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Global stability and bifurcations in a delayed discrete population model*

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Dedicated to Professor István Győri on the occasion of his 65th birthday

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Abstract. We consider a family of difference equations used in population dynamics. First we recall the most relevant results concerning the global stability of the positive equilibrium. Then, using the survival rate as a parameter, we investigate the changes in the dynamics when it ranges between zero (semelparous populations) and one.

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1. Introduction

The aim of this paper is the study of different aspects of the dynamics of the difference equation

$$x_{n+1} = \alpha x_n + (1-\alpha)h(x_{n-k}), \tag{1.1}$$

where $\alpha \in [0,1)$, $k \geq 1$ is an integer, and $h : [0,\infty) \to [0,\infty)$ is a continuous function.

The motivations for our interest in Eq. (1.1) are mainly two:

First, this equation was proposed by K. R. Allen in 1963 to model whale populations. Since it was popularized by Clark in 1976 [5], it is often referred to as *Clark's delayed recruitment model* (see also [4, 17, 34] and references therein). In this context, x_n represents the number of adult (sexually mature) members of the population in the year n, $\alpha \in [0,1)$ is the annual survival rate, and $f = (1-\alpha)h$ is the recruitment function, which is in general a nonlinear function of the size of population of adults a

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number of k years before. We refer to [13] for more details. We notice that the limit case $\alpha = 0$ in (1.1) reads

$$x_{n+1} = h(x_{n-k}), \tag{1.2}$$

which is usually used to model semelparous populations, characterized by the fact that individuals reproduce only once and die afterwards (see, e.g., [6, 8, 10]). Two famous examples are Pacific salmon [10] and magical cicadas (see Chapter 6 in [6] and references cited therein). These special cicadas emerge to the ground during a short period among two weeks and two months for mating and lying eggs every 13 or 17 years, and then they die. Recently, equation (1.2) has also attracted some attention from the point of view of its periodic structure (see [2, 9, 23, 31]).

The second motivation to study Eq. (1.1) is that it can be considered as the discretized version of the following well known delay differential equation used in mathematical biology:

$$x'(t) = -x(t) + h(x(t-\tau)), \quad \tau > 0. \tag{1.3}$$

In fact, an application of Euler's explicit method with discretization step $\delta = \tau/k$ leads to equation (1.1) with $\alpha = 1 - \delta$ (see, e.g., [26]). Many of the results in the literature concerning Eq. (1.1), in particular with regard to the stability of the equilibria, were motivated by this fact (see, e.g., [15, 18, 21, 24, 26, 27, 40]).

2. The choice of the recruitment function

In relation to Clark's model, several stock-recruitment functions have been suggested in the literature. Perhaps the most popular are the following:

- The Ricker function [4, 36]: $h(x) = pxe^{-\gamma x}, \quad p > 1, \gamma > 0.$
- The Shepherd function [34, 38]: $h(x) = \dfrac{ax}{1+x^n}, \quad a > 1, n > 0.$
- The Beddington-May function [3, 17]:

  $$h(x) = x\left[1 + q\left(1 - \left(\frac{x}{K}\right)^z\right)\right]_+,$$

  where $q, K, z > 0$, $[x]_+ = \max\{x, 0\}$.

All these nonlinearities share the common property to have a unique positive equilibrium and a unique local maximum (such maps are usually called unimodal). We emphasize that Eq. (1.1) with the Ricker nonlinearity is also the discretized version of the famous Nicholson's blowflies delay differential equation proposed in [19]. The same remark applies to Shepherd's function and the celebrated Mackey-Glass equation [33].

Some decreasing nonlinearities were also suggested as recruitment functions; we mention $h(x) = pe^{-\gamma x}, p > 0, \gamma > 0$, and $h(x) = a/(1 + x^n), a > 0, n > 0$, which correspond to discrete versions of models in hematopoiesis, see, e.g., [27, Section 4.6]).

In order to include the models cited above, we will consider throughout the paper that the recruitment function meets the following assumption:

Assumption 2.1. $h : [0, \infty) \to [0, \infty)$ *is continuous and has a unique fixed point* $\bar{x}$. *Furthermore,* $0 < x < h(x)$ *for* $0 < x < \bar{x}$, *and* $h(x) < x$ *for* $x > \bar{x}$.

We notice that some of the results included here can be proved under more general assumptions (see, e.g., [12, 13, 16]).

We recall that in most usual models, function h is either decreasing or unimodal, and some relevant papers in the literature of Eq. (1.1) only consider these cases.

