

## Asymptotic equations in growth studies — an analysis based on *Anodonta piscinalis* (Mollusca, Unionidae)

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The suitability of four asymptotic growth equations for describing growth of length in populations of *Anodonta piscinalis* was studied. The Krüger function showed the best fit with the observed values, but the other three equations (von Bertalanffy, Gompertz, logistic) were not much worse. The Krüger function was also the best when lengths of very old and young individuals were extrapolated from truncated data.

Although the equations closely simulated the sets of material, we could find little evidence that their parameters (growth constant, asymptotic length) were suitable for comparisons between populations. Different cohorts and sexes within a population produced very variable numerical values for these parameters. The correlation between the mean length of the third annulus in a population and the growth constant produced by different equations for the same set of data ranged from 0.539 to —0.640. The von Bertalanffy equation was the least unsuitable for producing parameters for comparisons between populations.

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### 1. Introduction

Asymptotic equations are used extensively in growth studies because they fit reasonably well with empirical data and because they include only three parameters, two of which are interpreted as biologically meaningful (growth constant, asymptotic level). In relation to their wide use, analyses of their biological relevance and comparisons between different equations are rare (e.g. Krüger 1969, 1973).

In the present paper we have analysed data on the growth in length of a freshwater mussel (*Anodonta piscinalis*) in 15 populations — with three aims: First, to compare five ways of solving the parameters of the von Bertalanffy (von Bertalanffy 1938) equation. Secondly, to compare the von Bertalanffy equation and three other asymptotic equations (Gompertz, logistic, Krüger) as regards their fit with empirical data and their usability for extrapolating values beyond the range used to

calculate the parameters. Thirdly, to show that in spite of a good fit of an asymptotic equation with empirical data, the biological validity of comparisons of parameters derived from different populations is highly dubious.

### 2. Material and methods

#### A. Determination of parameters

##### von Bertalanffy equation

The equation is usually presented in the form

$$L_t = L_{\infty} (1 - e^{-K(t-t_0)}) \quad (\text{e.g. Ricker 1958}),$$

where

$L_t$  = length of an animal at time  $t$

$L_{\infty}$  = asymptotic length

$K$  = growth constant

$t_0$  = theoretical time with zero length.

The parameters were solved in the following five ways:

- 1) by computing the Ford-Walford (Ford 1933, Walford 1946) line, 2) by fitting the Ford-Walford line by eye, 3) by Rafail's (1973) method (five iteration times), 4)

by Allen's (1966) method (five iterations), and 5) by iterating the asymptotic length from the linearized von Bertalanffy equation given by Rafail (1973).

#### Gompertz, logistic and Krüger equations

The Gompertz equation (Winsor 1932):

$$y_t = Y_{\infty} e^{-Be^{-Ct}},$$

where  
 $y_t$  = length of an animal at time  $t$   
 $Y_{\infty}$  = asymptotic length  
 $C$  = the growth constant  
 $B$  = a constant

and the logistic equation (Verhulst 1838):

$$y_t = \frac{Y_{\infty}}{1 + be^{-Kt}},$$

where  
 $K$  = the growth constant  
 $b$  = a constant

and the Krüger equation (Krüger 1962):

$$y_t = \frac{Y_{\infty}}{N(t+r)^{-1}},$$

where  
 $N$  = the growth constant and  
 $r$  = a constant

were solved by iterative procedures as given by Krüger (1973).

## B. Material

The *Anodonta piscinalis* measurements used in the computations were made in southwestern Finland in 1971–1974. They relate to samples from 15 different populations. Seven samples are from the river Paimionjoki, five from the Loimijoki (a tributary of the river Kokemäenjoki), two from different parts of the Kokemäenjoki, and one from the Uskelanjoki. The minimum sample size included 99 measurements. Calculations concerning a single population were made from material collected from the Paimionjoki at Santio, Koski commune.

Lengths (mm) of mussels at the beginning of each growth period were measured according to the dark winter rings. The usability of these as the basis for a growth study has been treated elsewhere (Haukioja & Hakala 1978). The method used is essentially the same as that used in measuring growth rings in scales or otoliths of fish. However, it is more exact in mussels, because the length of preceding winter rings can be measured directly without using the ring width/total length relationship.

Equations were computed from unweighted mean lengths of winter rings. This practice decreases the effects of growth-selective mortality (Parker & Larkin 1959).

