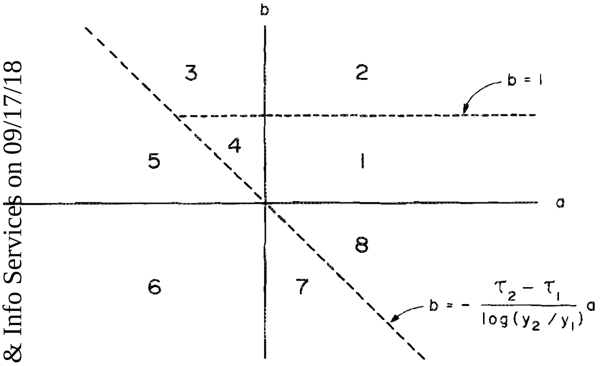

FIG. 1. Set of eight regions in the a,b-plane defined by four lines. The solid lines correspond to the a-axis and b-axis. The broken line parallel to the a-axis is defined by $b = 1$. The diagonal broken line with negative slope corresponds to equation (34) in the text.

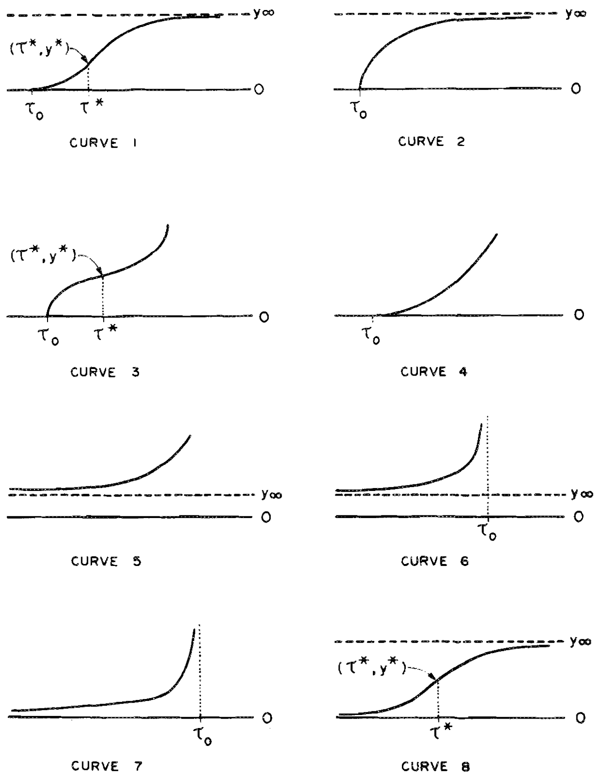

FIG. 2. Set of eight characteristic growth curves appropriate to a parameter pair (a,b) in each of the eight regions shown in Fig. 1. The curves all represent plots of size Y on the vertical scale against age t on the horizontal scale.

ferential equation (7) or (8) avoids this impression and leads one to consider the larger family of curves (15)−(18).

Model Properties

The parameters τ_0, y_∞, τ^*, and y^* are defined in (24)−(27) only when the expressions in square brackets are positive. As Appendix C shows, this seemingly troublesome problem turns out, in fact, to be a major clue for understanding the various faces of the model (15)−(18). There are eight possible characteristic shapes for growth curves. These depend primarily on the two parameters a and b. Figure 1 shows the a,b-plane divided into eight regions by four lines: the a-axis, the b-axis, the line $b = 1$, and the sloping line

$$(34) \quad b = -\frac{\tau_2 - \tau_1}{\log (y_2/y_1)}a.$$

Notice that only the fourth line (34) involves the remaining parameters τ_1, τ_2, y_1, and y_2. It is guaranteed to have negative slope by the assumptions that $\tau_2 > \tau_1$ and $y_2 > y_1 > 0$. Figure 2 displays a collection of eight typical growth curves. A simple rule determines which curve fits a particular parameter set (τ_1, τ_2, y_1, y_2, a, b). First determine the number of the region in Fig. 1 where the pair (a,b) lies; then find the curve so numbered in Fig. 2, Appendix C gives mathematical justification for this correspondence between Fig. 1 and Fig. 2. Notice that the curves in Fig. 2 show which parameters τ_0, y_∞, τ^*, y^* are defined for each case.

It may happen that the point (a,b) lies on a boundary between two regions in Fig. 1, or even on one of the three vertices where the boundary lines meet. In such cases, the appropriate characteristic curve in Fig. 2 may be unclear. This section concludes with a detailed description of all the various possibilities.

One general principle should be considered whenever the model (15)−(18) is applied: an empirical curve can represent size-at-age data only for those ages with known size. A curve may be quite unrealistic when applied to an entire fish life, yet may give a completely adequate description of one life phase. For example, models which predict eventual growth to infinite size are not necessarily inappropriate over a limited period of rapid growth, such as the larval stage.