Due to biological reasons, only nonnegative initial conditions will be considered; more precisely, the set of admissible initial conditions is defined by

$$S = \{(x_{-k}, \ldots, x_{-1}, x_0) \in \mathbb{R}^{k+1} \,:\, x_i \geq 0,\, i = -k, \ldots, 0,\, x_0 > 0\}.$$

Solutions of (1.1) corresponding to admissible initial conditions will be called *admissible solutions*. A simple induction argument shows that, if $\alpha > 0$, then for any admissible initial condition, the corresponding solution $\{x_n\}$ of (1.1) is well defined and satisfies $x_n > 0$ for all $n \geq 0$. Moreover, admissible solutions are permanent; more precisely, there exist positive constants A, B such that, for any admissible solution $\{x_n\}$ of (1.1) there exists an integer $N > 0$ such that

$$0 < A \leq x_n \leq B\,, \quad \forall\, n \geq N.$$

For a proof, see [12, Proposition 4.6]. Related results can be found in [16, 21, 24, 27], among others.

3. Stability of the positive equilibrium

Let $\bar{x}$ be the positive equilibrium of (1.1). Linearization of (1.1) at $\bar{x}$ gives equation

$$x_{n+1} = \alpha x_n + (1 - \alpha) h'(\bar{x}) x_{n-k}.$$

It is well known that $\bar{x}$ is asymptotically stable if all solutions of the associated characteristic equation

$$\lambda^{k+1} - \alpha \lambda^k - (1 - \alpha) h'(\bar{x}) = 0 \tag{3.1}$$

lie in the unit open disk of the complex plane. Necessary and sufficient conditions for this to happen can be found in [29, 35], see also [13]. Clark himself proved that $|h'(\bar{x})| < 1$ is a sufficient condition for the local asymptotic stability of $\bar{x}$. In fact, this condition can be improved to $|h'(\bar{x})| \leq 1$ if $\alpha > 0$, and it is the best asymptotic stability condition independent of the size of the delay k (this is usually called *absolute stability*).

Numerical experiments suggest that in some of the considered models the local asymptotic stability of the equilibrium implies its global stability. See related conjectures in [15, 16, 21, 40]. Although this is still an open problem, sufficient conditions for the global asymptotic stability were found by many authors (see [11, 12, 15, 16, 18, 21, 24, 26, 27, 28, 40] and other references cited therein).

We recall some of the most relevant results in this direction. As usual, we say that $\bar{x}$ is a *global attractor* for (1.1) if all admissible solutions converge to $\bar{x}$ as $n \to \infty$. On the other hand, $\bar{x}$ is called *globally stable* if it is a stable global attractor.

Starting with the absolute stability, it is a remarkable fact that $\bar{x}$ is globally stable for all values of k whenever it is a global attractor for the discrete dynamical system generated by the iteration

$$x_{n+1} = h(x_n). \tag{3.2}$$

Results in this direction were proved by Fisher [17], Karakostas *et al.* [26] and Ivanov [24]. A result more appropriate to include nonlinearities as the Beddington-May function is the following:

Theorem 3.1. [16, Theorem 1] *Define* $M = \max\{h(x) \ : \ 0 \le x \le \bar{x}\}$*. If* $h(x) \neq 0$ *for all* $x \in (0, M]$ *and* $\bar{x}$ *is a global attractor for (3.2) in* $(0, M]$*, then* $\bar{x}$ *is globally stable for Eq. (1.1).*

Notice that condition $h(x) \neq 0$ for all $x \in (0, M]$ always holds if $h(x) > 0$ for all $x > 0$, as in the Ricker and Shepherd functions, but it is necessary to require it when considering the Beddington-May function.

In order to apply Theorem 3.1, we need global stability results for the recurrence (3.2), in other words, sufficient conditions to ensure that all orbits $\{h^n(x)\}$, $x > 0$, converge to the positive equilibrium.

One of most known tools is the Schwarzian derivative. We recall that the Schwarzian derivative of a C^3 function h is defined as

$$(Sh)(x) = \frac{h'''(x)}{h'(x)} - \frac{3}{2}\left(\frac{h''(x)}{h'(x)}\right)^2$$

whenever $h'(x) \neq 0$.

Using Singer's results [39], it is not difficult to prove that if h is a decreasing or unimodal map with a unique fixed point $\bar{x}$ and negative Schwarzian in every point (except the critical one in the unimodal case), then $\bar{x}$ is globally stable if and only if $|h'(\bar{x})| \le 1$. This fact was used to get sharp results on the absolute stability of the positive equilibrium of (1.1) by Ivanov [24]. We notice that function h in the models of Ricker and Shepherd, and also the discrete versions of delay equations with decreasing nonlinearity cited in Section 2, have negative Schwarzian derivative everywhere.

