Journal of Engineering and Applied Sciences 12 (9): 2304-2309, 2017
ISSN: 1816-949X

Dynamics of a Discrete Non-Autonomous Ricker Model

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Abstract: In applications such as population dynamics, the environment is often assumed constant despite the fact that fluctuating environments may fundamentally affect the dynamics. In particular, environmental periodicity can enhance or diminish population sizes. In this study discrete non-autonomous Ricker population model is considered. Specifically the dynamics of the Ricker Model are investigated when subjected to environmental variability. This is achieved by periodically modulating the carrying capacity which is considered as a proxy variable for the state of the environment. We analyze a population whose growth is subject to an alternating environment. The parameter space is explored both periodic and chaotic behaviour including abrupt change of chaotic attractors are observed.

Key words: Ricker Model, discrete population dynamics, carrying capacity, environmental change, Malaysia

INTRODUCTION

Ecological modelling has a wide variety of applications and it is an important tool in environmental and resource management. It may be used to assess the survival or possible extinction of a species or ecosystem by evaluating the potential impact of changes to the environment. For example, chemical exposure from the use of pesticides or fertilizers in the environment, either by direct application in an ecosystem or due to drift, run-off or spillage has significant ramifications for an ecosystem and its biodiversity. Other possible sources of chemical exposure are industrial operations and oil spills in the ocean. Such exposure may have a negative impact on a specie's habitat, possibly threatening the survival of the species.

Invasive species of both flora and fauna are other well-known factors that can change an environment and provide competition for resources with endemic species. A similar situation may also occur in agriculture where native animals may be considered pests because they compete with stock for feed. The introduction of disease into an environment may also have negative impact on the survival of a given species. Another source of change in the environment that impacts both the survival and distribution of species is climate change with research on its potential impacts having increased significantly in recent years (Chapman *et al*., 2014). Using a continuous model, one option to incorporate a periodically changing environment is to utilize a periodic time-dependent carrying capacity (Swart and Murrell, 2008). It was observed that periodicity in the environment caused the population to exhibit a periodic behavior with all solutions having the same period as the carrying capacity. In this study, a discrete periodic form of carrying capacity is presented. It is applied to the Ricker Model (May, 1974) and the resulting population dynamics are analyzed.

Ricker Model: The periodically fluctuating environment can be used in a number of different models, according to that which best suits the population in question. While some analysis of the effect of periodic forcing on the Ricker Model has been performed (Henson, 1999; Zhou and Zou, 2003; Li and Chen, 2009; Morena and Franke, 2012) the method of forcing is varied and the analysis remains incomplete. Here, a similar analysis to that performed using the logistic map is performed. The model for a population of size N_n coupled to a periodic environment described via its carrying capacity K_n is:

$$N_{n+1} = N_n e^{r(1-\frac{N_n}{K_n})}, \quad K_{n+1} - K_0 + \in \left(-1\right)^n, \; n \in Z^+ \qquad (1)$$

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Where:
K_0 = The average value of the carrying capacity
ϵ = Determines the amplitude of the oscillations

In this model, the carrying capacity has an influence on the population but the population has no impact on its environment. The changes induced in the environment can be thought of as describing seasonal effects. It is well recognized that interactions occur in which a species will have an impact on its environment. However, if the population size is small then its effect on the environment may be considered negligible. An example of such a scenario is the well known Jillson (1980) experiment on the response of a population of flour beetles, Tribolium castaneum to environmental fluctuations. Thus, the simple model described by the system of Eq. 1 forms a first step in the development of better discrete population models. Iteration plots, bifurcation diagrams and typical attractor regions can give insight into the population dynamics predicted in a periodic environment.

MATERIALS AND METHODS

Constant environment ($\epsilon = 0$): Let us consider first the case of a constant environment that is $K_n = K_0$ for all $n \in Z^+$. The solutions to (1a) are given by the sequence N_0, N_1, N_2, ..., called the trajectory of N. When the sequence reaches some point for which consecutive values are the same it is said to have reached a fixed point (Groff, 2013) denoted N^*. For the Ricker Model there are two fixed points, $N^* = 0$ and $N^* = K_0$.

