

Dynamics of a discrete population model with variable carrying capacity

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Abstract: The carrying capacity is assumed to be constant in population growth models used for resource assessment and management. However, changes to the carrying capacity do occur due to both exogenic and endogenic processes. The need to treat the carrying capacity as a function of time has long been recognised in order to model population dynamics in an environment that undergoes change. Most populations experience fluctuations in their environment due to seasonal change.

The simplest approach is to specify some time-dependent function for the carrying capacity that reflects the observed behaviour of the changing environment. To date these models are deterministic with overlapping generations, the kind that are best described using continuous equations. However, the dynamics of some populations may not be appropriately described with continuous equations. Populations with non-overlapping generations are better described by discrete (difference equation) models.

In this paper, by considering the carrying capacity as a proxy for the state of the environment, we analyse a population whose growth is governed by a discrete logistic model and whose carrying capacity is modelled by a separate difference equation. The existence of fixed points is established and the stability of fixed points is discussed. Aperiodic behaviour is also shown to exist.

Keywords: *Population dynamics, carrying capacity, difference equation, discrete model*

1 INTRODUCTION

Ecological modelling has a wide variety of applications, and it is an important tool used in environmental and resource management. It is often used to assess the survival or possible extinction of a species or ecosystem, by evaluating the potential impact of changes to the environment. The concept of “carrying capacity” in ecological modelling was first introduced by Belgian mathematician Verhulst in 1838, as a limitation to exponential population growth (Banks, 1994). In ecology, it is generally used as a proxy representing the state of the environment, often related to the amount food, water, space or other resources, or the impact of pollutants having a detrimental effect on the environment. In general, carrying capacity is considered to be the maximum population an environment can sustain (Monte-Luna *et al.*, 2004).

In many applications, there is an underlying assumption that a finite level of resources implies a fixed level of resources. In particular, in resource management the carrying capacity is often assumed to be constant and unchanging (Monte-Luna *et al.*, 2004). Many efforts to predict the world’s carrying capacity, the maximum sustainable population, are based on this assumption (Cohen, 1995). However, technological developments have raised crop yields, allowing a greater population to be supported by a smaller land area (Waggoner, 1996). Thus for human populations, a constant carrying capacity is not realistic (Meyer and Ausubel, 1999). Similarly in nature, the inherent variability of natural systems (Ludwig *et al.*, 1993) means that assuming an unchanging carrying capacity fails to adequately represent the environment.

Monte-Luna *et al.* (2004) analysed different ways the concept of carrying capacity is applied to populations, communities, ecosystems and the biosphere, and proposed the following definition for carrying capacity:

“the limit of growth or development of each and all hierarchical levels of biological interaction, beginning with the population, and shaped by processes and interdependent relationships between finite resources and the consumers of these resources”.

This definition highlights the importance of defining the carrying capacity in a mathematical model so that it may vary with time. Such a treatment of the concept allows a more realistic portrayal of the way in which various processes and relationships, both biotic and abiotic, influence the environment.

2 A SIMPLE MODEL—THE LOGISTIC EQUATION

The logistic, or Verhulst, equation is the simplest of ecological models, and is given by (Banks, 1994):

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right), \quad N(0) = N_0, \quad (1)$$

where N is the population of a given species, r is the intrinsic growth rate and K is the constant carrying capacity – a proxy for the state of the environment. N_0 is the initial population at time $t = 0$. The exponential growth of the population governed by rN is limited by intra-species competition for resources described by the term $-\frac{rN^2}{K}$.

Now, it can be shown that all solutions to (1) with positive initial conditions, $N_0 > 0$, converge monotonically to the carrying capacity, K , as time t tends to infinity. This does not successfully represent reality, as physical and biological processes affect the environment, in turn changing the carrying capacity for a given species.