Case 1: $0 < a$, $0 < b < 1$.

This case represents the classical situation in which all parameters of Table 2 are defined. The curve is S-shaped and asymptotic with limiting size y_∞. It has an inflection point (τ^*, y^*), and it crosses the t-axis at age τ_0.

Case 2: $0 < a$, $1 \le b$,

In this case the curve is asymptotic and crosses the t-axis, but it has no inflection point. On the boundary where $b = 1$, the model corresponds to the specialized von Bertalanffy curve (1) with $p = 1$. This three-parameter curve (also called a Pütter No. 1 curve by Ricker (1979)) is typically used in the particular case when "size" refers to "length." There is really no a priori reason to limit the model in this way. Analysis of variance (described later) can be used to decide when it is appropriate to restrict one or more parameter values.

Case 3: $-b \log(y_2/y_1)/(\tau_2 - \tau_1) < a \le 0$, $1 < b$.

When (a,b) lies in this region, the growth curve is a not asymptotic, but becomes unbounded. It crosses the t-axis at age τ_0, and an initial period of decelerated growth begins at this age. The curve continues later with an indefinite period of accelerated growth. Such curves may not occur commonly, but it is easy to imagine circumstances in which they might be appropriate. If a young fish experiences a difficult struggle for food until it reaches a critical size y^* (when things get increasingly better), then its growth pattern might follow a curve of this type.

As the point (a,b) approaches the boundary where $a = 0$, the final period of accelerated growth moves to the right. When $a = 0$, the curve represents unbounded decelerated growth. The line $a = 0$ between regions 2 and 3 is also a limiting possibility for case 2, where y_∞ becomes infinite as a approaches 0.

Case 4: $-b \log(y_2/y_1)/(\tau_2 - \tau_1) < a \leq 0,\ 0 \leq b \leq 1.$

Here the corresponding curve starts on the t-axis and continues upward with unbounded accelerated growth. Such a curve might represent fish growth restricted, say, to the larval stage. The particular case $(a,b) = (0,1)$ corresponds to linear growth; that is, the curve becomes a straight line (no acceleration) with positive slope. This point (0,1) is on the boundary of regions 1, 2, 3, and 4. The reader can perhaps see from Fig. 2 how a straight line could be a limiting possibility for each of the four relevant curves.

Case 5: $a \leq -b \log (y_2/y_1)/(\tau_2 - \tau_1),\ 0 \leq b.$

As in case 4, the curve here also represents unbounded accelerated growth. The difference is that the curve in this case cannot be extrapolated back to a theoretical age τ_0 corresponding to size 0. Instead, there is a theoretical minimum size y_∞. Notice in Fig. 2 the unconventional significance of the parameter y_∞ here. Curves of this type might describe fish growth during a rapid developmental stage which begins slowly at size y_∞.

As the point (a,b) moves to the boundary of this region, the parameter y_∞ moves towards 0. Thus, on the region boundary, the t-axis is a lower asymptote to the curve. This property also applies to the special point $(a,b) = (0,0)$, which lies on the boundary of regions 1, 4, 5, 6, 7, and 8. At this vertex, the model reduces to t-th power growth, equation (18) or (20).

Case 6: $a < 0,\ b < 0.$

Here the curve is similar to the previous case, but with a rather dramatic extra feature. Growth is now so rapid that the fish theoretically reaches infinite size by the finite age τ_0. In this context both the parameters y_∞ and τ_0 have unconventional significance. Curves of this type might apply to a life stage where increased size continually makes the fish more accessible to an increased food supply. While it lasts, such a positive feedback effect could lead to extremely accelerated growth.

Case 7: $0 \leq a \leq -b \log (y_2/y_1)/(\tau_2 - \tau_1),\ b < 0.$

This case is almost the same as the previous one, except that the lower asymptote is now the t-axis. As the parameter pair (a,b) approaches the sloping line (34), that is, the boundary between regions 7 and 8, the parameter τ_0 becomes infinite. In this limiting situation, the curve simply represents unbounded accelerating growth.

Case 8: $-b \log (y_2/y_1)/(\tau_2 - \tau_1) < a,\ b \leq 0.$

Here the curve is S-shaped once again. Unlike the classical situation of case 1, however, the curve does not extrapolate back to the t-axis. Instead, it has the t-axis as a lower asymptote. Such a curve might be appropriate if early fish growth is extremely gradual.

