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Fitting and Using Growth Curves

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Summary. A technique is presented for fitting and analyzing growth patterns using Gompertz, power, and exponential curves. Data collection involves measuring growth rate as a function of size. This is useful because growth rates at many different sizes can be measured at the same time, which removes the effect of environmental change from the observed growth pattern. Using size instead of age as the independent variable is important because size is usually more closely related to growth rate than is age. The particular technique presented here yields estimates of the variance of the curve parameters so that growth curves for different populations can be compared.

Introduction

This paper presents a technique for fitting growth data to differential equations for several commonly used growth curves. Differential equations describe changes in growth rate and often this is better than describing changes in size, as do the integrated forms of the growth equations. It is not unusual to see authors discuss differences in growth rate in the text of an article, suggesting that they are indeed the better measure to use, and then to describe the data with both graphs and equations for the integrated form of the growth curve.

A useful way of recording growth rate is to measure the specific growth rate, or the rate of growth divided by the size. Changes in specific growth rate for a wide variety of organisms can be described with just two parameters. For colonial organisms in particular, but not exclusively, these parameters and the measure of specific growth rate itself can be shown to have great analytic and heuristic value.

The technique presented here for fitting differential equations involving specific growth rate has the following advantages. It allows a comparison of growth curves obtained from several different treatments of the test organism. It permits one to quickly determine which, if any, of several growth curves might best fit the data. It allows one to combine data from a number of different individuals and then to obtain estimates of the variance of the parameters of the curve. The kind of data needed is faster, easier and cheaper to collect than the kind often used for plotting growth curves. And finally, the technique is easier to use than those employed for plotting the integrated curves, often requiring only a hand calculator and the ability to fit a linear regression.

Five Commonly Used Growth Curves

Five growth curves have been used to describe not only the growth of animals, but also the growth of plants, populations, species during evolution, capital, tumors, and products of chemical reactions. They are the exponential, power, Gompertz, logistic and Bertalanffy curves (Fig. 1). The exponential curve describes a pattern of growth in which not only does the size increase with time, but the *rate* at which size increases, itself increases at a rapid rate. The power curve is similar except that the rate at which size increases is variable and the equation can be used to describe more gradual but nevertheless indeterminate growth. It can either be concave up or concave down. The Gompertz and the logistic curves are sigmoid in shape and approach an asymptote with time. The logistic curve is symmetrical about the inflection point, while the Gompertz curve is asymmetrical and approaches the asymptote more gradually than would a logistic curve with a similar early growth trajectory. (The equations for all of these curves are given in Table 1)

The techniques described here are best applied to the expontial, Gompertz, and power curves. They may be applied to the logistic and Bertalanffy curves, but the accuracy of the fit may be in doubt, particularly in the latter case. These two curves are included, however, in order to demonstrate how to tell from the analysis whether they might fit the data better than the others. If they do, more appropriate methods for fitting the curves (see below) can be employed.

Specific Growth Rate

The meaning of specific growth rate (sometimes called relative growth rate) is not at first easy to understand. It is defined as the rate of growth divided by the size. It can also be considered to be the percent increase in size per day and has units of 1/time. If the specific growth rate remains constant for the entire growth of an organism, then the growth curve is exponential. However, specific growth rate usually decreases with increasing size (Bertalanffy 1960) and it is possible to consider growth as an exponential increase in size but with the parameter describing the rate of increase to be constantly decreasing as size increases. The four growth curves other than the exponential curve can be considered to represent different schedules by which the specific growth rate decreases from its initial high value, b. For each different curve, the amount of decrease is mediated by the parameter a. Both a and b are defined more explicitly below.

When population growth is being described with a logistic curve, the equivalent to the initial value of the specific growth rate, b, is the intrinsic rate of increase, usually symbolized as r (Wilson and Bossert 1971). The specific growth rate is then written as r times a factor which decreases with increasing size and ultimately reaches zero when the size reaches K, called the carrying capacity. Here, K is equivalent to S_∞ (see below).

For colonial organisms, the use of specific growth rate is particularly apt because one would expect the rate of growth to be related to the ability to gather food, and often each additional individual added as a colonial organism grows has the

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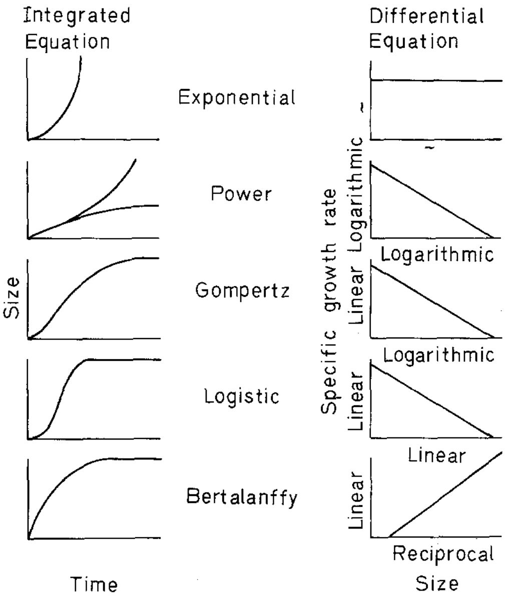

