Behaviour of simple population models under ecological processes

SOMDATTA SINHA* and S PARTHASARATHY

Centre for Cellular and Molecular Biology, Uppal Road, Hyderabad 500 007, India

Abstract. The two most popular and extensively-used discrete models of population growth display the generic bifurcation structure of a hierarchy of period- doubling sequence to chaos with increasing growth rates. In this paper we show that these two models, though they belong to a general class of one-dimensional maps, show very different dynamics when important ecological processes such as immigration and emigration/depletion, are considered. It is important that ecologists recognize the differences between these models before using them to describe their data—or develop optimization strategies—based on these models.

Keywords. Population dynamics; immigration and emigration; logistic equations; discrete models; chaos.

1. Introduction

Growth of populations can occur either by continuous breeding or propagation at discrete times. Examples of species that breed seasonally are annual plants and insects such as the 13 year periodical cicadas; and humans are an example of species that breed continuously. Therefore, depending on the type of growth process, generations can overlap or be seasonal *i.e.*, non-overlapping. For a continuously-breeding, single-species population, growth can be described by a simple differential equation known as the "logistic equation", which was first described by Verhulst in 1838 (Krebs 1978). The equation is

$$\frac{dN}{dt} = r N (1 - N/K).$$
(la)

Here *r* is the intrinsic growth rate and *K* the carrying capacity of the environment. Populations (*N*) growing according to this equation show a temporal variation described by a sigmoid curve (figure 1). Equation la has a globally stable equilibrium point at *N=K,* the level at which the population level equals the carrying capacity of the environment.

For populations growing in discrete time steps, *i.e.*, when generations do not overlap, the dynamics of growth can be described by a difference equation. Here the population at the next generation, *i.e.*, at (*t+* 1), is dependent on the magnitude of the population at the preceding generation *t.* For historical reasons two simple, nonlinear difference equations have been used extensively for describing such growth
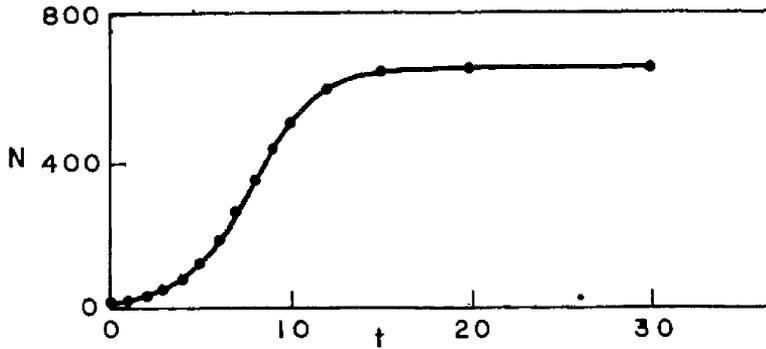
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* Corresponding author.

Figure 1. Growth curve of populations following continuous logistic model (eq. 1) for $r = 0.54$, $K = 665$.

processes in the ecological literature. Both have been considered by different workers to be the difference equation analogue of the logistic differential equation (1a) (Cooke 1965; Macfadyen 1963; Smith 1968; May 1974, 1975). The equations are

$$N_{t+1} = N_t[1 + r(1 - N_t/K)] \tag{1b}$$
$$N_{t+1} = N_t \exp[r(1 - N_t/K)]. \tag{1c}$$

Here also r and K are the intrinsic growth rate and the carrying capacity of the environment respectively. To make the equations independent of the units of measurements, simple changes in variables are introduced and N_t is measured in terms of the carrying capacity K. The new dimensionless population variables X_t and Y_t are related to N_t by

$$X_t = [r/(1+r)](N_t/K) \qquad \text{in equation 1b}$$
and
$$Y_t = N_t/K \qquad \text{in equation 1c.}$$

The two equations 1b and 1c can then be written as

$$X_{t+1} = RX_t(1-X) \tag{2}$$
$$Y_{t+1} = Y_t \exp[r(1-Y_t)], \tag{3}$$

where $R = (1 + r)$. Though equation (2) is the simplest possible non-linear difference equation, it has the following undesirable features: the population becomes negative whenever $X_t > 1$, and extinction takes place for $R > 4$, Equation (3) on the other hand does not suffer from these un-biological properties.

