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THE FITTING OF GROWTH CURVES FOR PECTEN MAXIMUS (L.)

by

J A Pope and James Mason
DAFS Marine Laboratory, Aberdeen, Scotland, UK

Abstract

The properties of some commonly used growth curves are described. The results of fitting the von Bertalanffy and Gompertz curves to growth data for the scallop *Pecten maximus* are contrasted. The von Bertalanffy equation gave curves which fitted the observed data reasonably well over the entire age range. The Gompertz equation gave curves which fitted the data well over the middle of the age range, but gave values of asymptotic size which were well below the observed sizes of scallops 10 or more years old. At the lower end of the age range the von Bertalanffy equation gave a very good fit with observed values, the different intercepts on the time axis reflecting different spawning times. The Gompertz curve cannot do this as it does not meet the time axis.

Résumé

On décrit les propriétés de quelques courbes de croissance d'usage courant. On met en contraste les résultats de l'ajustage des courbes de von Bertalanffy et de Gompertz aux données pour la croissance du pecten *Pecten maximus*. L'équation de von Bertalanffy a donné des courbes qui s'ajustaient assez bien aux données qu'on a observé à n'importe quel point sur la gamme des âges. L'équation de Gompertz a donné des courbes qui s'ajustaient bien aux données au milieu de la gamme des âges, mais elle a donné des valeurs de taille asymptotique bien au-dessous des tailles observées pour les pectens de dix ans et au-dessus. Sur la partie inférieure de la gamme des âges l'équation de von Bertalanffy s'est ajustée très bien aux valeurs observées, les différents points d'intersection sur l'axe du temps indiquant différentes fraiesons. La courbe de Gompertz ne peut pas en faire ainsi parce qu'elle ne touche pas l'axe du temps.

Introduction

Types of Growth Curves

Observations on the size of animals or plants at different stages of their life history can be used to fit a mathematically formulated relationship describing growth in size. Such curves are expressible in the form

$$Y_t = \phi(\underline{\theta}_n; t) \qquad (1)$$

where Y_t is the size of the organism, t is chronological time (or some quantity related to chronological time) and Θ_m represents m parameters which determine various characteristics of the curve. These parameters may be employed to provide precise comparisons between the growth patterns of different individuals of the same or different species.

A great deal has been written about the appropriateness, from a biological point of view, of different mathematical functions as growth descriptors. In some instances the analytical form of a function has been regarded as describing, or arising from, specific physiological processes occurring in the growth process being studied. However, it is not the intention to discuss such theories here. Suffice it to say that mathematical functions, whether or not biological significance can be attributed to them, do provide an obviously useful mechanism for describing and comparing observed growth in both plants and animals.

Having said this, however, one can recognise and usefully distinguish between two general classes of curves, namely those whose use is simply to summarize a given set of data and those which it is intended shall have a meaning beyond the range of the data used in their estimation. In the former situation, consideration of properties of the chosen curve outside the observed range of the data plays no part in the choice of curve. In the latter case, such considerations may be all important.

Undoubtedly the search for curves which have a practical and theoretical significance wider than the particular set of data which form their basis is a praiseworthy scientific objective. It may, however, be an unattainable goal. Growth is an extremely complicated process and to express all its complexities within a single mathematical function is likely to result in an extremely complicated function with a very large number of parameters whose estimation in practice would be highly difficult, if not entirely impossible. The search for such a function also militates against another important scientific principle, namely the principle of parsimony. This simply states that we should always choose the smallest possible number of parameters for adequate representation.

Perhaps the best that can be hoped for, therefore, is to seek the simplest function which will fit the data adequately and which will possess some of the more obvious properties which a sensible curve should have. Here again conflict can easily arise between these criteria, for instance because of the nature of the observed data. A curve which may suitably represent observations over a restricted part of the total growth cycle (eg over the very early stages of life) will in all likelihood quickly become meaningless if extrapolated beyond that restricted range.

It has already been noted that simple functions, such as first and second degree polynomials in time, provide convenient, easy to fit summaries, perfectly adequate in many situations for making comparisons between average growth patterns in different groups of individuals. Such comparisons may be made using straightforward analysis of variance techniques, or, where appropriate, by using developments of these techniques proposed by Mandel (1961, 1971) and adapted by Snee, Acuff and Gibson (1979). Polynomials cannot be recommended without reservation. They are not, for example, generally successful at describing the entire growth cycle, usually giving poor fits at the upper limits of growth.

