Analytical Solution to an Open-System Model of Population Growth

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ABSTRACT

The analytical solution to a system of differential equations is obtained. The equations were proposed by Williams [1] as a model for the growth of a population on a supply of a single limiting nutrient in an open system. The logistic equation is a special case of the solution.

A unique approach to biological theory construction has been described by Williams [1]. Williams developed a sequence of population models in order of increasing correspondence to reality, and he emphasized the importance of explicitly stating the assumptions behind the models.

Such an approach has not been popular with mathematical ecologists, however. One reason for this is that Williams's notions about theory building lead to models that are quite vulnerable to empirical testing. Another reason is that the models are often nonlinear, mathematically intractable, and best studied with the aid of a computer.

I wish to add a mathematical footnote to one of Williams's models. It is possible to analytically solve the model equations with straightforward techniques. I regard this simple presentation as a ray of hope for mathematicians who are faced with increasingly nonlinear-minded biologists.

The model pertains to the growth of a population of organisms on a supply of a single limiting nutrient in an open system:

$$\frac{dm(t)}{dt} = k_1 c(t) m(t) - k_0 m(t), \tag{1}$$

$$\frac{dc(t)}{dt} = k_0 C_0 - k_0 c(t) - \alpha k_1 c(t) m(t). \tag{2}$$

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In these equations $m(t)$ = population biomass at time t; $c(t)$ = concentration of the limiting nutrient; C_0 = input nutrient concentration; α = ratio of nutrient consumed to biomass produced; k_0, k_1 = rate constants. The equations correspond to a laboratory chemostat-type culture in which there is an input of fresh nutrient at concentration C_0 and at rate k_0 and a removal of nutrient and organisms at a rate k_0. The transformation of nutrient into biomass is assumed to be analogous to a bimolecular chemical reaction.

The total amount of the limiting nutrient in the system at any instant of time is $\alpha m(t)+c(t)$. Multiplying (1) by α and adding this to (2), it is seen that

$$\frac{d[\alpha m(t)+c(t)]}{dt}=k_0C_0-k_0[\alpha m(t)+c(t)],$$

or (3)

$$\alpha m(t)+c(t)=C_0+[\alpha m(0)+c(0)-C_0]e^{-k_0 t}.$$

The expression (3) is a relation for the conservation of mass in the system, and is what enables us to solve the system equations (1) and (2). This is accomplished by using (3) to substitute for $c(t)$ in (1). Equation (1) is thus transformed into an expression entirely in terms of $m(t)$; in fact, the resulting expression is a Bernoulli-type differential equation and is readily integrable:

$$\frac{dm(t)}{dt}=[k_1(C_0+\lambda e^{-k_0 t})-k_0]m(t)-\alpha k_1[m(t)]^2,$$

where $\lambda=\alpha m(0)+c(0)-C_0$, or

$$m(t)=\left\{\frac{\exp[(k_1C_0-k_0)t-k_1\lambda(1+e^{-k_0 t})/k_0]}{m(0)}\right.$$
$$\left.-\alpha k_1 g(t)\exp[(k_1C_0-k_0)t-k_1\lambda e^{-k_0 t}/k_0]\right\}^{-1}, \quad (4)$$

in which

$$g(t)=\int_0^t \exp\left[(k_0-k_1C_0)u+\frac{k_1\lambda e^{-k_0 u}}{k_0}\right]du.$$

The solution trajectory for $c(t)$ is obtained using (4) and the conservation relation (3):

$$c(t) = C_0 + \lambda e^{-k_0 t} - \alpha m(t).$$

Under the circumstance that $\lambda = 0$, the expression (4) is readily shown to be the logistic equation of population growth which is popular in the ecological literature. Indeed, it was this property of the equations (1) and (2) that was pointed out by Williams.

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REFERENCES

1 F. M. Williams, Mathematics of microbial populations, with emphasis on open systems, in *Growth By Intussusception: Ecological Essays in Honor of G. Evelyn Hutchinson* (E. S. Deevery, Ed.), Trans. Conn. Acad. Arts Sci., 1972, pp. 397–426.