When the population at the next generation (X_{t+1}, Y_{t+1}) is plotted against the population at the present generation (X_t, Y_t), both these equations show a curve with one hump as shown in figure 2. Other density-dependent population growth equations used in ecology (May and Oster 1976) also display "single-humped" shapes. On analysis they turn out to belong to a general class of one-dimensional maps that show a "universal" bifurcation structure. As a function of increasing
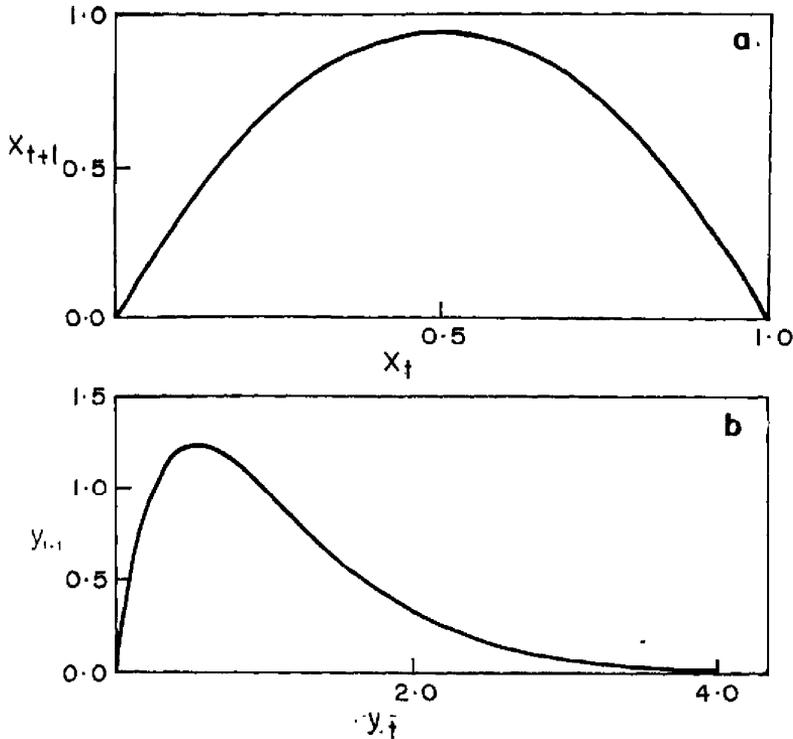
Figure 2. Successive generation population curves for discrete logistic models. (**a**) Quadratic logistic model (eq. 2) for $R = 3.8$. (**b**) Exponential logistic model (eq. 3) for $r = 1.8$.

growth rates these equations display complicated dynamics: solutions range from a stable equilibrium point to chaos through successive period-doublings. Because of these similarities in their dynamics, equations 2 and 3 have been used interchangeably to study a variety of growth and resource management problems (May and Oster 1976; May 1976; Krebs 1978; Clark 1985; Edelstein-Keshet 1988; Murray 1989), and no specific attempt has been made to differentiate between the two models. In this paper we show that models represented by equations (2) and (3) show very different dynamics when important ecological processes such as migration or harvesting are considered. This implies that these models are not equivalent, either mathematically or functionally. Therefore ecologists should recognise the differences between these models before using them to describe their data, or developing optimization strategies based on these models.