When the whole, or a large part, of the growth curve is to be modelled a more elaborate functional form is likely to be required. Three-parameter functions are often used to describe biological growth, the most frequently employed being

the von Bertalanffy : $Y_t = Y_\infty (1 - be^{-kt})$ (2)

the Gompertz : $Y_t = Y_\infty \exp(-be^{-kt})$ (3)

the logistic : $Y_t = Y_\infty \{1 + \exp(-(b+kt))\}$ (4)

These curves are special cases of a family derivable from a generalized growth curve for which the rate of growth is defined by

$$\frac{dY}{dt} = BY\{1 - (Y/A)^m\} \quad (5)$$

Both the Gompertz curve and the logistic curve have points of inflexion. In the case of the logistic curve this point occurs precisely half-way between zero and Y_∞ and the curve is symmetrical about this value. Growth rates which are symmetric in this way are unusual. On the other hand the point of inflexion of the Gompertz curve occurs at $Y_t = Y_\infty/e$ and the curve is not symmetric about the point of inflexion. For this reason the Gompertz curve may be a more attractive function than the logistic for describing growth. Growth in length, as Beverton and Holt (1957) have pointed out, does not usually show a point of inflexion and hence neither of these curves is likely to provide a reasonable model of linear growth. The Gompertz curve has, however, been studied by some writers as a possible alternative to the von Bertalanffy curve for representing growth in the size of pectinids.

The von Bertalanffy curve has no point of inflexion. It was derived from considerations of the physiological processes determining the growth in weight of an animal, the latter being assumed to obey the differential equation

$$\frac{dW}{dt} = hW - pW^{2} \quad (6)$$

On expressing W (weight) in terms of length the von Bertalanffy equation is obtained.

Of the three parameters involved in these curves, k, the growth constant, is related to the rate of growth of the animal and expresses the rate at which Y_∞, its final size, is approached. The constant b has no biological significance. In the von Bertalanffy curve the value of t corresponding to $Y_t = 0$ is $t_o = (\ln b)/k$, the point where the curve cuts the time axis, but the Gompertz and logistic curve do not touch the time axis at any finite value of t.

The von Bertalanffy curve has proved suitable for describing animal growth, particularly over the later stages, while, perhaps because of the greater flexibility of its shape for smaller values of t, the Gompertz curve might in some instances provide a more satisfactory description of the earliest stages of growth. The logistic curve, owing to its symmetry, is generally unsuitable for describing animal growth over the whole life cycle.

Materials and Methods

There is a high degree of correlation between overall length, breadth and thickness of the shell of *Pecten maximus* and also between the overall length and breadth of the flat valve (coefficient of correlation = 0.995) (Mason, 1957). These conclusions were reached as a result of examining scallops of all ages from 0+ (one growth period completed) to 13+ (fourteen periods completed). The annual increment of any one of these dimensions will, therefore, give a reliable indication of the rate of growth from one year to another.

Based on the data of Mason (1957), annual growth of scallops taken off Port Erin, Isle of Man, was plotted and von Bertalanffy and Gompertz curves were fitted, using the following two measurements:- (i) the distance (B) of successive growth rings on the flat valve from the umbo measured at right angles to the hinge line, and (ii) the overall length (L) of scallops of various ages during the winter cessation of growth during two winters 1950-51 and 1951-52. Since each growth ring represents the position of the edge of the shell at the end of an annual growth period, it is possible to measure directly on the shell of any scallop the breadth of the flat valve at the end of each growth period of its life. In the second method a scallop with no growth ring has completed its first growth period, one with one ring has completed two periods, and so on.

Mason (1957) found that the breadth of the first growth band gave a bimodal distribution, the great majority of scallops having a small band (<28mm wide) and a minority a large first band ($\geqslant 28$mm). He postulated that this was a result of the occurrence of two main spawnings each year, in spring and autumn, the fewer spring spawned scallops having longer to grow than the autumn spawned before the first winter cessation of growth.

In the preparation of growth curves, data from these so-called spring and autumn spawned scallops were treated separately. Autumn spawned scallops with eleven or fewer rings only were used because of difficulties arising from the crowding together of rings in older scallops. Few spring spawned scallops with more than seven rings were found.

Data from scallops of different year-classes are grouped together, thus, especially in the first method, masking any possible variation in growth from year to year.

The mean dimensions at age are presented in Tables I and II and the plotted values and fitted growth curves are shown in Figures 1 and 2 together with the growth constants.