Fig. 1. Graphs of the five growth curves discussed in this paper

Table 1. Growth equations for five common growth curves. In the left hand column are the more commonly used forms of the equations, giving the size (S) as a function of time (t). The center column contains differential equations showing the relationship between the specific growth rate (G), defined in Eq. (1), and the size. The relationship is linear if G and S are properly transformed. S_∞ is the asymptote of the three determinate growth equations. It is commonly used in the integrated forms of the equations. The relationship between S_∞, a, and b is in the right hand column. The parameter t_0 is the constant of integration

Integrated equation	Differential equation	Relation of parameters
Exponential $S=\exp[b(t+t_0)]$	$G=b$	$a=0$
Power $S=[ab(t+t_0)]^{1/a}$	$\ln G=-a\ln S+\ln b$	–
Gompertz $S=S_\infty\exp[-\exp-a(t+t_0)]$	$G=-a\ln S+b$	$\ln S_\infty=\frac{b}{a}$
Logistic $S=S_\infty[1+\exp-b(t+t_0)]^{-1}$	$G=-aS+b$	$S_\infty=\frac{b}{a}$
Bertalanffy $S=S_\infty[1-\exp-b(t+t_0)]$	$G=a\frac{1}{S}-b$	$\frac{1}{S_\infty}=\frac{b}{a}$

same apparatus for collecting food as any other. Specific growth rate can then be considered to be the rate of growth per unit food gathering ability. A similar approach used by botanists is to calculate the rate of growth divided by the total leaf area of a plant (Evans 1972, Ch. 13). Perhaps the same approach would be useful in the study of non-colonial animals where growth rate would be divided by say, gill area, siphon diameter, or gut length.

The use of specific growth rate, besides allowing differential equations to be plotted as straight lines, allows a certain systematic measurement error to be corrected. Such an error, described below, is often introduced when an instantaneous measurement, growth rate, is computed from discrete data points.

Kinds of Data

Two kinds of data can be collected to analyze growth, cross sectional, the kind of data used here, and longitudinal. Cross sectional data, also called mark and recapture data, are collected by recording the growth increment, over a short period of time, of different individuals of different sizes, all simultaneously. This is equivalent to measuring the slope of different parts of the growth curve all at once and effectively compresses the entire lifetime of an organism into one short measurement interval. My definition of cross sectional data is different from others (Tanner 1951; Cock 1966) in that the growth increments are determined at different sizes rather than at different ages. Longitudinal data is a record of the size of one individual at different ages and is collected sequentially as the organism grows.

The use of cross sectional data requires an implicit assumption. It is that all of the individuals represented in the data set are following the same growth trajectory, i.e. that if a small individual in the data set were observed at a later time when it was larger, it would have the same specific growth rate as one of the larger individuals in the data set. This, in fact, is not always so because under natural conditions, environmental changes with time affect the parameters of the growth curve being followed (Kaufmann in prep.). The data do describe, however, the average performance of individuals of different sizes, all under the same set of conditions. This averaging property of cross sectional data can be very useful for comparing different species growing in the same place or the same species growing in different places.

The difference between cross sectional data and longitudinal data is important but often not considered. If environmental conditions are kept constant during the growth of the test organism, then according to the implicit assumption above, a growth curve plotted from longitudinal data would be similar to one fitted from cross sectional data which had all been collected at one time but from different sized organisms. Often, however, longitudinal data are collected in the field while water temperature, amount of sunlight, food supply, and many other things are changing so that the resulting growth curve may not resemble at all the growth curve of the same animal grown under constant conditions. Collecting longitudinal data is appropriate if one is trying to determine how an animal will grow in a particular place and can assume that subsequent years will present the organism with similar conditions, but it does not distinguish between intrinsic growth responses of a species and growth responses due to differences in environment.

Cross sectional data are usually much cheaper and easier to collect than longitudinal data because it can be done in a much shorter time. Also, it is not necessary to raise the organism in the laboratory to keep conditions constant, because all different sizes of the test organism in the field are automatically exposed to the same conditions.

