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MODELS OF POPULATION GROWTH—II

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In the present paper four new models for the microbial population growth are given. They are based on the experimentally determined laws of Teissier (1942), Jost *et al.* (1973), Shehata and Maar (1971), Powell (1967) and Dabes *et al.* (1973) for the dependence of the specific growth rate of a population on the concentration of the rate-limiting substrate. It is shown that though these laws are apparently quite different, they all lead to logistic-type growth curves with limiting population sizes and with points of inflexion.

1. IMPORTANCE OF MODELS OF POPULATION GROWTH

Actuaries and demographers are interested in models of growth for human population for predicting expected duration of life at various ages and for estimating future population trends (Pollard 1973). Bioeconomists are interested in models of growth for populations of sheep, fish, forests and other renewable resources for the sake of their optimal exploitation (Clark 1976). Medical scientists and biologists are interested in models of growth of bacterial populations for the sake of controlling diseases, and epidemics and for genetical studies. Chemical engineers are interested in models of growth of populations of all microorganisms for the role they play or can play in four major areas, viz.

(i) fermentation technology where microorganisms are used for producing foods, beverages, antibiotics, vitamins, plant growth regulators, flavour enhancing compounds, amino acids, enzymes, polysaccharides, single-cell proteins and so on;

(ii) sanitary and environmental engineering where microorganisms are used to reduce water pollution;

(iii) ore and fuel processing where microorganisms can be used to leach certain undesirable substances from ores e.g. they can be used to remove sulphur from coal;

(iv) bioconversion of solar energy where microorganisms can be used to first absorb it and then they can be used as fuels. (Frederickson and Tsuchiya 1977).

One specific example is the release of methane gas from gobar gas plants which is due to the action of microorganisms. For increasing the amount of gas released, it is necessary to understand the mutual relationships between the growth of microorganisms, the change in the substrate and the amount of gas produced.

2. Some Earlier Models

Let $N(t)$ be the population of microorganisms at time t and let $c(t)$ be the concentration of the rate-limiting substrate, then we have the simple hypothesis

$$\frac{dN}{dt} = k(c)\, N \qquad ...(1)$$

where $k(c)$ is the specific growth rate of the population. The substrate is consumed by the population and according to Monod's hypothesis

$$\frac{dc}{dt} = -\frac{1}{Y}\, k(c)\, N \qquad ...(2)$$

where Y is called the yield coefficient. From (1) and (2)

$$N(t) + Yc(t) = N(0) + Yc(0) = \bar{c} \text{ (say)} \qquad ...(3)$$

so that (1) gives

$$\frac{dN}{dt} = N(t)\, k\left[\frac{\bar{c} - N(t)}{Y}\right]. \qquad ...(4)$$

Integration of this gives $N(t)$ as a function of t. In general $k(c) = 0$ when $c = 0$ so that $dN/dt = 0$ when $N(t) = \bar{c}$, so that the population will stop increasing when it reaches the value $\bar{c}$. Thus each such model will have a limiting population size. Further

$$\frac{d^2N}{dt^2} = \frac{dN}{dt}\left\{k\left[\frac{\bar{c} - N(t)}{Y}\right] - \frac{N(t)}{Y}\, k'\left[\frac{\bar{c} - N(t)}{Y}\right]\right\} \qquad ...(5)$$

and this may vanish before the final population size is reached in which case the population growth curve will have a point of inflexion.

If we take $k(c) = \alpha c$, we get

$$\frac{dN}{dt} = N(t)\,[a - bN(t)] \qquad ...(6)$$

which gives the logistic curve with limiting population size as a/b and a point of inflexion at half the final population size. This is the famous Pearl-Verlhust or M'Kendrick and Pai (1911) law.

If we take

$$k(c) = \frac{\gamma c}{\beta - \nu c} \qquad ...(7)$$

we get

$$\frac{dN}{dt} = \frac{\gamma(c - N)\, N}{\beta Y - \nu c + \nu N} \qquad ...(8)$$

which is similar to Smith's (1963) model, but is not identical with it:

$$\frac{dN}{dt} = \frac{\gamma(K - N)\, N}{K + \nu N}. \qquad \ldots(9)$$

In fact Smith's model does not belong to the family of models we are considering. Moreover (7) is not an experimental law.