Model Errors and Nonlinear Estimation

So far the model (15)−(18) has been posed deterministically, as if the data never deviated from the growth curve. Obviously this is unrealistic, and statistical assumptions are required to make the model workable. To be explicit, suppose that n fish are each sampled to determine an observed size $\hat{Y}$ and age t. This gives n data points $(t_i, \hat{Y}_i)$, $i = 1, 2, \ldots n$. For each age t_i, there is a corresponding size Y_i predicted by the model. Two common error assumptions are

$$(35)\quad \hat{Y}_i = Y_i + \sigma_1\epsilon_i; \qquad i = 1, \ldots, n;$$

$$(36)\quad \hat{Y}_i = Y_i e^{\sigma_2\epsilon_i}; \qquad i = 1, \ldots, n;$$

where the random variables ϵ_i $(i = 1, \ldots, n)$ are assumed to be independent and normal with mean 0 and variance 1. In (35) the errors are additive, and the parameter σ_1, which has units of size, measures the additive standard error in prediction. The second model (36) includes multiplicative errors. The dimensionless parameter σ_2 measures the logarithmic standard predictive error.

In some cases the data collection process may suggest more complex models which admit errors in both the size Y and age t. Such models could easily be formulated, but their analysis would be a digression from the main purpose of this paper. Regardless of the model, the practitioner is ultimately faced with a nonlinear parameter estimation problem. For example, parameter estimates for (35) are obtained by minimizing the sum of squares

$$(37)\quad S_1(y_1,y_2,a,b) = \sum_{i=1}^{n} \left[\hat{Y}_i - Y_i(y_1,y_2,a,b)\right]^2.$$

In (37) τ_1 and τ_2 are presumed fixed, so that the predicted sizes Y_i and the sum S_1 depend on the remaining parameters. Similarly, estimates for the model (36) require minimizing

$$(38)\quad S_2(y_1,y_2,a,b) = \sum_{i=1}^{n} \left[\log (\hat{Y}_i/Y_i(y_1,y_2,a,b))\right]^2.$$

At this point, the practitioner often feels alienated from the analysis. If the sums S_1 and S_2 could be minimized by linear regression, then the estimation problem would be considered finished. Since the parameters enter the model nonlinearly, the need to minimize S_1 or S_2 sometimes seems to be a tremendous technical impediment. Not surprisingly, the historical literature on this problem includes numerous intricate and specialized methods for estimating parameters in related models, like (1), (2), (3), or (4).

In my experience, there are two common misconceptions about nonlinear estimation. (I might add that I began work on nonlinear problems a few years ago with these misconceptions alive and well in my own mind.) The first is the belief that technical methods for finding a minimum are necessarily complex and difficult to use. The second is that, if such a method were easily available, then it would solve the problem completely, just as linear regression does. Reality often flies in the face of both beliefs. Modern computing technology makes it easy to interface with good minimization methods. Yet, when programs are implemented, mysterious problems may occur and the search for a minimum can seem endless.

As an explicit example, suppose that the practitioner wishes to describe a data set with model (1), generalized von Bertalanffy growth. The problem, apparently, is to estimate y_∞, g, t_0, and p. This can be done quite easily, for example, with the aid of a general function minimization program written by Schnute (1981). (See Appendix D for further details.) The practitioner need only supply a few lines of code to define model (1), and the computer does the rest. In spite of this simple implementation, the method may fail, as illustrated in the next section. The difficulty lies not with the search method, but with the model posed. Here is the crux of the issue, typical in nonlinear estimation. It's easy enough to set up a minimizing scheme; the real problem centers on formulating the model in terms of estimable parameters. That is why the bulk of this paper is spent placing the model on a proper parametric foundation. Once this is accomplished, statistical questions can be resolved rather easily.

Unfortunately, the concept of "proper parameters" isn't easy to define in general. There is an art to choosing the right parameters for a particular nonlinear model. The growth model in this paper illustrates three possible guidelines for making that choice. First, the parameters should, if possible, relate directly to the data. Here y_1 and y_2 have this property because they correspond to actual points on the growth curve. Second, the parameters should be influenced only slightly by minor changes in the model. Here, for instance, z_1 and z_2 might be poor choices of parameters. Minor curve changes would influence the slopes z_1 and z_2 more than the positions y_1 and y_2. Such reasoning led to the earlier decision to formulate the model here from problem (I), rather than (II).

The two guidelines just cited both relate to *local* dependence of the model on its parameters. The third guideline deals with *global* parameter variations. As the parameters tend to the limits of definition, they should not define a potentially useful curve. For instance, model (1) can tend to a perfectly reasonable Gompertz curve as t_0 and p become infinitely large negative and positive, respectively, as illustrated in the next section. The model (15)–(18) does not suffer a similar defect. It can be shown that, as the point (a,b) moves to infinity in any direction, the corresponding curve in Fig. 2 becomes one with a sudden jump at one of the ages τ_1, τ_2, or τ^*. Such curves are unrealistic; consequently, any useful curve must indeed correspond to a finite point (a,b).