Why Size is Used as the Independent Variable

In this paper, a regression is calculated, using the specific growth rate as the dependent variable and size as the independent variable. Size, rather than age, is used as the independent variable for several reasons. Size is easier to measure than age, especially among animals where there is a lack of age markers, such as growth rings on clams, or where there is little correlation between size and age. This may be common among colonial organisms such as corals (Hughes and Jackson 1980). Large seasonal differences in growth rate among many invertebrates suggest that age alone is an insufficient predicter of growth rate. The well known dependence of metabolic rate in a wide variety of animals

Table 2. Method of determining parameters of three common growth curves from cross sectional data using variations of the Ford-Walford plot. S_1 and S_2 are the sizes of the organism at the beginning and end of some measurement interval Δt days long. When all data pairs, S_1 and S_2, are plotted as indicated, the parameters a or b, and S_∞ may be determined from the slope of the regression using the formula indicated, and the intercept on the abscissa, respectively. The equations of the growth curves are given in Table 1. The value of t_0 must still be determined as explained in the text. 1. After Theisen (1973); 2. After Yamaguchi (1975); 3. Jones (1976)

Type of growth curve	Data to be plotted		Determination of the parameters	
	Ordinate	Abscissa	Slope of regression	Intercept on abscissa
Gompertz[1]	$\ln S_2 - \ln S_1$	$\ln S_1$	$1-e^{-a\Delta t}$	$\ln S_\infty$
Logistic[2]	$\frac{S_2-S_1}{S_2}$	S_1	$\frac{1-e^{-b\Delta t}}{S}$	S_∞
Bertalanffy[3]	S_2-S_1	S_1	$1-e^{-b\Delta t}$	S_∞

on size suggests that size, rather than age, determines growth rate (Bertalanffy 1960, p. 213). Among colonial organisms in particular, where senescence may not be a factor, it seems more realistic to associate growth rate with food gathering area, related to size, rather than with age. While age has most often been implicitly assumed to be a determinant of growth rate, in this paper, size will implicitly be assumed to be so.

Available Techniques for Plotting Cross Sectional Data

Available techniques for plotting cross sectional data are similar to those used most often by fisheries biologists for plotting Bertalanffy curves and are referred to as Ford-Walford plots. In one variation of the Ford-Walford plot (Gulland 1965), the size at the beginning of the measurement period is plotted against the growth increment during the period. The parameters of the curve are determined from a regression line through all of the points plotted in this manner. The same technique may be used to plot a Gompertz curve if the logarithm of the size is substituted for the size (Theisen 1973). This may be demonstrated by taking the logarithm of both sides of a Gompertz equation (see Table 1). With some manipulation, the result is the same as a Bertalanffy equation. A logistic curve may be fitted to the data by dividing the growth increment by the final size of the organism during the measurement period and plotting these values against the initial size (Yamaguchi 1975). A summary of these techniques, adapted to the form of the equations used here, appears in Table 2. The one advantage of Ford-Walford plots is that the estimates of the parameters are not biased in the way described below.

One drawback of Ford-Walford plots is that the time intervals for all the data points must be the same and so data taken with different time intervals cannot be pooled. But, a more important problem is that the parameters of the growth curves are not simply related to the axes of the graph (see Table 2). For example, the parameters a or b do not appear on the graph of the data as either slopes or intercepts but as exponents in a rather complicated term which describes the slope of the regression. In the method of treating cross sectional data described below, it is much easier to conceptualize the mathematical properties of the parameters and to analyze them statistically. In a later paper I will show how this approach makes it easier

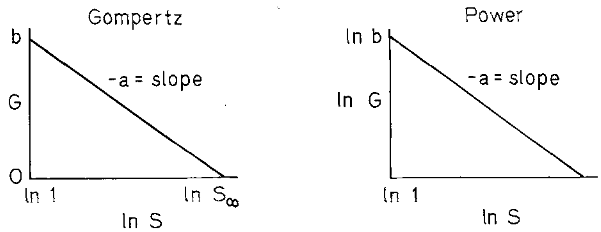

Fig. 2. Graphs of the differential equations of the Gompertz and power curves. G is the specific growth rate and S is the size. S_∞, a, and b are parameters of the curves as described in the text

to use growth equations to isolate different factors affecting growth.

An approach similar to that used here, but using growth rate, rather than specific growth rate, as the independent variable can be used to fit cross sectional data to a Bertalanffy curve (Van Devender 1978). The method takes advantage of the linear relationship between growth rate and size for a Bertalanffy curve. Elliot (1975), uses a method very similar to that used here for fitting a power curve to the growth of brown trout. Both Van Devender and Elliot demonstrate the advantage of using differential equations to describe growth.

Growth Equations – Differential and Integrated Forms

In this section, the integrated form of a Gompertz curve is derived by integrating a differential equation involving the specific growth rate. In practice, this differential equation will be obtained from a regression of the specific growth rate against the size, and the parameters of the regression, a and b, can then be used directly in writing the integrated form.