Method of Fitting

The fitting of the von Bertalanffy curve by maximum likelihood has been described by Stevens (1951). His method assumes that the variance of y_t, the observed value of Y_t, is constant over the entire range. By taking natural logarithms of (3) we obtain

$$\ln Y_t = \ln Y_\infty - be^{-kt} \quad \text{or} \qquad (7)$$

$$Z_t = Z_\infty (1 - ce^{-kt}) \qquad (8)$$

which is equivalent to (2). Hence Steven's method may be used to fit the Gompertz curve by fitting a von Bertalanffy curve to the natural logarithms of the observed lengths. This procedure assumes, of course, that the variance of the logarithm of the length is constant over the range, not that of the length itself. Therefore, the two models contrasted here differ in respect of both their functional forms and their error structures. Fitting procedures appropriate to other assumptions about the error structures are currently under consideration by the authors.

Results and Conclusions

The von Bertalanffy equation gave curves which fitted the observed data reasonably well over the entire age range, and the calculated values of L_∞ and B_∞ agreed well with the observed values of L and B in older scallops. While the Gompertz equation gave curves which fitted the observed data over most of the age range, the calculcated values of L_∞ and B_∞ were well below the observed values of L and B for scallops 10 or more years old. However, since on most exploited grounds few scallops older than nine years are taken, this probably is not serious from the point of view of population dynamics.

At the lower end of the curves, too, the von Bertalanffy equation gave a very good fit with observed values, the intercept (t_o) on the time axis being consistently larger in autumn spawned than in spring spawned scallops, reflecting the fact that spring spawned scallops grew for almost a complete growing period and lived for almost a year before laying down the first growth ring, whereas autumn spawned scallops grew for a correspondingly shorter time before doing so. The Gompertz curve did not reflect the difference in spawning times because it does not meet the time axis. There is no evidence that the annual growth of *Pecten maximus* can be meaningfully represented by a sigmoid curve like the Gompertz.

References

Bertalanffy, L. von	1957	Quantitative laws in metabolism and growth. Quart. Rev. Biol. 32, 218-231.
Beverton, R.J.H. and Holt, S.J.	1957	On the dynamics of exploited fish populations. Fish. Invest. Lond. (Ser II) 19, 533 pp.
Mandel, J.	1961	Nonadditivity in two-way analysis of variance. J. Amer. Stat. Ass. 56, 878-888.
Mandel, J.	1971	A new analysis of variance model for non-additive data. Technometrics. 13, 1-18.
Mason, J.	1957	The age and growth of the scallop, *Pecten maximus* (L.), in Manx waters. J. mar. biol. Ass. UK, 36, 473-492.
Richards, F.J.	1959	A flexible growth function for empirical use. J. Exper. Bot. 10, 290-300.
Snee, R.D., Acuff, S.K. and Gibson, J.R.	1979	A useful method for the analysis of growth studies. Biometrics 35, 835-848.
Stevens, W.L.	1951	Asymptotic regression. Biometrics 7, 247-267.

Table I Mean distances of the growth rings from the umbo (flat valve) of Port Erin scallops

Growth rings	Mean distance (mm) Autumn spawned	Spring spawned
1	19.0	36.2
2	48.0	65.8
3	76.4	88.1
4	94.6	101.8
5	104.9	109.1
6	112.3	113.4
7	114.2	114.6
8	119.2	-
9	121.6	-
10	123.9	-
11	126.1	-

Table II Length of Port Erin scallops at the end of successive annual growth periods

No. of completed growth bands	Mean length (mm) Autumn spawned	Spring spawned
1	21.2	37.5
2	53.5	73.3
3	87.7	98.0
4	108.1	114.7
5	118.6	118.9
6	128.0	134.4
7	131.8	134.2
8	136.8	140.8
9	137.9	-
10	142.8	-
11	142.1	-
12	148.1	-

Figure 1. Mean distances (B) of growth rings of Port Erin scallops from the umbo (• spring spawned, x autumn spawned), and fitted von Bertalanffy and Gompertz annual growth curves.

Parameters of fitted curves:-

	B_∞	k	t_o	b
Spring spawned				
von Bertalanffy	121mm	0.476	0.27	-
Gompertz	116mm	0.719	-	2.394
Autumn spawned				
von Bertalanffy	128mm	0.380	0.62	-
Gompertz	122mm	0.677	-	3.648

Functional forms:-

von Bertalanffy $Y_t = B_\infty (1 - e^{-k(t-t_o)})$

Gompertz $Y_t = B_\infty \exp(-be^{-kt})$

Figure 2. Length (L) of Port Erin scallops at the end of successive annual growth periods (• spring spawned, x autumn spawned), and fitted von Bertalanffy and Gompertz annual growth curves.

