Asymptotic analysis of a semelparous species model

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Abstract. We study a non-linear age-structured discrete-time population model and give necessary and sufficient conditions for stability of a positive stationary point. In the case of semelparous species we show that the population converges locally to a population consisted only of individuals at one age. It means that the long-time behaviour of the population depends only on an one-dimensional transformation $g$. If the reproduction age is an even number we prove that the positive stationary point is unstable and numerical simulations suggest that in this case almost all trajectories behave asymptotically as trajectories corresponding to $g$.

Keywords: age-structured discrete-time model, semelparous species, periodicity, chaos

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1. Introduction

Age-structured models describe the number of individuals in a single species population with given age and at given time. We consider a discrete-time model, which means that both the age and time are positive integers. If \( n \) is the maximal age then the evolution in time of the population can be written as a transformation \( x(t+1) = f(x(t)) \), where the coordinate \( x_a(t) \) of the vector \( x(t) \in \mathbb{R}_+^n \) is the number of individuals with age \( a \) at time \( t \). This general description called a non-linear Leslie model was introduced by Leslie [15, 16] and Lewis [17] and this pattern has been extensively used in a variety of population studies [3]. In age-structured models the decisive role is played by the death and birth processes. The death \( \mu \) and birth \( b \) rates at time \( t \) depend on age \( a \) of an individual and the density of the population, i.e. the vector \( x(t) \) (see e.g. [7]). Usually, we simply assume that \( \mu \) and \( b \) are functions of \( a \) and \( I = c_1x_1 + \cdots + c_nx_n \), where \( c_i \) denotes the impact of an individual at age \( i \) on the environment. \( I \) is sometimes called environmental variable (see [9]). In our paper we use a special case where \( I = N = x_1 + \cdots + x_n \) is the total population size. This restriction does not change the properties of the model but allows us to omit some technical difficulties.

We pay special attention to semelparous species. Semelparous species are those whose individuals reproduce only once in their lives and die afterwards. We restrict our considerations to semelparous species whose life span have a fixed length of \( n \) years. Semelparous models have been intensively studied recently [6, 7, 8, 9, 10, 11, 12, 14]. Some of these papers are devoted to study of special cases \( n = 2, 3 \) called, respectively, biennials [9, 10] and triennials [8, 9], which are usually called LPA models [6] (the name stands for larval, pupal, and adult). In [14] the authors consider biennials model but with Allee effect, which is not regarded in our paper. Other models concern arbitrary \( n \). In the papers [7, 11] the authors studied mainly the bifurcations that occur at the trivial and positive equilibrium. In [13] a criterion for permanence (survival) is given and in [12] the authors studied populations with periodical fluctuations of birth and death rates.

It is interesting that a population distribution might not converge to a stationary point but tend to a periodic limit with all but one year classes missing. Possibility of such a behaviour was suggested by Bernardelli [1] and this phenomenon was called by him the population waves. A formal proof of this property for a special linear model was given in [5]. Bulmer [2] observed that interactions between different age classes of insects, for instance by competition for food, may lead to the extinction of all but one year classes and he called the insects that exhibit such a property periodical insects. Some strict mathematical results in this direction for biennials and triennials are given in [6, 8, 10, 9]. In [7] it was shown that the bifurcations that occur at the trivial equilibrium can lead to one year classes cycles. These cycles together with connecting them heteroclinic orbits form loops which are attractors at some assumptions. It should be noted that if a population is not semelparous then one can observe periodic orbits with periods independent on \( n \), for example with period four [20].

We consider a model with death rates independent of \( N \) and a strictly decreasing birth function of \( N \). Our aim is to show that the distribution of the population converges locally to one year class cycle which is described by an one-dimensional transformation \( g \). We prove that if the transformation \( g \) has a stable periodic orbit, then this orbit is locally asymptotically stable in the whole system. Moreover, if the transformation \( g \) is shadowing then the orbits of the whole system are chaotic if \( g \) is chaotic.

The organization of the paper is the following. In Section 2 we introduce a general discrete age-structured model, we check when the total population is bounded, and give sufficient and necessary conditions for the existence of a positive equilibrium \( x^* \). In Section 3 we give conditions which guarantee
the asymptotic stability of $x^*$. Section 4 is devoted to a semelparous species model. The main result is the convergence of the distribution of the population to periodical behaviour, i.e. the model behaves, asymptotically as $t \to \infty$, like a one-dimensional model corresponding to a population consisted only of individuals at one age. In particular, we show that if the reduced model has a stable periodic point then the initial model has the same local behaviour. If, additionally, the reduced model is shadowing then also chaoticity of the reduced model implies chaoticity of the initial one. Some numerical results are presented in Section 5.