The specific growth rate (G) is the rate of growth divided by the size (S). S can be any measure such as length, weight, volume, or number of individuals in a colony. The rate of growth is expressed as the quotient of two differentials (dS/dt), where t is the time in days. Hence, the specific growth rate is:

$$G=\frac{1}{S}\frac{dS}{dt}. \quad (1)$$

For a Gompertz curve, G decreases in direct proportion to ln S, the natural logarithm of the size. G can be treated as a variable in an equation describing this relationship, ignoring for the moment that it is a term consisting of differentials. Hence:

$$G=-a\ln S+b \quad (2)$$

where G=specific growth rate; $-a$=constant of proportionality; b=specific growth rate for $\ln S=0$ (i.e. when $S=1$).

A graph of Eq. (2) (Fig. 2) with G on the ordinate and $\ln S$ on the abscissa is a straight line with a slope of $-a$ and an intercept on the ordinate of b.

Because of the definition of G (1), Eq. (2) is actually a differential equation and can be integrated:

$$S=\exp(b/a)\exp[-\exp -a(t+t_0)] \quad (3)$$

where t_0=constant of integration.

Although (3) is a valid equation for the Gompertz curve, it is useful to define a third parameter, S_∞, in terms of the other two parameters, a and b.

$$S_\infty=\exp(b/a). \quad (4)$$

The rationale for this definition is as follows. The intersection of the line described by (2) with the abscissa (Fig. 2) occurs when $G=0$, meaning that the animal has stopped growing. The point of intersection is thus the maximum size which the animal would reach. On the integrated form of the Gompertz curve (Fig. 1), this maximum size is approached by the animal as time approaches infinity, and hence this point is labelled S_∞. If (4) is solved for a:

$$a=b/\ln S_\infty \tag{5}$$

it is seen that the slope, a, is the intercept on the ordinate divided by the intercept on the abscissa, as would be expected from the definition of a slope.

Substituting (4) into (3), a more common equation for the Gompertz curve is derived:

$$S=S_\infty \exp[-\exp-a(t+t_0)] \tag{6}$$

where S_∞ = the asymptote of the curve.

The constant of integration, t_0, in (3) and (6) serves to set the size at which one starts counting the age of the organism. Suppose, for example, that one were describing the growth of a clam which grew according to a Gompertz curve and that one wanted to define its age to be zero when the veliger had just metamorphosed into a juvenile clam 0.5 mm long. Then in (6), set $S=0.5$ mm, $t=0$, and solve for t_0. Equation (6) would then give the size at any age measured from time of metamorphosis. The values of S_∞ and a are presumed to be known, because as will be explained below, these parameters can be determined without knowledge of the age of the clam. One could just as well have arbitrarily decided to set the age of a clam 10 mm long at zero and solved for a new value for t_0. Equation (6) would then give the size as a function of the number of days since the clam was 10 mm long. Changing t_0 then, does not affect the shape or the asymptote of the growth curve, these are determined by a and b, or a and S_∞. A change in t_0 merely moves the growth curve to the right or left along the abscissa.

Often, the scale in which the size, S, is measured is such that the initial size, or the arbitrary size at which one starts counting the age, is not 1. The ordinate in Fig. 2 then, which is placed at $S=1$ on a logarithmic scale, may be far to the left or right of the points plotted and the value for b may be much larger than any value for G in the data set, or even a negative number. This would make no difference if one were just plotting the integrated form, but it is often convenient for heuristic purposes to have b represent the value of G when the animal is at its initial size, S_0. A useful way to accomplish this is to measure size in units of the initial size. This is done by dividing all values of S by S_0. Then the initial size is $S_0/S_0=1$ and the asymptotic size is S_∞/S_0. In general, S/S_0 or S_∞/S_0 may be substituted for S or S_∞ in any equation of Table 2. The parameter b will then measure the specific growth rate at $S=S_0$. The parameter a is not affected by such a change.

The logistic, Bertalanffy, exponential, and power curves (Table 1) have differential equations that are very similar to that of the Gompertz curve, and in each case, G may be plotted against S to get a straight line if the proper set of axes (Fig. 1) are used. In each case the parameters have similar mathematical properties. For the logistic curve, the abscissa is a linear axis, as is the ordinate. For the Bertalanffy curve, the ordinate is linear while the abscissa must be a reciprocal axis, with the smallest values of S and hence the larger values of the reciprocal, furthest to the right. The line describing the linear relationship between G and the reciprocal of the size has a positive slope and intersects the abscissa at the reciprocal of the asymptote, $1/S_\infty$. For an exponential curve, the specific growth rate is constant for all values of S, so the scale of either axis is not relevant.

