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Exact solution of a non-autonomous logistic population model

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ABSTRACT

Growth models such as the logistic equation are widely studied and applied in population and ecological modelling. The carrying capacity in the logistic equation is usually regarded as a constant which is not often realistic. Functional forms of the carrying capacities are used to describe changes in the environment. The purpose of this study is to derive an exact solution of the non-autonomous logistic equation with a saturating carrying capacity. The solution is found via a power series resulting from a straightforward algebraic method. For practical applications the power series may be truncated, a simple criterion is established that leads to a good approximate solution. The approximate solution is in good agreement with the numerical simulations, even though only a small number of terms are used.

1. Introduction

The logistic equation was introduced to describe population growth with a self-limitation term which serves as a correction to the unlimited growth of the Malthusian model. It is commonly applied in the studies of human, plants, animal and bacterial populations, and is also used to forecast technological and economic growth. The classical logistic (or Verhulst's) equation is a nonlinear first order differential equation

$$\frac{dN(t)}{dt} = aN(t)\left(1 - \frac{N(t)}{K}\right), \qquad N(0) = N_0, \tag{1}$$

where $N(t)$ denotes the population density, a is the intrinsic growth rate, K is the environmental carrying capacity and N_0 is the population density at time $t=0$. Since a and K are constants the logistic equation (1) is said to be autonomous. The solution is

$$N(t) = \frac{KN_0}{Ke^{-at} + N_0(1 - e^{-at})}. \tag{2}$$

The carrying capacity K in (1) is a constant which is not often realistic. A changing environment may result in a significant change in the carrying capacity. For example, food production or new resources which can be regarded as positive changes in the environment will elevate the carrying capacity. Negative changes, however, such as food depletion or a toxic effect worsen the environment thus will degrade the carrying capacity.

As an alternative to the constant carrying capacity a number of studies have used a time-dependent carrying capacity, $K(t)$, for various applications. By using a time varying carrying capacity, the explicit time-dependence of $K(t)$ renders the logistic equation as non-autonomous.

The general mathematical properties of the non-autonomous logistic equation were deduced by Coleman (1979a) and later modified by Hallam and Clark (1981). Table 1 shows several functional forms for carrying capacities that have been used in the literature.

An oscillating carrying capacity was used to describe seasonal environments (Coleman et al., 1979b; Leach and Andriopoulos, 2004; Rogovchenko and Rogovchenko, 2009), a carrying capacity with saturation was used to model enrichment in an inland sea by a nutrient (Ikeda and Yokoi, 1980) and to describe the changing micro-environment beneath an occlusion on healthy human skin (Safuan et al., 2011). A carrying capacity which itself varies logistically was introduced by Meyer (1994) and Meyer and Ausubel (1999) to model the technological development of a population. A similar form of the carrying capacity was used in modelling the body size of a host infected by parasites (Ebert and Weisser, 1997). For these applications it is vital that the carrying capacity is not treated as a constant.

2. Non-autonomous logistic equation

The purpose of this paper is to derive an exact solution of the non-autonomous logistic equation used in Safuan et al. (2011). Consider the non-autonomous logistic equation

$$\frac{dN(t)}{dt} = aN(t)\left(1 - \frac{N(t)}{K(t)}\right), \tag{3}$$

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Table 1
Time-dependent carrying capacities $K(t)$.

$K(t)$	References
$K(t)=a+b\sin(ct+\phi)$	Coleman et al. (1979b), Leach and Andriopoulos (2004), and Rogovchenko and Rogovchenko (2009)
$K(t)=a+b(1-e^{-ct})$	Ikeda and Yokoi (1980) and Safuan et al. (2011)
$K(t)=K_1+K_2/(1+ae^{-bt})$	Meyer (1994) and Meyer and Ausubel (1999)
$K(t)=K_1K_2/[(K_2-K_1)e^{-bt}+K_1]$	Ebert and Weisser (1997)

where the carrying capacity, $K(t)$, takes the form

$$K(t)=K_s(1-be^{-ct}). \tag{4}$$

Here K_s is the bacterial saturation level, c is the saturation constant, $b=1-K_0/K_s$, with $K(0)=K_0$. Observe here $0<b<1$.

The model in Safuan et al. (2011) assumed that on the unoccluded skin, the environment is relatively constant and the density of the microbes is in equilibrium with its environment such that $K_0\approx N_0$. As a result, b is always a positive number since $N_0<K_s$. After an occlusion is applied to the skin the environment beneath it begins to change to one that is generally more favourable for microbial growth. Thus, a monotonically increasing function (4) was used to describe the changing environment beneath an occluded skin. Eq. (3) has the solution

$$N(t)=\frac{N_0e^{at}}{1+(aN_0/K_s)\int_0^t(e^{ax}/(1-be^{-cx}))\,dx}. \tag{5}$$

The exact solution of the non-autonomous equation can be derived by noting

$$\int_0^t\frac{e^{ax}}{1-be^{-cx}}\,dx=F(t)-F(0), \tag{6}$$

where

$$F(t)=\frac{e^{at}}{a}\,{}_2F_1\left(1,-\frac{a}{c};1-\frac{a}{c};be^{-ct}\right). \tag{7}$$

The function ${}_2F_1$ is a hypergeometric function which converges for $c>0$ and $0<b<1$. It can also be expressed as the series

$${}_2F_1\left(1,-\frac{a}{c};1-\frac{a}{c};be^{-ct}\right)=\sum_{n=0}^{\infty}\frac{(1)_n(-a/c)_n}{(1-a/c)_n}\frac{(be^{-ct})^n}{n!}, \tag{8}$$

where $(a)_n$ is a Pochhammer symbol: $(a)_n=a(a+1)\cdots(a+n-1)$ (Abramowitz and Stegun, 1972).

