Asymptotic Growth: An Example of Nonsense Disguised as Mathematics

"In the space of one hundred and seventy-six years the Lower Mississippi has shortened itself two hundred and forty-two miles. That is an average of a trifle over one mile and a third per year. Therefore, any calm person, not blind or idiotic, can see that in the Old Oölitic Silurian Period, just a million years ago next November, the Lower Mississippi River was upward of one million three hundred thousand miles long, and stuck out over the Gulf of Mexico like a fishing rod. And by the same token any person can see that seven hundred and forty-two years from now the Lower Mississippi will be only a mile and three quarters long, and Cairo and New Orleans will have joined streets together, and be plodding comfortably along under a single mayor and a mutual board of aldermen. There is something fascinating about science. One gets such wholesale returns of conjecture out of such a trifling investment of fact."

Mark Twain — Life on the Mississippi

A person seeking some mathematical curve to approximate growth data often chooses the von Bertalanffy (1938) or negative exponential curve for the job. This is reasonable both because it is simple and often fits the data about as well as anything else, and because the nature of a lot of growth models is such that they will generate an exponential curve or some related curve such as the logistic.

The now familiar notation for the von Bertalanffy curve is

$$\text{length at age } t = L_\infty \, [1 - \exp\,(K\,(t - t_o))] \qquad \ldots\ldots(1)$$

and has three parameters, L_∞, K, and t_o. Passing K and t_o by, I propose to discuss L_∞, commonly interpreted as the maximum length of the fish or other organism. It is a common, perhaps even standard, practice to fit a von Bertalanffy curve to a set of growth data and report the L_∞ thus obtained as the maximum size. This procedure, however, can be dubious.

Consider this business of maximum length in terms of a couple of sets of growth data, heights of human males after Thompson (1948) shown in Fig. 1, and lengths of cod after Graham (1933) shown in Fig. 2.

In the first instance cessation of growth is known from common acquaintance with the beast, the idea of maximum size makes sense, and the maximum height is well defined by the data at a little over 170 cm (5 ft 7 in) for these Belgian males.

In the case of the cod, the growth curve can be reasonably well approximated by a straight line although there is some small visible curvature. The data show a nearly constant growth rate of about 14 cm per year and it is

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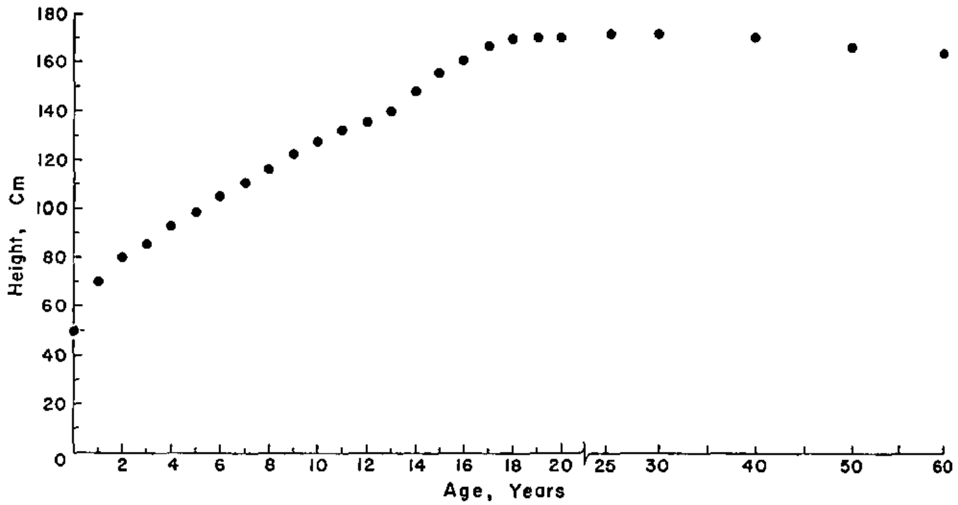

FIG. 1. Growth of Belgian human males. Source: Thompson (1948, p. 90)

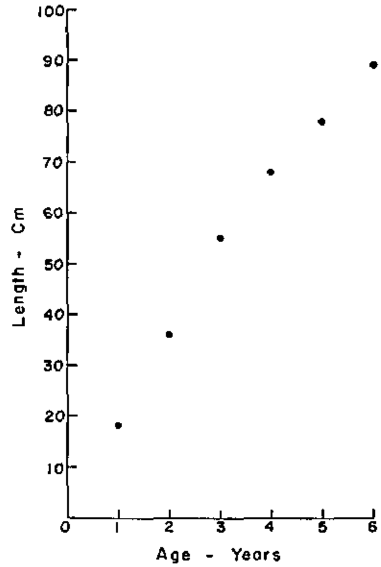

FIG. 2. Growth of cod. Source: Graham (1933).

not at all evident from the data alone at what length the growth stops, or even that it stops at all, and I believe that anyone who claims that this putative maximum is, say, the von Bertalanffy L_∞ (132 cm) (Beverton and Holt, 1957, p. 286) is either foolhardy or fortune telling.

