

A Periodical Population Model

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ABSTRACT

In this work, we propose a population model of difference equations to explore the phenomenon of periodicity which occurs frequently among biological populations, most notably in species of plants and insects.

Local stability analysis was made to determine the conditions under which the population will become periodical. The analysis was done for the cases of populations with 2 and 3 age-classes, and numerical simulations were made for the latter case to ensure its global properties. For the case of population with more than three age-classes, we used numerical examples to highlight the similarities and differences.

Key words: periodical population, stable equilibrium, semelparous species

1. Introduction

A biological population is said to be periodical if the life cycle of the individuals in the population has a fixed length of k time units, with $k \geq 1$ an integer, where the time unit may be in terms of year, month, day, or minute and if reproduction occurs only once at the end of the individual's lifetime.⁽¹⁾ Species with such phenomena are known as "semelparous" species [3] and occur frequently in many species of animals and plants, especially in insect species such as periodical cicada [7] or the May beetle (*Melolontha spp.*) [6].

In many cases, all but one of the age-classes are eliminated although it is possible for several of the age-classes to coexist, as in the case of the pink salmon (*Oncorhynchus gorbuscha*) or the wood cricket (*Nemobius sylvestris*) [1, 9].

It is then common to divide the members of the periodical population into k reproductively isolated age-classes with $N_i(t)$ being the number of individuals of the population in the i -th age-class at time t , t an integer. It has been suggested [4, 6] that periodical behavior might be the result of competitive exclusion between individuals of the population, particularly when the competition is stronger between individuals of different ages than be-

tween individuals of the same age-class.

In his work on periodical insects, Bulmer [2] concluded that the relative intensity of competition among the individuals of the population has a decisive influence on whether the population will tend to be a periodical population or not.

For his periodical insect model, Bulmer assumed that the competition that effects the survival rate of an individual comes from other individuals existing in the population at the same time as the individual in question. However, in many instances, the individuals of different age-classes appear in different form at different stages of their lifetimes, require different kinds of food resource, attract different predators and occupy a different type of habitats. For example, the effect of adult fishes on the survival rate of fish eggs at any time might not be directly dependent on the present number of the adult fishes, but on the number of that age-class when they were in egg form, since the more numerous they were, the more likely it was to attract predators to their natural habitat in the future. This is also competition, although the effect is delayed for some time. Similar phenomena also occur in many species of insects. Therefore it is reasonable to investigate this delayed effect of competition from ancestors on the periodical behavior of a population.

In Section 2, we propose a nonlinear difference equation model which takes into account this delayed competition from other members of the population. Sections 3 and 4 are devoted to the discussion of this model in the cases of the life cycle, k , equaling 2 and 3, respectively. In Section 5, we give numerical examples to illustrate the cases where the general model for $k > 3$ are

(1) In cases where the individuals reproduce at a precisely defined "age of fecundity" and continue to live without reproduction for the rest of their lifetimes, we can follow a practice commonly used and assume that their age of fecundity is the length of their lifetimes since they can be considered as inconsequential to the growth of the population once past their reproductive age.

similar or different from the earlier analysis and discuss the ecological significance of the results obtained from this model.

2. The Model

Let $N_j(t)$ be the number of individuals of the j th age-class of a population counted at the beginning of the time unit t , t an integer. Consider the following equations:

$$N_0(t+1) = \frac{BN_{k-1}(t)}{1 + \sum_{i=0}^{k-1} \alpha_i N_{k-1}(t-i)} \tag{2.1}$$

$$N_{j+1}(t+1) = \frac{S_{j+1} N_j(t)}{1 + \sum_{i=0}^{k-1} \gamma_i N_j(t-i)}, j=0,1,\dots,k-2. \tag{2.2}$$

Here S_{j+1} is the probability that an individual of age j will survive to the end of the time unit in absence of competition, B is the mean reproduction rate ⁽²⁾ of an adult (of age $k-1$) at the end of its lifetime, $\alpha_i > 0$ is the "competition coefficient" which specifies the amount of effect an adult i time units before (i.e., at time $t-i$) has on the survival rate of an adult, and $\gamma_i > 0$ is the corresponding competition coefficient for a non-adult individual (of age 0 to $k-2$) i time units before has on an individual of the same age-class ⁽³⁾.

The denominator terms on the right-hand sides of equations (2.1) and (2.2) account for the influence of all population members on the chance of survival of each individual. They take into account the effect of the other members of the population present at time t when they were of the same age-class as the individual in question, if they were older than the given individual; and the effect of their direct ancestors in the preceding generation if they were younger. Thus the denominators in (2.1) and (2.2) cover the delayed competition from all the population members present at time t on any given individual when they or their immediate predecessors were of the same age as the said individual.

As a convention, the number of the population at time t will be given in terms of an age composition vector:

$$N(t) = \begin{bmatrix} N_0(t) \\ \vdots \\ N_{k-1}(t) \end{bmatrix}.$$

(2) The mean reproductive rate B is used to denote $B^* S_k$, where S_k is the probability that an individual of age $k-1$ will survive to the end of its lifetime and B^* is the average number of newborns by an individual at the end of its lifetime.

(3) Note that we do not distinguish non-adults of different age-classes in the sense that they have the same competition coefficient. This is a simplification which shall have no effect on the conclusions of this work.