Example

In connection with his discussion of von Bertalanffy growth, Ricker (1975, p. 226) lists length and weight data for ciscoes (*Coregonus artedii*) from Vermilion Lake, Minnesota. The mean weights in grams for ages 2–11 are given, respectively, as 99, 193, 298, 383, 462, 477, 505, 525, 539, and 539. These means are based on different numbers of fish at each age, so parameter estimates might perhaps be found by minimizing a weighted sum of squares S_1 or S_2. For the sake of simple illustration, however, consider the problem of fitting model (1) with additive errors (35) to these 10 data points. This can be accomplished, as described earlier, with the aid of software by Schnute (1981). (See Appendix D.)

Table 3 summarizes the results of the fitting process, which begins with a wild guess at point No. 1 ($y_\infty = 550$, $g = 0.5$, $t_0 = 0$, $p = 1$). This rather poor choice gives a large initial sum of squares S_1. For a start, model (1) is restricted to the special case $p = 1$, the Pütter No. 1 curve (Table 1). After about 160 calculations of S_1, the algorithm easily locates point No. 2, where S_1 is minimized subject to the requirement that $p = 1$.

Traditionally, the Pütter No. 1 curve ($p = 1$) is used to describe lengths, while weights are presumed to follow a Pütter No. 2 ($p = 3$). The logical basis for this choice is that weight is volumetric and should therefore relate to length cubed. Point No. 3 in Table 3 shows the relevant parameter estimates with this assumption. Notice that the sum of squared model errors S_1 at point No. 3 (615.3) is only about 35% of its value at point No. 2 (1755.3). Consequently, the three-parameter Pütter No. 2 curve really does fit the cisco weight data better than the three-parameter Pütter No. 1 curve.

It remains only to free the fourth parameter p to see how much the fit can be improved with the general model (1). Point No. 4 in Table 4 represents a failed attempt to do so. Once the algorithm is allowed to tamper freely with p, it succeeds in reducing S_1 gradually by increasing p and decreasing t_0 endlessly. Here this search is arbitrarily stopped at point No. 4 in Table 4, after several hundred calculations of S_1. Apparently, an optimum model (1) cannot be located.

TABLE 3. The sum of squares S_1 for cisco weight data (see text) and model (1) at four points. Point No. 1 is a starting point for the search algorithm. Points 2 and 3 correspond to minima for S_1 when $p = 1$ and $p = 3$, respectively. Point No. 4 is reached by stopping the algorithm arbitrarily during an endless search for a general minimum.

	1	2	3	4
		S_1		
	171660	1755.3	615.3	429.0
y_∞	550	584.0	555.5	548.1
g	0.5	0.3031	0.4574	0.5304
t_0	0	1.488	0.2746	−4.363
p	1	1	3	50.38

TABLE 4. The sum of squares S_1 for cisco weight data (see text) and model (15)−(16) at six points. The first four points are taken from Table 3. Points 5 and 6 correspond to minima for S_1 in (15) and (16), respectively. Parameters absent from this Table are not defined.

	1	2	3	4	5	6
			S_1			
	171660	1755.3	615.3	429.0	398.0	423.1
y_1	347.7	84.02	90.32	94.83	97.81	95.05
y_2	547.8	551.3	543.3	540.2	538.2	539.9
a	0.5	0.3031	0.4574	0.5304	0.5801	0.5356
b	1	1	0.3333	0.01985	−0.1890	0
τ_0	0	1.488	0.2746	−4.363	—	—
τ^*	0	1.488	2.676	3.027	3.218	3.046
y_∞	550	584.0	555.5	548.1	544.1	547.6
y^*	0	0	164.6	199.6	217.7	201.4
z^*	—	—	0.6861	0.5411	0.4879	0.5356
z_1	0.2910	1.804	1.142	0.9469	0.8502	0.9380
z_2	0.002052	0.01796	0.01023	0.007731	0.006339	0.007560
Region	2	2	1	1	8	8

The first four columns of Table 4 present the same four points as Table 3, except that all parameters cited in Table 2 are listed. Throughout Table 4, τ_1 and τ_2 have been fixed at 2 and 11, respectively, the lowest and highest observed ages. Notice particularly the key parameters of this paper: y_1, y_2, a, and b. These reveal the essence of the apparent problems in Table 3. For example, the initial point No. 1 is obviously ill-chosen because the parameter y_1 (weight at age 2) surely should be somewhere near 100 g, rather than 347.7 g as shown. (See the data at the start of this section.) More importantly, the convergence problem for model (1) at point No. 4 now comes into focus. Table 4 shows that b is nearly 0 at this point. In fact, p becomes positive infinite and t_0 becomes negative infinite as b approaches 0. Using model (15), rather than model (1), the search algorithm easily finds point No. 5, where S_1 is minimized for all four parameters in (15). Explicitly, starting at point No. 1, the algorithm requires fewer than 300 calculations of S_1 to locate point No. 5. This point has the remarkable property that, while it determines just another curve (15), it corresponds to no curve at all of the form (1). This happens because t_0 is not defined at point No. 5.

