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SOME MATHEMATICAL MODELS FOR POPULATION GROWTH

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One of the most successful models for explaining the growth of populations of bacteria and even of humans is the so-called logistic model. Its characteristic features are: (i) a limiting population size and ultimate zero growth rate and (ii) an S-shaped graph with a point of inflexion. Many observed populations show these features but do not fit the logistic model very well. Smith (1963) gave another model with these features giving a better fit in some situations. We give here two more models of the same type based on considerations of enzyme kinetics and compare these with the existing models.

1. THE LOGISTIC CURVE

The simplest growth model is

$$\frac{dN}{dt} = aN \qquad \ldots(1)$$

where $N(t)$ is the population at time t and a is the excess of births over deaths per unit time. This is known as the law of Malthus and gives on integration

$$N(t) = N_0\, e^{at}. \qquad \ldots(2)$$

This model is valid when there are unlimited resources available to the population. However limitation of resources suggest the introduction of an inhibiting term on the right-hand side of (1) to take into account the competition for resources among members of the population. The simplest modified law is the logistic law

$$\frac{dN}{dt} = aN - bN^2. \qquad \ldots(3)$$

Integration of (3) gives (Pielou 1969)

$$N = \frac{N_e}{1 + \left(\frac{N_e}{N_0} - 1\right) e^{-at}}, \quad N_e = \frac{a}{b}. \qquad \ldots(4)$$

The logistic curve is S-shaped and has a point of inflection when

$$N = \frac{a}{2b} = \tfrac{1}{2}N_e. \qquad \ldots(5)$$

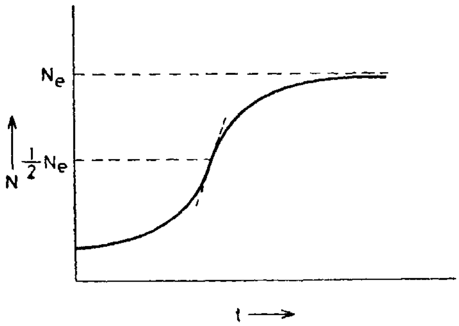

FIG. 1.

This law explained very well the growth of a bacterial colony in a nutrient medium or broth, provided the initial inoculum N_0 is taken from an exponentially growing colony (Gause 1934, Rabinow 1975). It has also been successfully used to fit data for human populations. Equation (3) is sometimes replaced by

$$\frac{dN}{dt} = a(t)\,N - b(t)\,N^2 \qquad \ldots(6)$$

which gives on integration

$$\frac{1}{N} = \frac{1}{N_0}\,e^{-\alpha(t)} + \int_0^t e^{\alpha(t)}\,b(t)\,dt \qquad \ldots(7)$$

where

$$\alpha(t) = \int_0^t a(t)\,dt. \qquad \ldots(8)$$

2. The Model of Smith

According to (2), $\frac{1}{N}\frac{dN}{dt}$ should be a linear function of N. Smith (1963) (Pielou 1969) found in his experiments on bacterial cultures that while the graph of N against t was a sigmoid or S-shaped curve, the graph of $\frac{1}{N}\frac{dN}{dt}$ against N was not a straight line but it was a concave curve. He argued that the term $a - bN$ in (3) should be replaced by the rate of food supply 'not' being used by the population i.e. it should be replaced by $\gamma(S - F)/S$ where F is the rate at which food is being used and S is the saturation rate. He assumed that

$$F = \lambda N + \mu\,\frac{dN}{dt} \qquad \ldots(9)$$

so that

$$\frac{1}{N}\frac{dN}{dt} = \gamma\,\frac{S-F}{S} = \frac{\gamma\left(\lambda K - \lambda N - \mu\frac{dN}{dt}\right)}{\lambda K} \quad ...(10)$$

or

$$\frac{1}{N}\frac{dN}{dt} = \frac{\gamma(K-N)}{K+\nu N} \quad ...(11)$$

where $\nu = \frac{\gamma\mu}{\lambda}$. This model gave a good fit for his data.

If $N_0 < K$, we find that $dN/dt > 0$, the population goes on increasing at a decreasing rate and ultimately as $N \to K$, the growth rate $\to 0$ so that K is the limiting size of the population. If $N_0 > K$, the population decreases to the limiting size K.