Time-dependent carrying capacities have been successfully used in many models (Banks, 1994). In these cases, the carrying capacity is defined explicitly as a function of time, $K = K(t)$. A periodic form of the carrying capacity, for example:

$$K(t) = K_0 + \epsilon \sin(\omega t), \quad (2)$$

where ϵ and ω are constants, might be used to represent seasonal variations in the environment, possibly influencing the amount of vegetation available for food. It is important to note that the carrying capacity is completely independent of the population, meaning that the population does not have any impact on the environment. Figure 1 plots two solutions to the logistic equation with carrying capacity given by (2), with $r = 1.2$ and $r = 5$. It can be seen that both solutions tend to follow the carrying capacity curve, and while a larger growth rate r causes the population to always be much closer to the carrying capacity K , solutions have the same period. As opposed to the monotonic convergence when the carrying capacity is constant, a periodic carrying capacity forces periodicity onto the population.

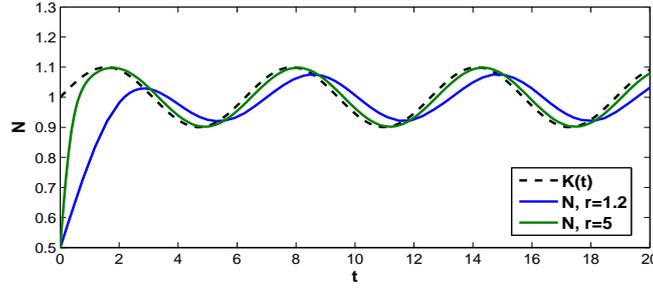


Figure 1: Plot of N against t for equations (1) and (2), with $K_0 = 1$, $N_0 = 0.5$, $\omega = 1$ and $\epsilon = 0.1$.

Models of a similar form to this have been used in many applications, representing population growth in a periodic environment (Coleman *et al.*, 1979; Cushing, 1986). Multiple time scales have also been used, representing environmental fluctuations on a longer time scale than that of the population (Grozdanovski *et al.*, 2009; Shepherd and Stojkov, 2007). Other time-dependent carrying capacities have been used to model fish population dynamics (Ikeda and Yokoi, 1980), microbial biomass (Safuan *et al.*, 2011) and technological phenomena (Meyer, 1994). Carrying capacity has also been defined as a state-variable in various applications (Huzimura and Matsuyama, 1999; Meyer and Ausubel, 1999; Safuan *et al.*, 2012). This allows better portrayal of changes in the environment as it is shaped by various processes and relationships within an ecosystem.

3 DISCRETE MODELS

While continuous models have been successfully applied in a variety of situations, one fundamental assumption is that the species in question has continuous, overlapping generations. However, it is observed in nature that many species do not possess this quality. For example, some anadromous fishes, such as salmon, have annual spawning seasons, with births taking place at the same time every year. Many insects breed and die before the next generation emerges, often having overwintered as eggs, larvae or pupae. Annual plant species also set seed and die before the next generation germinates. Populations with this characteristic of non-overlapping generations are much better described by discrete-time models than continuous equations (Hu *et al.*, 2011).

In order to derive a discrete form of the logistic equation, consider the approximation,

$$\frac{dN}{dt} \approx \frac{N_{n+1} - N_n}{\Delta t}, \quad (3)$$

where N_n and N_{n+1} are consecutive points, separated by a time step Δt . Now, by letting $\Delta t = 1$ and applying the approximation to the logistic equation (1), then the logistic map is obtained:

$$N_{n+1} = \alpha N_n \left(1 - \frac{(\alpha - 1)}{\alpha} \cdot \frac{N_n}{K_0} \right), \quad n \in \mathbb{Z}^+ \quad (4)$$

where $\alpha = 1 + r$, N_n is the population at time-step n and K_0 is the constant carrying capacity.