In terms of the regions in Fig. 1, the search algorithm starts at point No. 1 on the lower boundary of region 2. It then moves across region 1 to locate a minimum for S_1 at point No. 5 in region 8. Consequently, when guided by model (1), the search is doomed to failure. Curves in region 8 can't be described by model (1) because t_0 is not defined there. Consequently, a legendary piece of comic advice to the lost traveller applies literally in this case: "Come to think of it, sir, you can't get there from here." This difficulty epitomizes the importance of the third guideline for choosing parameters, discussed in the last section.

Table 4 also illustrates the other two guidelines. In connection with the first, notice that the estimates for y_1 and y_2 in Table 4 are reasonably close to the observed sizes 99 and 539 g, respectively, at ages 2 and 11. Also, the estimates for z_1 and z_2 vary more with small changes in S_1 than y_1 and y_2. This confirms parameter behavior anticipated by the second guideline.

The analysis does not stop with the determination of point No. 5. It may be that a three-parameter submodel could be used to describe the data adequately. Earlier discussion shows that, for two particular such curves, a Pütter No. 2 ($b = \frac{1}{3}$) should be chosen in preference to a Pütter No. 1 ($b = 1$). Yet point No. 5, the optimum four-parameter model, has a small negative value for b. This suggests considering a Gompertz model ($b = 0$, Table 1), defined in the notation of this paper by (16). Point No. 6 in Table 4 shows the parameter estimates in this case. Since S_1 is even smaller at point No. 6 than at point No. 3, a Gompertz model works even better than a Pütter No. 2.

For the cisco weight data, then, the really interesting choice lies between the general four-parameter model (15) and the three-parameter Gompertz submodel (16). To make this choice, consider the variance ratio defined by the residual sum of squares for model (16) divided by the sum of squares for (15):

$$\frac{(423.1 - 398.0)/1}{398.0/6} = 0.378.$$

If the models were linear in their parameters, this statistic would be F-distributed with 1 and 6 df under the null hypothesis that $b = 0$. (Here 1 df comes from the single parameter b, and $10 - 4$ (i.e. 6) df comes from the 10 data points and the four parameters y_1, y_2, a, and b.) Even for nonlinear models, the above variance ratio is approximately F-distributed when sample sizes are large. Under this approximation, one would reject the null hypothesis at the 5% level if the ratio exceeds

$$F_{0.05}(1,6) = 3.78.$$

The much smaller observed ratio (0.378) suggests retaining the null hypothesis $b = 0$, so that a Gompertz model appears adequate for the data. Once again, this conclusion could not be reached in the context of model (1), because t_0 is not defined when $b = 0$.

This example illustrates how the data can be used objectively in selecting an appropriate model. The general procedure is to begin by locating an optimal four-parameter model (15). Then one can inspect the parameter estimates for a and b in the context of the models listed in Table 1. It may happen that the estimated curve lies close to a three-parameter (or even two-parameter) submodel. In this case, one might estimate the parameters for the submodel and use analysis of variance to make a final choice. Since the latter analysis is approximate at best, this procedure should be considered an informal process, rather than a rigorous statistical analysis. Very often, the action of the search algorithm itself helps to suggest which parameters are well defined. For example, in Table 5, the estimates for y_1, y_2, and a are similar at points 3, 4, 5, and 6, while the estimate for b varies considerably as the sum of squares S_1 changes only slightly. This reinforces the idea of fixing b at some prescribed value (like 0) and determining the other three parameters accordingly.

The example here focuses on problems associated with models in which the parameter pair (a,b) lies near the a-axis in Fig. 1. As the example illustrates, such models lead to difficulties in the definition of τ_0. Other examples can easily be found in which the data indicate a parameter pair (a,b) near the b-axis. In such cases there are similar problems with the definition of y_∞. These problems are precisely the ones which have led writers like Knight (1968) and Ricker (1979) to question the validity of asymptotic growth. Using the right parameters, it would probably be possible to stir up controversy in the literature associated with the boundary between each of the 10 pairs of adjacent regions in Fig. 1. Here is fertile ground for 20 scientific papers, including one for each rebuttal.