Also

$$\frac{1}{\gamma}\frac{d^2N}{dt^2} = -\frac{\nu}{(K+\nu)^2}\left[\left(N+\frac{K}{\nu}\right)^2 - K^2\left(\frac{1}{\nu}+\frac{1}{\nu^2}\right)\right] \quad ...(12)$$

so that there is a point of inflexion when

$$\frac{N}{K} = \left[\sqrt{\frac{1}{\nu}+\frac{1}{\nu^2}} - \frac{1}{\nu}\right]. \quad ...(13)$$

As $\nu \to 0$, $N/K \to \frac{1}{2}$ and as $\nu \to \infty$, $N/K \to 0$, so that the point of inflexion always occurs when N lies between 0 and $K/2$. As ν (or μ/λ) increases, the point of inflexion occurs for lower and lower values of N and if

$$\nu > \frac{1}{(N_0/K)^2} - \frac{2}{N_0/K} \quad ...(14)$$

there is no point of inflexion.

Thus Smith's model is likely to fit the data better when the point of inflexion in the sigmoid curve occurs before half the final population size is reached. We may also note that (11) has one parameter more than (3) and in fact includes (3) as a special case.

3. Our First Model for the Growth of a Bacterial Colony in a Nutrient Medium

The law of growth is given by

$$\frac{dN}{dt} = k(c)\,N \quad ...(15)$$

where Monod (Rabinow 1975) proposed that the mathematical form for $k(c)$ should be taken as

$$k(c) = k_m \frac{c}{K + c} \qquad \text{...(16)}$$

where c is the concentration of the nutrient in the medium. The law is supported by the theoretical possibility that the uptake of nutrient is governed by enzyme action. A more general form of (16) is given by Hill's equation

$$k(c) = k_m \frac{c^n}{K + c^n}. \qquad \text{...(17)}$$

The concentration c is reduced due to the consumption of the nutrient by the bacteria according to the law

$$\frac{dc}{dt} = -\frac{1}{y} k(c) N \qquad \text{...(18)}$$

so that the consumption rate is being assumed proportional to both the population size of the bacteria and saturation function of the nutrient.

From eqns. (15) and (18)

$$\frac{dN}{dc} = -y \qquad \text{...(19)}$$

which gives on integration

$$N = y(c_1 - c). \qquad \text{...(20)}$$

From (15), (17), and (20), we get

$$\frac{dN}{dt} = k_m \frac{\left(c_1 - \frac{N}{y}\right)^n N}{K + \left(c_0 - \frac{N}{y}\right)^n} = k_m \frac{(\bar{c} - N)^n N}{\bar{K} + (\bar{c} - N)^n} \qquad \text{...(21)}$$

where

$$\bar{K} = Ky^n, \ \bar{c} = c_1 y. \qquad \text{...(22)}$$

We note that

(i) If $N_0 < \bar{c}$, then $\frac{dN}{dt} > 0$, N goes on increasing and as $N \to \bar{c}$, $\frac{dN}{dt} \to 0$ so that $\bar{c}$ is the limiting size of the population. In our model $\frac{dN}{dt}$ cannot be negative.

(ii) The graph of $\frac{1}{N}\frac{dN}{dt}$ against N is not a straight line but may be a concave or convex curve.

(iii) There are two equilibrium points vix $N = 0$ and $N = \bar{c}$. The first is unstable and the second is stable. If N is initially zero, it always remains zero, but if N_0 is slightly greater than zero, then N grows with time and approaches $\bar{c}$ asymptotically.

$$\text{(iv)} \quad \frac{d^2N}{dt^2} = k_m (\bar{c} - N)^{n-1} \frac{[(\bar{c} - N)^{n+1} + \bar{K}(\bar{c} - N) - N\bar{K})}{[\bar{K} + (\bar{c} - N)^n]^2}. \qquad \ldots(23)$$

Let

$$f(N) = (\bar{c} - N)^{n+1} + \bar{K}(\bar{c} - N) - nN\bar{K} \qquad \ldots(24)$$

$$= (\bar{c})^{n+1} \{(1 - x)^{n+1} + A(1 - \overline{n+1}\, x)\} = (\bar{c})^{n+1} \phi(x) \qquad \ldots(25)$$

where

$$x = \frac{N}{\bar{c}}, \; A = \frac{\bar{K}}{\bar{c}^n} = \frac{K}{c_1^n}. \qquad \ldots(26)$$

In general $x_0 = \dfrac{N_0}{\bar{c}} \ll 1$ and we can assume

$$\phi(x_0) = (1 - x_0)^{n+1} + A(1 - x_0) > nAx_0. \qquad \ldots(27)$$

Also $\phi(1)$ is negative and so the population curve has a point of inflexion at x^* between x_0 and 1. The position of the point of inflexion will depend on A and n.