3.1 Logistic map: Constant carrying capacity

The dynamics of the logistic map (4) when varying the growth rate are very well known. For $0 < \alpha < 1$, the intrinsic growth rate r is negative (since $\alpha = 1 + r$), and thus the population becomes extinct. For $1 < \alpha < 3$, the intrinsic growth rate of the population is positive, and an equilibrium is reached with the environment due to the interaction between reproduction and limited resources. The population will converge to its carrying capacity, K_0 . Increasing α beyond 3, a period-doubling cascade occurs, with the population displaying periodic behaviour with cycles of period 2^k , $k \in \mathbb{N}$, beginning at period 2 and increasing as α increases. At $\alpha \approx 3.57$, the behaviour becomes aperiodic, although this is intermittent as windows of periodic behaviour occur. In particular, an orbit of period 3 is evident for $3.828 \lesssim \alpha \lesssim 3.842$, thus chaos is present in the dynamics (Li and Yorke, 1975). When $\alpha > 4$, the population is no longer bounded below, and it thus becomes rapidly extinct. This behaviour can be summarised in a bifurcation diagram (figure 2).

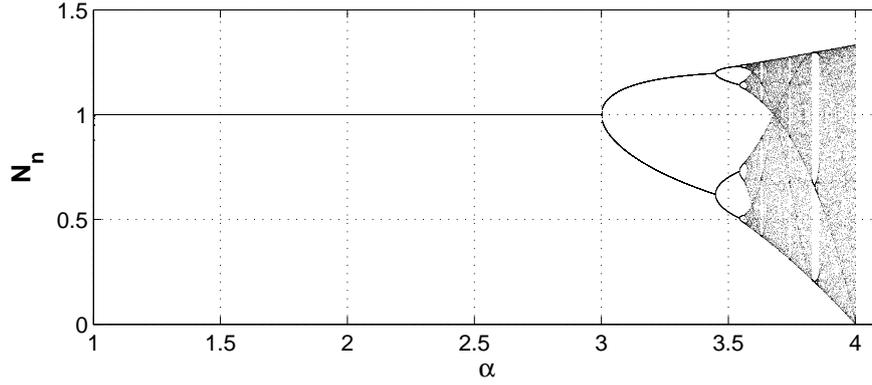


Figure 2: Bifurcation diagram of equation (4), plotting N_n against α , for $K_0 = 1$.

3.2 Discrete periodic carrying capacity

The dynamics resulting from the logistic map with constant carrying capacity are very well known (Thunberg, 2001), having been applied to a wide variety of phenomena as well as being very interesting from a purely mathematical perspective (López-Ruiz and Fournier-Prunaret, 2004). The dynamics of various forms of coupled logistic equations representing interspecies interactions in symbiosis models and predator-prey models have also been investigated and applied (Hu *et al.*, 2011; López-Ruiz and Fournier-Prunaret, 2004; Saha and Sahni, 2012; Thunberg, 2001). However, these all consider the carrying capacity to be some fixed value. In order to better replicate the natural environment, a time-dependent form of carrying capacity will now be considered in a discrete model.

In (2), the carrying capacity was represented by a periodic function. It was observed that periodicity in the environment forced population dynamics into periodic behaviour, with all solutions having the same period as the carrying capacity. One way a periodic time-dependent function may be replicated in a discrete model is by using the system

$$\begin{aligned} N_{n+1} &= \alpha N_n \left(1 - \frac{(\alpha - 1)}{\alpha} \cdot \frac{N_n}{K_n} \right) \\ K_{n+1} &= K_0 + \epsilon(-1)^n, \end{aligned} \quad (5)$$

where K_0 is the average value of the carrying capacity, and ϵ determines the amplitude of the oscillations. As for the continuous system, the carrying capacity has an influence on the population, but the population of the species has no impact on its environment.