As an example, for the discrete model

$$x_{n+1} = \alpha x_n + (1-\alpha) p e^{-\gamma x_{n-k}}, \quad p > 0, \gamma > 0, \tag{3.3}$$

the equilibrium $\bar{x}$ is the unique solution of equation $h(x) = pe^{-\gamma x} = x$. Since h is decreasing and $(Sh)(x) = -\gamma^2/2 < 0$ for all $x \in \mathbb{R}$, condition $|h'(\bar{x})| \le 1$ implies the global stability of the equilibrium. This condition is equivalent to $p\gamma \le e$, and it was already found in [26] using a different approach.

Clark's model with the Beddington-May recruitment function

$$x_{n+1} = \alpha x_n + (1-\alpha)x_{n-k}\left[1 + q\left(1 - \left(\frac{x_{n-k}}{K}\right)^z\right)\right]_+, \tag{3.4}$$

requires a more subtle analysis since function $h(x) = \left[1 + q\left(1 - \left(\frac{x}{K}\right)^z\right)\right]_+$ does not have negative Schwarzian everywhere. In [16] it was proved that condition $|h'(\bar{x})| \leq 1$ also implies the global stability of the equilibrium $\bar{x} = K$ in (3.4). This condition reads $qz \leq 2$.

At this point, one should be happy with the obtained results for the global absolute stability of the equilibrium in the considered models because they are sharp. However, for a fixed k, the equilibrium of (1.1) is locally asymptotically stable even if $|h'(\bar{x})| > 1$ when α is close to one, that is, when the survival rate is large enough (see [13] for more discussions). Thus, we should expect to get results of global stability in the same direction.

Some interesting results were proved by several authors as discrete analogues of stability theorems for the delay differential equation (1.3). After the pioneering work of Karakostas *et al.* [26], some remarkable conditions were obtained by Győri and Trofimchuk in [21]. A very useful result is their Corollary 18, which, roughly speaking, establishes that to ensure the global stability of the positive equilibrium in (1.1) with $\alpha \in (0,1)$, the condition that $\bar{x}$ be a global attractor for the map h may be replaced for the weaker condition that $\bar{x}$ is globally stable for the map $g : [0,\infty) \to (0,\infty)$ defined by $g(x) = \alpha^{k+1}\bar{x} + (1-\alpha^{k+1})h(x)$.

In particular, the global stability condition $p\gamma \leq e$ for Eq. (3.3) is improved to $p\gamma \leq \nu e^{\nu}$, where $\nu = (1-\alpha^{k+1})^{-1} > 1$ for all $\alpha \in (0,1)$.

The same function g is used by El-Morshedy and Jiménez to improve the global stability condition $qz \leq 2$ for Eq. (3.4) up to $qz \leq 1 + \nu$, where ν is defined as before (cf. [12, Corollary 4.7]).

We emphasize that these results show that, as it was noticed for the local stability, for fixed k in equations (3.3) and (3.4), the positive equilibrium is globally attracting whenever α is close enough to one.

Now, if h has negative Schwarzian derivative and is decreasing or unimodal, then the same conditions hold for g and hence a sufficient condition for the global stability of the positive equilibrium is $|g'(\bar{x})| \leq 1$. This can be written in the form

$$\alpha^{k+1} \geq \frac{c-1}{c}, \text{ where } c = |h'(\bar{x})|.$$

Actually, Győri and Trofimchuk obtained sharper conditions in [21]. In particular, their Corollary 17 can be written in the following form:

Theorem 3.2. [21, Corollary 17] *Define $c = |h'(\bar{x})|$. If h has negative Schwarzian derivative, is decreasing or unimodal, and $h(x) > 0$ for all $x > 0$, then $\bar{x}$ is globally stable for Eq. (1.1) if either $c \leq 1$ or $c > 1$ and*

$$\alpha^{k+1} \geq \frac{c^2 - c}{1 + c^2}. \tag{3.5}$$

Remark 3.1. *In the unimodal case, we assume that $h'(\bar{x}) < 0$. Otherwise, Corollary 10 in [21] ensures that $\bar{x}$ is globally stable for (1.1). An analogous result was proved in [16, Theorem 3] in a more general setting.*

We emphasize that the result of Theorem 3.2 is exactly the discrete version of a global stability theorem established by the same authors in [20] for the delay differential equation (1.3). In fact, they proved that, in the conditions of Theorem 3.2, the positive equilibrium of (1.3) is globally stable if

$$e^{-\tau} \geq \frac{c^2 - c}{1 + c^2}. \tag{3.6}$$

This is not surprising, since (1.1) may be obtained as a discretization of (1.3) with $\alpha = 1 - \tau/k$. Since the discretization step goes to zero when k tends to ∞, and

$$\lim_{k\to\infty} \alpha^{k+1} = \lim_{k\to\infty} \left(1 - \frac{\tau}{k}\right)^{k+1} = e^{-\tau},$$

it turns out that condition (3.5) is the natural discrete version of (3.6).