Let $f(N_n)$ be the right-hand side of Eq. 1a. A fixed point is stable if $|f(N^*)|<1$, unstable otherwise. Using this criterion, $N^* = 0$ is unstable for $r>0$ all while $N^* = K_0$ is stable for all $0<r<2$. An iteration plot of the Ricker Model with growth rate $r = 1$ (Fig. 1a) demonstrates that the population reaches this fixed point. A similar plot may be shown when the value of r is increased above 2 (the threshold value for the stability of $N^* = K_0$). Consider Fig. 1b where $r = 2.4$. The iteration plot clearly shows that after initial transient behavior, the population settles to oscillate between two values-a cycle of period 2 has formed around what was previously a stable fixed point $N^* = K_0$.

A 2-cycle is when every second iteration gives the same result $N_{n+2} = f(f(N_n)) = N_n = N^{**}$ with $N_{n+1} \neq N_n$ where the two solutions N_1^{**} and N_2^{**} map onto each other. A 2-cycle is stable if and only if $|f(N_1^{**})\ f(N_2^{**})|<1$. At $r = 2$ the fixed point, $N^* = K_0$ becomes unstable and the stable 2-cycle emerges. This change in stability is called a period-doubling bifurcation and the point at which it occurs is called a bifurcation point.

For increasing values of r stable 4 and 8-cycles, etc., exist. The bifurcation Fig. 2a shows this period-doubling behavior with cycles of period 1, 2, 4 and 8 clearly visible. It can be seen that it undergoes period doubling bifurcations on a route towards chaos which occurs at $r \approx 2.69$. Windows of periodic behavior are also evident in particular a cycle of period three at $r \approx 3.12$. The windows of periodic behavior break up the chaotic dynamics. This phenomenon is called intermittency.

While all orbits are bounded, the Ricker model, being exponential, predicts population dynamics with increasingly large maximums as the growth rate increases. However, it conversely predicts minimums approaching $N_n = 0$. Thus, one of the disadvantages of the Ricker Model is that it never explicitly predicts extinction, unless the minimum population on a cycle is less than one individual. However, it does describe increasing vulnerability to extinction in the form of very small

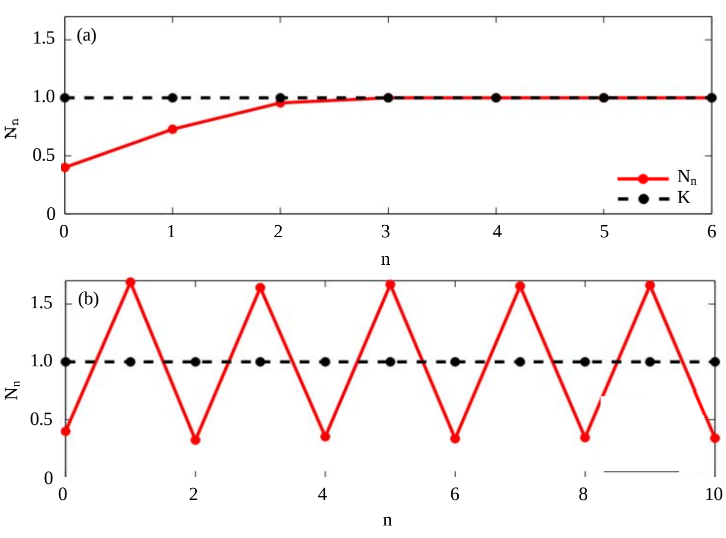

Fig. 1: Iteration plots, N_n versus n with: a) $r = 1$ and b) $r = 2.4$. Here $K_0 = 1$ and $N_0 = 0.4$