Iteration plots of system (5) are shown in figure 3, with $K_0 = 1$, $N_0 = 0.5$ and $\epsilon = 0.1$ for two different values of α . When $\alpha = 1.7$, if the carrying capacity is constant then the population reaches a stable fixed point, as in figure 2. However, in figure 3a, the periodic carrying capacity has caused the population to have cyclic dynamics, with a 2-cycle evident. Hence variations in the environment are forcing changes in the population dynamics. Variations in the population are delayed by one time step from the environment. This is because the population dynamics, as determined by system (5), depend only on the value of K_n for the time-step. Any increases or decreases in the population reflect conditions of the previous season. Increasing α to 2.8, which would for a constant carrying capacity also mean eventually reaching a fixed point (figure 2), the population has been forced into a 4-cycle. Hence we notice that a period-doubling bifurcation has occurred.

This behaviour can be represented in a bifurcation diagram (figure 4). It is clear that there is no 1-cycle, but the periodic environment has forced periodic behaviour onto the population. Increasing α , the amplitude of the 2-cycle increases before a period-doubling bifurcation occurs, producing a 4-cycle. This behaviour continues in a period-doubling cascade towards chaos. It can be seen that the range of physically meaningful values of α has decreased from when the environment is unchanging. The regions of aperiodic behaviour are bounded for $\alpha < 3.273$, but increasing α beyond this critical point results in extinction. Intermittency between periodic and aperiodic behaviour is also evident.

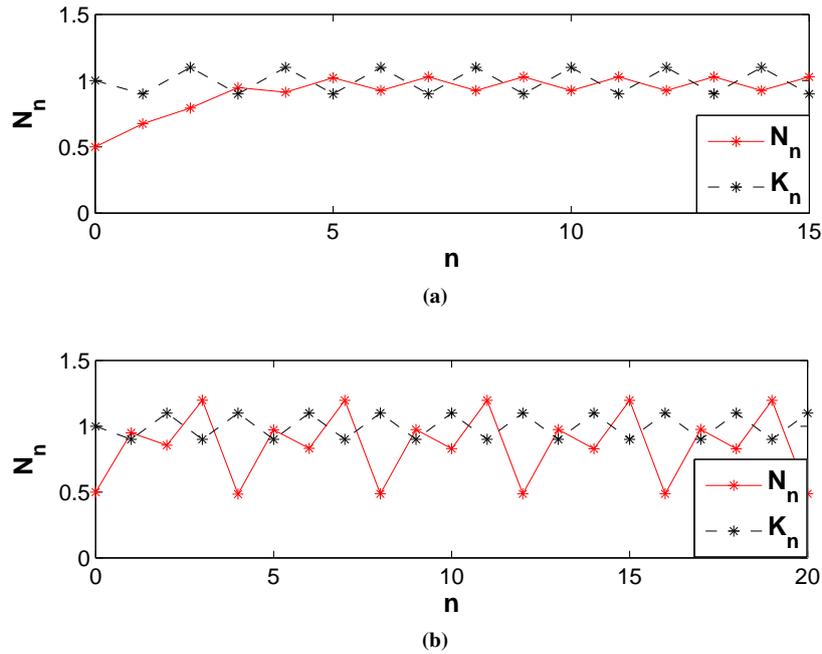


Figure 3: Iteration plots of N_n against n , with (a) $\alpha = 1.7$ and (b) $\alpha = 2.8$.

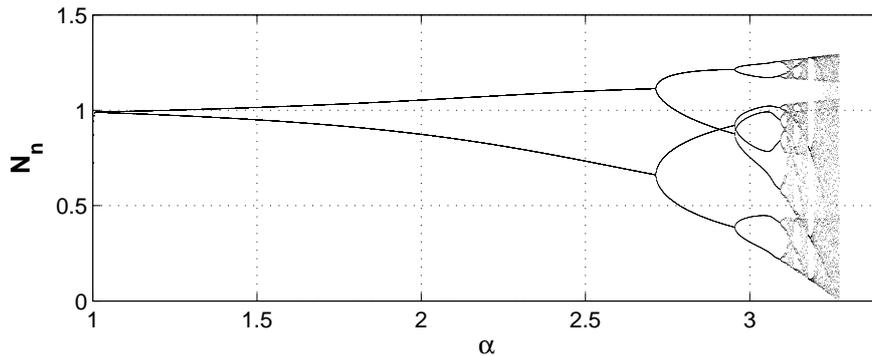


Figure 4: Bifurcation diagram of N_n against α , for $K_0 = 1$, $N_0 = 0.5$ and $\epsilon = 0.1$.