## C. Aims and methods

The most common use of a growth curve is obviously to calculate the length or weight of an animal from its age. This is needed especially in calculating biological production. What is required is an equation that accurately simulates the empirical values from which its parameters were determined. At the same time it smooths the possible irregularities in the data. In practice it is useful if the equation is also able to predict values outside the measured range. It is further advantageous if the equation is widely applicable and easy to compute.

The primary aim, agreement between predicted and observed values, was tested using the logarithmic deviations between simulated and observed values, according to the equation proposed by Krüger (1973):

$$s_{\log} = \sqrt{\frac{(\log y - \log \hat{y})^2}{n - 3}}$$

This meant that samples with less than four age classes could not be used and therefore calculations with truncated data (see later) had to be based on fewer than 15 populations.

From the above formula, the so-called percentage mean deviation (Krüger 1973) was calculated:

$$s_{\%} = (10^{s_{\log}} \cdot 100) - 100$$

The use of logarithms in the above formulae reduces the effects — perhaps large absolutely but small relatively — of deviations caused by large individuals. This is a meaningful practice, as mean lengths in the older age classes are usually based on smaller samples than in the more abundant younger year classes. In production biology the young age classes usually make up the bulk of production, which also emphasizes the accuracy in the lower part of the growth curve.

Another aim for growth equations is to obtain parameters for comparing different sexes, populations, species etc. In this case the most important parameters are the growth constant and the asymptotic length. For meaningful comparisons these parameters must indicate some real biological features of the group studied. This was checked by comparing within-population and between-population variances in the above parameters.

## 3. Accuracy of iteration

If numerical values for all parameters in growth equations are obtained arithmetically, deviations between observed and predicted values are directly comparable. When parameters are determined by iteration, discrepancies may also be due to the inaccuracy of iteration. The accuracy can be raised to a high level. But this is justified only if the point minimizing the difference between observed and predicted values can be found by an efficient searching method.

The step length in iterations was 0.5 mm in

the von Bertalanffy, Gompertz, and logistic equations. Values in iterations were computed from 30 below to 125 mm above the mean length of the oldest age class. Computation took practically the same time in each case, and the von Bertalanffy equation gave better results than the Gompertz or logistic equations, especially the latter (Table 1).

Table 1. Sensitivity of the von Bertalanffy (vB), Gompertz (G) and logistic (l) equations to step size of the iterated parameter near the minimum value of  $L_{\infty}$ . Calculated for material from Santio.

	vB		G		l	
	$s_{\log}$	%	$s_{\log}$	%	$s_{\log}$	%
min - 0.5 mm	0.0085	4.9	0.0186	6.3	0.0374	4.8
min	0.0081	2.5	0.0175	4.0	0.0357	16.8
min + 0.5 mm	0.0083		0.0182		0.0417	

When the additive term ( $r$ ) in the Krüger function was iterated, the step size was put at 0.05 and the range from 0.0 to 10.0. A step size near the minimum point gave the same relative change for  $s_{\log}$  as in the logistic equation, although absolutely the result was more accurate:

iterated value	$s_{\log}$	difference as a percentage of the minimum
minimum - 0.05	0.0075	11.9
minimum	0.0067	9.0
minimum + 0.05	0.0073	

To sum up, the step size in iteration had the least effect on the von Bertalanffy equation. The following in order were the Gompertz, logistic and Krüger equations. When equations were evaluated according to the computing time needed for iteration, the Krüger equation was the best. The others did not differ significantly, the time needed for iteration being largely determined by the step size and the range which the programmer sets for the parameter iterated.

#### 4. Comparison of different methods of fitting the von Bertalanffy equation

The computed Ford-Walford plot gave much lower  $s_{\log}$  values than the method based on graphical fitting (mean values for  $s_{\log}$  were 4.8 and 18.8, respectively). It is difficult to generalize this result, because the graphical method is subjective, especially in weighting the extreme values. Therefore graphical determi-

nation of the Ford-Walford line has not been used further in the present treatment.

When the other methods were compared, the iteration method gave the best fit, but Allen's method was also good (Table 2). The results of the iteration method are used later when the von Bertalanffy equation is compared with the others. Rafail's and Allen's methods were economical in computation. However, on account of its accuracy, Allen's method was the most suitable for calculating without an electronic computer.

