PART I

Chapter I: Modelling of Biological Growth:

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CHAPTER - I

MODELLING OF BIOLOGICAL GROWTH:

PRELIMINARY DISCUSSIONS
1.1 *Introduction*:

The term growth denotes those changes of a system that are manifested as measurable changes particularly as increase in biomass, matter, concentration, population size or density etc. Growth is one of those biological phenomena which invites mathematical modelling and analysis for a rational quantitative theory [Bertalanffy, 1960]. One of the most useful concepts in the mathematical modelling of growth is that of the net specific growth rate which is defined by

\[ g = \frac{1}{m} \frac{dm}{dt} \]  \hspace{1cm} (1.1)

where \( m \) is the growth indicator of a species (biomass, population size etc.). By itself (1.1) is not a mathematical model. It is simply a definition of the net specific growth rate which might be a function of \( x, t \) and a whole host of other variables and parameters. It may become a mathematical model, however, as soon as assumptions are made about the form of that function \( g \) (e.g. linear, quadratic in \( x \), independent of \( t \), etc.) [Gibbons, 1989].
1.2 Law of Natural Growth : Malthus Model

A constant specific growth rate is given by

\[ \frac{1}{x} \frac{dx}{dt} = g = k \text{ (constant)} \]

\[ \text{.........(1.2)} \]

The solution of the equation (1.2) leads to the exponential law, frequently called the law of natural growth. The exponential growth is thus characterized as the growth of a large number of uncoupled and self-reproducing elements which are fed by unrestricted resource and refuse of which is put into a sink of unlimited capacity. Every element grows independently of each other without influencing its neighbour or its environment. Historically, the exponential growth is known as Malthus growth. In 1798 Malthus published "an essay on Principle of population as it effects the future improvement of Society". There he stated

"Population when unchecked, increases in a geometric ratio. Subsistence increases only in an arithmetic ratio. A slight acquaintance with numbers will show the immensity of the first power in comparison with the second".

The tendency towards geometric progression of population growth is clear from the solution of (1.2), but the arithmetic (or linear) growth of subsistence may be less plausible today. We think of increasing agricultural output through the use of
chemical fertilizers, heavy machinery and genetic engineering. But in Malthus day those methods did not exist, the only way to increase harvest significantly was to bring more land under cultivation --- the limitation of which is obvious. Malthus argued that only war, famine and pestilence (and as Darwin later emphasized, infanticide) prevented the human population from outrunning its means of subsistence. He concluded that any effect to relieve the misery of the poor (who included practically everyone) was bound to fail, because any temporary improvement would only lead to an increase in population, which in turn meant less food and worsened living conditions in general. The discrepancy between supply and demand for food for ever-increasing world-population will grow very fast, and already for this reason, mankind cannot avoid future catastrophe. Malthus thus brought a gloomy message for the mankind.

Malthus thesis was enormously influential for the start. From Malthus day to now, economists have taken Malthus argument very seriously. Besides his influence in economics, Malthus effect on biology has been far reaching. Both Darwin and Wallace obtained inspiration from Malthus essay for their independent discoveries of natural selection. Darwin found Malthus' Essay new and striking not because of the truth of Malthus law - but because of the fact that Malthus presented his idea in law like, quantitative form with a deductive approach. This was just what Darwin was looking for in the Newtonian philosophy of science. As
soon as Darwin had read Malthus, he started to think in terms of forces and pressures that were pushing organism into the available not so-available gaps in the economy of nature.

1.3 Biological Growth: Mathematical Model

Before we go into the explicit form of the different growth equations, let us first clarify some basic mathematical characteristics of growth function. For simplicity, we consider only one-dimensional continuous growth. One-dimensional continuous growth usually appear in the form of s-formed continuous and monotonic state-transition as can be seen from the Fig - I given below for \( x = F(t) \):

![Graph of \( F(t) \) vs \( t \)]

If \( F(t) \) is differentiable then transition process can be written in the form of the ordinary differential equation

\[
\frac{dx}{dt} = f(t) \quad \ldots \ldots \ldots (1.3)
\]
or more generally by

\[ \frac{dx}{dt} = f(x, t) \] .......(1.4)

The r.h.s. of this equation i.e. \( f(x, t) \) is the driving force.