2. Nonlinear discrete age-structured model

We consider a nonlinear version of a discrete-time-age model. We assume that the birth and death rates depend on two factors: the age $a$ of an individual and the total number of individuals $N$ at the given time. Let $x(t,a)$ be a number of individuals at age $a$ and at time $t$, where both time and age are positive integers and $a \leq a_{\text{max}}$, where $a_{\text{max}} \leq \infty$ is the maximal age. Let $N(t) = \sum_{a=1}^{a_{\text{max}}} x(t,a)$ be a total number of individuals at time $t$. We also assume that $N(t) \leq N_{\text{max}}$, where $N_{\text{max}} \leq \infty$ is the maximal size of the population. Usually, it is assumed that $N_{\text{max}} < \infty$ and the number $N_{\text{max}}$ is called the carrying capacity of a species in an environment. We denote by $b = b(a,N(t)) \geq 0$ and by $\mu = \mu(a,N(t))$, $0 \leq \mu \leq 1$ the birth and death rates for an individual with age $a$ at time $t$. In the whole paper we assume that all rates are continuous functions. The function $q = q(a,N(t)) = 1 - \mu(a,N(t))$ is called the survivorship rate.

The relation between two consecutive generations is described by the following system of equations

$$
N(t) = \sum_{a=1}^{a_{\text{max}}} x(t,a),
$$

$$
x(t + 1, a + 1) = q(a, N(t)) x(t,a),
$$

$$
x(t + 1, 1) = \sum_{a=1}^{a_{\text{max}}} b(a, N(t)) x(t,a),
$$

which is often called a non-linear Leslie model. If $a_{\text{max}} < \infty$ we should assume that $\mu(a_{\text{max}}, N) = 1$. If we omit this assumption, then the age of some individuals may be greater than $a_{\text{max}}$, but we do not take them into consideration. Such models are reasonable if, for example, $a_{\text{max}}$ is the maximal reproductive age.

If we assume $N_{\text{max}} < \infty$, then we expect that from $N(t) \leq N_{\text{max}}$ it follows that $N(t + 1) \leq N_{\text{max}}$. This implication is fulfilled if we provide some additional assumptions concerning the rates $b$ and $q$. Note that, if the population at time $t$ consists only of $x$ individuals at age $a$, then at time $t + 1$ it consists of $b(a,x)x$ individuals at age $1$ and $q(a,x)x$ individuals at age $a + 1$. Since the total population may not exceed $N_{\text{max}}$, so

$$
b(a,x)x + q(a,x)x \leq N_{\text{max}} \quad \text{for } a \in [0, a_{\text{max}}], x \in [0, N_{\text{max}}].
$$

This condition is also sufficient for $N(t)$ to be bounded by $N_{\text{max}}$. Indeed, let $x := N(t) \leq N_{\text{max}}$. Since

$$
N(t + 1) = \sum_{a=1}^{a_{\text{max}}} b(a,x)x(t,a) + q(a,x)x(t,a),
$$
from formulas (2) and (3) we obtain

\[ N(t + 1) = \sum_{a=1}^{a_{\text{max}}} (b(a, x) + q(a, x))x \frac{x(t, a)}{x} \leq \sum_{a=1}^{a_{\text{max}}} N_{\text{max}} \frac{x(t, a)}{x} = N_{\text{max}}. \]

3. Behaviour near stationary points

Let us now check when the system (1) has a steady state. The steady state \( x^* = (x_1^*, \ldots, x_{a_{\text{max}}}^*) \) satisfies the system of equations

\[
N = \sum_{a=1}^{a_{\text{max}}} x_a^*,
\]

\[
x_{a+1}^* = (1 - \mu(a, N))x_a^*, \quad \text{for } a \geq 1,
\]

\[
x_1^* = \sum_{a=1}^{a_{\text{max}}} b(a, N)x_a^*.
\]

Let us define

\[
r(1, N) = 1,
\]

\[
r(a, N) = (1 - \mu(1, N)) \cdot \ldots \cdot (1 - \mu(a - 1, N)) \quad \text{for } a > 1.
\]

Then \( r(a, N) \) is the probability that an individual survives to the age of \( a \) provided that the total population is constant and equals \( N \). Using the second and third equations of the system (4) we get

\[
\sum_{a=1}^{a_{\text{max}}} b(a, N)r(a, N) = 1.
\]

One can interpret the expression \( \phi(N) = \sum_{a=1}^{a_{\text{max}}} b(a, N)r(a, N) \) as an average reproduction coefficient of the population. For a distribution near the steady state the population grows if \( \phi(N) > 1 \), and decreases if \( \phi(N) < 1 \). If we consider a population living in a bounded-resource environment and if we neglect the Allee effect, we may assume that \( b(a, N) \) is strictly decreasing in \( N \). Likewise, we may assume that \( \mu(a, N) \) is a non-decreasing function of \( N \), and thereby \( r(a, N) \) is a non-increasing function of \( N \). Therefore, function \( \phi(N) \) is strictly decreasing. So, the condition

\[
\phi(0) > 1, \quad \lim_{N \to N_{\text{max}}} \phi(N) < 1
\]

is sufficient for the existence of \( N \) satisfying (5) and, moreover, such an \( N \) is unique. Let us assume that \( \phi \) satisfies condition (6) and let \( N_0 \) be a number such that \( \phi(N_0) = 1 \). Since the steady state \( x^* \) satisfies a condition \( x_a^* = r(a, N_0)x_1^* \), we have

\[
\sum_{a=1}^{a_{\text{max}}} r(a, N_0)x_1^* = N_0.
\]
Therefore

\[ x_a^* = \frac{r(a, N_0) N_0}{\sum_{i=1}^{\alpha_{\text{max}}} r(i, N_0)}. \] (8)

We summarize the above considerations with the following proposition.

