Short communication

Integration of logistic and kinetics equations of population growth

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ABSTRACT

The procedure proposed by Sakanoue [Sakanoue, S., 2007. Extended logistic model for growth of single-species populations. Ecological Modelling 205, 159–168] is used to derive the kinetics equations of population growth. It is based on three assumptions: resource availability changes with population size; resource supply to population and population demand for resources are defined as functions of resource availability and population size; and resource availability and population size shift in the supply function attracted to the demand function. These assumptions are organized into an abstract equation, which can be transformed into the Verhulst logistic equation under certain supply and demand functions. On the other hand, by setting "per capita resource availability" as an independent variable, the abstract equation can also be transformed into some existing kinetics equations and new kinetics ones involving intraspecific interactions such as facilitation and interference. The procedure provides a unified means of deriving and relating the two types of population growth equation.

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1. Introduction

In the maxim of Occam's razor, we should choose the simplest model that describes the observed data well. Furthermore, it is ideal that different and related types of observations are depicted by a model composed of a small number of equations. Sometimes, one fundamental phenomenon is expressed by different types of mathematical model. As a well-known example in the field of physics, quantum motion was modelled in the form of either matrix mechanics or wave mechanics in the beginning. Shortly thereafter, it became clear that the two mechanics are essentially equivalent. The numerical correspondence of phenomena to models is preferred to be many-to-one, and should be at least one-to-one.

In the field of ecology, there are two classical and influential equations for describing and analysing the growth of biological populations: the Verhulst logistic equation (Verhulst, 1838; Pearl and Reed, 1920) and the Monod kinetics equation (Monod, 1949, 1950). The former equation can trace the sigmoid curve that is a well-known characteristic of population growth with time. The latter equation is known as a hyperbola with an upper asymptote, which denotes the maximum specific growth rate. Although the dependent variables of both equations are the same, i.e., the growth rate of a population, the independent variable of the logistic equation is only population size, whereas those of the kinetics equation are population size and resource availability. Nevertheless, the two

equations have common mathematical characteristics. The intrinsic rate of natural increase in the logistic equation is probably the same as the maximum specific growth rate in the kinetics equation. Furthermore, the two equations are composed of simple quadratic forms that indicate that a negative feedback control is included in the growth system. These characteristics suggest that the adoption of adequate variables and some ingenuity may integrate the two equations.

The ratio-dependence approach becomes widespread in understanding the interactions between consumer species (predator species) and their resources (prey species) (Arditi and Ginzburg, 2012). For the growth of single-species populations, Contois (1959) firstly examined and proposed a ratio-dependent kinetics model in the experiment on bacterial growth, although he was interested in the constant rather than the variable of his equation. Droop (1968) and Getz (1984) formulated another type of ratio-dependent kinetics model. The procedure proposed by Sakanoue (2007) from which some logistic equations are derived is a kind of ratio-dependence approach in the sense that the ratio of population size to population demand for resources is treated as a variable. Because the procedure was oriented towards the generation and expansion of the Verhulst logistic equation, it was necessary to substitute an independent variable for only population size in the resultant equations. However, note that resource availability was also included and treated as a variable in the execution of the procedure. This means that the procedure is a mechanistic approach (refer to Schoener, 1986), which has often been addressed in the construction of kinetics models, to modelling population growth. There is room for ingenuity in the integration of logistic and kinetics equations.

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The purpose of the present study is to show that the procedure can generate not only the logistic equation but also the kinetics equation of population growth. First, the procedure is outlined and organized into an abstract equation. Second, the Verhulst logistic equation is derived from the abstract one under certain assumptions on the population demand for resources. Third, some kinetics equations, one of which indicates Contois kinetics rather than Monod kinetics, are also derived from the abstract one under the same assumptions. Fourth, new kinetics equations involving intraspecific interactions are developed from the abstract one. It is wise and important to introduce the ratio of resource availability to population size as an independent variable in the derivation of the kinetics equations.

2. Outline of the procedure

Let the variable x and the constant x_m be the resource availability and its maximum, respectively. Similarly, let the variable y and the constant y_m be the population size and its maximum, respectively. Assuming that the quantity of a limiting resource is finite, a high resource availability is supplied to a small population and a low resource availability is supplied to a large population. This relationship is expressed as $X + Y = 1$, where x/x_m and y/y_m are substituted for X and Y, respectively, to simplify the mathematical expressions used. Studies of bacterial growth showed that this relationship is valid under appropriate conditions with various limiting nutrients serving as either carbon, nitrogen, phosphorus, or sulfur sources (Contois, 1959). With the constant flow of resources such as in streams (i.e., $x = x_m$), the relationship becomes $X = 1$. Both functions are simple mathematical expressions for mass conservation.

On the other hand, a large population requires a high resource availability and a small population requires a low resource availability for increasing their size. This relationship can be expressed as a function $f(X, Y)$, provided that it is impossible for the population to exist amidst the vacuity of resource availability (i.e., $f(0, Y) = 0$). Studies of bacterial growth also suggested the existence of this relationship. For example, the relationship between the total growth of bacteria (denoted by G) and the initial concentration of a limiting nutrient (denoted by C) was shown to be linear and conformed to the equation $G = KC$, where K is a constant (Monod, 1949).