2. Methods

The method used for describing the dynamic behaviour of the equations is through "bifurcation diagrams" (Baker and Gollub 1990). This method gives a global view of the long term behaviour of the model over a range of parameter values and allows a simultaneous comparison of periodic and chaotic behaviours that a model may exhibit with changing parameters. For obtaining the bifurcation diagrams (figure 3) the
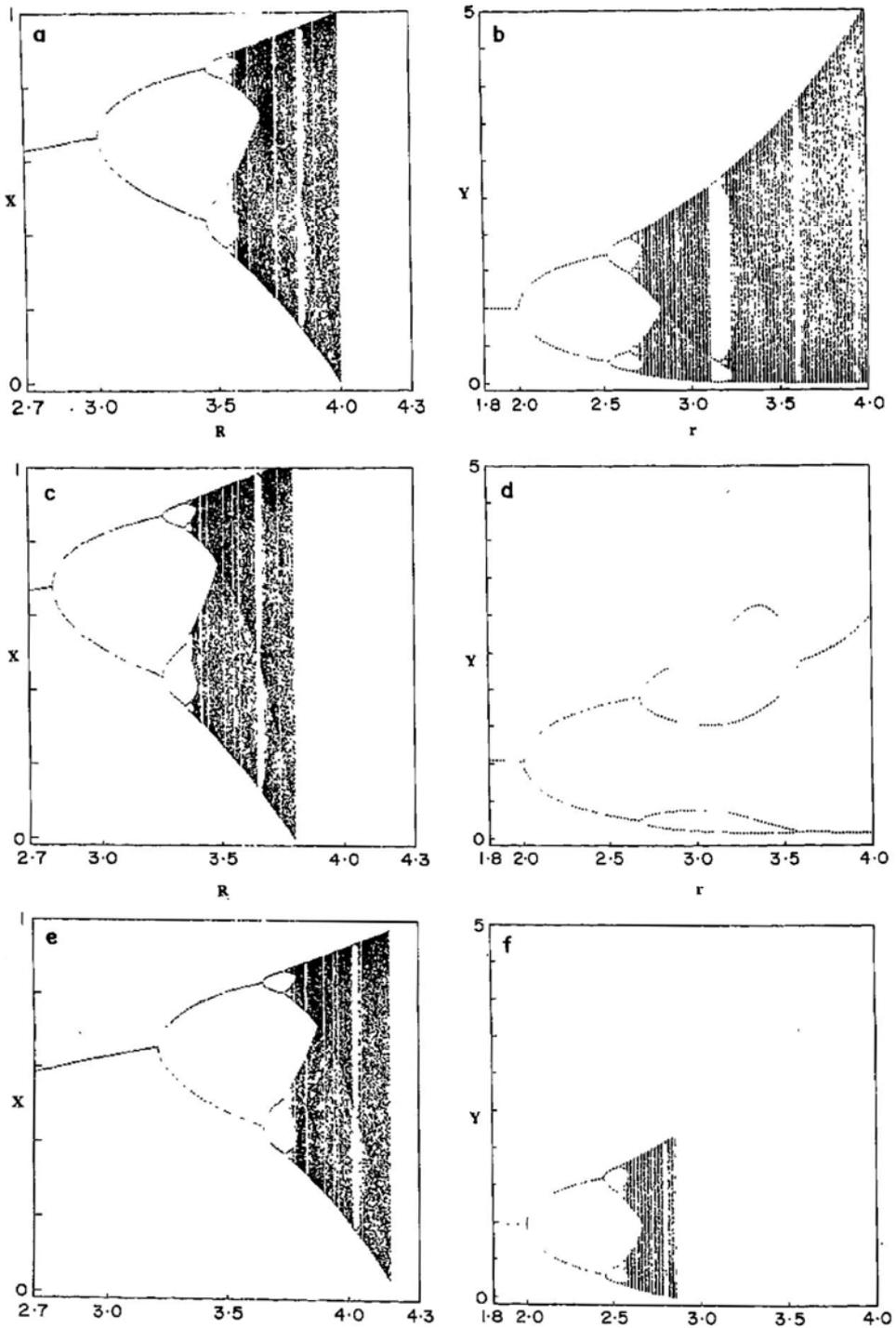
Figure 3. Bifurcation diagrams of the discrete models with varying growth rates for: Free growth: (a) Model (2); (b) Model (3). Immigration with $L = 0.07$: (c) Model (2), (d) Model (3). Emigration/depletion with $L = 0.07$: (e) Model (2), (f) Model (3).

equations were iterated for 1000 generations and the X (or Y) values for the last 200 iterations plotted for each R (or r) value in the given range. The results have been further checked after 5000 iterations. The criteria used for population extinction is that X_t or Y_t becomes zero or negative within 1000 generations.