First, let us consider a restriction on the values of the mean reproduction rate B and the survival rates S_j . Note that for t integer and for $j = 1, 2, \dots, k-1$.

$$N_j(t+1) = \frac{S_j N_{j-1}(t)}{1 + \sum_{i=0}^{k-1} \gamma_i N_{j-1}(t-i)} < S_j N_{j-1}(t), \tag{2.3}$$

and thus

$$N_{k-1}(t+k) < \left(\prod_{i=1}^{k-1} S_i\right) N_0(t+1). \tag{2.4}$$

Since

$$N_0(t+1) = \frac{BN_{k-1}(t)}{1 + \sum_{i=0}^{k-1} \alpha_i N_{k-1}(t-i)} < BN_{k-1}(t), \tag{2.5}$$

combining (2.4) and (2.5), we get

$$N_{k-1}(t+k) < B \left(\prod_{i=1}^{k-1} S_i\right) N_{k-1}(t), \text{ for each integer } t \tag{2.6}$$

If $B \prod_{i=1}^{k-1} S_i = M < 1$, then, for all integer values of t ,

$N_{k-1}(t+kn) < N_{k-1}(t+k(n-1))$ for positive integers n . Let $\{N_{k-1}(t+kn)\}_{n=1}^{\infty}$ be a sequence of the $k-1$ th age-class at time $t+kn$ for $n=1, 2, \dots$, if $N_{k-1}(t)$ is the $k-1$ th age-class at time t . It is a strictly decreasing sequence bounded below by 0 and $N_{k-1}(t+kn) > 0$ as $n \rightarrow \infty$ provided $N_{k-1}(t)$ is bounded. (2.7)

For the case when $B \prod_{i=1}^{k-1} S_i = 1$, consider that

$$N_0(t+1) < \frac{BN_{k-1}(t)}{1 + \alpha_0 N_{k-1}(t)}. \tag{2.8}$$

The together with (2.4) give us, for all $t > 0$,

$$N_{k-1}(t+k) < \frac{B \left(\prod_{i=1}^{k-1} S_i\right) N_{k-1}(t)}{1 + \alpha_0 N_{k-1}(t)} = \frac{N_{k-1}(t)}{1 + \alpha_0 N_{k-1}(t)}, \tag{2.9}$$

when $B \prod_{i=1}^{k-1} S_i = 1$.

Note that the function $f(N) = \frac{N}{1 + \alpha_0 N}$, $\alpha_0 > 0$

has $N = 0$ as its only nonnegative fixed point. Hence the sequence $\{N_{k-1}(t+kn)\}_{n=1}^{\infty}$ is strictly decreasing and decreases to 0 as $n \rightarrow \infty$.

Therefore we have the following theorem:

Theorem 2.1

A population as described in (2.1) and (2.2) will not become extinct only if $B \prod_{i=1}^{k-1} S_i > 1$

As was given in the theorem, $B \prod_{i=1}^{k-1} S_i > 1$ is only a necessary condition; in no way does it guarantee the survival of a population, much less its periodicity. As was noted in Bulmer [2], the periodical behavior of populations of this type depends very much on the relative intensity of competition. To analyze further, we shall first consider the relatively simple case when n is small.

3. Analysis of the Case $k=2$

The model for $k=2$ can be written as follows:

$$\frac{B N_1(t)}{1 + \alpha_0 N_1(t) + \alpha_1 N_1(t-1)}, \quad (3.1)$$

$$N_1(t+1) = \frac{S_1 N_0(t)}{1 + \gamma_0 N_0(t) + \gamma_1 N_0(t-1)}. \quad (3.2)$$

The model has a periodical equilibrium with the population alternating between $\begin{bmatrix} \hat{N}_1 \\ \hat{n}_1 \\ 0 \end{bmatrix}$ and $\begin{bmatrix} 0 \\ \hat{n}_2 \end{bmatrix}$

$$\text{with } \hat{n}_1 = \frac{B S_1 - 1}{\gamma_0 + S_1 \alpha_0} \text{ and } \hat{n}_2 = \frac{B S_1 - 1}{\alpha_0 + B \gamma_0}. \quad (3.3)$$

(Note that the condition in Theorem 2.1, $B S_1 > 1$, guarantees that \hat{n}_1, \hat{n}_2 are positive).

It is clear that in this equilibrium the population is periodical, existing only in the 1st or the 2nd age-class alternatively. To investigate its stability, let us consider a vector-valued function

$\tilde{X}: Z \rightarrow \mathbb{R}^4$ defined by

$$\tilde{X}(m) = \begin{bmatrix} \tilde{N}(2m) \\ \tilde{N}(2m+1) \end{bmatrix} = \begin{bmatrix} N_0(2m) \\ N_1(2m) \\ N_0(2m+1) \\ N_1(2m+1) \end{bmatrix}, \quad m \text{ integer.} \quad (3.4)$$

Then from (3.1) and (3.2), we get

$$\tilde{X}(m+1) = \begin{bmatrix} N_0(2m+2) \\ N_1(2m+2) \\ N_0(2m+3) \\ N_1(2m+3) \end{bmatrix} = \begin{bmatrix} \frac{B N_1(2m+1)}{1 + \alpha_0 N_1(2m+1) + \alpha_1 N_1(2m)} \\ \frac{S_1 N_0(2m+1)}{1 + \gamma_0 N_0(2m+1) + \gamma_1 N_0(2m)} \\ \frac{B S_1 N_0(2m+1)}{\alpha_0 S_1 N_0(2m+1) + [1 + \gamma_0 N_0(2m+1) + \gamma_1 N_0(2m)] [1 + \alpha_1 N_1(2m+1)]} \\ \frac{B S_1 N_1(2m+1)}{\gamma_0 B N_1(2m+1) + [1 + \alpha_0 N_1(2m+1) + \alpha_1 N_1(2m)] [1 + \gamma_1 N_0(2m+1)]} \end{bmatrix} \quad (3.5)$$