**Proposition 3.1.** Assume that \( b(a, N) \) is a strictly decreasing and \( \mu(a, N) \) is a non-decreasing function of \( N \). Let \( \varphi(N) = \sum_{a=1}^{\alpha_{\text{max}}} b(a, N) r(a, N) \) satisfy condition (6). Then system (1) has a unique positive steady state \( x^* \) given by formula (8).

Now we consider only the case when \( \alpha_{\text{max}} < \infty \) and \( \mu(a, N) = 1 - q(a) \). In order to simplify notation we set \( n = \alpha_{\text{max}} \). The system (1) is a special case of the general nonlinear Leslie model

\[ x^{k+1} = f(x^k), \]

where \( x = (x_1, \ldots, x_n) \) and the function \( f \) defined on some subset \( G \) of \( \mathbb{R}^n \) is given by the formula

\[ f_1(x) = \sum_{a=1}^{n} b(a, N)x_a, \]

\[ f_{a+1}(x) = q(a)x_a, \quad \text{for} \quad 1 \leq a \leq n - 1, \] (9)

where \( N = \sum_{i=1}^{n} x_i \). Let \( x^* \) be a fixed point of the map \( f \). The point \( x^* \) is called **asymptotically stable** if for each \( \varepsilon > 0 \) there is \( \delta > 0 \) such that

(i) if \( x \in B(x^*, \delta) \), for all positive integers \( n \) we have \( f^n(x) \in B(x^*, \varepsilon) \),

(ii) if \( x \in B(x^*, \delta) \), then \( \lim_{n \to \infty} f^n(x) = x^* \).

By \( B(x^*, \delta) \) we denote the ball with centre in \( x^* \) and radius \( \delta \). We use the following well known criterion for asymptotic stability.

**Theorem 3.1.** If all eigenvalues of the matrix \( A = f'(x^*) \) have the absolute values less than 1, then the fixed point \( x^* \) of the map \( f \) is asymptotically stable. If at least one eigenvalue has the absolute value greater than 1, the point \( x^* \) is unstable (the condition (i) does not hold).

In our case

\[ \frac{\partial f_1}{\partial x_a} = b(a, N) + \sum_{i=1}^{n} \frac{\partial b(i, N)}{\partial N} x_i, \]

\[ \frac{\partial f_{a+1}}{\partial x_a} = q(a), \quad \text{for} \quad 1 \leq a \leq n - 1, \]

\[ \frac{\partial f_{a+1}}{\partial x_j} = 0, \quad \text{for} \quad 1 \leq a \leq n - 1 \quad \text{and} \quad j \neq a. \] (10)
Thus the eigenvalues of the matrix $A$ can be found by solving the following equation

$$\begin{vmatrix} \frac{\partial f_1}{\partial x_1} - \lambda & \frac{\partial f_1}{\partial x_2} & \frac{\partial f_1}{\partial x_3} & \cdots & \frac{\partial f_1}{\partial x_n} \\ q(1) & -\lambda & 0 & \cdots & 0 \\ 0 & q(2) & -\lambda & \ddots & 0 \\ \vdots & \ddots & \ddots & \ddots & 0 \\ 0 & 0 & \cdots & q(n-1) & -\lambda \end{vmatrix} = 0.$$ 

We can expand this determinant along the first column and obtain

$$\begin{align*}
(n-1)\partial f_1 & (\partial f_1 \partial x_1 - \lambda) (-\lambda)^{n-1} - q(1)\partial f_1 \partial x_2 (-\lambda)^{n-2} + q(1)q(2)\partial f_1 \partial x_3 (-\lambda)^{n-3} \\
&- q(1)q(2)q(3)\partial f_1 \partial x_4 (-\lambda)^{n-4} + \cdots = 0.
\end{align*}$$

We set $r(1) = 1$ and $r(i) = q(1) \cdots q(i-1)$ for $i \geq 2$. Then the last equation can be written in a simpler form

$$\lambda^n - \sum_{i=1}^{n} r(i) \partial f_1 \partial x_i \lambda^{n-i} = 0.$$ 

(11)

**Corollary 3.1.** If $x^*$ is a stationary point of $f$ and

$$\sum_{i=1}^{n} r(i) \left|\frac{\partial f_1}{\partial x_i}(x^*)\right| < 1,$$

then the point $x^*$ is asymptotically stable.

**Proof:**

From (12) it follows that for $|\lambda| \geq 1$ we have

$$\sum_{i=1}^{n} r(i) \left|\frac{\partial f_1}{\partial x_i}(x^*)\lambda^{n-i}\right| \leq |\lambda|^{n-1} \sum_{i=1}^{n} r(i) \left|\frac{\partial f_1}{\partial x_i}(x^*)\right| < |\lambda|^n.$$ 

It means that for such a $\lambda$ equation (11) does not hold. 

The values of derivatives $\frac{\partial f_1}{\partial x_i}$ in the stationary point $x^*$ can be found by using equations (5) and (8).