Parameters of fitted curves:-

	L_∞	k	t_o	b
Spring spawned				
von Bertalanffy	146mm	0.396	0.24	-
Gompertz	138mm	0.661	-	2.512
Autumn spawned				
von Bertalanffy	147mm	0.372	0.62	-
Gompertz	141mm	0.658	-	3.651

Functional forms:-

von Bertalanffy $Y_t = L_\infty (1 - e^{-k(t-t_o)})$

Gompertz $Y_t = L_\infty \exp(-be^{-kt})$

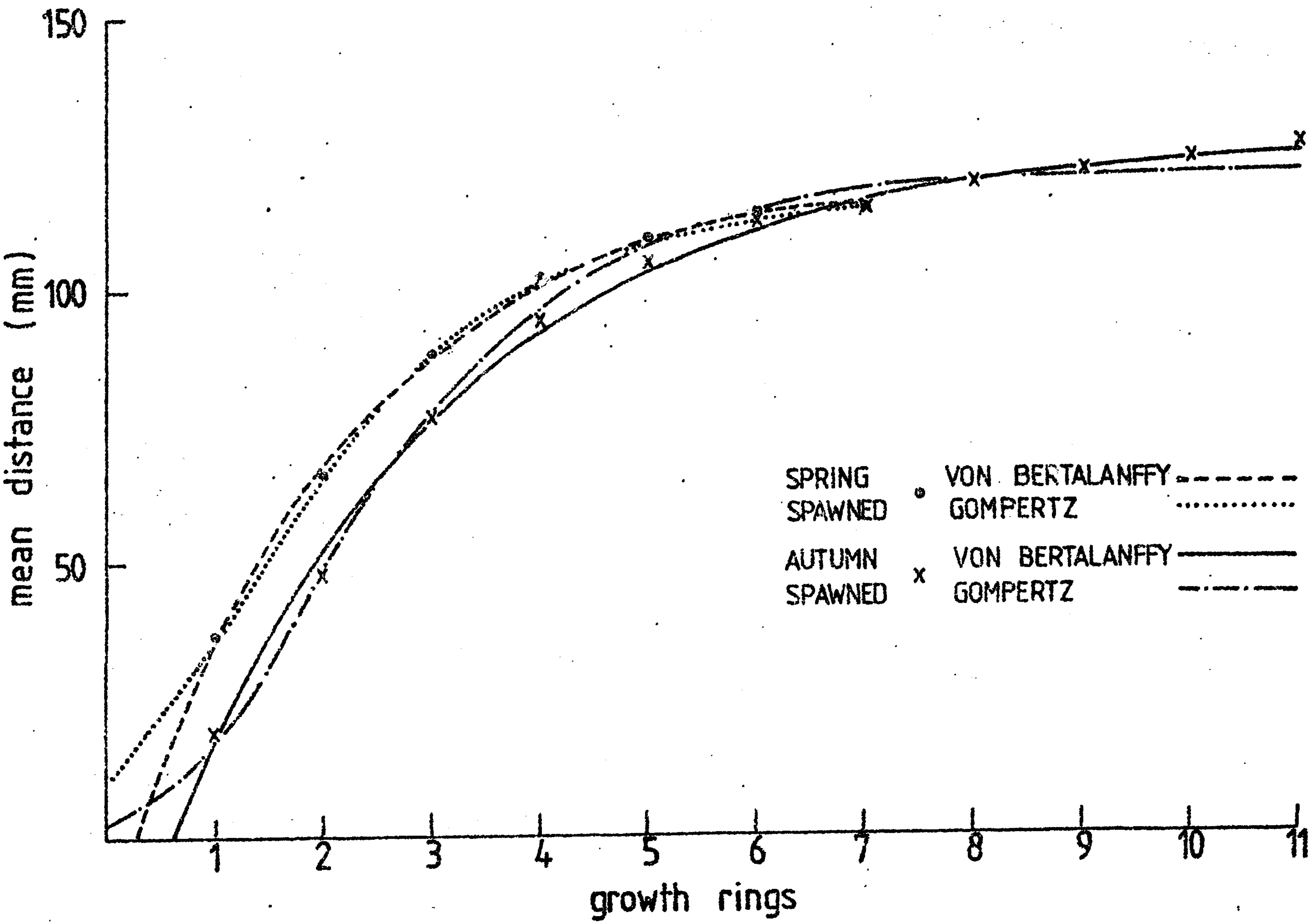