For a power curve, both axes for the plot of the differential equation are logarithmic (Fig. 2). Consequently, there is no value of S for which the specific growth rate becomes zero, and no parameter S_∞ can be defined. This is consistant with the lack of an asymptote for this curve. The intersection of the abscissa on the ordinate in Fig. 2 can be at any convenient value for G, and will not be zero. The form of the differential equation for the power curve (Table 1) has been altered from a more simple form by taking the logarithm of both sides so that it can be plotted as a straight line.

Estimating the Specific Growth Rate

The first step in determining the parameters of the Gompertz, power, or exponential curves is to estimate the specific growth rate from cross sectional data and to plot this estimate against the size, using appropriate axes. If the points plotted lie along a straight line, then a regression of the size against the specific growth rate will yield estimates for the parameters of one of the curves.

The specific growth rate is estimated by:

$$\frac{\ln S_2-\ln S_1}{\Delta t} \tag{7}$$

where S_1 = size at the beginning of time interval, Δt; S_2 = size at the end of the time interval.

The size against which this approximation is plotted is taken as the geometric mean of S_1 and S_2:

$$\bar{S}=(S_1 S_2)^{\frac{1}{2}}. \tag{8}$$

The error in the estimation can be represented by the ratio of the true value of the specific growth rate at $\bar{S}$ (2), to the estimated specific growth rate (7). The ratio then becomes a correction factor which, when multiplied by any estimated value for the specific growth rate, in particular b, gives the true value:

$$\text{correction factor}=\frac{\text{true value of } G \text{ at } \bar{S}}{\text{estimated value of } G}; \tag{9}$$

The value of the correction factor for a Gompertz curve was determined empirically using Eqs. (2), (6), (7), and (8) for many different positions along the curve. For a given curve and sampling interval, the correction factor was found to be the same for all values of S. For different curves, those that had the same values for b or for S_∞ also had the same correction factor. Only differences in a, and the sampling interval, Δt, affected the correction factor, and a graph can be drawn showing the correction factor as a function of the product $a\Delta t$ (Fig. 3).

Consequently, if the estimated values for specific growth rate were plotted against the natural logarithm of the mean size, the locus of points would still be in a straight line and the intercept on the abscissa would still be at the point $\ln S_\infty$, but the values for a and b would both be proportionally less than their true values by the same amount. The correction factor then, can be applied to an estimate of a, or b or any value of G.

Because the correction factor for a Gompertz curve is a function of the true parameter a, and a cannot be determined without knowing the correction factor, a series of successive approximations must be made, starting with an estimate for a from the regression. Using the graph (Fig. 3), the estimate

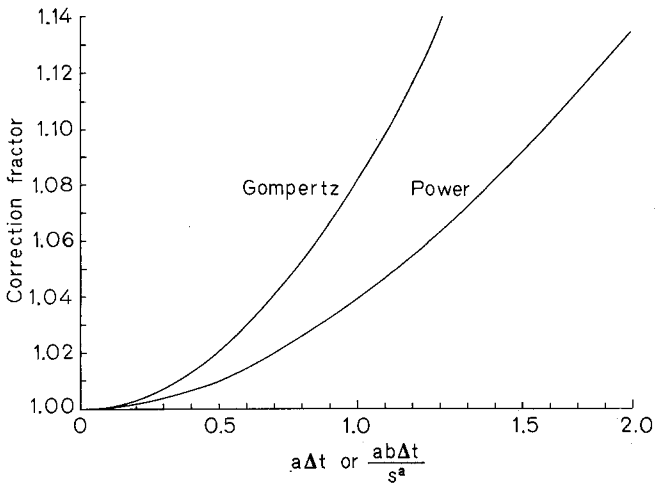

Fig. 3. Correction factors for the estimate of specific growth rate when applied to the Gompertz and power curves. For a Gompertz curve with a given parameter a (and any parameter b or S_∞) for which the differential equation is plotted using the method described in the text and using a time interval Δt, the ratio of the true value to the estimated value of the specific growth rate (called the correction factor) will have the value indicated on the graph as a function of $a\Delta t$. The product of the correction factor and an estimated specific growth rate gives the true specific growth rate. Because the true parameters of the curve under investigation are not initially known, a process of successive approximations, starting from the estimated parameters, may be used to determine them, as explained in the text. For a power curve with given parameters a and b, the correction factor will vary as a function of $ab\Delta t/S^a$. Unlike the Gompertz curve, the correction factor varies with S

of a is multiplied by the first estimate of the correction factor to obtain a new estimate for a which is in turn used to determine a new estimate for the correction factor. If each time the new estimate of the correction factor is multiplied by the *original* estimate for a, the estimates will rapidly converge to the true parameter a.