Let $N_0$ be the solution of

$$\sum_{a=1}^{n} b(a, N_0) r(a) = 1.$$

Since

$$x_i^* = \frac{r(i)N_0}{r(1) + \cdots + r(n)},$$
from (10) it follows that
\[
\frac{\partial f_1}{\partial x_a} = b(a, N_0) + \sum_{i=1}^{n} \frac{\partial b(i, N_0)}{\partial N} \frac{r(i)N_0}{r(1) + \cdots + r(n)}.
\] (13)

**Example 3.1.** Let \( b(a, N) = (1 - N/N_{\text{max}})p \) for all \( a \). Then
\[
\frac{\partial f_1}{\partial x_a}(x^*) = \frac{2}{\sum_{i=1}^{n} r(i)} - p
\]
and condition (12) is fulfilled if and only if \(|2 - \sum_{i=1}^{n} pr(i)| < 1\). The non-zero stationary point \( x^* \) exists if \( \sum_{i=1}^{n} pr(i) > 1 \). Thus the stationary point is asymptotically stable if
\[
1 < \sum_{i=1}^{n} pr(i) < 3.
\]
This result agrees with the well known result for the logistic transformation
\[
x^{t+1} = \sigma x^t(1 - x^t),
\]
because this transformation has an asymptotically stable positive stationary point if and only if \( \sigma \in (1, 3] \).

In our model the term \( \sum_{i=1}^{n} pr(i)(1 - N/N_{\text{max}}) \) is the average reproduction coefficient and in the logistic model \( \sigma(1 - x) \) plays the same role.

4. **Semelparous species model**

Now we restrict our investigation to the *semelparous species*, i.e. we assume that only individuals at age \( n \) reproduce and die. We also assume that the death rate depends only on age \( a \), so we have a model with functions
\[
\mu(a, N) = 1 - q(a), \quad b(a, N) = \begin{cases} 
0, & \text{for } a < n, \\
\tilde{b}(N), & \text{for } a = n,
\end{cases}
\]
where \( n \) is the maximal age, \( \tilde{b} \) is a continuously differentiable function defined on some interval \([0, M)\), where \( 0 < M \leq \infty \). We assume that
\[
0 < q(a) < 1 \text{ for } a < n \text{ and } q(n) = 0,
\]
\[
\tilde{b}(x) > 0 \text{ and } \tilde{b}'(x) < 0 \text{ for } x \in [0, M),
\]
\[
r(n)\tilde{b}(0) > 1 \text{ and } \lim_{N \rightarrow M} r(n)\tilde{b}(N) < 1.
\]

Typical examples of the function \( \tilde{b} \) are \( \tilde{b}(x) = \sigma(1 - x/M) \) in the logistic model, \( \tilde{b}(x) = \sigma e^{-cx} \) in the Ricker model, and \( \tilde{b}(x) = \frac{\sigma}{1+cx} \) in the Beverton-Holt model. We assume here that \( \sigma r(n) > 1 \).
From the assumptions concerning \( \tilde{b} \) and \( r(n) \) it follows that there exists a unique \( N_0 \in (0, M) \) such that \( r(n) \tilde{b}(N_0) = 1 \) and the point

\[
x^* = [x^*_1, x^*_2, \ldots, x^*_n] \text{ with } x^*_i = \frac{r(i)N_0}{r(1) + \cdots + r(n)}
\]

is the only positive stationary point of the transformation \( f \). Let \( h(x) = r(n)\tilde{b}(x) \). Then \( h(N_0) = N_0 \) and \( h(x) < x \) for \( x > N_0 \). Let \( M_0 = \tilde{b}(0)N_0 \). If \( M < \infty \) we extend the function \( \tilde{b}(x) \) on the interval \([M, \infty)\) setting

\[
r(n)\tilde{b}(x) = \lim_{N\to M} r(n)\tilde{b}(N)M \quad \text{for } x \in [M, \infty).
\]

First we prove the existence of a global attractor \( A \) for the transformation \( f \), i.e. a compact set \( A \) which is invariant \( f(A) = A \) and for each point \( x \in \mathbb{R}^n_+ \) the distance between \( f^k(x) \) and \( A \) converges to zero as \( k \to \infty \).

**Proposition 4.1.** The transformation \( f \) has a global attractor.

**Proof:**

It is enough to show that there exists a compact absorbing set \( S \) for the transformation \( f \), i.e. \( f(S) \subset S \) and for each point \( x \in \mathbb{R}^n_+ \) there exists an integer \( k = k(x) \) such that \( f^k(x) \in S \). In order to do it we need two functionals

\[
\alpha(x) = x_1 + \cdots + x_n, \quad \beta(x) = \frac{x_1}{r(1)} + \cdots + \frac{x_n}{r(n)}.
\]

The set \( S \) is defined by

\[
S = \left\{ x \in \mathbb{R}^n_+ : \beta(x) \leq \frac{M_0}{r(n)} \right\}.
\]

First we prove that \( f(S) \subset S \). According to the definition of the function \( f \) we need to check that from the inequality

\[
\frac{x_1}{r(1)} + \cdots + \frac{x_n}{r(n)} \leq \frac{M_0}{r(n)}
\]

it follows that

\[
\tilde{b}(\alpha(x))x_n + \frac{x_1}{r(1)} + \cdots + \frac{x_{n-1}}{r(n-1)} \leq \frac{M_0}{r(n)}.
\]