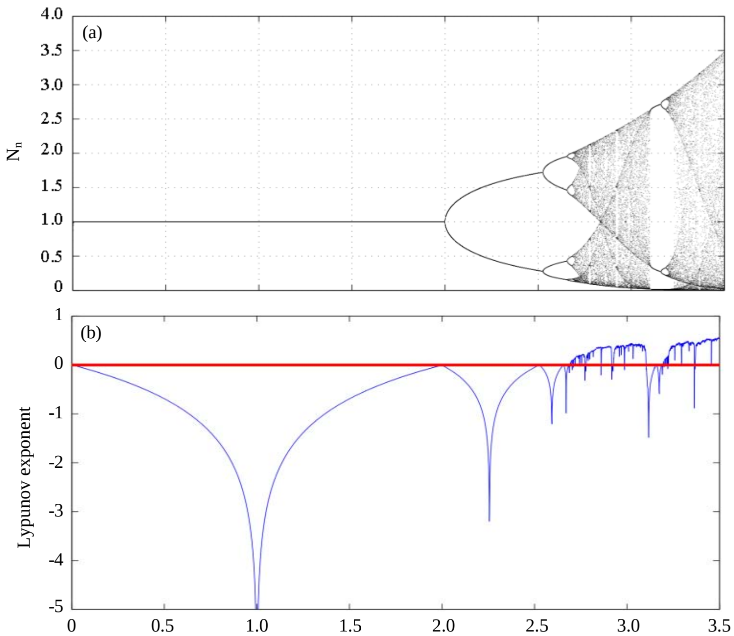

Fig. 2: a) Bifurcation diagram and b) Lyapunov exponents with K_0 = 1

minimum populations. The values of r for which stable periodic orbits exist can be more precisely determined using Lyapunov exponents. Lyapunov exponents are a means of quantifying sensitivity to initial conditions, relating the exponentially fast divergence or convergence of orbits with close but different initial conditions. Such sensitivity is a trait of chaotic dynamics and thus a system is defined to be chaotic if (and only if) it has one or more positive Lyapunov exponents (Wolf *et al*., 1985). The Lyapunov exponent λ for a function $f(N_n)$ is defined by Young (2013) (Fig. 2):

$$\lambda = \lim_{n\to\infty} \frac{1}{n}\sum_{k=0}^{n-1} \text{In}\left|\frac{df(N_k)}{dN_k}\right| \tag{2}$$

Applying Eq. 2 to system Eq. 1, Fig. 2b shows the existence of stable, periodic orbits ($\lambda<0$) bifurcation points ($\lambda = 0$) and chaotic dynamics ($\lambda>0$). It should be noted that however, the Lyapunov exponents do not give any indication of the period of the orbits, merely indicating stable or chaotic dynamics.

Periodic environment ($\epsilon\neq0$): We now return to system Eq. 1. Iteration plots show that even for a relatively small growth rate, r = 1 the population is forced into a 2-cycle (Fig. 3a). Observe also that the population is displaced by one time step from changes in the environment, since only the previous generation and the environmental conditions it experienced influence the population. If the growth rate is increased to r = 2.4 (Fig. 3b) the population is forced into a 4-cycle and thus a period-doubling bifurcation has occurred for $1<r<2.4$. Summarizing this behavior in a bifurcation diagram allows comparison of the dynamics with the case of constant carrying capacity (May, 1974). Setting ϵ-0.1 and comparing Fig. 4a with Fig. 2a, it is clear that the periodic carrying capacity has forced the population into a 2-cyclic even for $0<r<2$. The period-doubling route to chaos is the same for both the periodic and constant carrying capacities. Bifurcations into 4 and 8-cycles for example, occur earlier than in the case of a constant environment. The bifurcation diagram for the periodic environment show richer dynamics. Additional windows of periodic orbits are present as a result of crisis-induced (Kubo *et al*., 2008) intermittency initiated by a saddle-node bifurcation at $r\approx2.69$, resulting in a 2-cycle.

In the region $2.69<r<3.06$ the process of period-doubling starts over leading again to chaotic dynamics. At $r\approx3.6$ the chaotic region experiences a sudden expansion resulting in a attractor-merging crisis (Young, 2013) a feature absent in the population with a constant carrying capacity. If the size of the oscillations of the carrying capacity is increased to ϵ = 0.4 the bifurcation in Fig. 5 is obtained. Comparing the bifurcation diagrams for ϵ = 0.1 (Fig. 4a) and ϵ = 0.4 (Fig. 5) it is apparent that structural changes have occurred. Period-doubling bifurcations occur at smaller r values compared to the ϵ = 0.1 case.

