DETERMINISTIC MODEL FOR THE EVOLUTION OF A POPULATION IN A LIMITED ENVIRONMENT

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ABSTRACT

Systems which are closed to matter transfer are specially interesting in population studies. A deterministic model for the time evolution of growth and extinction is outlined in this note and is tested with bacterial experimental data.

RESUM

Els sistemes que són pròxims a la transferència de matèria són especialment interessants en els estudis de poblacions. Es formula un model determinístic per a l'evolució en el temps de creixement i d'extinció, que es demostra amb dades experimentals de bacteris.

Deterministic model

Let us represent the population function by $n(t)$; it is the number of viable individuals of the specie under consideration. We represent its sourroundings —the nutrients— by the magnitude $M(t)$. The working hypothesis will be that the evolution of $n(t)$ results only from the interaction between each individual and its environment. Interactions between individuals will not be taken into account; we start in a certain sense from the idea of a «ideal gas population».

The first law for population growth was given by T. R. MALTHUS (1798) under conditions of unlimited sources:

$$\frac{\ddot{n}}{n} = k \qquad (1)$$

where k is the growth rate «constant». According to (1) the population function will grow exponentially,

$$n(t) = n(o) \exp (kt) \tag{2}$$

In a closed system solution (2) is in accord with the observation only after a short period of adaptation and until a certain critical point $M(t_o) = M_o$ of the evolution has been reached. After this point the ambient environment intervenes to inhibit growth. This situation can be expressed by means of a system of two differential equations:

$$\frac{\dot{n}}{n} = k \tag{3a}$$

$$\dot{k} = f(n) \qquad \text{with} \quad f(n) = o \quad \text{for} \quad t > t_o \tag{3b}$$

where (3b) should express the environment-population interaction through the function $f(n) = g(M(n))$ for $t > t_o$. To etablish a model means to suggest a concrete form for $f(n)$. If we consider the qualitative evolution of

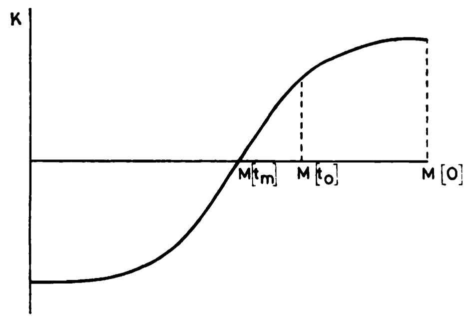

FIG. 1. — Qualitative evolution of the growth rate with the nutrient concentration

Evolució qualitativa de la taxa de creixement amb la concentració de nutrients

the growth rate $k(t)$ as a function of the nutrients $M(t)$ as shown in fig. 1, we can develop $k(t)$ around the inflection point $M(t_m) = M_m$:

$$k(t) \sim - a + b\ M(t) \qquad \text{with } a,b > o \tag{4}$$

where the point t_m is the maximum population state $(n(t_m) = n_m,$ $k(t_m) = o)$. This aproximation which becomes exact in the limit $t \rightarrow t_m$, is sufficient for our purposes. On the other hand, the instantaneous value $M(t)$ of the nutrients (in which toxic effects are conceptually included) is a direct function of the history of the population until time t. We will assume that this dependence has the linear form:

$$M(t) = M(t_o) - c \int_{t_o}^{t} n(t)\, dt \qquad \text{with } c > o \tag{5}$$

Equations (4) and (5) allow us to rewrite system (3) in the form:

$$\frac{\dot{n}}{n} = k \tag{6a}$$

$$\dot{k} = - p\, n => \qquad \text{for } t > t_o \tag{6b}$$

where the interaction constant $p = bc$ is a positive number. This is a set of two differential equations of first order; it is equivalent to a second order differential equation for the population function:

$$\frac{\ddot{n}}{n} - \left(\frac{\dot{n}}{n}\right)^2 + p\, n = o \tag{7}$$

from which we derive the population function by direct integration:

$$n(t) = \frac{\mu^2}{2p} \left[1 - \left(\frac{1 - \alpha \exp \mu\, (t - t_o)}{1 + \alpha \exp \mu\, (t - t_o)} \right)^2 \right] \tag{8}$$

using the following initial conditions at $t = t_o$: a) $n(t_o) = n_o$ b) $k(t_o) = k_p$, the parametres μ and α are given by:

$$\mu^2 = k^2_o + 2\, p\, n_o \tag{9}$$

$$\alpha = \frac{1 - \left[1 - \frac{2pn_o}{\mu^2}\right]^{1/2}}{1 + \left[1 - \frac{2pn_o}{\mu^2}\right]^{1/2}} \tag{10}$$

Equation (6a) then yields the function $k(t)$:

$$k(t) = \mu \left[\frac{1 - \alpha \exp \mu (t - t_o)}{1 + \alpha \exp \mu (t - t_o)} \right] \qquad (11)$$