We consider two cases. If \( \alpha(x) > N_0 \) then \( \tilde{b}(\alpha(x)) \leq \tilde{b}(N_0) = 1/r(n) \) and the second inequality is obvious. Now consider the case \( \alpha(x) \leq N_0 \). Since \( \tilde{b}(\alpha(x)) \leq \tilde{b}(0) \) and \( 1/r(a) < 1/r(n) < \tilde{b}(0) \) for \( a \leq n - 1 \) we have

\[
\tilde{b}(\alpha(x))x_n + \frac{x_1}{r(1)} + \cdots + \frac{x_{n-1}}{r(n-1)} \leq \tilde{b}(0)\alpha(x).
\]

But since \( \alpha(x) \leq N_0 \) we have \( \tilde{b}(0)\alpha(x) \leq M_0/r(n) \), which proves our claim.

Now, we check that for each \( x \in \mathbb{R}^n_+ \) we have \( f^k(x) \in S \) for sufficiently large \( k \). We have

\[
f^n(x) = \left[ \tilde{b}(\alpha(f^{n-1}(x)))x_1r(n), \tilde{b}(\alpha(f^{n-2}(x)))x_2r(n), \ldots, \tilde{b}(\alpha(x))x_nr(n) \right].
\]
If \( f^k(x) \notin S \) for all \( k \geq 0 \) then \( \tilde{b}(\alpha(f^k(x))) \leq \tilde{b}(N_0\tilde{b}(0)) \) and

\[
\beta(f^n(x)) \leq \tilde{b}(N_0\tilde{b}(0)) \sum_{a=1}^{n} \frac{x_a r(a)}{r(a)} = \gamma \beta(x),
\]

where the constant \( \gamma = \tilde{b}(N_0\tilde{b}(0))r(n) \) is less than 1, because \( \tilde{b}(N_0\tilde{b}(0)) < \tilde{b}(N_0) = 1/r(n) \). This implies that \( \lim_{n \to \infty} \beta(f^n(x)) = 0 \), which contradicts the assumption that \( f^k(x) \notin S \). Thus \( f^k(x) \in S \) for sufficiently large \( k \).

Properties of the positive stationary point depend surprisingly on evenness of \( n \).

**Proposition 4.2.** If \( n \) is an even number then the point \( x^* \) is unstable.

**Proof:**

According to equation (13)

\[
\frac{\partial f_k}{\partial x_a} = \begin{cases} 
\tilde{b}'(N_0)x_n^*, & \text{for } a \leq n - 1, \\
\tilde{b}(N_0) + \tilde{b}'(N_0)x_n^*, & \text{for } a = n.
\end{cases}
\]

Since \( r(n)\tilde{b}(N_0) = 1 \) equation (11) can be written in the form

\[
\lambda^n + \alpha \sum_{i=1}^{n} r(i)\lambda^{n-i} - 1 = 0,
\]

(16)

where \( \alpha = -\tilde{b}'(N_0)x_n^* \) is a positive constant and the sequence \( (r(n)) \) satisfies inequalities \( r(1) > r(2) > \ldots > r(n) > 0 \). Let us denote by \( \psi(\lambda) \) the left hand side of the equation (16). Then \( \lim_{\lambda \to -\infty} \psi(\lambda) = \infty \) and \( \psi(-1) < 0 \), which implies that the characteristic equation has a real root less than \(-1 \) and according to Theorem 3.1 the stationary point \( x^* \) is unstable.

**Remark 4.1.** It is an interesting problem if the positive stationary point can be stable for odd numbers \( n \). It is well known that for \( n = 1 \) the logistic transformation \( x^{t+1} = \sigma x^t(1 - x^t) \) with \( \sigma \in (1, 3] \) has a stable positive stationary point. For \( n = 3 \) Dr. Dorota Kubalińska helped us to construct an example of a transformation with a positive stable stationary point. We omit details here.

Our transformation \( f \) has only two non-negative stationary points: the one with positive coordinates, which is unstable for even \( n \) and the second trivial one which is unstable if \( \tilde{b}(0)r(n) > 1 \). It means that asymptotic behaviour of the iterates of \( f \) can strongly depend on periodic points of this transformation. Our model can have a lot of periodic points also with positive entries, but as we will check the significant role is played by periodic points with only one year class present. Notice that if we start with a population consisted only of individuals at age one, then in the next generation we obtain only individuals at age two and so on. After a full life cycle, i.e. after \( n \) iterations, we return to the population of age one individuals only. We then have

\[
f^n([z, 0, \ldots, 0]) = \tilde{b}(r(n)z)r(n)z, 0, \ldots, 0].
\]

Apparently, if \( z_* \) is a fixed point of the function \( g(z) = \tilde{b}(r(n)z)r(n)z \), then the point \([z_*, 0, \ldots, 0] \) is \( n \)-periodic under the action of \( f \). Since \( \tilde{b} \) is decreasing, such a point always exists and is unique, and
in fact \(z_\ast = N_0/r(n)\). Furthermore, if \(z_0\) is a \(k\)-periodic point of \(g\), then \([z_0, 0, \ldots, 0]\) is a \(kn\)-periodic point of \(f\). The question arises if we can say something about the stability of such periodic points under the transformation \(f^{kn}\).