(3.5) can be written as

$$\tilde{X}(m+1) = \tilde{F}(\tilde{X}(m)),$$

where the vector-valued function $\tilde{F}: \mathbb{R}^4 \rightarrow \mathbb{R}^4$ is defined as:

$$\tilde{F} \begin{pmatrix} X_1 \\ X_2 \\ X_3 \\ X_4 \end{pmatrix} = \begin{bmatrix} \frac{B X_4}{1 + \alpha_0 X_4 + \alpha_1 X_2} \\ \frac{S_1 X_3}{1 + \gamma_0 X_3 + \gamma_1 X_1} \\ \frac{B S_1 X_3}{\alpha_0 S_1 X_3 + (1 + \gamma_0 X_3 + \gamma_1 X_1) (1 + \alpha_1 X_4)} \\ \frac{B S_1 X_4}{\gamma_0 B X_4 + (1 + \alpha_0 X_4 + \alpha_1 X_2) (1 + \gamma_1 X_3)} \end{bmatrix} \quad (3.6)$$

From (3.3), we know that

$$\tilde{F} \begin{pmatrix} \hat{n}_1 \\ 0 \\ 0 \\ \hat{n}_2 \end{pmatrix} = \begin{bmatrix} \hat{n}_1 \\ 0 \\ 0 \\ \hat{n}_2 \end{bmatrix} \quad (3.7)$$

i.e. $\begin{bmatrix} \hat{n}_1 \\ 0 \\ 0 \\ \hat{n}_2 \end{bmatrix}$ is a fixed point for $\tilde{F}(\cdot)$.

To study the local stability of the fixed point, we use a local linearization method to obtain:

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$$[\nabla_{\tilde{F}}] \begin{pmatrix} \hat{n}_1 \\ 0 \\ 0 \\ \hat{n}_2 \end{pmatrix} = \begin{bmatrix} 0 & \frac{-\alpha_1 B \hat{n}_2}{(1+\alpha_0 \hat{n}_2)^2} & 0 & \frac{B}{(1+\alpha_0 \hat{n}_2)^2} \\ 0 & 0 & \frac{S_1}{1+\gamma_1 \hat{n}_1} & 0 \\ 0 & 0 & \frac{B S_1}{(1+\gamma_1 \hat{n}_1)(1+\alpha_1 \hat{n}_2)} & 0 \\ 0 & \frac{-\alpha_1 B S_1 \hat{n}_2}{(1+(\alpha_0+\gamma_0 B) \hat{n}_2)^2} & \frac{-\gamma_1 B S_1 \hat{n}_2 (1+\alpha_0 \hat{n}_2)}{(1+(\alpha_0+\gamma_0 B) \hat{n}_2)^2} & \frac{B S_1}{(1+(\alpha_0+\gamma_0 B) \hat{n}_2)^2} \end{bmatrix} \quad (3.8)$$

after elementary but complicated computation. The matrix in (3.8) has eigenvalues

$$\lambda = 0, \frac{B S_1}{(1+(\alpha_0+B\gamma_0)\hat{n}_2)^2}, \frac{B S_1}{(1+\gamma_1 \hat{n}_1)(1+\alpha_1 \hat{n}_2)} \quad (3.9)$$

with zero being a double root of the characteristic equation.

Using the values of \hat{n}_1 and \hat{n}_2 in (3.3), we know that

$$0 < \frac{B S_1}{(1+(\alpha_0+\gamma_0 B)\hat{n}_2)^2} = \frac{1}{B S_1} < 1, \quad (3.10)$$

and

$$\frac{B S_1}{(1+\gamma_1 \hat{n}_1)(1+\alpha_1 \hat{n}_2)} = \frac{B S_1 (\gamma_0 + S_1 \alpha_0) (\alpha_0 + B \gamma_0)}{[\gamma_0 + S_1 \alpha_0 + \gamma_1 (B S_1 - 1)] [\alpha_0 + B \gamma_0 + \alpha_1 (B S_1 - 1)]} > 0. \quad (3.11)$$

For the fixed point to be an attractor, we need $\rho(\lambda)$, the magnitude of the largest eigenvalue of the matrix in (3.8), to be less than unity. From (3.9), (3.10), and (3.11), we know that this is the case if and only if the expression in (3.11) is less than 1. It is clear that this depends on the relative size of the competition coefficients, α_i 's and γ_i 's. Hence, we will discuss them case by case.

- (1) $\alpha_1 \neq \alpha_0, \gamma_1 = \gamma_0 = \gamma$.

The term in (3.11) then becomes

$$\frac{B(\gamma + S_1 \alpha_0)}{(\alpha_0 - \alpha_1) + B(\gamma + \alpha_1 S_1)},$$

which is greater than 1 when $\alpha_0 > \alpha_1$ and less than 1 when $\alpha_0 < \alpha_1$. Thus the periodical equilibrium with one

age-class present is an attractor if and only if $\alpha_1 > \alpha_0$.

The only other non-zero fixed point of equation

(3.6) is the stationary equilibrium $\begin{bmatrix} \hat{N}_1 \\ \hat{N}_2 \\ \hat{N}_1 \\ \hat{N}_2 \end{bmatrix}$ with

$$\hat{N}_1 = \frac{B S_1 - 1}{2\gamma + S_1(\alpha_0 + \alpha_1)}, \quad \hat{N}_2 = \frac{B S_1 - 1}{(\alpha_0 + \alpha_1) + 2B\gamma}. \quad (3.12)$$

It is the only attractor when $\alpha_1 < \alpha_0$. Therefore, the system converges to a periodical equilibrium when $\alpha_1 > \alpha_0$ and a stationary equilibrium when $\alpha_1 < \alpha_0$.

- (2) $\gamma_1 \neq \gamma_0, \alpha_1 = \alpha_0 = \alpha$.