If different time intervals, Δt, are used in collecting the data, the error cannot be exactly determined. However, Fig. 3 can be used to determine whether the largest possible error, corresponding to the largest value of Δt, can be safely ignored.

The same estimate of specific growth rate (7) may be used to fit the differential equations of the other curves in Table 2. However, except for the exponential curve, the correction factor (9) for these curves varies with the sizes, S_1 and S_2, used to calculate the specific growth rate and as a result, the exact amount of systematic error in the regression is difficult to determine. For the logistic and Bertalanffy curves, it is necessary in this paper only to demonstrate that they do not fit a set of data points as well as do the Gompertz or power curves, so the error does not make any difference. If there is any doubt, the data may be plotted as described in Table 1 which will yield an unbiased estimate for the parameters.

The estimate, (7), when applied to the exponential curve, is free of this kind of bias for all values of Δt and all values of b.

For the power curve, the correction factor may also be determined empirically and plotted as a function of a, b, Δt, and $\bar{S}$ (Fig. 4). Although an exact correction cannot be made because the correction factor changes with $\bar{S}$, the largest value of the correction may be determined for any given curve. It corresponds to the smallest value of $\bar{S}$ in the data set or to that size for which the curve is otherwise deemed to apply. Usually, this error will be small enough compared to the scatter in the data that it can be disregarded.

A useful characteristic of Gompertz, power, and exponential curves which is not shared by logistic and Bertalanffy curves is that the measure of the size used (length, area, or volume) does not change the type of curve needed to fit the data as long as the measures are related by the allometric equation. Thus, if one measures the area (A) of an organism and finds that it increases according to a Gompertzian growth curve, then a measure of length, ($A^{\frac{1}{2}}$), or of volume ($A^{\frac{3}{2}}$) will also be fit by a Gompertz curve, but with different parameters. However, an animal that follows a Bertalanffy curve when length is used as a measure of size will follow a different curve, a sigmoid one, when weight is used (Bertalanffy 1960; Schoener and Schoener 1978).

Practical Application of Techniques for Fitting Gompertz, Power, and Exponential Curves

From a set of cross sectional data, estimates for G are calculated using Eq. (7). For each pair (S_1, S_2), a value for $\bar{S}$ is determined using (8). The estimate for G is then plotted against $\bar{S}$ on semi-logarithmic paper. As an example, the growth of *Schizoporella biaperta*, an encrusting bryozoan, is plotted (Fig. 4). Most of the data were collected using a time interval (Δt) of 14 days, but nine of the points were collected using a time interval of 16 days. In this case, the size is measured as a count of the number of zooids in the colony, N. Although there is some scatter, the data appear to be fit by a straight line, indicating that a Gompertz curve would adequately describe the growth of colonies of *S. biaperta* during the time interval when the data were collected. From a regression with the natural logarithm of the size ($\ln N$) as the independent variable, the intercept with the ordinate, b, is determined as 0.0837 (S.E.$=$0.0078, $n=25$). The slope a is 0.0103 (S.E.$=$0.0020). N_∞ is 3421 zooids.

The correction factor can be estimated from the product of the estimate for the slope, a, and the largest value for Δt used to collect the data. In this case it is $(0.0103)(16)=0.1648$. From Fig. 3, the approximate correction factor is 1.002. The value is approximate because first, it was determined from an estimated value for the slope rather than from the true value and second, two values for Δt were used to collect the data and the correction factor curve only strictly applies to a data set with one value of Δt. It is evident, however, that the error involved is so small that it may be neglected.

To see whether the slope is different from zero, a one-tailed t test is used because one would not expect the slope to be positive. The parameter a is different from zero ($P \ll 0.001$) so an exponential curve would not fit the data. If the results were not different from zero, the mean value for G could be taken as the value of b in the exponential equation in Table 1.

If the same data is plotted on logarithmic paper (Fig. 5), again the data appear to be fit by a straight line, so that there is a power curve which would also fit the data. From a linear regression of $\ln G$ against $\ln \bar{S}$, the parameters of the power curve are found to be $a=0.2360$ (S.E.$=$0.0476, $n=25$) and $b=0.0991$ (S.E. of $\ln b=0.1851$). Note that while a Gompertz curve has an asymptote, suggesting that *S. biaperta* has determinate growth, the power curve does not, suggesting an indeterminate growth pattern for the same data set. In fact, the extrapolation of the regression on the Gompertz curve plot to the asymptotic value on the abscissa is not justified, even though the distance of the extrapolation appears relatively small. The inflexion point for a Gompertz curve is $0.37\, S_\infty/S_0$ (Bertalanffy 1960) which in this case is 1,266 zooids. The largest size in the data set