For a given n, we can choose A so that the point of inflexion is at a given point x^* where $\dfrac{1}{n+1} < x^* < 1$.

(v) For a given observed population curve with a point of inflexion and a limiting population size, $\bar{c}$ is given by the limiting population size, then $x_0 = \dfrac{N_0}{\bar{c}}$ is given by the initial population size. The existence of the point of inflexion shows that $n > \dfrac{1}{x^*} - 1$ and then A is given by

$$A = \frac{(1 - x^*)^{n+1}}{(n + 1)\, x^* - 1}. \qquad \ldots(28)$$

We can then choose n to get the best fit to the data.

(vi) This model is more general than the logistic model as well as Smith's model in the sense that it can give population curves with points of inflexion both before and after $\bar{c}/2$ while logistic model gives a point of inflexion only at $\bar{c}/2$ and

Smith's model gives it only before $\bar{c}/2$. This is not surprising since our model is a four-parameter model, whereas the earlier models were two and three parameter models respectively.

(vii) From (21) and (26)

$$\frac{1}{x}\frac{dx}{d\tau} = \frac{(1-x)^n}{A + (1-x)^n} \qquad \ldots(29)$$

where

$$\tau = k_m t. \qquad \ldots(30)$$

Integrating

$$\int_{x_0}^{x} \left[\frac{A}{x(1-x)^n} + \frac{1}{x}\right] dx = \tau. \qquad \ldots(31)$$

when $n = 1$, this gives

$$(A+1)\log\frac{x}{x_0} + A\log\frac{1-x_0}{1-x} = \tau. \qquad \ldots(32)$$

If n is a positive integer greater than unity, we get

$$(A+1)\log\frac{x}{x_0} + A\log\frac{1-x_0}{1-x} + A\left[\frac{1}{1-x} + \frac{1}{2(1-x)^2} + \ldots \frac{1}{(n-1)(1-x)^{n-1}}\right]_{x_0}^{x} = \tau. \qquad \ldots(33)$$

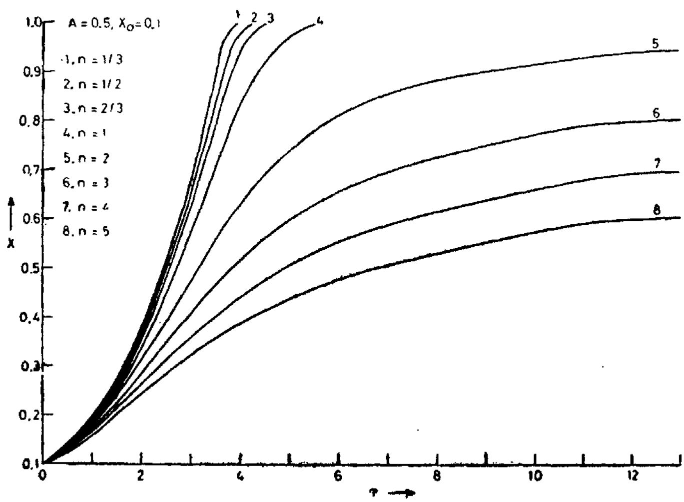

FIG. 2.

When n is not an integer, we have to integrate numerically. We note that τ increases with A, x and n and decreases with x_0.

Figures 2–5 show population growth curves for different values of A and n and for $x_0 = 0.1$

4. Another Population Model

Another equation for enzyme moderated reaction is

$$k(c) = k_m \frac{c(1 + c)^3 + Bc^4}{(1 + c)^4 + Bc^4}. \qquad \ldots(34)$$

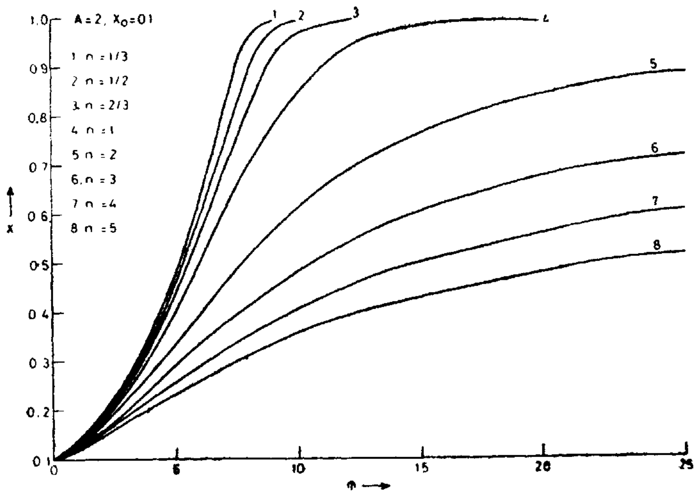

FIG. 3.