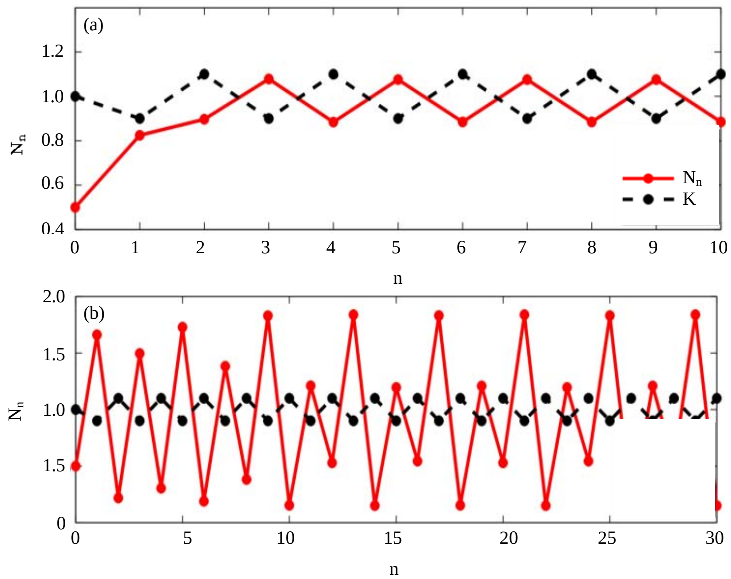

Fig. 3: Iteration plots of N_n against n with: a) r = 1 and b) r = 2.4. Other parameters are K_o 1 = N_o = 00.5 and ϵ = 0.1

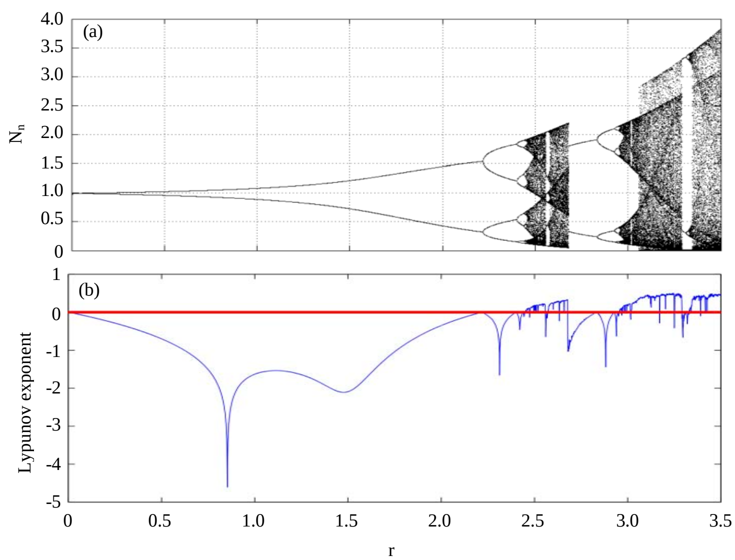

Fig. 4: Bifurcation diagram: a) Lyapunov exponents and b) with K_0 = 1, N_o = 0.5 and ϵ = 0.1

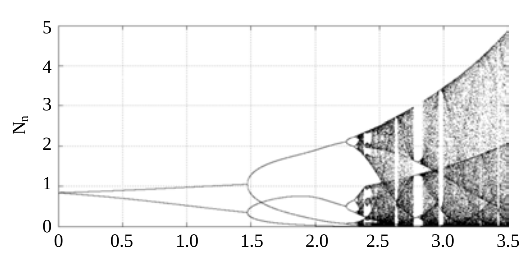

Fig. 5: Bifurcation diagram of N_n against r with parameters K_o = 1, N_o = 0.5 and ϵ = 0.4

RESULTS AND DISCUSSION

It is noticeable that very small population values occur in 4-cycles for intermediate growth rates (such as when r = 2). This makes the population more vulnerable to additional environmental perturbations such as natural disasters or increased competition for resources, factors that may place the population at risk of extinction. Figure 6 shows bifurcation diagrams for fixed growth rates r but varying amplitudes of oscillations ϵ in the carrying capacity. Interesting dynamical behaviour is evident with intermittent windows of stable periodic