The situation is similar to that of case (1). Here

(3.11) becomes $\frac{S_1(\alpha + B\gamma_0)}{[(\gamma_0 - \gamma_1) + S_1(\alpha + B\gamma_0)]}$, which is greater

than 1 when $\gamma_0 > \gamma_1$ and less than 1 when $\gamma_0 < \gamma_1$. Again, the system converges to the periodical equilibrium given in (3.3) when $\gamma_0 < \gamma_1$; and when $\gamma_0 > \gamma_1$, the

system converges to the stationary equilibrium $\begin{bmatrix} \hat{N}_1 \\ \hat{N}_2 \\ \hat{N}_1 \\ \hat{N}_2 \end{bmatrix}$ with

$$\hat{N}_1 = \frac{B S_1 - 1}{2S_1\alpha + (\gamma_0 + \gamma_1)}, \quad \hat{N}_2 = \frac{B S_1 - 1}{2\alpha + B(\gamma_0 + \gamma_1)}. \quad (3.13)$$

- (3) $\alpha_0 = \alpha_1 = \alpha, \gamma_0 = \gamma_1 = \gamma$.

Here (3.11) becomes

$$\frac{BS_1(\gamma+S_1\alpha)(\alpha+B\gamma)}{[\gamma+S_1\alpha+\gamma(BS_1-1)][\alpha+B\gamma+\alpha(BS_1-1)]} = 1.$$

Hence, the periodical equilibrium with one age-class present is a stable equilibrium but not an attractor.

In this case, there is an infinite number of non-zero

equilibria $\begin{pmatrix} \hat{N}_1 \\ \hat{N}_2 \\ \hat{N}_3 \\ \hat{N}_4 \end{pmatrix}$ satisfying the relation

$$\hat{N}_1 + \hat{N}_3 = \frac{BS_1-1}{\gamma+S_1\alpha}, \quad \hat{N}_2 + \hat{N}_4 = \frac{BS_1-1}{\alpha+B\gamma}. \quad (3.14)$$

We note that (3.3) is a special case of the above relations

when $\hat{N}_3 = \hat{N}_2 = 0$. We note further that relations (3.14) also include the case of stationary equilibrium with

$$\hat{N}_1 = \hat{N}_3 = \frac{BS_1-1}{2(\gamma+S_1\alpha)} \quad \text{and} \quad \hat{N}_2 = \hat{N}_4 = \frac{BS_1-1}{2(\alpha+B\gamma)}. \quad (3.15)$$

In fact, all sets of $\{\hat{N}_1, \hat{N}_2, \hat{N}_3, \hat{N}_4\}$ satisfying (3.14) are stable equilibria of the system and the set $A \subset \mathbb{R}^4$

with $A = \{(\hat{N}_1, \hat{N}_2, \hat{N}_3, \hat{N}_4) \mid \hat{N}_1, \hat{N}_2, \hat{N}_3, \hat{N}_4 \text{ satisfying (3.14)}\}$ constitutes an invariant set which is a global attractor for equation (3.6).

(4) $\gamma_1 \neq \gamma_0, \alpha_1 \neq \alpha_0$.

Here (3.11) can be rewritten as

$$\frac{B(\gamma_0+S_1\alpha_0)}{[B(\gamma_0+S_1\alpha_0)+(\alpha_1-\alpha_0)(BS_1-1)]} \cdot \frac{S_1(\alpha_0+B\gamma_0)}{[S_1(\alpha_0+B\gamma_0)+(\gamma_1-\gamma_0)(BS_1-1)]} \quad (3.16)$$

It is clear that when $\alpha_1 > \alpha_0$ and $\gamma_1 > \gamma_0$, both terms in (3.6) above are less than 1, and when $\alpha_1 < \alpha_0$ and $\gamma_1 < \gamma_0$, both terms are greater than 1. Therefore the periodical equilibrium with one age-class present is an attractor in the former case but not in the latter when $\alpha_1 < \alpha_0$ and $\gamma_1 < \gamma_0$.

For the latter case, we must go back to consider the situation where both age-classes are present. A periodical equilibrium in this case is an equilibrium which oscillates between $\begin{bmatrix} a \\ b \end{bmatrix}$ and $\begin{bmatrix} c \\ d \end{bmatrix}$ where $a, b, c,$ and d are positive and finite. Then these constants must satisfy the set of equations

$$a = \frac{Bd}{1+\alpha_0d+\alpha_1b}, \quad b = \frac{S_1c}{1+\gamma_0c+\gamma_1a}, \quad (3.17)$$

$$c = \frac{Bb}{1+\alpha_0b+\alpha_1d}, \quad d = \frac{S_1a}{1+\gamma_0a+\gamma_1c}. \quad (3.17)$$

Eliminating b and d from (3.17), we get the simple equation for a and c :

$$S_1(c-a)[\gamma_0(\alpha_0-\alpha_1)(c+a) + (\alpha_0-\alpha_1)+B(\gamma_0-\gamma_1)] = 0 \quad (3.18)$$

Thus we have two solution:

$$c = a \text{ and } a+c = \frac{B(\gamma_1-\gamma_0)+(\alpha_1-\alpha_0)}{\gamma_0(\alpha_0-\alpha_1)}. \quad (3.19)$$

Note that when $\alpha_1 < \alpha_0$ and $\gamma_1 < \gamma_0$, the second solution in (3.19) is negative, thus the only positive equilibrium is the stationary equilibrium with

$$a = c = \frac{BS_1-1}{(\gamma_1+\gamma_0)+S_1(\alpha_1+\alpha_0)}, \quad \text{and} \quad (3.20)$$

$$b = d = \frac{BS_1-1}{(\alpha_1+\alpha_0)+B(\gamma_1+\gamma_0)}.$$

Since this is the only choice of non-zero equilibrium which is stable, it must be an attractor and the system becomes stationary when $\alpha_1 < \alpha_0$ and $\gamma_1 < \gamma_0$.