If we take $k(c)$ according to Hill's equation or the law of Moser (1958) viz.

$$k(c) = \frac{k_m c^n}{K^n + c^n} \qquad \ldots(10)$$

we get

$$\frac{dN}{dt} = k_m \frac{(\bar{c} - N)^n\, N}{K^n + (\bar{c} - n)^n}. \qquad \ldots(11)$$

This has a point of inflexion between $\frac{\bar{c}}{n+1}$ and $\bar{c}$. When $n = 1$, Moser's law reduces to Monod's law and the point of inflexion lies between $\bar{c}/2$ and $\bar{c}$. In Part I, we (Kapur and Khan 1979) also investigated the case when

$$k(c) = k_m \frac{c(1 + c)^3 + Bc^4}{(1 + c)^4 + Bc^4} \qquad \ldots(12)$$

All the models corresponding to (6), (8), (9), (10) and (12) give growth curves with limiting population sizes and points of inflexion. However since S-shaped curves are of very common occurrence, more models of this type are needed to give a sufficiently wide choice to the experimentalists.

3. Population Growth Model Based on the Law of Teissier

Teissier (1942) found that the equation

$$k(c) = k_m \left[1 - \exp\left(-\frac{c \log 2}{K}\right)\right] \qquad \ldots(13)$$

fitted his data quite well. From (4) and (13)

$$\frac{dN}{dt} = k_m \left[1 - \exp\left(-\frac{\bar{c} - N}{KY} \log 2\right)\right] N. \qquad \ldots(14)$$

On integration, this gives

$$\int_{X_0}^{X} \frac{dX}{X\,[1 - \exp\{-B(1 - X)\}]} = \tau \qquad \ldots(15)$$

where

$$B = \frac{\bar{c} \log 2}{KY},\ \tau = k_m t,\ X = \frac{N}{\bar{c}}. \qquad ...(16)$$

Figure 1 shows the population curves for $X_0 = 0.1$ and for $B = 0.10, 0.15, 0.20, 0.25, 0.30$.

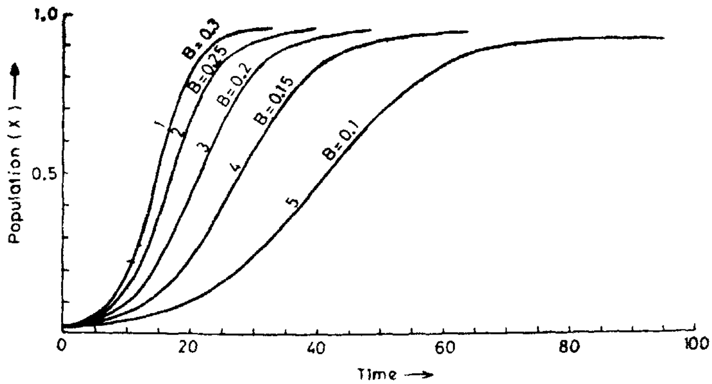

FIG. 1. Model based on the law of Teissier.

The point of inflexion X^* is obtained by putting $\frac{d^2X}{d\tau^2} = 0$ so that

$$1 - (BX^* + 1) \exp(-B(1 - X^*)) = 0. \qquad ...(17)$$

This gives the table

B	0.10	0.15	0.20	0.25	0.30
X^*	0.506	0.509	0.512	0.515	0.518

When B is very small, (17) gives on neglecting third and higher powers of B

$$1 - 2X^* - B[X^{*2} + \tfrac{1}{2}(1 - X^*)^2] = 0 \qquad ...(18)$$

so that as $B \to 0$, $X^* \to \frac{1}{2}$.

Let

$$f(X) \equiv 1 - (1 + BX) \exp(-B(1 - X)) \qquad ...(19)$$

then

$$f(0) = 1 - \exp(-B) > 0,\ f(\tfrac{1}{2}) = 1 - \left(1 + \frac{B}{2}\right) \exp(-\tfrac{1}{2}B) > 0$$

$$f(1) = -B < 0 \qquad ...(20)$$

so that

$$\tfrac{1}{2} < X^* < 1. \qquad \ldots(21)$$

Also as $B \to \infty$, $X^* \to 1$.

Thus for this model, a point of inflexion always exists and occurs after half the final population size is reached.