**Theorem 4.1.** Let \(z_0 = g^k(z_0)\). Then the point \(z_0 = [z_0, 0, \ldots, 0]\) is a \(kn\)-periodic point of \(f\) and there exist a neighbourhood \(V \subset \mathbb{R}^n_+\) of \(z_0\) and \(\alpha \in (0, 1)\) such that for each point of \(x \in V\) we have

\[
(f^{kn}(x))_i \leq \alpha^i|x_i|
\]

for \(i \geq 2\) and the integer \(t\) such that \(f^{knj}(x) \in V\) for \(j = 0, 1, \ldots, t\). In particular, if \(z_0\) is an asymptotically stable stationary point of the transformation \(g^k\) then \(z_0\) is an asymptotically stable stationary point of the transformation \(f^{kn}\).

**Proof:**

Let \(z_0 = g^k(z_0)\) and let us denote \(z_i = g^i(z_0)\) and \(z_i = [z_i, 0, \ldots, 0]\) for \(i \geq 0\) (\(k\) is an arbitrary positive integer and we do not distinguish here the case \(k = 1\)). Then \(f^k(z_0) = z_0\). For an arbitrary \(x \in \mathbb{R}^n_+\) we have

\[
f^{kn}(x) = [\gamma^k_1(x)x_1, \gamma^k_2(x)x_2, \ldots, \gamma^k_n(x)x_n],
\]

where

\[
\gamma^k_j(x) = \bar{b}(\alpha(f^{knj}(x))) \cdots \bar{b}(\alpha(f^{n-n-j}(x))) \gamma^k_j(0)
\]

and \(\bar{b}(r(n)) = r(n)\) for \(i \geq 0\). Note that \(f^{kn+n-j}(z_0) = [0, \ldots, 0, r(n-j+1)z_i, 0, \ldots, 0]\) with the only positive value at \((n-j+1)\)-th position, and thereby \(\bar{b}(\alpha(f^{kn+n-j}(z_0))) = \bar{b}(r(n-j+1)z_i)\). Since \(z_0 = g^k(z_0) = r(n)\prod_{i=0}^{k-1} \bar{b}(r(n)z_i)\), we have \(r(n)\prod_{i=0}^{k-1} \bar{b}(r(n)z_i)\). Therefore, for \(j = 2, \ldots, n\) we have \(\gamma^k_j(0) < 1\), because \(r(n-j+1) > r(n)\) and \(\bar{b}\) is strictly decreasing. Thanks to the continuity of \(\gamma^k_j\), \(\gamma^k_j\) is less then one in some neighbourhood of \(z_0\). So if we start from \(x\) in this neighbourhood then after iterations of \(f^{kn}\) all but the first coordinates decrease. Since \(\gamma^k_1([z_0, 0, \ldots, 0]) = 0\), the behaviour of the first coefficient depends on the stability of \(z_0\) under the transformation \(g^k\). Thus, if \(z_0\) is a stable steady point of \(g^k\), then \(z_0\) is a stable steady point of \(f^{kn}\). \(\square\)

Now we prove a little stronger result which allows us to reduce the problem of asymptotic behaviour of the map \(f\) to a study of the only one-dimensional map \(g(x) = \bar{b}(r(n)x)r(n)x\).

**Theorem 4.2.** If \(\bar{b}\) is a positive function then for each \(\rho_0 \in (0, M_0)\) there exists an \(\varepsilon > 0\) such that for each point \(x = (x, \varepsilon_2, \ldots, \varepsilon_n)\) with \(\varepsilon_i \in [0, \varepsilon)\) for \(i = 2, \ldots, n\) and \(x \in [\rho_0, M_0]\) the sequence \(f^{mn}(x)\) converges to 0 as \(m \to \infty\) for \(i = 2, \ldots, n\).

**Proof:**

The point \(0 = [0, \ldots, 0]\) is an *ejective* (or *repulsive*) fixed point of the transformation \(f\), i.e. there is some neighbourhood \(U\) of 0 such that for each \(x \in U \setminus \{0\}\) there is a positive integer \(j\) such that \(f^j(x) \notin U\).

Indeed, all eigenvalues of the matrix \(f'(0)\) are the numbers \(\lambda = \sqrt[n]{r(n)\bar{b}(0)} > 1\), which implies the ejectivity of the fixed point 0. Since \(\bar{b}\) is a positive function \(0 \notin f(U)\). From this it follows that we find a \(\rho \in (0, \rho_0)\) such that \(B(0, \rho) \subset U\) and for each \(x \in S \setminus \{0\}\) there exists an integer \(j_0\) such that \(f^j(x) \notin B(0, \rho)\) for \(j \geq j_0\). It means that we can consider the transformation \(f\) only on the
set $S \setminus B(0, \rho)$. Let us observe that since the function $h(x) = \tilde{b}(x)r(n)x$ is the transformation of the interval $[0, M_0]$ into itself the function $g$ is the transformation of the interval $[0, M_1]$ into itself, where $M_1 = M_0/r(n)$ and $g(x) > 0$ for all $x \in (0, M_1]$. The function $g$ can be restricted to the interval $[\rho, M_1]$ Let $z = (z, 0, \ldots, 0)$, $z \in [\rho, M_0]$. Then from the formula (18) and the definition of $g$ it follows that

$$
\gamma_i^k(z) = \tilde{b}(r(n-i+1)g^{k-1}(z))\tilde{b}(r(n-i+1)g^{k-2}(z)) \ldots \tilde{b}(r(n-i+1)z)r(n)^k. \quad (19)
$$