We can now obtain the dependence of the interaction with the initial conditions of the sourroundings and the population. From (5) we have:

$$M(\infty) = o \qquad : \qquad M(t_o) = c \int_{t_o}^{\infty} n(t) \, dt \qquad (12)$$

where the constant c is the nutrient that one individual needs in order to live one unit of time. If we write the nutrients in «c» units $m(t) = \frac{1}{c} M(t)$, we derive from equations (8), (9), (10) and (12):

$$m_o = \left[(\frac{k_o}{p})^2 + \frac{k_o}{p} \right]^{1/2} + \frac{k_o}{\text{ı}p} \qquad (13)$$

and therefore, for a given environment (m_o), the interaction depends on the quantity (n_o) and the quality (k_o) of the initial biomass in the linear form:

$$p = \frac{2}{m_o} \left[\frac{n_o}{m_o} + k_o \right] \qquad (14)$$

Experimental test and concluding remarks

To make an experimental test of the model we need a more accessible form of eq. (8). We use the maximum population state ($k(t_m) = o$, $n(t_m) = n_m$) in order to supress k_o and to adjust the constant p. We rewrite then:

$$n(t) = n_m \left[1 - \left(\frac{1 - \alpha \exp \mu (t - t_o)}{1 + \alpha \exp \mu (t - t_o)} \right)^2 \right] \qquad (15)$$

with

$$\alpha = \frac{1 - \left[1 - \frac{n_o}{n_m}\right]^{1/2}}{1 + \left[1 - \frac{n_o}{n_m}\right)^{1/2}} \qquad (16)$$

$$\mu = - \frac{\ln \alpha}{t_m - t_o} \qquad (17)$$

$$p = \frac{\mu^2}{2\, n_m} \qquad (17)$$

Figure 2 shows a test of eq. (15) applied to a bacterial culture of Citrobacter intermedium C_3 (Clotet *et al.* 1968), inoculated in a hermetically closed vessel of 10 ml with 6.7 ml of liquid medium (Torra *et al.* 1976). The experimental points (dark circles) represent the number of

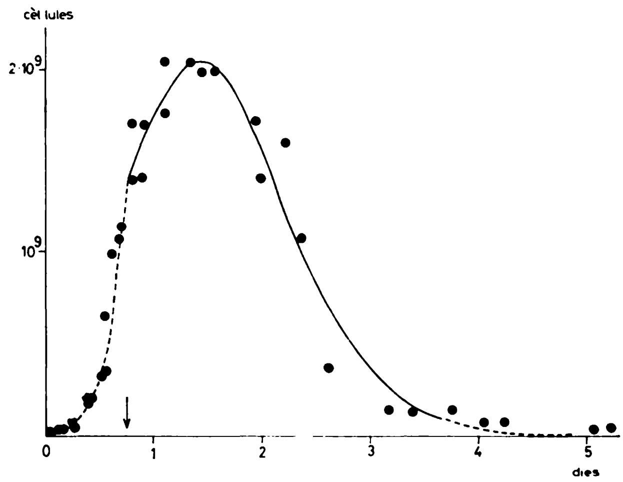

FIG. 2. — Equation (2) (...) and (15) (—) applied to a bacterial culture of *Citrobacter intermedium*. The arrow indicates the critical point t_0

Equacions (2) (...) i (15) (—) aplicades a un cultiu bacterià de *Citrobacter intermedium*. La sageta indica el punt crític t_0

viable bacteria in the vessel, determined by plate count from a serie of evolutions prepared identically at constant temperature (20 °C) (Torra *et al.* 1976). The evolution follows the Malthus' law after a latency phase of two hours until the critical instant $t_o = 18$ h:

$$n(t) = 0.15 \times 10^9 \exp (0.26\ t) \text{ cells for } 2 < t < 18 \qquad (18)$$

For $t > 18h$ equation (15) is applied with the following values of the initial and maximum population states:

$$n_o = 1.4 \times 10^9 \text{ cells} \quad \text{at} \quad t_o = 18 \text{ h}$$
$$n_m = 2.1 \times 10^9 \text{ cells} \quad \text{at} \quad t_m = 34 \text{ h}$$

We conclude that population function in a closed system has a different behavior before and after the critical point t_o. Before the critical point, the behavior is given by the Malthus' law (2). After the critical point the behavior follows solution (15). There is a discontinuity at t_o and this is in contrast with the behavior predicted from the so-called S-shaped curve for open systems (models of EIGEN, VERHULST'S, GOMPERTZ) (EIGEN, 1971) (GOEL, 1974, p. 74). This discontinuity has an important biological meaning. A minimum value of the nutrient concentration is needed in order that the population may grow freely following Malthus' law; on the other hand below this minimum nutrient concentration the interaction becomes important and it drives the population to total extinction, after reaching a single characteristic maximum.

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DISCUSSIÓ

MARGALEF

Aquest procés, que depèn d'un impuls inicial i unes constants, podria aplicar-se al consum de petroli en estudis com els del Club de Roma.

J. WAGENSBERG

Potser sí, però aquest model està pensat per a experiments de laboratori. El model no inclou el paràmetre, decisió intelligent, malgrat que, també és veritat, en el cas del petroli potser sigui irrelevant considerar-lo.

D. LURIÉ

Fins a quin punt és lineal el model?

J. WAGENSBERG

L'expressió: $k(t) = - a + b\ M(t)$, és certa en el punt d'inflexió; si s'en allunya va deixant de ser vàlida. Si es vol augmentar la validesa del sistema cal prendre més termes en el desenvolupament de k(t). L'ideal seria cobrir el sistema del començament al final.

VALLESPINÓS

¿I el cas dels bacteris marins que has estudiat amb el microcalorímetre, on després d'una aparent extinció reapareixen processos metabòlics?

J. WAGENSBERG

Per al model, això fóra un miracle. Hauria de canviar qualitativament el sistema. En el cas dels bacteris marins l'he ajustat fins a la primera extinció.

MARGALEF

Després d'un impuls inicial, arriba un moment en que es redueix el canvi d'energia i poden introduir-se noves possibilitats.