4. Model Based on the Law of Jost-Drake-Tsuchiya-Frederickson

Jost *et al.* (1973) obtained from their experiments the law

$$k(c) = \frac{k_m c^2}{(K_1 + c)(K_2 + c)}. \qquad \ldots(22)$$

This gives for the growth of the population

$$\frac{dN}{dt} = \frac{k_m c^2}{(K_1 + c)(K_2 + c)} N. \qquad \ldots(23)$$

From (4) and (23), we get

$$\int_{X_0}^{X} \frac{(H - \bar{c}X)(G - \bar{c}X)}{\bar{c}^2 X(1 - X)^2} \, dX = \tau \qquad \ldots(24)$$

where

$$H = K_1 Y + \bar{c},\ G = K_2 Y + \bar{c},\ X = \frac{N}{\bar{c}},\ \tau = k_m t. \qquad \ldots(25)$$

Figure 2 shows the population growth curves for $X_0 = 0.02$, $\bar{c} = 1.0$, $G = 3.0$ and $H = 2.4, 2.6, 2.8, 3.0, 3.2$.

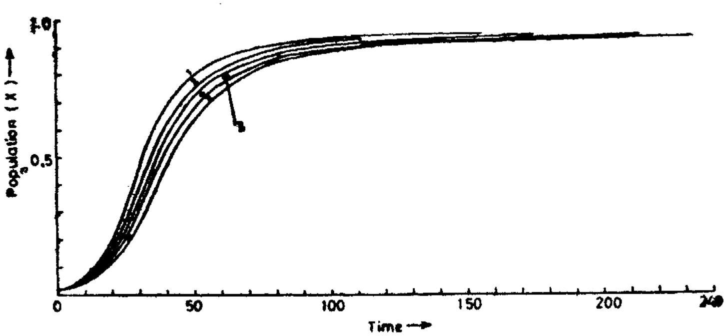

Fig. 2. Model based on the law of Jost *et al.*

From (24), the point of inflexion is given by

$$\phi(X) \equiv (H - \bar{c}X)(G - \bar{c}X)(1 - 3X) + \bar{c}X(G + H - 2\bar{c}X)(1 - X) = 0 \qquad \ldots(26)$$

so that

$$\phi(\tfrac{1}{3}) > 0, \phi(1) < 0. \qquad ...(27)$$

As such a point of inflexion always exists and occurs after one-third the final population size is reached.

If $G = H$, (26) gives

$$\phi(X) \equiv (G - \bar{c}X)\,[(G - \bar{c}X)\,(1 - 3X) + 2\bar{c}X(1 - X)] = 0. \qquad ...(28)$$

Since $G > \bar{c}$, the first factor cannot be zero when $0 < X < 1$ and as such the point of inflexion is given by

$$X^2 + X(1 - 3\bar{G}) + \bar{G} = 0,\ \bar{G} = \frac{G}{\bar{c}}. \qquad ...(29)$$

Equation (29) has two positive roots, one greater than and the other less than unity. The latter root determines the point of inflexion so that

$$X^* = \tfrac{1}{2}\,[(3\bar{G} - 1) - ((9\bar{G} - 1)\,(\bar{G} - 1))^{1/2}] \qquad ...(30)$$

and as $\bar{G} \to \infty$, $X^* \to \frac{1}{3}$.

Equation (30) determines the point of inflexion for the law

$$k(c) = \frac{k_m c^2}{(k + c)^2}. \qquad ...(31)$$

For the general law (22), the basic eqn. (26) is a cubic in X and its root lying between $\frac{1}{3}$ and 1 can be determined numerically. For the curves in Fig. 2, we get the table

H	2.4	2.6	2.8	3.0	3.2
X	0.4045	0.4005	0.3972	0.3945	0.3921

5. Model Based on the Law of Shehata and Marr

Shehata and Marr (1971) found from their experiments the law

$$k(c) = \frac{k_1 c}{K_1 + c} + \frac{k_2 c}{K_2 + c} \qquad ...(32)$$

or a generalization of this involving the addition of more terms of the same form. They pointed out that this equation would arise if growth involves different and parallel processes of substrate intake.

The equation for population growth comes out to be

$$\int_{X_0}^{X} \frac{(D - \bar{c}X)\,(E - \bar{c}X)}{X(1 - X)\,(B - AX)}\,dX = \tau \qquad ...(33)$$

where

$$D = K_1Y + \bar{c},\ E = K_2Y + \bar{c},\ X = N/\bar{c},\ \tau = k_m t \qquad \text{...(34)}$$

and A and B are positive constants.