Since the function \( F(t) \) is assumed to be monotonic in principle, it is possible to write the growth equation in the autonomous form:

\[ \frac{dx}{dt} = f(x) \] .......(1.5)

or in terms of specific-growth rate we can rewrite (1.5) as

\[ \frac{1}{x} \frac{dx}{dt} = \frac{1}{x} f(x) = g(x) \] .......(1.6)

The indicator 'x' may be vector-valued quantity representing the biomasses, concentrations and population sizes of the different species of a biological community. The form of the function \( f(x) \) or \( g(x) \) in equation (1.6) will depend on different models of
different systems based on different phenomenologies. To place
the growth on a broader context, we start with the equation of
growth (1.5) i.e.
\[
\frac{dx}{dt} = f(x)
\] ..........(1.7)

If \( f(x) \) is sufficiently smooth as assumed earlier, we can expand
\( f(x) \) by Taylor's series

\[
f(x) = \sum_{n=0}^{\infty} a_n x^n = a_0 + a_1 x + a_2 x^2 + a_3 x^3 + ... 
\] ..........(1.8)

Thus every growth function may be written as a polynomial [See
Lamberson and Biles, 1981]. We should, however, make the
assumption \( f(0) = 0 \) to discuss the possibility of spontaneous
generation, the production of living organism from inanimate
matter, known as the axiom of Parenthood: Every organism must
have parents. This is equivalent to

\[
\left. \frac{dx}{dt} \right|_{x=0} = f(0) = 0
\] ..........(1.9)

So that we may assume that

\[
a_0 = 0
\]

\[
\frac{dx}{dt} = a_1 x + a_2 x^2 + a_3 x^3 + ... 
\]

\[
= x (a_1 + a_2 x + a_3 x^2 + ... )
\]

\[
= x g(x)
\] ..........(1.10)
The polynomial \( g(x) \) is thus the special growth rate.

We note that Malthus model of growth corresponds to \( a_1 = k \) and \( a_2 = a_3 = \ldots = 0 \). The model predicts exponential growth for \( k > 0 \) and exponential decline for \( k < 0 \). To correct Malthus prediction that a population can grow infinitely at an exponential rate, we can consider a non-constant intrinsic growth rate. The simplest extension of Malthus model is the logistic growth which takes account of intraspecies interaction and is described by the equation

\[
\frac{dx}{dt} = x(a_1 + a_2 x) \quad \ldots \ldots (1.11)
\]

which can be written in the form

\[
\frac{dx}{dt} = r \left( 1 - \frac{x}{K} \right) x \quad \ldots \ldots (1.12)
\]

where \( r = a_1 \) is the growth rate and \( K = - \frac{a_1}{a_2} \) is the carrying capacity of the environment of the species. We can rewrite (1.12) in the form

\[
\frac{dx}{dt} = \alpha (x^* - x) \quad \alpha = \frac{r}{K} \quad \ldots \ldots (1.13)
\]

where the steady state value \( x^* = K \).

The logistic growth equation (1.12) is widely used in population growth as well as in organismic growth [Zotin and Zotina, 1983]. There is extensive literature on it and also on its various stochastic extensions. So we shall not go far with this model.
1.4 Conclusion:

Malthus and logistic equations, the two simple models are discussed above only to explain the process of mathematical modelling of the phenomena of biological growth. These model equations, however, do not represent the real picture of the growth process. A general model equation of growth proposed by Peshel and Mende [1983] is given by the hyper-logistic differential equation

\[ \frac{dx}{dt} = k(x-a)^k \left\{ B - (x-A)^w \right\}^l, \]

where \( a \) and \( A \) are shift parameters, \( B \) is the saturation or steady-state value, the exponent \( k \) characterizes autonomous growth in the extensive phase and \( l \) is the autonomous saturation in the intensive phase. As particular case of the above generalized hyper-logistic model equation we can obtain the well-known and frequently used growth equation:

\[(1) \quad \text{Power growth} : \quad \frac{dx}{dt} = k x^k \]

\[(11) \quad \text{Power Saturation} : \quad \frac{dx}{dt} = k (B - x)^l \]

\[(111) \quad \text{Allometric Saturation} : \quad \frac{dx}{dt} = k (B - x^v) \]
Logistic growth: \( \frac{dx}{dt} = k (B - x) \)

Bertalanffy's growth: \( \frac{dx}{dt} = A x^m - B x^n \)

Gompertzian growth: \( \frac{dx}{dt} = k x \ln (B/x) \)

The list of growth equations given above is not exhaustive and unique. There are other types of growth equations obtained from different observations and phenomenologies. The applicability and utility of the different growth equations depend on different systems, situations, necessities and requirements.

Finally, we should make it clear that the growth is not only the increase of the growth indicator, it is a process of inner organization based on inner programme. The inner programme is determined by the co-operation and competition and in general by interaction of the different elements of the living system in relation to its environment [Peshel and Mende, 1983].