It is necessary to derive an equation for governing the dynamics of resource availability and population size. Let the parameters b and d, respectively, denote the per capita birth rate and per capita death rate of a population. Assume that growth rate is proportional to the ratio of population size to the function $f(X, Y)$ (i.e., $rY/f(X, Y)$, where $r \equiv b - d$ and denotes the intrinsic rate of natural increase) and that death rate is proportional to population size (i.e., dY). Furthermore, assume that the dead and waste products are immediately recycled as resources for the population. Given these assumptions, Sakanoue (2007) achieved the abstract equation

$$\frac{\dot{y}}{y} = \frac{rf - dY}{f + (f_X - f_Y)Y}, \tag{1}$$

where $\dot{y}$ is the derivative of population size with respect to time, f_X is the partial derivative of $f(X, Y)$ with respect to X, and f_Y is the partial derivative of $f(X, Y)$ with respect to Y. Eq. (1) is an integrated model of population growth involving the relationships between resource availability and population size. The effects of intraspecific interaction such as facilitation and interference between individuals of a population could be included in the function $f(X, Y)$. Refer to Appendix A of Sakanoue (2009) for the detailed derivation of Eq. (1). In addition, the procedure described above could be extended to modelling the dynamics of interacting populations (Sakanoue, 2009).

3. Derivation of logistic equation

The logistic equation proposed by Verhulst (1838) and Pearl and Reed (1920) can be expressed as

$$\frac{\dot{y}}{y} = \frac{r(\hat{y} - y)}{\hat{y}}, \tag{2}$$

where $\hat{y}$ denotes the carrying capacity of the environment. It is simple to derive Eq. (2) from Eq. (1) and either expression of mass conservation. First, a certain mathematical expression is set to the function $f(X, Y)$. Second, by using $X + Y = 1$ or $X = 1$, Eq. (1) is transformed into the logistic equation.

Assume that $f(X, Y) \equiv X$. This means that the relationship between the population's demand and resource availability is directly proportional. By using $X + Y = 1$ as the expression of mass conservation, X can be substituted for $1 - Y$. These treatments transform Eq. (1) into Eq. (2), where $\hat{y} \equiv (r/b)y_m$. If all members in a population are immortal (i.e., $d = 0$), Eq. (1) also becomes Eq. (2), where the intrinsic rate of natural increase is equivalent to the per capita birth rate (i.e., $r \equiv b$), and the carrying capacity is identical to the maximum population size (i.e., $\hat{y} \equiv y_m$).

On the other hand, using $X = 1$ as the expression of mass conservation, Eq. (1) is also transformed into Eq. (2), where $\hat{y} \equiv (r/b)y_m$. If all members in a population are immortal (i.e., $d = 0$), Eq. (1) particularly becomes the exponential growth equation $\dot{y}/y = b$, where $\hat{y} \equiv \infty$. Although there is a variation in carrying capacity depending on the type of mass conservation and per capita death rate, Eq. (1) results in the same form as the Verhulst logistic equation. Note that intraspecific interactions are not included in the derivation of Eq. (2).

4. Derivation of kinetics equations

It is not difficult to derive the kinetics equations of population growth from Eq. (1) and either expression of mass conservation. In common with the derivation of the logistic equation, assume that $f(X, Y) \equiv X$. First, consider the case in which $X + Y = 1$ is adopted as the expression of mass conservation. Differently from the derivation of the logistic equation, X should not be substituted for $1 - Y$. Furthermore, the ratio of resource availability to population size is qualified as a variable. This variable can be termed "per capita resource availability" like that of Getz (1984). As an actual example, it may correspond to "cell nutrient quota" or "cell quota", defined as the weight of internal nutrient per unit biomass in the field of phycology (refer to Droop, 1968). Let s denote the per capita resource availability (i.e., $s \equiv x/y$). The treatments described above transform Eq. (1) into the kinetics equation

$$\frac{\dot{y}}{y} = \frac{-r(\hat{s} - s)}{s_m + s}, \tag{3}$$

where $s_m \equiv x_m/y_m$ and $\hat{s} \equiv (d/r)s_m$. Note that s_m denotes the equivalent coefficient of consumers to resources. Eq. (3) is of the same form as the models proposed by Schoener (1978) in his theoretical study, Tilman et al. (1981) for the growth rate of two species of freshwater diatoms, and Houtsma et al. (1994) for the growth rate of *Listeria innocua*, and identical to the model of Getz (1984) in his theoretical study. One difference of Eq. (3) and the Getz model from other existing models is in the variable. In Eq. (3), the variable is the per capita resource availability. On the other hand, in the existing models, the variable is the resource availability or concentration. If all members in a population are immortal (i.e., $d = 0$), Eq. (3) becomes

$$\frac{\dot{y}}{y} = \frac{bs}{s_m + s}. \tag{4}$$