The mean values of  $L_{\infty}$  and  $K$  generated in different ways did not deviate significantly (Table 2).

Table 2. Comparison of four methods for fitting the von Bertalanffy equation to 15 populations of *Anodonta piscinalis*.

	Ford-Walford	Rafail	Allen	iteration
$S\% \bar{x}$	4.80	7.46	3.42	3.15
SE	1.265	1.783	0.690	0.629
$L_{\infty} \bar{x}$	106.2	107.8	106.9	107.9
SE	5.93	6.64	5.76	5.77
$K \bar{x}$	0.315	0.332	0.312	0.305
SE	0.024	0.045	0.024	0.024

#### 5. Comparison of the four equations

##### A. Fit between measured and predicted values

Table 3 gives the mean difference between simulated and measured values in the four equations with the same original data. The best fit was arrived at by the Krüger function, followed by the von Bertalanffy, Gompertz, and logistic equations. The differences were small, however, and each of the equations gave the best fit in more than one population (Table 3).

Table 3. Compatibility between actual and simulated lengths fitted by four growth equations for 15 populations of *Anodonta piscinalis*. vB = von Bertalanffy, G = Gompertz, l = logistic, K = Krüger. The row "best" indicates in how many cases each equation gave the best compatibility between actual and simulated lengths.

	vB	G	l	K
$S\% \bar{x}$	3.15	4.40	7.22	2.82
SE	0.629	0.493	0.907	0.561
min.	0.09	1.97	0.57	0.66
max.	8.31	7.91	12.15	8.14
best	4	3	2	6

The value for the first year often decreases the fit between the actual and predicted values. This was tested with the above set of data but omitting the first annulus from the computation. With these data, also, the order of the different equations was the same as with untruncated material (Table 4). The differences between the equations were even smaller than with the complete set of data.

Table 4. Compatibility between actual and simulated lengths from the second annulus onwards. Equations were fitted for 11 *Anodonta piscinalis* populations. For explanations, see Table 3.

	vB	G	l	K
$S\% \bar{x}$	3.02	3.21	3.48	2.98
SE	0.898	0.836	0.786	0.917
min.	0.55	0.68	1.18	0.50
max.	9.66	9.67	9.90	9.65
best	1	1	2	7

## B. Suitability for extrapolation

When studying aquatic animals, such as fishes — and the same is true to a lesser extent of mussels —, it is not always possible to catch and/or measure enough specimens of even the abundant age classes. Difficulties may arise with the first age-class, which, owing to its small size, cannot be caught by the same methods as older age classes. In the young age classes also, the catching method may take a disproportional number of large individuals. Furthermore, in back-calculation of annulus lengths, it is not always possible to recognize the first, worn annuli. If the material consists only of individuals with distinct annuli, the results will be biased. In the old year classes the number of individuals may also be so low that it does not allow reliable observed values. If, in situations of this kind, estimates of the first and/or very old year classes are needed, they may be calculated by extrapolation from growth equations.

### *Finding the length of the first annulus by extrapolation*

Table 5 gives deviations between empirical first-year values and the values simulated by different growth equations. Fitting of these was performed from the second ring onwards. Here also, the Krüger function gave the best fit,

followed by the Gompertz, von Bertalanffy, and logistic equations.

Table 5. Percentage difference between actual and simulated length of the first annulus in 11 populations of *Anodonta piscinalis*. Simulated values were derived from equations fitted without the first-year length. For explanations, see Table 3.

	vB	G	l	K
Error (%)				
$\bar{x}$	41.5	32.7	43.9	23.6
SE	11.01	5.74	6.95	3.67
min.	13.2	4.3	1.4	2.2
max.	142.6	58.2	73.1	42.7
best	2	3	1	5

### *Finding the length of old year classes by extrapolation*

For Table 6 the growth equations were determined from data truncated by 2 years from the upper end of the age distribution. Values were then calculated for the year class 2 years older than the highest age used in deriving the equations. When these values were compared with the actual values, the Krüger function was again the best and the von Bertalanffy equation the next best.