Where immigration takes place regularly, the population is described by the addition of a constant term, L, to the equations (2) and (3). It is necessary to mention that in this work L has not been considered as a floor below which the population can not go, *i.e.*, it is not considered as a refuge. In contrast to immigration, regular emigration or depletion from a population is modelled by subtracting a constant term L from equations (2) and (3). A small value of $L = 0.07$, which is only 7% of the carrying capacity (if K is chosen as 1) is considered in this study.

As mentioned earlier, both the models show a sequence of bifurcations from stable equilibrium to chaos for increasing growth rates. The scales for representing the growth rates (R and r) for the two models in the bifurcation diagrams have been chosen such that they display all types of dynamics for both free growth and with migration. The starting population has been taken as 0·3 for all simulations.

All numerical calculations have been done on a 80486-based IBM compatible PC.

3. Results

The results of the numerical study are presented together in figure 3 as bifurcation diagrams to allow simultaneous comparison of the dynamics at different growth rates for the two models given by equations (2) and (3). First we describe the free population growth dynamics of the two models, and then the growth dynamics under immigration and emigration. Comparison of the dynamics are made between the two models and also within the same model with and without the migratory processes.

3.1 *Free growth*

Figures 3a and 3b show bifurcation diagrams for models (2) and (3) with increasing growth rates. The figures show that both the models display a similar sequence of dynamical behaviour with increasing growth rates. Slow-growing populations show stable dynamics. As the growth rate increases, the population shows oscillatory variation with increasing amplitudes leading to period-doubling bifurcations giving rise to period 2, 4, 8, etc., oscillations. At higher growth rates, infinite period emerges and chaos sets in. At these high values of growth rates the population fluctuates between very high and very low values. Model (2) shows population extinction at $R = 4$, whereas populations persists for higher values of r for model (3). This sequence of bifurcations and the precise values of the growth rates at which these events occur for models (2) and (3) have been documented earlier (May 1974, 1975, 1976).

3.2 *Immigration*

The population dynamics with a low level of recurrent immigration are shown in the bifurcation diagrams depicted in figures 3c and 3d for models (2) and (3)

respectively. It is clear from the diagrams that the two models lead to qualitatively different dynamics with increasing growth rates. Figure 3c shows that populations of model (2) can undergo all the variety of dynamics with increasing growth rates; but figure 3d shows reversal of bifurcations and suppression of chaos at higher growth rates for model (3).

The dynamics shown by model (2) under immigration qualitatively resembles that in the absence of immigration; but comparison of figure 3a and 3c shows the following two differences. First, under immigration the population shows increased levels at lower growth rates and increased maxima of oscillations at higher growth rates. Secondly, all the bifurcations to simple oscillations and consecutive period-doublings to chaos take place at lower growth rates under immigration. Extinction also occurs at an earlier growth rate $R = 3.8$ (figure 3c).

The dynamics exhibited by model (3) with immigration (figure 3d), on the other hand, is very different when compared to free growth (figure 3b). Under immigration populations stabilize at a slightly higher value at lower growth rates; but as growth rate increases the population maxima during oscillations reduce for model (3). In contrast to model (2), in this case the first bifurcation—to a simple oscillation—takes place at the same growth rate ($r = 2$) as observed without immigration (compare figures 3b and 3d). Populations continue to oscillate at higher growth rates leading to period four oscillation which then reverses *via* period-halving bifurcations to simple oscillation again with increasing growth rates. Thus in model (3) immigration tends to stabilize oscillations which would otherwise produce chaotic dynamics.

3.3 *Emigration/depletion*

Figures 3e and 3f show the bifurcation diagrams for the two models with increasing growth rates when small but regular emigration or depletion from the population is considered. In general a population balances certain level of depletion by surviving at a lower density. Both models exhibit this feature. Both models also show the sequence of complex dynamics as growth rate increases. But closer inspection of figures 3e and 3f would show the differences in the behaviour of the two models clearly.