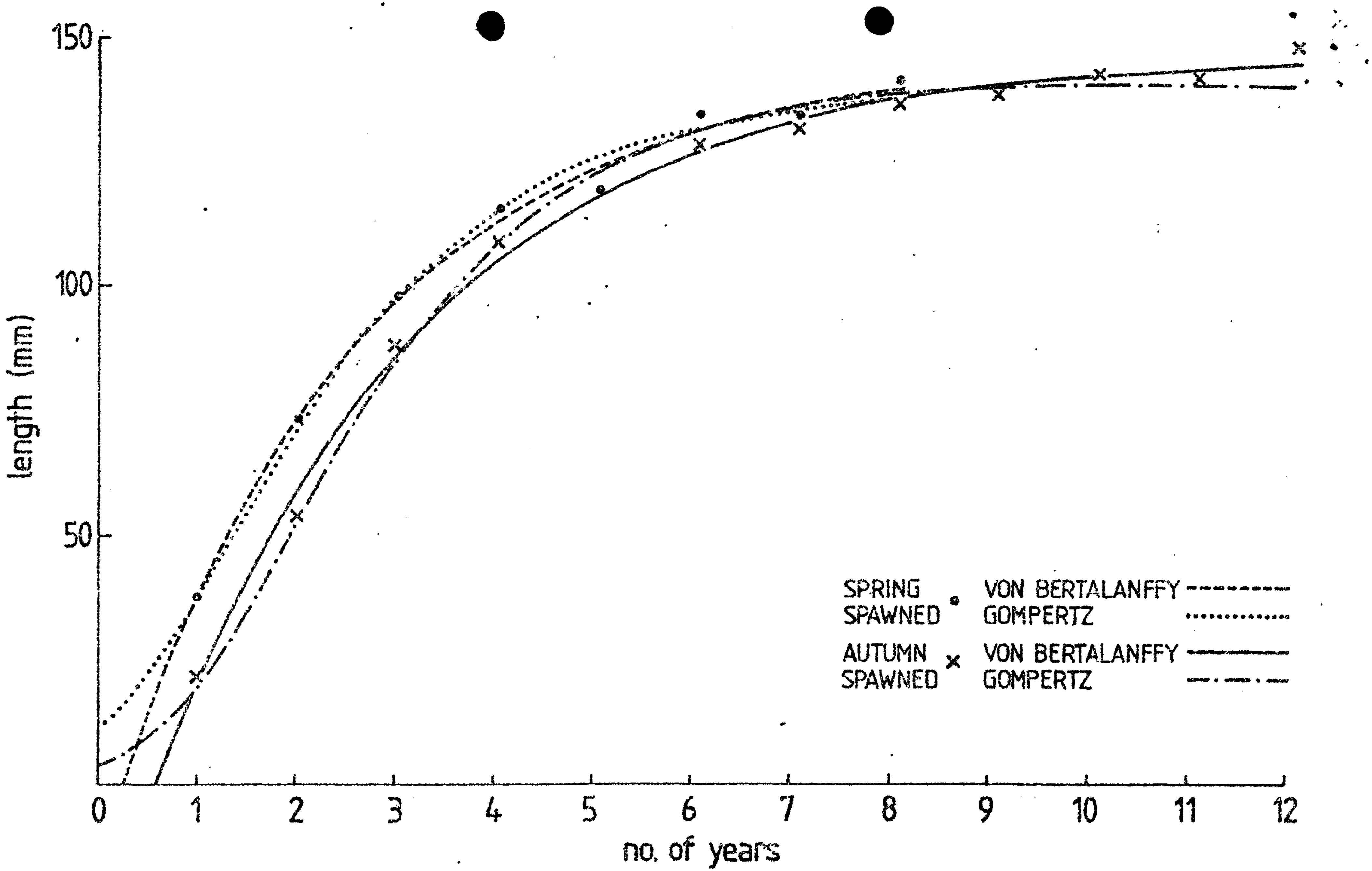

150
100
50
mean distance (mm)
1
2
3
4
5
6
7
8
9
10
11
growth rings
SPRING SPAWNED
VON BERTALANFFY
GOMPERTZ
AUTUMN SPAWNED
VON BERTALANFFY
GOMPERTZ

FIGURE 1



150
100
50
length (mm)
0
1
2
3
4
5
6
7
8
9
10
11
12
no. of years
SPRING SPAWNED
VON BERTALANFFY
GOMPERTZ
AUTUMN SPAWNED
VON BERTALANFFY
GOMPERTZ

FIGURE 2