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Appendix A. Solutions to Problems (I) and (II)

The solution Y to Problem (I) consists of equations (15)–(18). The corresponding solution Z is:

Case 1: $a \neq 0,\ b \neq 0$

$$\text{(A1)}\quad Z(t) = \frac{a}{b}\,\frac{y_2^{\,b} - y_1^{\,b}}{y_2^{\,b}[e^{a(t-\tau_1)} - 1] + y_1^{\,b}[1 - e^{-a(\tau_2 - t)}]},$$

Case 2: $a \neq 0,\ b = 0$

$$\text{(A2)}\quad Z(t) = \frac{a \log (y_2/y_1)\, e^{-at}}{e^{-a\tau_1} - e^{-a\tau_2}},$$

Case 3: $a = 0,\ b \neq 0$

$$\text{(A3)}\quad Z(t) = \frac{1}{b}\,\frac{y_2^{\,b} - y_1^{\,b}}{y_2^{\,b}(t - \tau_1) - y_1^{\,b}(t - \tau_2)},$$

Case 4: $a = 0,\ b = 0$

$$\text{(A4)}\quad Z(t) = \frac{\log (y_2/y_1)}{\tau_2 - \tau_1}.$$

The solutions Y and Z to Problem (III) are given similarly in the equations:

Case 1: $a \neq 0,\ b \neq 0$

$$\text{(A5)}\quad Y(t) = y_1\left[\frac{a + bz_1\,(1 - e^{-a(t-\tau_1)})}{a}\right]^{1/b},$$

$$\text{(A6)}\quad Z(t) = \frac{az_1\, e^{-a(t-\tau_1)}}{a + bz_1\,(1 - e^{-a(t-\tau_1)})},$$

Case 2: $a \neq 0,\ b = 0$

$$\text{(A7)}\quad Y(t) = y_1 \exp\left[\frac{z_1(1 - e^{-a(t-\tau_1)})}{a}\right],$$

$$\text{(A8)}\quad Z(t) = z_1\, e^{-a(t-\tau_1)},$$

Case 3: $a = 0,\ b \neq 0$

$$\text{(A9)}\quad Y(t) = y_1\left[1 + bz_1(t - \tau_1)\right]^{1/b},$$

(A10) $Z(t) = z_1/[1 + bz_1(t - \tau_1)]$,

Case 4: $a = 0$, $b = 0$

(A11) $Y(t) = y_1 \, e^{z_1(t-\tau_1)}$,
(A12) $Z(t) = z_1$.

To prove the 16 formulas (15)−(18) and (A1)−(A12), begin with problem (II) when $a \neq 0$ and $b \neq 0$. Equation (10) can be written in the form

$$\text{(A13)} \quad \frac{1}{a}\left(\frac{b}{a + bZ} - \frac{1}{Z}\right) dZ = dt.$$

Integrating (A13) with the initial condition (14) gives

$$\text{(A14)} \quad \frac{1}{a}\log\left(\frac{a + bZ}{Z} \cdot \frac{z_1}{a + bz_1}\right) = t - \tau_1.$$

It is possible to solve for Z in (A14), and the result is (A6). Furthermore, it turns out that both the right and left sides of (A6) are logarithmic derivatives. Explicitly, (A6) can be written as

$$\text{(A15)} \quad \frac{d}{dt}\log Y = \frac{1}{b}\frac{d}{dt}\log\left[a + bz_1(1 - e^{-a(t-\tau_1)})\right].$$

Integrating (A15) with the initial condition (13) gives

$$\text{(A16)} \quad \log\left(\frac{Y}{y_1}\right) = \frac{1}{b}\log\left[\frac{a + bz_1(1 - e^{-a(t-\tau_1)})}{a}\right].$$

Solving (A16) for Y gives (A5). This completes the proof of (A5)−(A6).

Equations (A7)−(A12) can now be obtained from (A5)−(A6) by taking limits as the parameters a or b or both tend to 0. The proofs depend on the two results

$$\text{(A17)} \quad \lim_{a \to 0} (1 - e^{-\alpha a})/a = \alpha,$$

$$\text{(A18)} \quad \lim_{b \to 0} (1 + \beta b)^{1/b} = e^{\beta},$$

where α is an expression independent of a, and β is similarly independent of b. For example, equations (A9)−(A10) follow from (A5)−(A6) with the aid of (A17). Similarly, (A7) follows from (A5) because of (A18). The transitions from (A6) to (A8) to (A12) are obvious, and (A11) follows from (A7) by (A17). This completes the proof of solutions (A5)−(A12) for Problem (II).