The estimate given in [20] for the global stability in equation (1.3) was later improved in [32], where (3.6) was refined to

$$e^{-\tau} \geq c \ln\left(\frac{c^2 + c}{1 + c^2}\right). \tag{3.7}$$

This condition is sharper than (3.6) since $\ln(1 + y) < y$ for all $y > 0$. (Take $y = (c - 1)/(1 + c^2)$.)

Tkachenko and Trofimchuk proved that the corresponding condition also ensures that $\bar{x}$ is a global attractor for (1.1):

Theorem 3.3. [40, Theorem 1] *In the conditions of Theorem 3.2, the positive equilibrium $\bar{x}$ of (1.1) is globally stable if either $c \leq 1$ or $c > 1$ and*

$$\alpha^{k+1} \geq c \ln\left(\frac{c^2 + c}{1 + c^2}\right). \tag{3.8}$$

In fact, Theorem 7 in [40] applies to a model more general than (1.1), since it is allowed the recruitment function to depend on the variables $x_n, x_{n-1}, \ldots, x_{n-k}$.

For the particular case of Eq. (3.3), El-Morshedy proved in [11] that, under additional assumptions, a condition sharper than (3.8) is sufficient for the global stability of the equilibrium. This condition reads

$$\alpha^{k+1} \geq \frac{c - 1}{c + 1}. \tag{3.9}$$

Remark 3.2. *We emphasize that condition (3.9) without additional assumptions does not imply even the local asymptotic stability of the equilibrium for large k.*

The approach in [11] was generalized in [15] to the general case of decreasing h with negative Schwarzian. A remarkable improvement was made by Tkachenko and Trofimchuk; they found a sequence of numbers α_k, $k = 1, 2, \ldots$, such that condition (3.9) implies the global stability of the equilibrium in (1.1) if $\alpha \in (0, \alpha_k]$ (see Theorem 2, Theorem 3 and Corollary 4 in [40]). For example, when $k = 1$, they proved the following result:

Theorem 3.4. [40, Corollary 5] *Assume that $k = 1$. In the conditions of Theorem 3.2, the positive equilibrium $\bar{x}$ of (1.1) is globally stable if one of the following conditions holds:*

(a) Either $c \leq 1$ or $c > 1$, (3.9) holds and $\alpha \leq 0.88$.

(b) $\alpha \geq \max\{0.88, (c - 0.88)/c\}$.

For $k = 1$ in (1.1), the equilibrium is locally asymptotically stable if $\alpha > (c-1)/c$. It can be checked that in this case Theorem 3.4 gives sharper conditions for the global stability than Theorem 3.3.

Example 3.1. Consider the following particular case of equation (3.3):

$$x_{n+1} = \alpha x_n + (1 - \alpha)2e^{2-x_{n-1}}. \tag{3.10}$$

The unique equilibrium is $\bar{x} = 2$. Since $h(x) = 2e^{2-x}$ and $c = |h'(2)| = 2 > 1$, Theorem 3.1 does not apply. We know that $\bar{x} = 2$ is asymptotically stable for $\alpha > (c - 1)/c = 0.5$.

Using the previously stated results, we have that Theorem 3.2 provides the global stability of the equilibrium for $\alpha > (2/5)^{1/2} \approx 0.6324$. Theorem 3.3 improves this condition to $\alpha > (2\ln(6/5))^{1/2} \approx 0.6038$. Finally, Theorem 3.4 ensures that $\bar{x}$ is globally stable for $\alpha > (1/3)^{1/2} \approx 0.577$. Numerical simulations suggest that in fact the equilibrium attracts all admissible solutions of (3.10) if $\alpha > 0.5$, that is, whenever it is asymptotically stable.