Table 6. Percentage difference between the actual length of the maximum age recorded and the value calculated for the corresponding age in seven populations of *Anodonta piscinalis*. The latter values were obtained from equations fitted without the values for the two oldest age classes in each population. For explanations, see Table 3.

	vB	G	l	K
Error (%)				
$\bar{x}$	5.33	9.54	14.19	4.20
SE	1.209	2.177	1.514	1.174
min.	1.0	0.4	7.4	0.2
max.	10.2	18.9	18.6	8.1
best	3	1	0	3

## 6. Are the parameters of asymptotic growth equations susceptible of biological interpretation?

Next we study how growth constants and asymptotic lengths derived from the above growth equations correlate with independent estimates of growth rate and maximum length.

### A. Growth constant versus growth rate

The mean length of mussels at a given annulus indicates how fast they grow at a particular site. It is subjective to take a specific annulus as a criterion for comparisons, but the effects of such a decision are slight (Fig. 1). We chose the length of the third annulus for the reasons mentioned by Haukioja & Hakala (1978).

Fig. 2 shows correlations between growth rates (indicated by the length of the third annulus) and growth constants included in the different equations. The Krüger equation gave the best correlation but unfortunately a negative one.

The positive correlation given by the von Bertalanffy equation was almost as good, and an attempt in which the parameters of the von Bertalanffy equation were obtained by fitting the Ford-Walford line by eye yielded an even higher correlation ( $r = 0.813$ ,  $p < 0.001$ ). The correlations obtained with the Gompertz and logistic equations were low.

Krüger (1970) states that the slope of the Ford-Walford line is a better indicator of the growth rate than the parameter  $K$  in the von Bertalanffy equation. Using the slope ( $b$ ) does not seem to change the situation (Fig. 3), although Krüger's (1970) argument is logical.

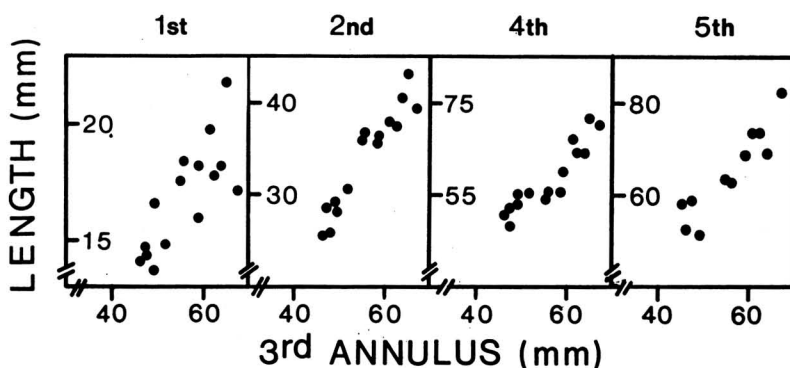


Fig. 1. The mean length of the third annulus in relation to the mean length of the first, second, fourth and fifth annuli in *Anodonta piscinalis* populations.

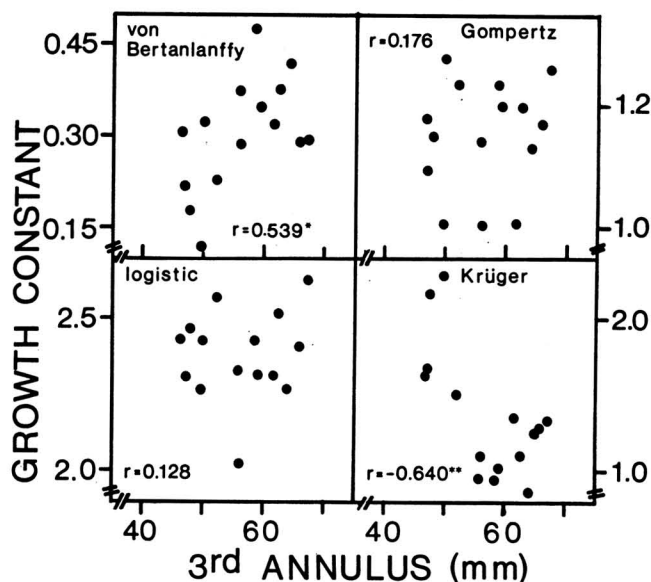


Fig. 2. Correlation between the mean length of the third annulus and growth constants derived from four growth equations in 15 populations of *Anodonta piscinalis*.