Curves 1 to 5 in Fig. 3 show patterns for $X_0 = 0.02$, $\bar{c} = 1.0$, $D = 2.2$, $E = 2.4$, $A = 5.0$ and $B = 18, 16, 14, 12, 10$.

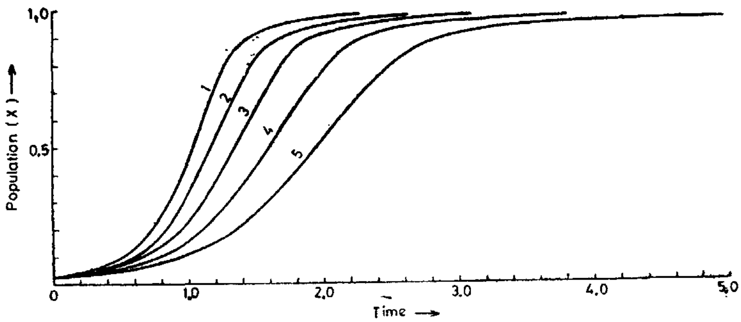

FIG. 3. Model based on the law of Shehata and Marr.

The point of inflexion is given by

$$\psi(X) \equiv k_1(\bar{E} - X)^2 (2X\bar{D} - \bar{D} - X^2) + k_2(\bar{D} - X)^2 (2\bar{E}X - \bar{E} - X^2) \qquad \text{...(35)}$$

where

$$\bar{D} = \frac{D}{\bar{c}} > 1,\ \bar{E} = \frac{E}{\bar{c}} > 1 \qquad \text{...(36)}$$

$$\left.\begin{aligned} &\psi(0) < 0,\ \psi(\tfrac{1}{2}) = -\frac{k_1}{4}(\bar{E} - \tfrac{1}{2})^2 - \frac{k_2}{4}(\bar{D} - \tfrac{1}{2})^2 < 0 \\ &\psi(1) = k_1(\bar{E} - 1)^2 (\bar{D} - 1) + k_2(\bar{D} - 1)^2 (\bar{E} - 1) > 0. \end{aligned}\right\} \qquad \text{...(37)}$$

As 'such a point of inflexion always exists and occurs after the population has reached half the final population size'. In fact $\psi(X)$ is negative when $X \leqslant \frac{1}{2}$, $\psi(1) > 0$, $\psi(\infty) < 0$ and as such $\psi(X)$ has one positive zero between $\frac{1}{2}$ and 1 and at least one positive zero between 1 and ∞.

If $\bar{D} = \bar{E}$, then

$$X^* = \bar{D} - (\bar{D}^2 - \bar{D})^{1/2} \qquad \text{...(38)}$$

but in this case the law (32) reduces to Monod's law. For the growth curves in Fig. 3, the points of inflexion are given by

B	10	12	14	16	18
X^*	0.552	0.534	0.513	0.507	0.505

6. Models Based on Powell and Dabes-Finn-Wilkie Laws

Powell (1967) pointed out that a differential resistance to substrate transfer through the medium could affect the growth rate. When Monod's model was modified to account for this, Powell obtained

$$k(c) = \frac{k_m(K + L + c)}{2L}\left[1 - \left(1 - \frac{4Lc}{(K + L + c)^2}\right)^{1/2}\right] \qquad ...(39)$$

where L is the parameter having the dimension of concentration which depends on the diffusional resistance around the cell. Powell's equation reduces to that of Monod if L is set equal to zero.

Recently Dabes *et al.* (1973) have proposed a number of new growth rate equations. One of the most interesting of these is

$$k(c) = (1/2A)\,[B + Ak_m + c - ((B + Ak_m + c)^2 - 4Ak_mc)^{1/2}]. \qquad ...(40)$$

For the law (40), we get

$$\int_{X_0}^{X} \frac{dX}{X[(H' - \bar{c}X) - \{(H' - \bar{c}X)^2 - G'(1 - X)\}^{1/2}]} = \tau \qquad ...(41)$$

where

$$\tau = k_mt,\ (B + Ak_m)\,Y + \bar{c} = H',\ 4Ak_m\bar{c} = G'. \qquad ...(42)$$

Figure 4 shows the growth curves for $X_0 = 0.02$, $G' = 1.2$, $\bar{c} = 1.0$ and $H' = 2.4, 2.6, 2.8, 3.0$ and 3.2.