To obtain solutions to Problem (I), notice from (A5) and the end condition (12) that

$$\text{(A19)} \quad y_2 = y_1\left[\frac{a + bz_1\,(1 - e^{-a(\tau_2-\tau_1)})}{a}\right].$$

Solving (A19) for z_1 gives

$$\text{(A20)} \quad z_1 = \frac{a(y_2{}^b - y_1{}^b)}{by_1{}^b(1 - e^{-a(\tau_2-\tau_1)})}.$$

Substituting (A20) into (A5) and (A6) gives the general solutions (15) and (A1) to Problem (I). The remaining equations (16)−(18) and (A2)−(A4) are limiting forms of (15) and (A1). The transitions require the use of

$$\text{(A21)} \quad \lim_{b \to 0}\left[1 + \beta(\gamma^b - 1)\right]^{1/b} = e^{\beta\log\gamma},$$

where β and γ are independent of b. A related limit, essentially a special case of (A21), is

$$\text{(A22)} \quad \lim_{b \to 0} \frac{y_2{}^b - y_1{}^b}{b} = \log\,(y_2/y_1).$$

Using (A17), (A21), and (A22), one can obtain (16)−(18) and (A2)−(A4) from (15) and (A1). This completes the derivation of solutions to Problem (I).

Appendix B. Parameter Relationships

To obtain the expressions (22)−(23) for z_1 and z_2, simply substitute $t = \tau_1$ and $t = \tau_2$ in (A1)−(A4). Also, if there is a time τ_0 when $y(\tau_0) = 0$, then by (15)

$$\text{(B1)} \quad y_1{}^b + (y_2{}^b - y_1{}^b)\frac{1 - e^{-a(\tau_0-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}} = 0,$$

provided that $b > 0$. Solving (B1) for τ_0 gives the first expression (24). Similarly, the second expression (24) follows from (17). Notice that τ_0 in (24) is not defined for $b = 0$ because, in either case, the fraction has denominator 0 and numerator nonzero.

From the definition (6) for Z, it follows by differentiation that

$$\text{(B2)} \quad \frac{dZ}{dt} = \frac{1}{Y}\frac{d^2Y}{dt^2} - Z^2.$$

Notice that equations (10) and (B2) both describe dZ/dt. Equating right-hand sides and solving for d^2Y/dt^2 gives

$$\text{(B3)} \quad \frac{d^2Y}{dt^2} = YZ[(1 - b)Z - a].$$

Incidentally, by (9), this proves (8). Now if there is a time τ^* when d^2Y/dt^2 vanishes, it follows from (B3) that at least one of three possibilities holds:

(B4) $y^* = 0$,
(B5) $z^* = 0$,
(B6) $(1 - b)z^* - a = 0$.

The possibility (B4) is eliminated by requiring a positive size y^*. Also (B5) can be eliminated because $Z = 0$ gives a singular point for the system (9)−(10); consequently, if Z ever vanishes, then Y and Z must be constant. This leaves (B6) and proves (28).

Define the quantity

(B7) $$k = Y^b(a + bZ).$$

Apparently k is a function of time t, since Y and Z are. However, differentiating k gives

$$\frac{dk}{dt} = bY^b\left[(a + bZ)\frac{1}{Y}\frac{dY}{dt} + \frac{dZ}{dt}\right] = bY^b[Z(a + bZ) - Z(a + bZ)] = 0.$$

Consequently, k is a constant; in particular

(B8) $$k = y_1{}^b(a + bz_1).$$

Combining (B8) and (22) gives the alternative form

(B9) $$k = a\frac{y_2{}^b e^{a\tau_2} - y_1{}^b e^{a\tau_1}}{e^{a\tau_2} - e^{a\tau_1}},$$

when $a \neq 0$. It follows from (B7) that

(B10) $$Y = \left[k/(a + bZ)\right]^{1/b},$$

(B11) $$Z = (kY^{-b} - a)/b,$$

when $b \neq 0$. Equations (B10) and (B11) allow $Y(t)$ and $Z(t)$ to be expressed in terms of each other. Equivalently, these equations describe trajectories in the YZ-plane for the system (9)−(10).

In particular (B10) implies that

(B12) $$y^* = [k/(a + bz^*)].$$

The expression (27) for y^* follows by substituting (28) and (B9) into (B12). As usual, the second expression (27) is a limiting form of the first, where, in this case, (A21) is helpful. Once y^* is found, then τ^* can be determined from (15) by solving

$$y^* = \left[y_1{}^b + (y_2{}^b - y_1{}^b)\frac{1 - e^{-a(\tau^* - \tau_1)}}{1 - e^{-a(\tau_2 - \tau_1)}}\right]^{1/b}$$

for τ^*. This gives (26), where the second expression follows from the first by (A22).

Finally suppose that

$$y_\infty = \lim_{t \to \infty} Y(t)$$

exists. Then the limiting value of Z must be 0, since the growth rate must slow to a stop as the limiting size is reached. Consequently, from (B10)

(B13) $$y_\infty = (k/a)^{1/b}.$$

The formula (25) follows from (B9) and (B13). This completes the proof of all parametric relationships (22)−(28). The final two equations (29) and (30) are simple consequences of (24)−(27). Furthermore, (33) can be proved by combining (B11), (B13), and (6).