In the case of the human data then, there is no objection to fitting an appropriate growth curve and reporting L_∞ or some equivalent symbol as the "average maximum height" or some such words. But I maintain that however well the von Bertalanffy curve may fit the cod data, and in fact the fit is good, it is misleading to the reader to report any value for L_∞ at all, particularly if accompanied by an intimation that it represents the maximum size the fish can or does attain.

It is very easy to construct examples of the danger of extrapolation though these are apt to be artificial. Suppose that in the growth data given for human males only age classes 1 through 13 were available and the reckless endeavour by von Bertalanffy curves and mathematical magic to obtain L_∞, the size of the adult male (?). How to fit a von Bertalanffy curve is a knotty subject which I do not altogether understand, but I have picked two of the stronger contenders for a good method and fitted curves to the truncated growth data. (The actual methods were the fitting of a Walford (1946) line by least squares and an iterative least squares procedure (Allen, 1966a, b), but these details are not germane to the main line of thought.) The two methods yield L_∞ = 195 cm (6 ft 5 in) and L_∞ = 211 cm (6 ft 11 in) respectively. The divergence from the correct 170 cm might be excessive sampling error, but as both estimates are 2.5 or more standard errors therefrom, it is probably not sampling error which is the trouble in this case. In point of fact the real trouble is not mathematical and is well known, especially to parents of adolescents: the human growth pattern changes at about age 13.

In principle this sort of thing might happen whenever any growth curve, von Bertalanffy or other, is forced on inappropriate data. The forcing of curves certainly happens and may even be common. The first example I happen to find is some growth data for the petrale sole (*Eopsetta jordani*) presented by Ketchen and Forrester (1966, p. 111). Figure 3 is a plot of growth against size. This is equivalent to the standard Walford plot but exhibits curvature rather better. Although this plot shows consistent curvature, the authors used the von Bertalanffy curve in their analysis.

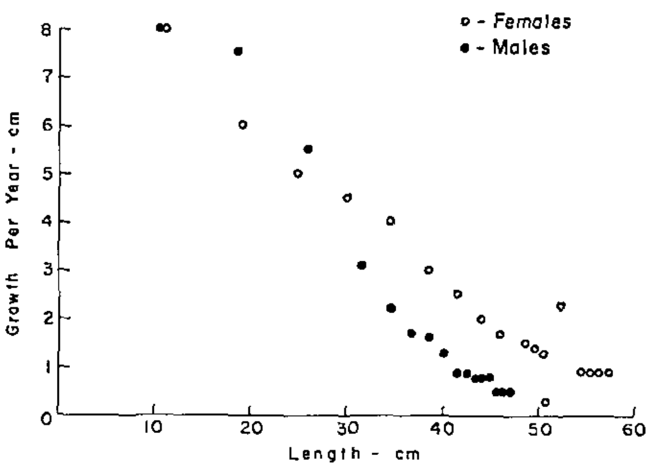

FIG. 3. Modified Walford plot of the petrale sole. Source: Ketchen and Forrester (1966).

However, Ketchen and Forrester do not fall into the trap of attempting a serious interpretation of the L_∞'s so calculated. Despite what I have said, I do not think that is an important danger in this study or any other. Indeed, to expect anything so blatant is to misunderstand the role of theory in science. More important is the distorted point of view engendered by regarding L_∞ as a fact of nature rather than as a mathematical artifact of the data analysis.

In comparative population studies one is tempted to tabulate L_∞ for a lot of species and environments and start comparing. This certainly calls for caution. If the L_∞'s are extrapolated from a lot of truncated growth data, the sampling error will be considerable at best, and the whole set of L_∞'s completely meaningless at worst. One example of such a comparative population study is Beverton and Holt's (1959). It includes, by the by, the 132 cm L_∞ for cod taken, apparently, from their own earlier analysis of Graham's data, tabled with no special comment, and not even rounded to 130 or 135 cm.

This same study contains an example of the way mathematical spectacles can distort an outlook in the remark: "The parameters T_{max} and M are, of course, closely linked on mathematical grounds; there is no reason why L_∞ and K should be, but it appears from the data that they are fairly closely correlated (inversely) although there are some important exceptions." (T_{max} and M are of no concern here.) However the von Bertalanffy K and L_∞ are mathematically linked; if K is zero, necessarily L_∞ is infinite. K among other things is a measure of curvature, and a large curvature relates to a small L_∞ in rather the same way that you have to bend a wire more sharply to make a small loop than a big one. If a growth curve is roughly straight as with Graham's cod and some other heavily fished species, some small apparent curvature, introduced by sampling error, will not merely be related to L_∞, it might cause it! Whether or not this is the actual cause of the observed correlation is irrelevant to this polemic. What does matter is the role a conceptual framework may have played in a possible cause being overlooked. Indeed, I believe the relation described above is obvious as soon as you consider K and L_∞ as descriptive summaries of data rather than as laws of nature.

For better or worse the use of mathematical tools in biology is growing. Any tool can, and occasionally will, be misused. A mathematical tool which the author believes is misused has been discussed. The unexpected point, to the author, is that the purported misuse seemingly did not come about because the user could not understand the mathematics since the mathematics is simple and the mistake not mathematical.

Thus the moral: That the main danger in a mathematical tool lies in the user's not understanding the mathematical foundations is obvious, but not necessarily true.

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