Let

$$
L = \max_{i \leq n-1} \sup_{x \in [\rho, M_1]} \frac{\tilde{b}(r(i)x)}{\tilde{b}(r(n)x)}
$$

Then since $\tilde{b}$ is a strictly decreasing function we have $L < 1$. From the formula (19) it follows that

$$
\gamma_i^k(z) \leq L^k \gamma_i^1(z) = L^k \frac{g^k(z)}{z} \leq L^k \frac{M_0}{\rho} \leq 1/4
$$

for $k \geq k_0$, where $k_0$ is a sufficiently large positive integer. Now let us fix $\varepsilon > 0$ such that $\gamma_i^k(x) \leq 1/2$ for $x = (z, \varepsilon_2, \ldots, \varepsilon_n)$ and $\varepsilon_i < \varepsilon$ and $k = k_0, k_0 + 1, \ldots, 2k_0 - 1$. It is easy to check by using induction argument that $\gamma_i^m(x) \leq 2^{-m/k_0}$ and, consequently, $[F^{mn}(x)]_i$ converges to 0 as $m \to \infty$ for $i = 2, \ldots, n$.

We now check that, under some additional assumptions concerning the function $g$, the asymptotic behaviour of the transformation $F^n$ near the axis $(x, 0, \ldots, 0)$ is the same as the transformation $g$. In order to do it we need some auxiliary definitions. A sequence $(y_k)$ is called a $\eta$-pseudo-orbit of a transformation $g$ if $|g(y_k) - y_{k+1}| < \eta$ for all $k \geq 1$. The transformation $g$ is called shadowing, if for every $\delta > 0$ there exists $\eta > 0$ such that for each $\eta$-pseudo-orbit $(y_k)$ of $g$ there is a point $x$ such that $|y_k - g^k(x)| < \delta$.

**Theorem 4.3.** If $\tilde{b}$ is a positive function and $g$ is shadowing then for each $\delta > 0$ and for each $\rho_0 \in (0, M_0)$ there exists $\varepsilon$ such that for each point $x = (x, \varepsilon_2, \ldots, \varepsilon_n)$ with $\varepsilon_i \in [0, \varepsilon)$ for $i = 2, \ldots, n$ and $x \in [\rho_0, M_0]$ there exists $y \in (0, M_0)$ such that

$$
|[F^{kn}(x)]_1 - g^k(y)| < \delta \quad \text{for all } k \geq 1. \quad (20)
$$

**Proof:**

Let us fix a $\delta > 0$ and let $\eta > 0$ be a constant from the shadowing property of $g$. Take $\rho \in (0, \rho_0)$ such as in the proof of Theorem 4.2. Then from the uniform continuity of the function $F^n$ there is an $\varepsilon > 0$ such that for each $w \in [\rho, M_0] \times [0, \varepsilon)^{n-1}$ we have $|[F^n(w)]_1 - [F^n([w_1, 0, \ldots, 0])]_1| < \eta$. From Theorem 4.2 it follows that there is $\varepsilon \in (0, \varepsilon)$ such that $F^{nk}([\rho, M_0] \times [0, \varepsilon)^{n-1}) \subset [\rho, M_0] \times [0, \varepsilon)^{n-1}$. Let $x \in [\rho, M_0] \times [0, \varepsilon)^{n-1}$ and we define $y_k = [F^{nk}(x)]_1$. Then

$$
|y_{k+1} - g(y_k)| = |[F^n(F^{nk}(x))]_1 - g([F^{nk}(x)]_1)| = |[F^n(w)]_1 - [F^n([w_1, 0, \ldots, 0])]_1| < \eta,
$$

where $w = F^{nk}(x)$ and $w \in [\rho, M_0] \times [0, \varepsilon)^{n-1}$. Therefore, the sequence $(y_n)$ is an $\eta$-pseudo-orbit of $g$ and since $g$ is shadowing we have (20). \qed
Remark 4.2. The proof of Theorems 4.2 and 4.3 in case \( \hat{b}(M) = 0 \) needs some attention at the beginning because for some \( x \neq 0 \) we have \( f'(x) = 0 \) and \( \hat{b} \) is not strictly decreasing function in the whole interval \( (0, M_0) \). But if we assume, for example, that \( M \) is the maximal size of the population, then \( \hat{b}(x)x \leq M \) for all \( x \leq M \). This assumption is sufficient to prove our result. In fact, it is enough to assume a weaker inequality that \( r(n)\hat{b}(x)x < M \) for all \( x \leq M \). Let

\[
N_{\max} = \max\{\hat{b}(x)x : x \leq M\}.
\]

We have \( N_{\max} < M/r(n) \) and if \( \alpha(x) \leq N_{\max} \) then \( \alpha(f(x)) \leq N_{\max} \). Let \( z = (z, 0, \ldots, 0) \), then \( f^n(z) = (g(z), 0, \ldots, 0) \). Since \( \hat{b}(0)r(n) > 1 \) for sufficiently small \( \rho > 0 \) we have \( g([\rho, N_{\max}]) \subset [\rho, N_{\max}] \), and the rest of the proof goes as in the case \( \hat{b}(M) > 0 \) if we replace the interval \([\rho, M_0]\) by \([\rho, N_{\max}]+(n)\).