The situation becomes more difficult when $(\alpha_1-\alpha_0)(\gamma_1-\gamma_0) < 0$, since the magnitude of $\rho(\lambda)$ then depends on the relative size of the parameters $\alpha_0, \alpha_1, \gamma_0, \gamma_1, B,$ and S_1 . Furthermore, when $(\alpha_1-\alpha_0)(\gamma_1-\gamma_0) < 0$, the second solution in (3.19) could be positive; that is, there could be a non-stationary equilibrium for the system, in addition to the stationary and periodical equilibria. The third solution is the form of an invariant set $[a, b, c, d]$, as happens in case (3), with

$$a + c = \frac{B(\gamma_1-\gamma_0)+(\alpha_1-\alpha_0)}{\gamma_0(\alpha_0-\alpha_1)}, \quad \text{and} \quad (3.21)$$

$$b + d = \frac{S_1(\alpha_1-\alpha_0)+(\gamma_1-\gamma_0)}{\alpha_0(\gamma_0-\gamma_1)}.$$

We can demonstrate through numerical simulations that, starting with any nonzero initial population, the system will tend to be periodical when the values of the parameters render the magnitude of $\rho(\lambda)$ less than 1, and becomes stationary otherwise.

4. Analysis for $k=3$

For the case of $k = 3$, we once again consider the periodical equilibrium with only one age-class present. We then look for $\hat{n}_1, \hat{n}_2, \hat{n}_3$ so that the population will

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oscillate between $\begin{bmatrix} \hat{\alpha}_1 \\ 0 \end{bmatrix}$, $\begin{bmatrix} 0 \\ \hat{n}_2 \\ 0 \end{bmatrix}$ and $\begin{bmatrix} - \\ \hat{n}_3 \end{bmatrix}$. Using the same method as we did in Section 3, we solve for $\hat{\alpha}_1, \hat{n}_2, \hat{n}_3$ to obtain

$$\left. \begin{aligned} \hat{n}_1 &= \frac{BS_1 S_2 - 1}{\gamma_0 + \gamma_0 S_1 + S_1 S_2 \alpha_0} \\ \hat{n}_2 &= \frac{BS_1 S_2 - 1}{\gamma_0 + \alpha_0 S_2 + BS_2 \gamma_0} \\ \text{and } \hat{n}_3 &= \frac{BS_1 S_2 - 1}{\alpha_0 + \gamma_0 B + BS_1 \gamma_0} \end{aligned} \right\} \quad (4.1)$$

To analyze the stability of this equilibrium we construct a vector-valued function $X: \mathbb{R}^9 \rightarrow \mathbb{R}^9$ as described in Section 3, where

$$\tilde{X}(m) = \begin{bmatrix} \tilde{N}(3m) \\ \tilde{N}(3m+1) \\ \tilde{N}(3m+2) \end{bmatrix} \text{ gives the age composition of}$$

the population at the m th generation.

Consider the vector-valued function $\tilde{F}: \mathbb{R}^9 \rightarrow \mathbb{R}^9$ such that

$$\tilde{X}(m+1) = \tilde{F}(\tilde{X}(m)) \quad (4.2)$$

and we note that $(\hat{n}_1, 0, 0, 0, \hat{n}_2, 0, 0, 0, \hat{n}_3)^T$ is a fixed point of $\tilde{F}(\cdot)$. To study the local stability of this fixed point, \tilde{n} , we use the linearization technique used in Section 3 and obtain a characteristic equation $P(\lambda)$ for $\nabla \tilde{F}(\tilde{n})$ as follows:

$$P(\lambda) = -\lambda^6 \left(\frac{BS_1 S_2}{Y_1} - \lambda \right) \left(\frac{BS_1 S_2}{Y_2} - \lambda \right) \left(\frac{1}{BS_1 S_2} - \lambda \right) = 0, \quad (4.3)$$

where

$$Y_i = (1 + \gamma_i \hat{n}_1) (1 + \gamma_i \hat{n}_2) (1 + \alpha_i \hat{n}_3) > 1 \text{ for } i = 1, 2. \quad (4.4)$$

Hence $\lambda = 0, \frac{BS_1 S_2}{Y_1}, \frac{BS_1 S_2}{Y_2}, \frac{1}{BS_1 S_2}$, all of which are nonnegative.

Since $\frac{1}{BS_1 S_2} < 1$, the magnitude of the dominant eigenvalue of $\nabla \tilde{F}$ depends on the relative values of Y_1 and Y_2 as compared to $BS_1 S_2$.

Equation (4.4) yields

$$Y_i = \left[\frac{S_1(\gamma_0 + \alpha_0 S_2 + \gamma_0 BS_2) + (BS_1 S_2 - 1)(\gamma_i - \gamma_0)}{\gamma_0 + \gamma_0 S_1 + \alpha_0 S_1 S_2} \right].$$

$$\begin{aligned} & \left[\frac{S_2(\alpha_0 + \gamma_0 B + \gamma_0 BS_1) + (BS_1 S_2 - 1)(\gamma_i - \gamma_0)}{\gamma_0 + \alpha_0 S_2 + \gamma_0 BS_2} \right], \\ & \left[\frac{B(\gamma_0 + \gamma_0 S_1 + \alpha_0 S_1 S_2) + (BS_1 S_2 - 1)(\alpha_i - \alpha_0)}{\alpha_0 + \gamma_0 B + \gamma_0 BS_1} \right], \\ & i = 1, 2. \end{aligned} \quad (4.5)$$

Note that when $\alpha_i = \alpha_0$ and $\gamma_i = \gamma_0$, $Y_i = BS_1 S_2$ for $i = 1, 2$.