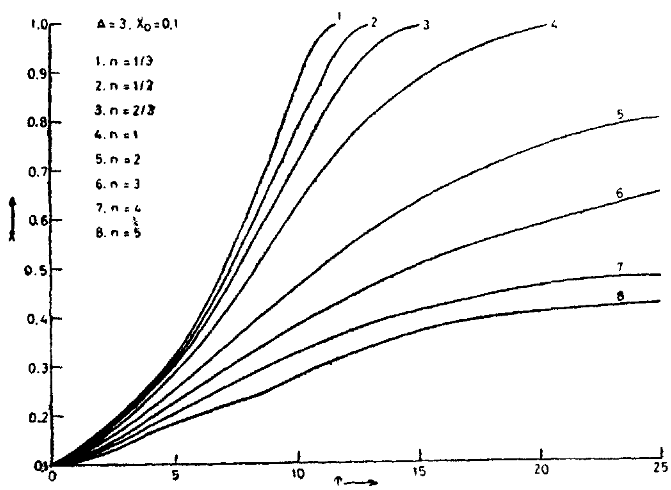

FIG. 4.

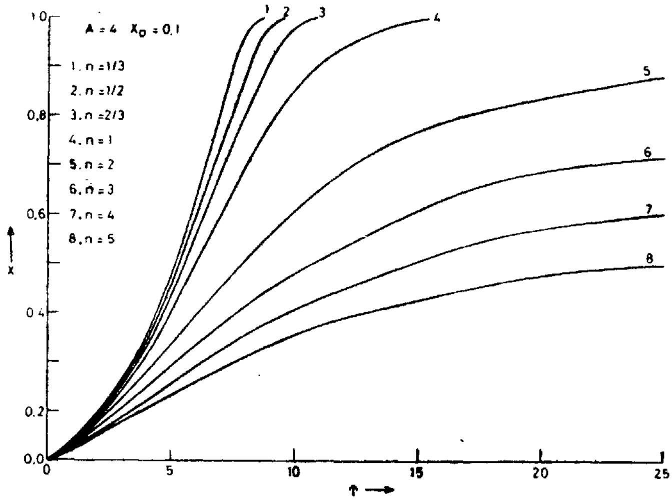

FIG. 5.

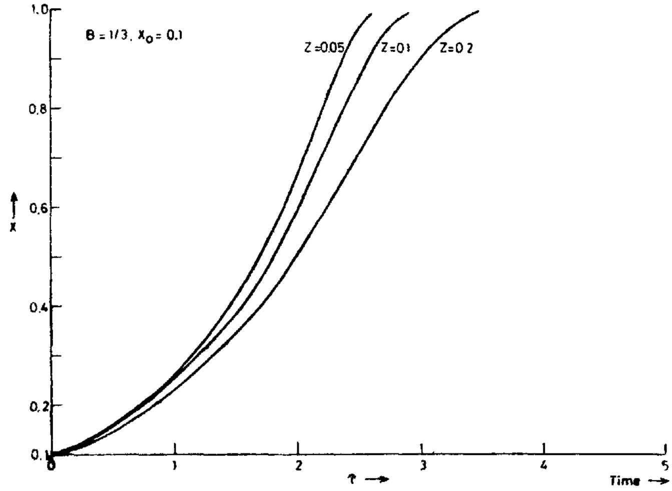

FIG. 6.

From (15), (22), (26) and (34)

$$\frac{dx}{d\tau} = \frac{(1 - x)\, x\,[(z + 1 - x)^3 + B(1 - x)^3]}{(z + 1 - x)^4 + B(1 - x)^4} \qquad \ldots(35)$$

when

$$z = \frac{y}{c}. \qquad \ldots(36)$$

Equation (35) can be easily integrated by quadrature.