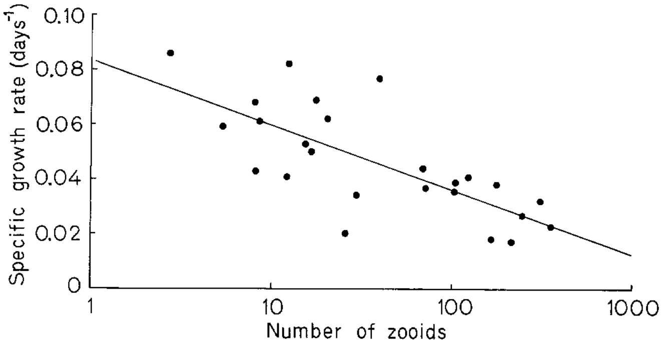

Fig. 4. Gompertz curve plot of the growth of *Schizoporella biaperta* during the period 8/17/75–9/2/75 at Woods Hole, Massachusetts

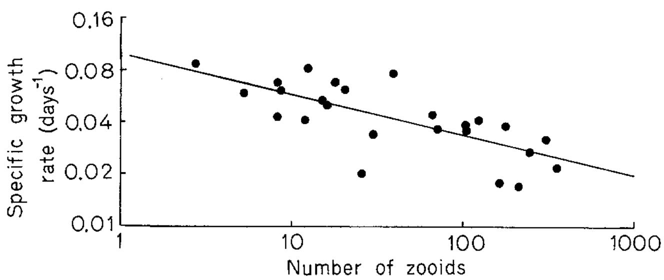

Fig. 5. Power curve plot of the growth of *Schizoporella biaperta* using the same data as in Fig. 4

then is substantially less than the inflexion point, and it is not unexpected that either the lower part of a Gompertz curve or a power curve would fit the data. Similarly, one would not want to extrapolate in the opposite direction back to a colony size of one unless other evidence showed that *S. biaperta* grew according to either a power or a Gompertz curve at those small sizes.

The correction factor for the power curve can be estimated for a size of one zooid, the size at which the largest error would occur in the estimation of G. At $S=1$, the term $(ab\Delta t/S^a)=(0.236)(0.0991)(16)=0.374$. From Fig. 3, the correction factor is 1.006, a negligible amount.

In order to fit a linear regression, several assumptions must be made about the data, including the assumption that the distribution of the points about the regression line is normal and that the variance of the distribution is not different for different sizes. Normally, if these assumptions were valid for values of G, they would not be valid for $\ln G$, and vice versa. In fact, the scatter of points about the regression line in Fig. 5 is uniform while in Fig. 4 the variance appears larger for smaller sizes of N. If it is necessary to fit a Gompertz curve but the dependent variable only fits the assumptions of a regression under a log transform, it is possible to fit a curvilinear regression to the data on a log-log plot and then to transform the fitted parameters back to the semilog plot.

The same data set is plotted on a graph with both axes linear (Fig. 6) to determine whether a logistic curve might be used to describe the data. Here, it is quite evident that the points do not lie along a straight line. The line fitted to these points is the trajectory of the Gompertz curve fitted in Fig. 5. Note, however, that if colonies with a size of less than 45 zooids had been omitted from the data, then a logistic curve would have been an adequate description of the data, but that an extrapolation of the line to small values of N would have predicted erroneous values for G.

To write the integrated form of the growth equation, a value for t_0 must be found. To do this for a Gompertz curve, a colony of a size of one zooid is arbitrarily assigned an age of zero. Setting $t=0$ and $N=1$ (i.e. $S=1$) in (3), and solving for t_0:

$$t_0=-\frac{1}{a}\ln\frac{b}{a}=203.4 \tag{10}$$

and, from Table 1,

$$N=3421\exp[-\exp-0.0103(t-203.4)]. \tag{11}$$

To write the integrated form of the power curve, a similar argument is used and

$$N=[0.0234(t+42.76)]^{4.24}. \tag{12}$$

Because the range of data is from 3 to 350 zooids, the use of equations (11) and (12) to predict the ages of colonies larger or smaller than these sizes requires extrapolation, which as shown above, must be done with care.

The same technique could be used to fit a growth curve to longitudinal data. From a sequential series of measurements of the size and age of an organism, adjacent values can be selected in pairs and a value for the specific growth rate (G) and the size (S) determined. The procedure is then the same as above. In some cases, this may be more convenient than using existing computer programs (Silliman 1967; Conway et al. 1970; Marubini 1971) because it requires only a small hand calculator.