Therefore the local stability of the periodical equilibrium can be discussed in three separate cases:

- (1) $Y_1 \geq BS_1 S_2$ and $Y_2 \geq BS_1 S_2$ with at least one equality. In this case, the dominant eigenvalue of $\nabla \tilde{F}(\tilde{n})$ is 1. This implies that the periodical equilibrium is stable but not an attractor and therefore convergence to the periodical equilibrium is not guaranteed. Furthermore, there is an invariant set of non-zero equilibria of the form $(\hat{N}_1, \hat{N}_2, \dots, \hat{N}_9)^T$ with

$$\begin{aligned} \hat{N}_1 + \hat{N}_4 + \hat{N}_7 &= \frac{BS_1 S_2 - 1}{\gamma + \gamma S_1 + \alpha S_1 S_2}, \\ \hat{N}_2 + \hat{N}_5 + \hat{N}_8 &= \frac{BS_1 S_2 - 1}{\gamma + \alpha S_2 + \gamma BS_2}, \end{aligned} \quad (4.6)$$

$$\text{and } \hat{N}_3 + \hat{N}_6 + \hat{N}_9 = \frac{BS_1 S_2 - 1}{\alpha + \gamma B + \gamma BS_1},$$

when $\alpha = \alpha_i$ and $\gamma = \gamma_i$ for $i = 0, 1, 2$ (and thus $Y_i = BS_1 S_2$ for $i = 1, 2$).

In this case, the system converges to any point in the set, depending on the value of its initial populations age composition, and the population becomes stable, but not periodical.

- (2) $Y_i > BS_1 S_2$ for $i = 1, 2$. Here both $BS_1 S_2 / Y_1$ and $BS_1 S_2 / Y_2$ are less than unity and we have $1 > \lambda \geq 0$. In this case, the periodical equilibrium is an attractor and the system will converge to this equilibrium if the initial population is close to it. We will show by means of numerical simulation that the periodical equilibrium is also a global attractor in this instance.
- (3) $Y_i < BS_1 S_2$ for $i = 1$ or 2. In this case, the dominant eigenvalue of $\nabla \tilde{F}(\tilde{n})$ is greater than 1 and the periodical equilibrium is unstable. As a result, the system will converge to the stationary equilibrium

$$\begin{bmatrix} \hat{N}_1 \\ \hat{N}_2 \\ \hat{N}_3 \end{bmatrix} \text{ with } \hat{N}_1 = \frac{BS_1 S_2 - 1}{\bar{\gamma} + S_1 \bar{\gamma} + S_1 S_2 \bar{\alpha}},$$

$$\hat{N}_2 = \frac{BS_1S_2 - 1}{\bar{\gamma} + \bar{\alpha}S_2 + BS_2\bar{\gamma}}, \tag{4.7}$$

and $\hat{N}_3 = \frac{BS_1S_2 - 1}{\bar{\alpha} + \bar{\gamma}B + BS_1\bar{\gamma}}$,

where $\bar{\alpha} = \alpha_0 + \alpha_1 + \alpha_2$ and $\bar{\gamma} = \gamma_0 + \gamma_1 + \gamma_2$.

For population with more than three age-classes, the dependence of its asymptotic behavior on the relative size of the parameters is similar to that of population with three age-classes discussed above except in one instance which was mentioned in Bulmer [2] and will be discussed later.

5. Numerical Examples and Discussions

To illustrate the analysis made in previous sections, we use the computer to simulate different case for $k = 3$. Each simulation was made for 100 generations (or 100 k time units) starting from a random initial age composition $\hat{N}(0) = (N_1(0), \dots, N_{k-1}(0))^T$. Graphs were made from the simulations plotting population density of each age-class, $N_f(t)$, versus generation time. In each simulation, $S_1 = S_2 = 0.8$ and $B = 5$.

In Figures (1.a) and (1.b), all competition coefficients equal 0.1 and, as discussed in case (1) of Section IV, all initial positive age compositions $\hat{N}(0)$ will approach the invariant set characterized in (4.7). However the two figures point out that the population's initial age composition will determine which point in the set does the population converge to. Therefore, when individuals in the population are equally competitive within or between age-classes, the population will become stable but

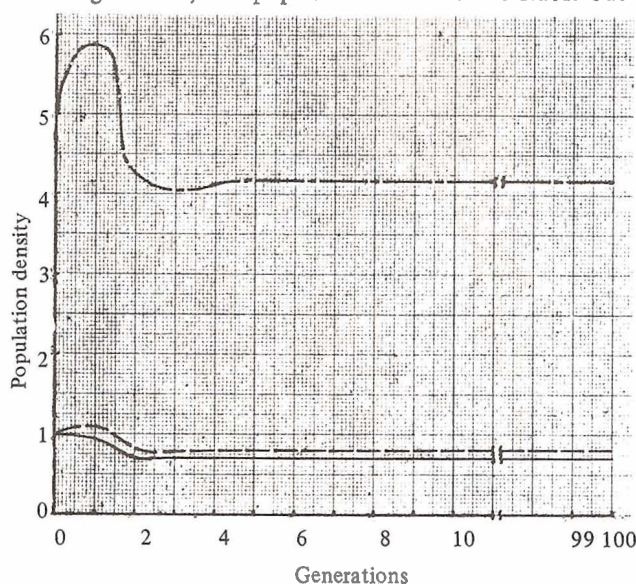


Fig. 1a. Simulation for $\alpha_i = \gamma_i = 0.1$ for $i = 0, 1, 2$; - - - age-class 1, - · - age-class 2, — age-class 3. Initial population = (5, 1, 1).

not periodical, and its eventual age composition depends on its initial age composition. This, as nature tells us, is not what really happens. It is therefore reasonable to conclude that all individuals are not equally competitive.