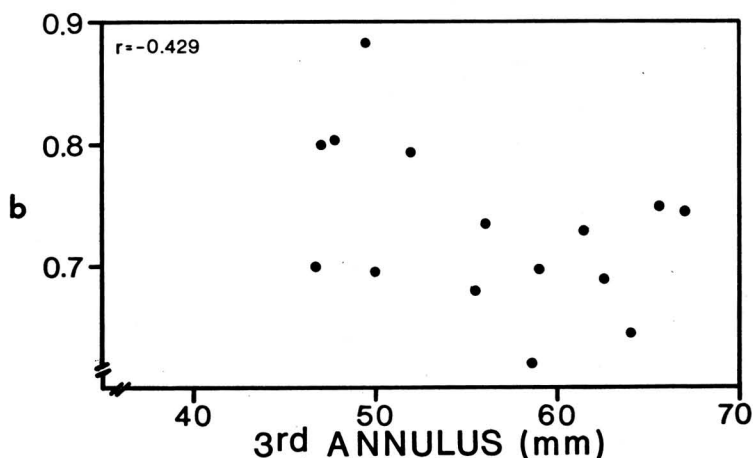


Fig. 3. Correlation between the mean length of the third annulus and the slope ( $b$ ) of the Ford-Walford line in 15 populations of *Anodonta piscinalis*.

### B. Asymptotic length versus maximum length

In the Santio population, where more than 2 000 individuals of *Anodonta piscinalis* were measured, the maximum length recorded was 116 mm. We suppose that this value is not far from the "true" maximum, because in this population the oldest individuals die at ages of 7–9 years. The different growth equations gave the following maximum lengths for the Santio population:

von Bertalanffy	126.0 mm
Gompertz	107.5 mm
logistic	100.0 mm
Krüger	163.6 mm

The Krüger function gave an impossibly high value for a realistic maximum length. The Gompertz and logistic equations gave values typical of the oldest age classes. The von Bertalanffy equation overestimated the value realized in any cohort.

### C. Differences between cohorts

The use of growth equation parameters to characterize certain populations assumes that growth equations can sift out figures that characterize growth in a particular population. The best equation is thus the one that is least sensitive to intrapopulation variation.

The most important factors responsible for variance in growth statistics in an *Anodonta piscinalis* population are annual variation in growth and sex (Haukioja & Hakala 1978).

For studying the effects of these factors on growth parameters we calculated growth equations separately for the different cohorts and for both sexes in a sample of 650 specimens collected at Santio in September 1974. The material allowed equations to be computed for cohorts 1967–1970.

Table 7 gives the range of growth parameters in this material as well as the range obtained when the same parameters were computed for each of the 15 populations. Variation between cohorts accounted, on average, for more than half the range found when the 15 populations were compared. The von Bertalanffy equation seems to give the best (least variable) index for the growth rate, and the logistic equation for the maximum length. Owing to the variance between cohorts, none of the equations gave parameters which could be regarded as characteristic of the Santio population.

Summarizing, any one of the parameters of a growth equation is meaningful when combined with the other two parameters. Together they dictate the form and position of the growth curve. When separated from this complex, they are mathematical quantities lacking any clear biological significance. This statement does not rule out the possibility that they may be correlated with some environmental factors or other parameters of growth.

### 7. Polynomials as a description of growth

Ordinary growth equations are considered preferable to purely mathematical equations

Table 7. The magnitude of the scatter and the extreme values (in parentheses) of parameters indicating asymptotic lengths (L, in mm) and of the growth constants (C) given by the four growth equations. The entire material gives the interpopulation variance in the values derived from 15 populations when both sexes were combined. The Santio sample gives the intrapopulation variance when a growth equation was fitted separately for each sex and cohort.

		Entire material (♂ + ♀)	♂	Santio	♀
L)	vB	88.0 (81.0–169.0)	62.5 (112.5–175.0)	27.0 (142.5–169.5)	
	G	38.0 (69.5–107.5)	12.0 (89.5–101.5)	18.0 (97.0–115.0)	
	I	35.0 (65.0–100.0)	5.5 (82.5–88.0)	7.5 (86.5–94.0)	
	K	61.8 (110.9–172.7)	61.5 (144.9–206.4)	105.5 (174.6–280.1)	
C)	vB	0.354 (0.122–0.476)	0.155 (0.174–0.329)	0.046 (0.179–0.225)	
	G	0.234 (1.045–1.279)	0.168 (1.215–1.383)	0.216 (1.184–1.400)	
	I	0.612 (2.015–2.629)	0.409 (2.488–2.897)	0.510 (2.472–2.982)	
	K	1.344 (0.944–2.288)	0.746 (1.179–1.925)	1.133 (1.586–2.719)	

for two reasons: they have fewer parameters and these are biologically interpretable. But as the latter argument does not seem to hold, what is the case with the former?