It is obvious that if \( g \) has an asymptotically stable periodic orbit then \( g \) is shadowing on the basin of attraction of this orbit. It means that Theorem 4.1 follows from Theorem 4.3. But also chaotic maps may be shadowing e.g. \( g(x) = 4x(1-x) \). The shadowing property was intensively studied for the last twenty five years and there are a lot results concerning the shadowing property for one dimensional maps (cf. a survey paper by Ombach and Mazur [18]). In particular, in the paper [4] the authors study tent maps \( g_s : [0, 2] \to [0, 2] \) defined by \( g_s(x) = sx \) for \( 0 < x < 1 \) and \( g_s(x) = s(2-x) \) for \( 1 < x < 2 \). They prove shadowing of \( g_s \) for almost all parameters (see Theorem 6.1 [4]). In this case the function \( \hat{b} \) is constant for \( x \in [0, r(n)] \) and equals \( s/r(n) \) and \( \hat{b} \) is strictly decreasing in the interval \([r(n), 2r(n)]\). Although such a function \( \hat{b} \) does not satisfy directly the assumptions of the Theorems 4.2 and 4.3 one can check that these theorems remain true also in this case and we have (20). A logistic map \( f(x) = \sigma x(1-x) \) is topologically conjugated with a tent map for a large set of parameters near \( \sigma = 4 \), and thus the behaviour of these two maps is identical under iteration. In particular, if one map is shadowing then a topologically conjugated map is also shadowing. In particular the logistic map is shadowing for a large set of parameters \( \sigma \). On the other hand the logistic map is chaotic for \( \sigma \) close to \( \sigma_0 = 4 \). It means that if \( \hat{b}(x) = \sigma x(1-x) \), then the function \( g \) is both chaotic and shadowing for a large set \( \sigma \) such that \( \sigma r(n) \) is close to 4 and the trajectories of the transformation \( f \) behaves chaotically.

5. Numerical simulations and conclusions

In this section we present some numerical simulations which can help us to predict the global behaviour of semelparous species models. The numerical simulations where obtained with use of the R environment [19].

First interesting problem is the behaviour of the system near a positive stationary point \( x^* \). As we have checked before, in the case when \( n \) is an even number this stationary point is unstable. If \( n \geq 3 \) is an odd number then \( x^* \) can be a stable point but it happens rarely. Usually \( x^* \) is a hyperbolic point and, generally, the dimensions of the stable and unstable manifolds \( M_s, M_u \) highly depend on \( n \) and constants \( r(1), \ldots, r(n) \) and \( \alpha = -\hat{b}'(N_0)x_n \). Only the case \( n = 2 \) is simple. Then \( x^* \) is a saddle point and the behaviour of trajectories is shown on the Fig. 1.

Even in the biennials model we can observe different behaviour of trajectories of \( x_k = f^k(x) \). If \( g(x) = \hat{b}(r(n)x)r(n)x \) has a stable fixed point, then trajectories \( (x_k) \) converge to a periodic orbit with period two; if \( g \) has a stable periodic point with period \( p \), then trajectories \( (x_k) \) converge to a periodic
Figure 1. Trajectories of $f$, that pass near the positive stationary point $x^*$ in the biennials model with logistic (a), Ricker (b) and Beverton-Holt (c) birth rate. The dotted and solid lines are, respectively, the stable and unstable manifolds. The trajectories $x_k = f^k(x)$ starting from a point near the stable manifold $M_s$ first approach $x^*$ along $M_s$ and then go to a periodic orbit along the unstable manifold $M_u$, jumping from one side of this manifold to the second side.

Figure 2. Trajectories of the biennials model with logistic birth rate in case of (a) 2-periodic point ($q = 2/3$, $\sigma = 3$), (b) of 4-periodic point ($q = 0.99$, $\sigma = 3.3$), and (c) chaotic behaviour ($q = 0.99$, $\sigma = 3.9$). A number of initial iterations are marked by circles and the next iterations by crosses, therefore, the asymptotic behaviour is illustrated by the x-shaped points.
orbit with period \( pn \); and in the case when \( g \) is a chaotic logistic map then trajectories \( (x_k) \) are also chaotic (see Fig. 2). Fig. 3 presents different behaviour of the triennials model with logistic birth rate.

Of course, these simulations presumably do not present all possible trajectories, but we were not able to observe different behaviour than the convergence of \( (x_k) \) to one year classes cycle. So, we can state the following conjecture.

If \( n \) is an even number then for each \( \varepsilon > 0 \) and for almost every initial values of \( x^* \) there exists \( y = (y, 0, \ldots, 0) \) and an integer \( k_0 \) such that \( \|f^k(x^*) - f^k(y)\| < \varepsilon \) for \( k \geq k_0 \).

The biological interpretation of this condition is obvious. The competition of different age classes leads to the extinction of all but one year classes and long time behaviour of the age distribution imitates a periodical population.

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References