Discussion

It is evident that more than one curve can fit a given data set. It is also evident that a large enough range in sizes, or a small enough variance, limits the number of simple curves which can be used to describe the data. In this case, perhaps a test could be applied to determine whether the power curve or the Gompertz curve provided the better fit, but that is not the point. Bryozoans, or any other organisms, are not constrained to grow according to one of five growth curves specified in advance by scientists, and there are undoubtably many other curves which would have fit the data even better. Growth is a complicated process and the observed patterns are controlled by many different factors. The point is to describe and use the data in such a way that these factors can be separated from one another.

The technique presented here has three salient characteristics which make it useful for comparing growth patterns. First, it uses cross sectional data which can be collected all at one time in the field so that environmental factors affecting growth can be controlled. The cross sectional data also introduces an averaging effect which allows a statistical comparison of growth rates. Second, it describes growth in terms of specific growth rate which allows several growth curves to be plotted as straight lines and hence needs only two parameters to describe the pattern. For colonial organisms, it also has a certain heuristic value. Third, it uses size rather than age as the independent variable. Size is both easy to measure and has a more direct relationship to growth rate than does age. The cost of using this technique is that the size at any given age is not described. For this, the value for t_0, the constant of integration, must be determined. In other words, if a size-age relationship is not needed, a very useful and complete descrption of growth may be made using differential equations. The integrated forms are not needed at all and, in fact, may obscure some kinds of information.

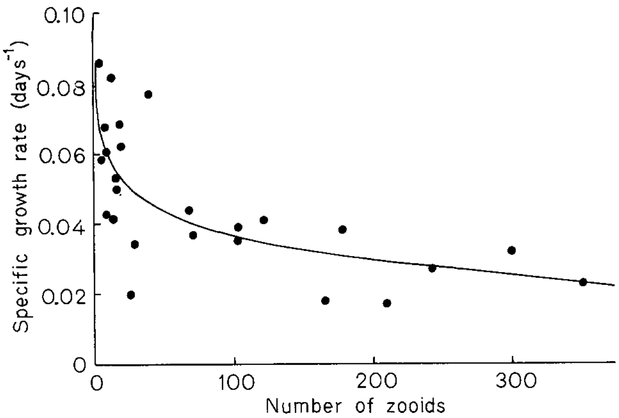

Fig. 6. Logistic curve plot of the growth of *Schizoporella biaperta* using the same data as in Fig. 4. The line is the trajectory of the Gompertz curve regression line

Often, however, it is useful to predict the size from the age of an organism, or vice versa, and the curve fitting technique presented here can be used to do this. Cross sectional data, however, cannot distinguish between a population where some individuals consistantly grow faster or slower than the average and a population where all individuals vary randomly about the mean specific growth rate at any given size. The latter will have a smaller variance in size at any given age and hence cross sectional data cannot be used to predict the variance of the size for a population at a given age.

Two other problems are sometimes encountered in fitting growth curves. Fabens (1965) presents a computer prgram for fitting the Bertalanffy growth curve from cross sectional data and states that in order to calculate the parameter equivalent to the constant of integration here, that the size of the organism at a given age would be needed, and that the size at birth would be ideal. This would only be true if the Bertalanffy curve accurately described the early growth of an organism, but this is often not the case (Frank 1969; Yamaguchi 1975; Sakawa and Kimura 1976). In fact, there are probably few organisms for which the Bertalanffy curve fits early growth well, for the curve requires that the highest growth rates (not specific growth rates) occur at the smallest sizes. Hence, the extrapolation implied by using the size at birth to determine the constant of integration would probably lead to an error in predicting the size at a given age of larger individuals. Brousseau (1979), using Fabens' (1965) computer program, properly determined the age of her clams at a larger size than at settlement and used that value to set the constant of integration, as was provided for in the original program.

Yamaguchi (1975) demonstrated that if an organism follows a sigmoidal growth pattern, and if the sampling period, Δt, is too long, that a Bertalanffy curve may appear to fit the data when plotted on a Ford-Walford plot, even if the smallest sizes are included in the survey. However, while this conclusion appears to be correct, the logistic curve used by Yamaguchi as an example to fit the growth of an asteroid *Acanthaster planci*, was not the best curve to use to fit his data. His Fig. 2 shows that the data points extend up along the abscissa for initial sizes less than about 25 mm. For a Ford-Walford plot, this pattern is characteristic of a Gompertz curve plotted on a logistic plot. The effect is similar to that shown in Fig. 6 here, although Fig. 7 is not a Ford-Walford plot. As a result, even though he had data points including the smallest sizes, these sizes were overestimated by the fitted logistic curve.

To use cross sectional data to fit the integrated forms of growth equations, then, care must be taken not to inadevertantly extrapolate when setting the constant of integration, and to use the appropriate curve to fit the data.

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