For Figure (2), we use $\alpha_0 = \gamma_0 = 0.01$ and $\alpha_1 = \alpha_2 = \gamma_1 = \gamma_2 = 0.05$. This is the case where competition is more intense between than within age-classes, so the population converges to the periodical equilibrium with one age-class present.

For Figure (3), $\alpha_0 = \gamma_0 = 0.5$, $\alpha_1 = \gamma_1 = 0.1$, and $\alpha_2 = \gamma_2 = 0.01$. From equation (4.5), we have $Y_1 = Y_2 < BS_1S_2$. Since the competition within an age-class (given by the competition coefficients α_0 and γ_0) is greater than that of other age-classes (described by the coefficients α_i and γ_i , $i = 1$ and 2), the presence of individuals of the same age-class greatly effects the chance of survival of the individuals. Here, as we see, the population converges to the stationary equilibrium since the intense competition within the age-classes lessens the possibility for any one age-class to dominate.

The above examples show that the convergence of the system depends on the relative size of Y_1 and Y_2 as compared to BS_1S_2 . Moreover, when $(\alpha_i - \alpha_0)(\gamma_i - \gamma_0) \geq 0$, there is no ambiguity to the sign of $Y_i - BS_1B_2$. (That is, it is positive when both $\alpha_i - \alpha_0$ and $\gamma_i - \gamma_0$ are positive and nonpositive when both terms are nonpositive).

When $(\alpha_i - \alpha_0)(\gamma_i - \gamma_0) < 0$ for either $i = 1$ or 2 , whether Y_1 and Y_2 are greater than BS_1S_1 or not is determined by the relative size of $(\alpha_i - \alpha_0)$ and $(\gamma_i - \gamma_0)$. So the resulting system could either approach a periodical equilibrium if $Y_i > BS_1S_2$, or the stationary equilibrium if $Y_i < BS_1S_2$. For example, when $\alpha_i > \alpha_0$, Y_i will be greater than BS_1S_2 even if $\gamma_i < \gamma_0$, provided $|\alpha_i - \alpha_0| \gg$

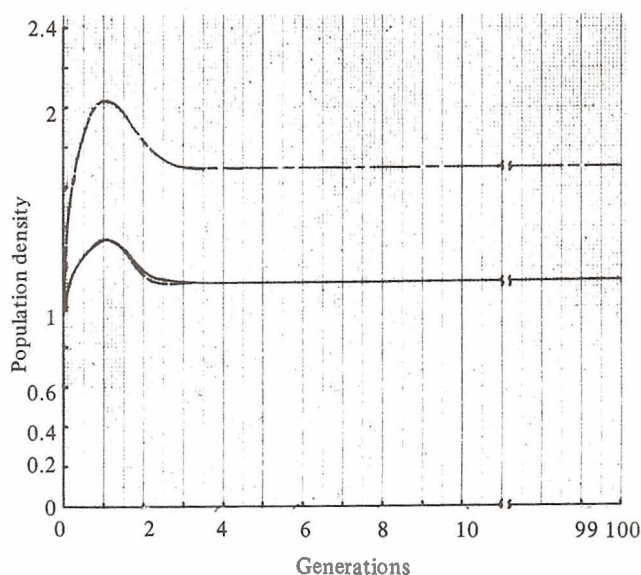


Fig. 1b. Simulation for $\alpha_i = \gamma_i = 0.1$ for $i = 0, 1, 2$; - - - age-class 1, - · - age-class 2, — age-class 3. Initial population = (1, 1, 1).

A Periodical Population Model

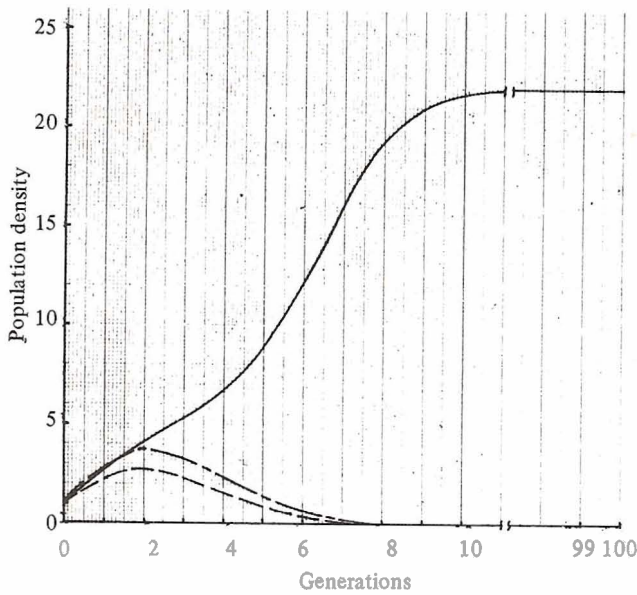


Fig. 2. Simulation for $\alpha_0 = \gamma_0 = 0.01$; $\alpha_i = \gamma_i = 0.05$, for $i = 1, 2$; --- age-class 1, - · - age-class 2, — age-class 3. Initial population = (1, 1, 1).

$|\gamma_i - \gamma_0|$.