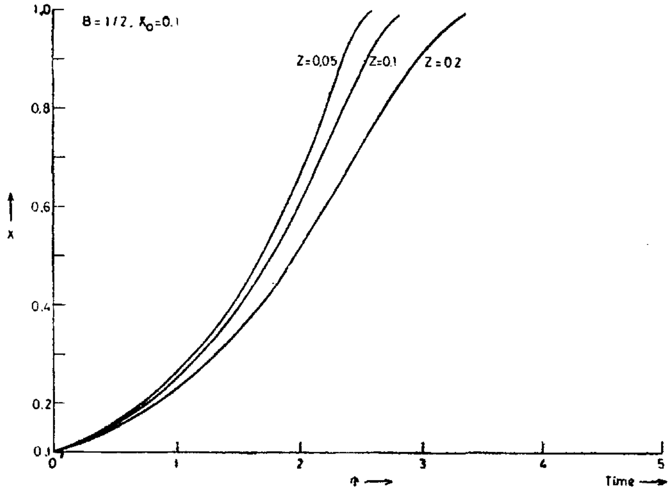

FIG. 7.

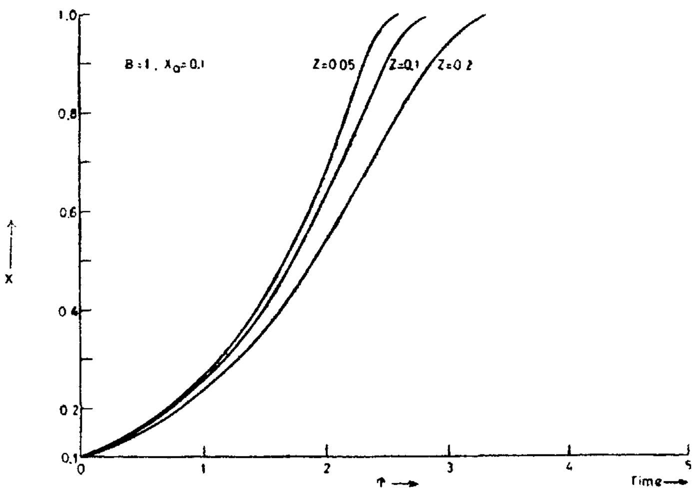

FIG. 8.

For the point of inflexion we find

$$\frac{d^2x}{d\tau^2} = \frac{\psi(x)}{[(z+1-x)^4 + B(1-x)^4]^2} \qquad \ldots(37)$$

where

$$\begin{aligned}\psi(x) = {} & [(z+1-x)^4 + B(1-x)^4]\,\{[(z+1-x)^3\,(1-x) + B(1-x)^4] \\ & - x\,[(z+1-x)^3 + 3(1-x)\,(z+1-x)^2\} - 4B(1-x)^3] \\ & + x\{[(1-x)\,(z+1-x)^3 + B(1-x)^4] \\ & \quad \times [4(z+1-x)^3 + 4B(1-x)^3]\}\end{aligned} \qquad \ldots(38)$$

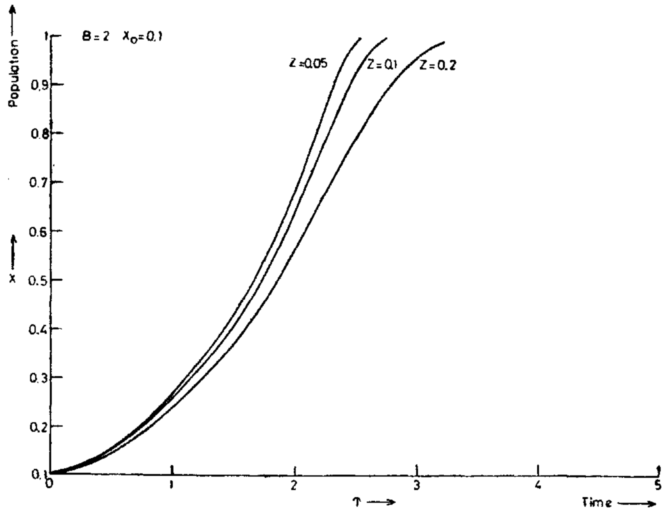

FIG. 9.

so that

$$\psi(1) = -z^7 < 0. \qquad \ldots(39)$$

Also $\psi(x_0) > 0$ if x_0 is sufficiently small. As such the population curve is an S-shaped curve with a limiting population size and each curve has in general a point of inflexion.

We have got here a three-parameter family of curves. Figures 6–9 show populations curves for different values of B and z.

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