Polynomials were fitted for each of the 15 populations up to the point at which adding a new term did not significantly improve the result. The mean  $s_{\%}$  between actual and simulated values was  $1.23 \pm 0.690$ , a lower value than in any of the growth equations considered above (Table 2). The upper limit was reached with a third-degree polynomial in 11 samples, with a second-degree polynomial in three samples and with a fourth-degree polynomial in one sample. Therefore, with the present material, polynomials contained at most one or two parameters more than ordinary growth equations and were more accurate. For extrapolation and for comparisons between populations they are totally unsuitable.

## 8. Conclusions

Above we postulated two requirements for growth equations, ability to describe the data and to produce parameters for comparisons. The Krüger function was the best for describing the material, whether entire or truncated. In extrapolations it also gave the best fit with actual values. The von Bertalanffy equation was usually the second in order. The results arrived at by the Gompertz and logistic equations were not much worse. If the time needed for iterations is taken into account, the Krüger function was again the best. On the other hand, the von

Bertalanffy equation gives good and rapid arithmetic solutions. When the two latter equations are evaluated, perhaps the chief disadvantage of the Krüger function is that it was developed so late. The von Bertalanffy equation already had an established position and consequently a large number of applications, e.g. in fishery research. However, the presence of a turning point in the Krüger equation, but not in the von Bertalanffy equation, gives the former a potentially wider field of application. This could be seen especially in the good fit on extrapolating the length of the first annulus. On the other hand, the von Bertalanffy equation can be fitted (by the Ford-Walford line) even if the ages of some growth rings are unknown.

It is worth stressing that if one simply wants a good description of measurements, it matters little which equation is used. The material analysed in the present paper indicates that the equation with the best fit is not specific for *Anodonta piscinalis*. As different equations may give the best fit in different populations, caution is needed in drawing conclusions based on one or a few populations only.

None of the equations used proved good in providing information for interpopulation comparisons. In the case of the growth constant this is easy to understand. The growth rate, the derivative of a growth curve, changes along the curve. Therefore it is impossible to find a single figure to describe an absolute growth rate. That the asymptotic length is not suitable for comparisons is less obvious, although its purely mathematical nature has been recognized



earlier (e.g. Krüger 1969). Therefore, when asymptotic growth equations are used, it is important that the asymptote takes a value so high that it is not reached in practice. This condition is fulfilled by Krüger's function and probably by the von Bertalanffy equation, too. With these equations it is possible to operate with the ages actually observed in the field.

As the differences in suitability between the equations seem to be slight, it is more fruitful to discuss why and when to use growth curves, instead of discussing their relative suitability.

For the purposes mentioned above growth equations are not especially suitable. Data can be described more accurately with polynomials of a low degree than with asymptotic growth equations. In practice this is an easy way, as computer programmes for fitting polynomials are to be found in standard programme libraries. As a source of extrapolated values ordinary growth equations are useful but, until results like those in Tables 5 and 6 are generally available, there is no reason to believe that they yield more realistic values than fitting by eye.

To us it seems more reasonable to present lengths of animals at different ages as a vector than to compute a growth equation for the same data, unless the equation is to be used for

some meaningful purpose, e.g. in a model. Formulating a growth equation does not *per se* add anything essential as compared with a vector of lengths. It does not facilitate the making of critical comparisons, either. On the contrary, a certain amount of information is lost, and the false accuracy arrived at may even be disadvantageous if it creates a feeling that the growth process is understood. Furthermore, growth equations are usually unrealistic because they smooth out the seasonal variation in growth, a characteristic feature of growth.

Presenting variances of lengths is easy when vectors of lengths are used. They can be calculated for growth equations, too, but again at the price of losing information.

Growth rates within a species or between related species of the same size can be compared by using the length at a certain age as a criterion. This criterion is not valid if the groups compared have clearly different final lengths; for such comparisons no good method is known to us.

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