This seems to imply that when the competition between age-classes are of intermediate intensity (i.e., the competition from other age-classes are stronger than within the age-class at some stage of the individual's lifetime but weaker at other times), the population will tend to periodicity only if the competition from a particular age-class (other than its own) at a certain stage of its lifetime is much stronger than at other times. Such is the case in the example above, where the delayed competition from the age-class i time units older, α_i , is much greater than the competition within the age-class at its

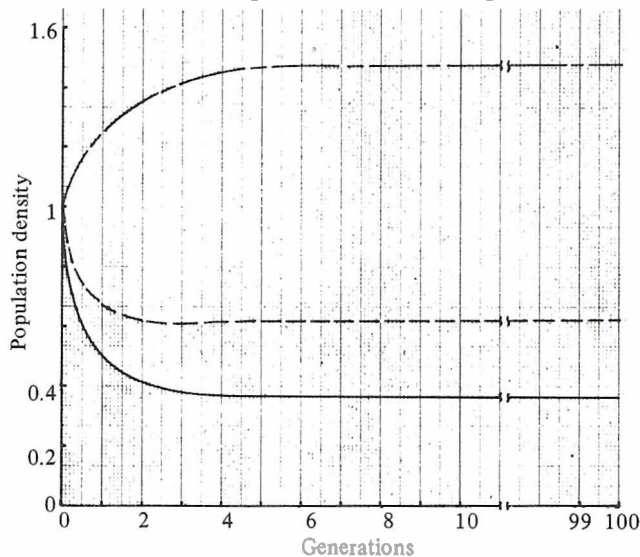


Fig. 3. Simulation for $\alpha_0 = \gamma_0 = 0.5$, $\alpha_1 = \gamma_1 = 0.1$, $\alpha_2 = \gamma_2 = 0.01$; --- age-class 1, - · - age-class 2, — age-class 3. Initial population = (1, 1, 1).

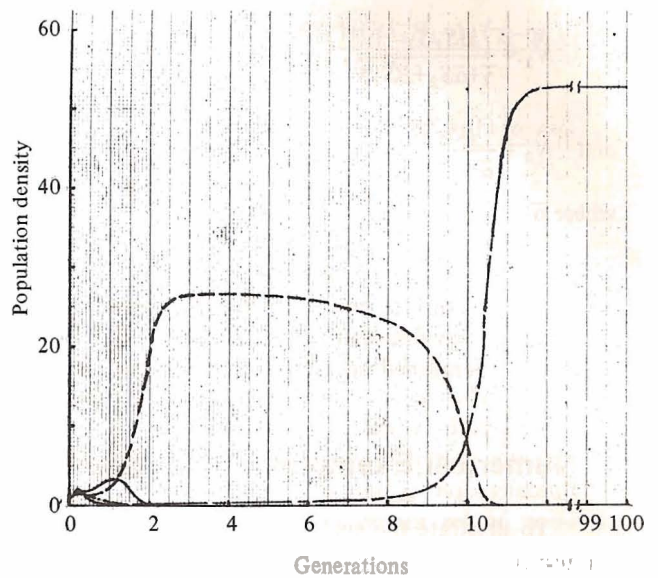


Fig. 4. Simulation for $\alpha_i = \gamma_i = 0.01$ for $i = 0, 1$; $\alpha_2 = \gamma_2 = 0.05$; $\alpha_3 = \gamma_3 = 0.1$; --- age-class 1, - · - age-class 2, — age-class 3, - - - age-class 4. Initial population = (1, 1, 1, 1).

birth, α_0 , as compared to the corresponding competition coefficients at later stages of its lifetime, γ_i and γ_0 . When $\alpha_i - \alpha_0$ is sufficiently large (so that $Y_i > BS_1S_2$ regardless of the value of $\gamma_i - \gamma_0$), the system will converge to its periodical equilibrium. It is, therefore, reasonable to deduce that this intense competition will enhance the population's tendency toward a dominating age-class. Thus we can conclude that the emergence of one intensely competitive age-class does not necessarily guarantee the periodicity of a population, but could be a major factor which reinforces the population's tendency toward periodical behaviour.

Finally, we consider the case of $k > 3$. As mentioned earlier, the general properties are similar to the case of three age-classes. However, when the periodical equilibrium is not a stable equilibrium, the asymptotic behaviour of the system is quite different.

Observe Figure (4) where $B = 5$, $S_i = 0.8$ for $i = 1, 2, 3$, $\alpha_i = \gamma_i = 0.01$ for $i = 0, 1$ and $\alpha_2 = \gamma_2 = 0.05$, $\alpha_3 = \gamma_3 = 0.1$. Using an initial value of $N_i(0) = 1$ for $i = 1, 2, 3, 4$, simulation was done for 100 generations and the number of individuals of age 0 in each age-class during each generation was plotted.

Note that there is a dominant age-class at each generation, but a different age-class dominates at different times. The dominant age-class is alternated among the four age-classes and the period of domination lengthens as time increases. From the 7th generation to the 50th generation, age-class 2 is the dominant age class with its maximum occurring at the 17th generation with value of 26.35757. But from the 51st generation to the 100th generation, age-class 1 is dominant with value of 52.84553

at the 100th generation, when the simulation ceases, while the other three age-classes are zero to 6 decimal places. By all biological interpretations, it would imply extinction for all but the dominant age-class. In other words, the system converges, nonetheless, to the unstable periodical equilibrium.

Thus what might seem unstable mathematically could be really stable. This was pointed out by May and Leonard [8] and by Gilpin [5] in their simultaneous but independent study on Lotka-Volterra models for three or more competing species and discussed with a numerical example of a periodical insect model by Bulmer [2].

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週期性生物棲群模型

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摘 要

本研究報告以非線性差分方程之生物棲群模型來探討植物及昆蟲界中常見之週期性現象。本人利用穩定性分析來尋求生物棲群趨向週期性之條件，並以數值模擬驗證之。當生物棲群之週期大於 3 時，本人將以數值實驗舉例提出可能發生之特殊現象。