Appendix C. Curve Shapes

Substituting the expression (B11) for Z into (8) gives

(C1) $$\frac{d^2Y}{dt^2} = \frac{dY}{dt}\frac{a}{b}(k^*Y^{-b} - 1),$$

where the constant k^* is

(C2) $$k^* = (1 - b)\frac{e^{a\tau_2}y_2{}^b - e^{a\tau_1}y_1{}^b}{e^{a\tau_2} - e^{a\tau_1}}.$$

It is shown in Appendix B that $Z \neq 0$ on any curve; in fact, from the assumptions $y_2 > y_1 > 0$ and $\tau_2 > \tau_1$, it can be proved that $Z > 0$ on the entire curve. Consequently, for positive sizes $Y > 0$, it follows that $dY/dt > 0$. The sign of the curvature (C1), then, is determined by the two factors a/b and $k^*Y^{-b} - 1$. In particular, the curvature is independent of Y if $k^* = 0$. From (C2) this happens if either

(C3) $b = 1$, or

(C4) $$e^{a\tau_2}y_2{}^b = e^{a\tau}y_1{}^b.$$

Equation (C4) is equivalent to (34). Consequently (C3) and C(4) define the two broken lines in Fig. 1.

To prove the correspondence between Fig. 1 and Fig. 2, it is necessary to answer the following two questions for each of the eight regions in Fig. 1:

a) For what values of t is the expression (15) for Y defined?
b) For what values of Y is the curvature (C1) positive, and for what values is it negative?

The answer to (a) hinges on solving the inequality

(C5) $$y_1{}^b + (y_2{}^b - y_1{}^b)\frac{1 - e^{-a(t - \tau_1)}}{1 - e^{-a(\tau_2 - \tau_1)}} > 0$$

for t. Similarly, the answer to (b) involves solving the pair of inequalities

(C6) $$\frac{a}{b}(k^*Y^{-b} - 1) \gtrless 0$$

for Y. Equivalent formulations for (C5) and (C6) are

(C7) $$a\left[e^{a\tau_2}y_2{}^b - e^{a\tau_1}y_1{}^b - (y_2{}^b - y_1{}^b)e^{a(\tau_1 + \tau_2 - t)}\right] > 0,$$

(C8) $$b\left[(1-b)(e^{a\tau_2}y_2{}^b - e^{a\tau_1}y_1{}^b) - (e^{a\tau_2} - e^{a\tau_1})Y^b\right] \gtrless 0.$$

The details of working through (C7)–(C8) in each of the eight regions are too lengthy to present here, but they are straightforward. For example, in region 8 it turns out that

$$a > 0,$$
$$e^{a\tau_2}y_2^{\,b} - e^{a\tau_1}y_1^{\,b} > 0,$$
$$y_2^{\,b} - y_1^{\,b} < 0.$$

These inequalities show that (C7) holds for any t; consequently the curve in region 8 is defined for all time. By contrast, in regions 1, 2, 3, and 4 (C7) holds when $t > t_0$. Similarly (C7) is always true in region 5, but holds only for $t < t_0$ in regions 6 and 7. The analysis of (C8) follows in much the same way. For example, in region 2 the inequalities

$$1 - b < 0,$$
$$e^{a\tau_2}y_2^{\,b} - e^{a\tau_1}y_1^{\,b} > 0,$$
$$e^{a\tau_2} - e^{a\tau_1} > 0,$$

guarantee that the left-hand side of (C8) is always negative. Consequently the curvature is always negative and the corresponding curve in Fig. 2 is convex downward.

To establish the role of y_∞ in Fig. 2, it is necessary to consider the limit of $Y(t)$ in (15) as $t \to -\infty$ or $t \to +\infty$ whenever the curve is defined for arbitrarily large negative or positive t. After the relevant range for t is established from (C7), the required limits in (15) follow easily from the properties of e^{-at}.

Appendix D. Computer Methods

The data analysis in this paper was done with the aid of a general function minimization program written in BASIC by Schnute (1981). The program employs the simplex search method of Nelder and Mead (1965). It will run on many computers, including the Apple II desk-top microcomputer for which it was developed. Schnute's (1981) documentation shows not only how to minimize the particular functions (37) and (38), but also how to employ this software in nonlinear estimation for any small model like the one discussed here. Typically, the practitioner needs to write just a few lines of code describing the model of interest and to key in the relevant data. Of course, the caveats in this paper still apply. For example, the model must be posed so that the search can proceed fruitfully.

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