The overall pattern of dynamics shown by model (2) with and without emigration (figures 3a and 3e) is similar, except that all bifurcations take place at higher values of R under emigration. In this case extinction at high growth rate occurs at $R = 418$.

The dynamics of model (3) is similar with and without emigration (figures 3b and 3f): the population takes the same period-doubling route to chaos. But the effect of emigration is to confer an additional feature in the dynamics of model (3). *i.e.*, extinction. Figure 3f shows that populations with high growth rates ($r > 2.86$) cannot survive even a small level of regular depletion and go extinct. On the other hand, populations in model (2) can balance depletion to this extent at all growth rates studied (figure 3e).

4. Discussion

The major point of this study is to bring out the strikingly different dynamical behaviours that the two most popular and extensively-used models of population

growth exhibit when simple but important ecological processes such as immigration and emigration are considered.

When a fixed amount of addition to the population (immigration) is considered, model (3) shows predominantly stable dynamics and simple oscillations with a small region of period four-oscillations with increasing growth rate. In such a situation model (2) exhibits the entire gamut of complex dynamics and chaos with all bifurcations occurring at lower growth rates. From the point of view of dynamics, immigration seems to effectively increase the growth rate [compare with the case when there is no immigration in model (2) (figures 3a and 3c)]. Depending on the model used, one can predict that immigration either helps in *stabilising* population variation [as in model (3)], or introduces *instability and chaos* at lower growth rates [as in model (2)]. Natural populations tend to display stable behaviour (Hassel *et al* 1976; Pimm *et al* 1988), and model (3) with immigration has been used to describe such data (McCallum 1992; Stone 1993). It is clear that the prediction would change completely if one uses model (2) in such a situation. Our results show that these two models give conflicting predictions regarding growth dynamics when additions are made to populations. Therefore it will be necessary to consider these results while planning conservation strategies for determining critical population sizes or for introducing endangered species in habitats (Bailey 1984; Soule' 1987).

Emigration or depletion seem to have exactly the opposite effects for the two models in the sequence of stable and unstable dynamics as observed in figures 3e and 3f. In model (2) low emigration has the effect of *decreasing* the effective growth rate when compared to the case with no depletion since the sequence of bifurcations occurs at higher growth rates. In contrast, it has the effect of *increasing* the effective growth rate in model (3) in the region of period four oscillations and beyond till extinction occurs. Therefore even under emigration the two models behave very differently with increasing growth rates. These models have been used for predicting optimal use of natural biological resources and deciding on harvesting strategies for maximum sustainable yields in fisheries (Krebs 1978; Clark 1985). Our results indicate that the difference between the predictions based on the two models could actually be a matter of "survival" and "extinction" at certain growth rates ($r > 2 \cdot 8$) as can be seen from figures 3e and 3f.

There is considerable theoretical interest (Stone 1993 and references quoted therein) in the universality of the bifurcation structure shown by single-humped functions and the robustness of their dynamics under small but realistic perturbations. Breakdown or distortion of universal behaviour by initiating period-doubling reversals have been shown earlier for model (3) with positive perturbation (Stone 1993), and consequently its role in controlling or preventing chaos in biological populations has been speculated. But this behaviour is not exhibited by model (2). We have compared the behaviour of the two population models under two common ecological processes and shown that they exhibit very different dynamics. The implications of these differences can be important when one attempts to correlate experimental data with models and also predict conditions for future trends in population growth or develop harvesting strategies depending on the effect of catches on the population density. We have chosen a small value of *L* (*L*=0·07) to highlight differences even at low levels of perturbation. The models show many more differences when larger values of *L* are considered (unpublished results); for example, the ability of model (3) to balance depletion depends strongly on the growth rate and at higher

growth rates the population persists at a small range of high values of emigration, even when it goes extinct at lower depletion rates—a property not exhibited by model (2). Thus simple nonlinear models not only show very complicated dynamics (May 1976), they also differ qualitatively when used to model ecological processes.

Acknowledgement

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