3. An alternative approach

Suppose $a>0$ and $c>0$. Since $0<b<1$, we may formally write

$$\frac{1}{1-be^{-cx}}=\sum_{n=0}^{\infty}b^ne^{-ncx},\quad x\geq 0. \tag{9}$$

The integral in the denominator of (5) then becomes

$$\int_0^t\frac{e^{ax}}{1-be^{-cx}}\,dx=\int_0^t\sum_{n=0}^{\infty}b^ne^{(a-nc)x}\,dx,=\sum_{n=0}^{\infty}\frac{b^n}{a-nc}(e^{(a-nc)t}-1). \tag{10}$$

Accordingly, the exact solution is

$$N(t)=\frac{K_sN_0}{K_se^{-at}+aN_0\sum_{n=0}^{\infty}(b^n/(a-nc))(e^{-nct}-e^{-at})}. \tag{11}$$

Although this solution is exact for $t\geq 0$, for practical applications the series solution needs to be truncated. Note that for some $n\in\mathbb{N}$, $a-nc<0$, the index of the exponential in (10) is negative and so this term's contribution to the series solution falls off rapidly for increasing t. Consequently, truncating the series at the $(n-1)$th term incurs a maximal error of $\mathcal{O}(b^n)$.

Using (11), we can derive a number of approximate solutions of the non-autonomous logistic equation simply by terminating the series at different values of n.

4. Special cases

For $c=0$, $K(t)=K_0$ for all t. The solution for this case is given by (2) with K replaced by K_0,

$$N(t)=\frac{K_0N_0}{K_0e^{-at}+N_0(1-e^{-at})}. \tag{12}$$

As $c\to\infty$, the carrying capacity is a step function ($K_0<K_s$),

$$K(t)=\begin{cases}K_0, & t\leq 0,\\ K_s, & t>0.\end{cases} \tag{13}$$

Suppose $N(t_1)=N_1<K_0$ for some $t_1<0$. The solution is

$$N(t)=\begin{cases}\dfrac{N_1K_0}{K_0e^{-a(t-t_1)}+N_1(1-e^{-a(t-t_1)})}, & t\leq 0,\\[2ex] \dfrac{K_sN_0}{K_se^{-at}+N_0(1-e^{-at})}, & t>0,\end{cases} \tag{14}$$

where

$$N_0=\frac{N_1K_0}{K_0e^{at_1}+N_1(1-e^{at_1})}. \tag{15}$$

Further, if for $t<0$ the population is in equilibrium with its environment, then $K_0\approx N(t_1)=N_1$ implies $K_0\approx N_0$. The solution for $N(t)$ can then be written in terms of the carrying capacities K_0 and K_s,

$$N(t)\approx\frac{K_sK_0}{K_se^{-at}+K_0(1-e^{-at})}. \tag{16}$$

5. Application: growth under an occlusion of the skin

Provided the initial population, N_0, and the saturation level, K_s, can be obtained from experimental data, we can then estimate parameter b. The parameters a and c are estimated to fit the data. The parameters used in the model in Safuan et al. (2011) were $a=6.6$/day, $b=0.99996$, $c=1.9$/day, $N_0\approx K_0=920$ counts/cm^2 and $K_s=2.3\times 10^7$ counts/cm^2.

As mentioned previously, using the exact solution (11) is a little cumbersome, instead the numerical solution of (3), N_{num}, is used to compare with the various approximations generated by (11) for the same parameters used in Safuan et al. (2011). N_{app1}, N_{app2}, N_{app3}, N_{app4} and N_{app5} represent one (open circle), two (cross), three (closed circle), four (left arrow) and five (right arrow) terms retained in the approximation, respectively. Fig. 1 shows that with one term, the approximation is in good agreement with the numerical result. With more terms in the approximation, even better agreement is achieved. However, due to the large scale of N, differences in the curves are not clearly visible.

To determine the accuracy of the various approximate solutions, relative errors were calculated (see Fig. 2). The maximum relative error at $t=2$ for the five term approximation (retaining terms up and including $n=4$) is only 0.06%, four terms (0.06%), three terms (0.07%), two terms (0.18%) and with only one term (3.2%). These values indicate that our approximations are reasonably good. Maximum relative error is clearly reduced by using more terms in the solution (11). According to our simple criterion, the series may be terminated at the $n-1$ term when $a-nc<0$. Here, the series may be terminated at $n=3$ (N_{app4}).