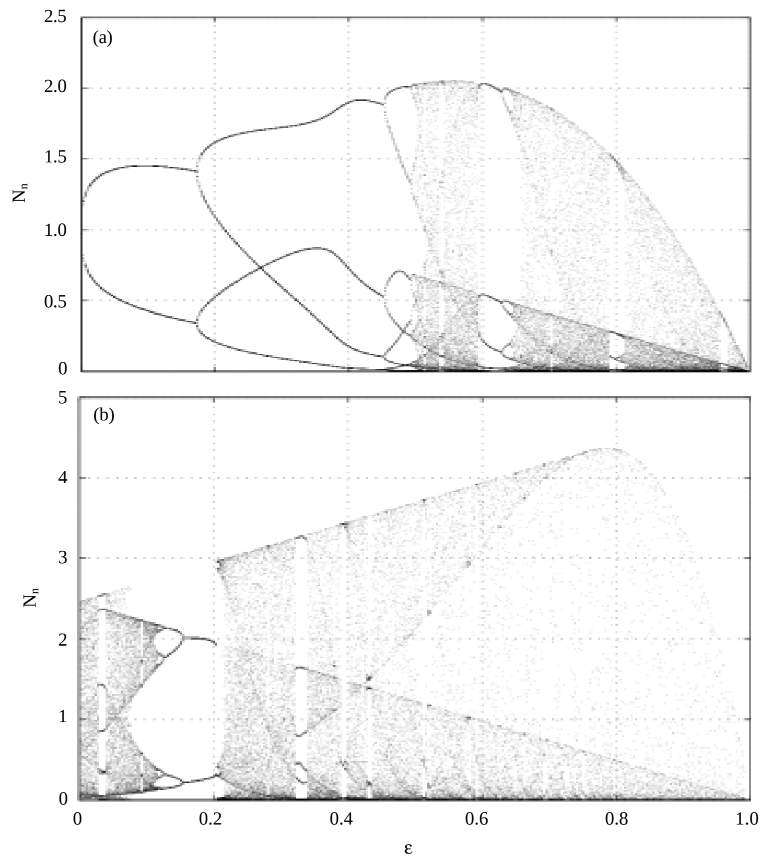

Fig. 6: Bifurcation diagrams of N_n for ϵ with: a) r = 2 and b) r = 2.5. Initial conditions K_n = 1 and N_0 = 0.5

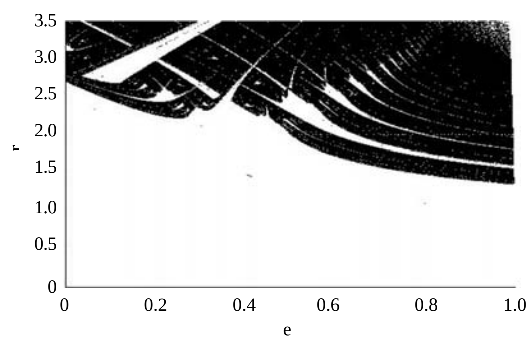

Fig. 7: Typical attractor regions in the (r, ϵ) parameter space for the Ricker Model with alternating carrying capacity. White regions $\lambda>0$ indicate periodic attractors while black regions $\lambda<0$ indicate chaotic attractors

behaviour and aperiodic dynamics. While extinction is not described, very small population sizes are predicted for larger values of ϵ and r. By using the Lyapunov exponents, a plot of typical attractor regions in the (r, ϵ) parameter space was produced in Fig. 7. White regions represent stable periodic population dynamics while areas of black represent chaotic behaviour. Note again that extinction is not possible in the Ricker Model. Comparison with the logistic map with periodic carrying capacity shows that the Ricker Model gives rise to far more stable periodic behavior than the logistic map with the same model for carrying capacity (Monte *et al*., 2004).

Although, neither population size nor the length of an orbit before reaching a stable cycle can be determined from this plot, regions of stability can be determined. Reference can then be made to iteration plots or bifurcation diagrams for relevant values of r and ϵ for more detailed information regarding the population dynamics.

CONCLUSION

In this study, a discrete periodic carrying capacity was applied to the Ricker Model. It was observed that the alternating carrying capacity forced periodic behavior onto the population. It was demonstrated that the larger the size of the environmental oscillations the earlier the onset of chaos. However for smaller growth rates $0<r<2$ and larger oscillations $0.6<\epsilon<1$, chaos was not a precursor to extinction. It was observed that larger periodic changes in the environment were better tolerated by populations with smaller growth rates as population increases in time intervals of high carrying capacity were restricted by the smaller growth rate. The subsequent collapse in time intervals of lower carrying capacity was much less and thus a small growth rate moderates the reactions of a population to changes in the environment.

The overall dynamics resulting from applying the discrete periodic carrying capacity to the Ricker Model were similar to the logistic model. The primary difference is that the Ricker Model does not explicitly predict extinction. Increasing the size of oscillations in the carrying capacity caused the onset of chaos to occur earlier with respect to growth rate. Despite extinction not being described, it was seen that populations with smaller growth rates $0<r<1$ tolerated larger environmental oscillations without experiencing chaos.

ACKNOWLEDGEMENT

The research is supported by the Fundamental Research Grant Scheme, Ministry of Higher Education Malaysia Vot number 1563 and Universiti Tun Hussein Onn Malaysia.

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