Thus far only a constant value of $\epsilon = 0.1$ has been considered. Figure 5 shows a bifurcation diagram for when the amplitude of the carrying capacity oscillations are increased to $\epsilon = 0.4$. Clearly, the acceptable range of α for species survival has been significantly reduced.

4 CONCLUSIONS AND FURTHER WORK

Discrete population models have advantages over their continuous counterparts in various applications, and have more interesting dynamics that can better represent some natural systems. A discrete function representing carrying capacity is proposed, and the population dynamics when used with the logistic map are explored. Table 1 summarises the dynamics in comparison with a constant carrying capacity. It is observed that changing the amplitude of the carrying capacity's oscillations could have significant ramifications for management. If a species with growth rate $\alpha = 2.5$ is comfortably in equilibrium with its environment with periodic changes in carrying capacity of 10% ($\epsilon = 0.1$), increasing the oscillations to 40% ($\epsilon = 0.4$) will cause the population to become extinct extremely rapidly. Smaller changes that do not directly cause extinction will increase suscep-

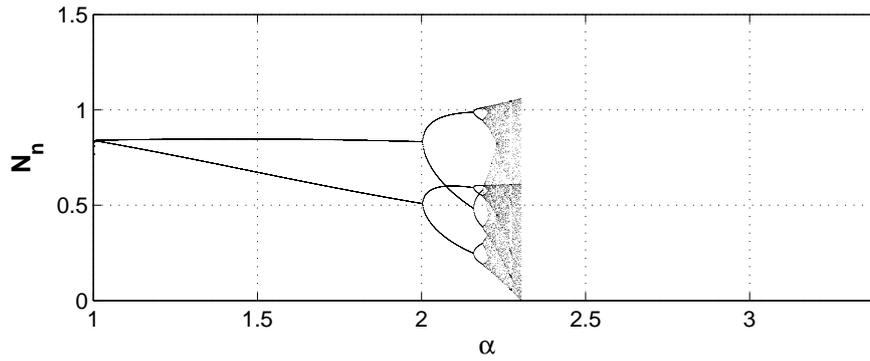


Figure 5: Bifurcation diagram of N_n against α , for $K_0 = 1$, $N_0 = 0.5$ and $\epsilon = 0.4$.

Table 1: A summary of the onset of n -cycles for the logistic map, for a constant carrying capacity (equation (4)) and a periodic carrying capacity (system (5)) with $\epsilon = 0.1$ and $\epsilon = 0.4$.

| n-cycle | $\mathbf{K} = \mathbf{K}_0$ | $\mathbf{K} = \mathbf{K}_0 + \epsilon(-1)^n,$ $\epsilon = 0.1$ | $\mathbf{K} = \mathbf{K}_0 + \epsilon(-1)^n,$ $\epsilon = 0.4$ |
|------------|-----------------------------|---|---|
| | onset at $\alpha \approx$ | onset at $\alpha \approx$ | onset at $\alpha \approx$ |
| 1 | 1 | none | none |
| 2 | 3 | 1 | 1 |
| 4 | 3.449 | 2.713 | 2 |
| 8 | 3.544 | 2.953 | 2.158 |
| 16 | 3.564 | 3.094 | 2.188 |
| \vdots | \vdots | \vdots | \vdots |
| extinction | 4 | 3.273 | 2.305 |

tibility to other changes in the environment. In such a situation, management must take care no such changes occur that threaten survival of the species. The model will be tested against data from Jillson (1980), however it is recognised that the logistic model is an oversimplification of reality. The consequences of using discrete models as opposed to their continuous counterparts will be explored.

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