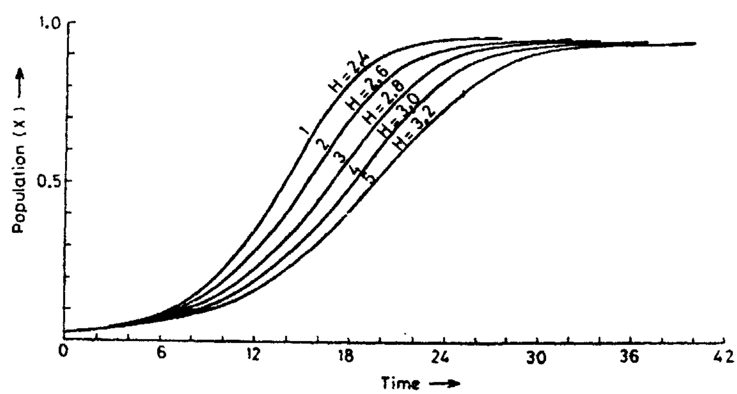

FIG. 4. Model based on the law of Dabes-Finn-Wilkie. (Read H' for H)

The points of inflexion on these curves are found to be as follows:

H'	2.4	2.6	2.8	3.0	3.2
X^*	0.5604	0.5548	0.5502	0.5463	0.5430

It can also be proved that a point of inflexion always exists.

7. General Class of Models With Points of Inflexion

Besides the Pearl-Verhulst and Smith's models, we have given six more models of population growth based on experimental laws connecting specific growth rates with the concentration of the rate-limiting substrates. Though these laws are different, yet they lead to similar population growth curves. This is not entirely unexpected because these laws are based on laboratory experiments on micro-organisms deriving nourishment from one rate-limiting substrate in each case

We now investigate mathematically general class of models with the same features viz. points of inflexion and limiting population sizes. Consider the model

$$\frac{dN}{dt} = g(N)\,[N_e - N]. \qquad \text{...(43)}$$

It will have a point of inflexion if

$$\frac{d^2N}{dt^2} = [-g(N) + g'(N)\,(N_e - N)]\,\frac{dN}{dt} = 0 \qquad \text{...(44)}$$

is satisfied by kN_e with $0 < k < 1$. We consider some particular cases.

(i) $g(N) = AN + B$. In this case eqn. (44) gives

$$AN_e(2k-1) + B = 0,\ k = \tfrac{1}{2} - \frac{B}{2AN_e},\ \frac{B}{A} = (1-2k)\,N_e. \qquad \text{...(45)}$$

If $B = 0$, $k = \frac{1}{2}$ satisfies it. This corresponds to the logistic law. If $|B/AN_e| < 1$, then the point of inflexion occurs before half the final population size is reached if B and A have same sign and after that if B and A have opposite signs.

The simplest model with given final population size and given position of point of inflexion is given by

$$\frac{dN}{dt} = A\,[N + N_e(1-2k)]\,[N_e - N]. \qquad \text{...(46)}$$

(ii) $g(N) = AN^2 + BN + C$. In this case (44) gives

$$Ak^2N_e^2 + BkN_e + c + (2AkN_e + B)\cdot(kN_e - N_e) = 0 \qquad \text{...(47)}$$

and we can choose A, B, C to satisfy (47). Similarly we can take $g(N)$ to be a polynomial of any degree m or a rational function with denominator which does not vanish between 0 and 1.

(iii) If $g(N) = Ae^{aN}$, we get

$$1 + aN_e(k - 1) = 0 \quad \text{or} \quad a = [(1 - k) N_e]^{-1} \qquad ...(48)$$

so that

$$\frac{dN}{dt} = A [N_e - N] \exp [(1 - k) N_e]^{-1} N \qquad ...(49)$$

gives a model with limiting population size N_e and with point of inflexion at kN_e.

We may note that models in this section have been obtained from purely mathematical consideration while the models in sections 2–6 have empirical foundations.

Conversely for any of the laws of this section we can find the $k(c)$ which will give this law. Thus corresponding to (49) we have

$$k(c) = \frac{AYc}{\bar{c} - cY} \exp\left(\frac{\bar{c} - cY}{(1 - k)N_e} \right). \qquad ...(50)$$

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