4. Bifurcations and periodic points

In order to study the dynamics of equation (1.1), we notice that there is a natural correspondence between the solutions of a difference equation

$$x_{n+1} = F(x_n, x_{n-1}, \ldots, x_{n-k})$$

and the orbits of the discrete dynamical system associated to the map $\bar{F} : \mathbb{R}^{k+1} \to \mathbb{R}^{k+1}$ defined by

$$\bar{F}(x_0, x_1, \ldots, x_k) = (x_1, x_2, \ldots, x_k, F(x_0, x_1, \ldots, x_k)).$$

Namely, if $\{x_n\}$ is the solution of the difference equation with initial vector $\mathbf{u} = (x_{-k}, \ldots, x_{-1}, x_0)$, then $\bar{F}^n(\mathbf{u}) = (x_{n-k}, \ldots, x_{n-1}, x_n)$ for every n. Hence the study of the dynamics of (1.1) can be reduced to the study of the discrete dynamical system generated by the map

$$H_\alpha(x_0, x_1, \ldots, x_k) = (x_1, x_2, \ldots, x_k, \alpha x_k + (1-\alpha)h(x_0)). \tag{4.1}$$

When we talk about bifurcations and periodic points for (1.1), we are considering this equivalent dynamical system. We refer to [22, 37, 41] for definitions.

Contrary to the global stability issue, the dynamics of (1.1) when the equilibrium is unstable has not received much attention in the literature. There are two possible approaches to this problem. One of them was suggested by An der Heiden and Liang [23], who claim that the pair of equations (1.1) and (1.2) form a discrete singular perturbation problem (as $\alpha \to 0$) parallel to the well-known continuous perturbation problem between the pair (1.3) and (3.2). We recall that the limit form of (1.3) as $\tau \to \infty$ is the difference equation with continuous argument $x(t) = h(x(t-1))$ (see [25] for more details). In this way, it would be interesting to study the correspondence between the asymptotic properties of the $(k+1)$-dimensional dynamical system generated by the recurrence (1.2) and the asymptotic behaviour of the solutions of (1.1) for α close to zero.

The periodic structure for Eq. (1.2) based on that of (3.2) is studied in [23]; see also [2, 9, 31]. However, the same problem for $\alpha \neq 0$ was not addressed. As far as we know, the first perturbation theorem was proved in [13] for the case when h is a C^1 function having a hyperbolic repelling fixed point $\bar{x}$, a hyperbolic attracting 2-cycle $\{a, b\}$ and no other periodic points. Under some mild additional conditions, if $\alpha \geq 0$ is small enough, then Eq. (1.1) has exactly as many cycles (with the same periods and local dynamics) as Eq. (1.2) and these cycles attract all solutions of (1.1). (See [13, Theorem 8]).

Since we are assuming that $h'(\bar{x}) < 0$, the local stability of the equilibrium in (3.2) is usually lost in a period-doubling bifurcation, and therefore the previous result applies for values of $|h'(\bar{x})|$ close to 1. In fact, when h is decreasing and has negative Schwarzian derivative, this situation holds for all $|h'(\bar{x})| > 1$, according to the following dichotomy result:

Theorem 4.1. *Assume that $h : [0, \infty) \to [0, \infty)$ is three times differentiable, and $(Sh)(x) < 0, h'(x) < 0$ for all $x \geq 0$. Let $\bar{x}$ be the unique fixed point of h. Then one of the following occurs:*

- *(a) If $|h'(\bar{x})| \leq 1$, then $\lim_{n\to\infty} h^n(x) = \bar{x}\,,\ \forall\, x \geq 0$.*
- *(b) If $|h'(\bar{x})| > 1$, then the equilibrium is unstable and there is a globally attracting 2-cycle. More precisely, there exist $a, b \in [0, \infty)$, $a < b$, such that $h(a) = b$, $h(b) = a$, and $\lim_{n\to\infty} h^{2n}(x) = a$ if $x < \bar{x}$, $\lim_{n\to\infty} h^{2n}(x) = b$ if $x > \bar{x}$.*

The proof of Theorem 4.1 follows easily from Singer's results [39].

From Theorem 1.2 in [23], it follows that if (3.2) has cycles with minimal periods 1 and 2, then the set of minimal periods of (1.2) is

$$S_k(2) = \{1\} \cup \{2r \,:\, r \in \mathbb{N},\ r|(k+1) \text{ and } ((k+1)/r, 2) \text{ is coprime}\}\,.$$

Recall that the pair of natural numbers (m, n) is called *coprime* if 1 is the only common divisor of m and n. For example,

$$k = 1 \Longrightarrow S_1(2) = \{1, 4\} \quad ; \quad k = 2 \Longrightarrow S_2(2) = \{1, 2, 6\}\,.$$

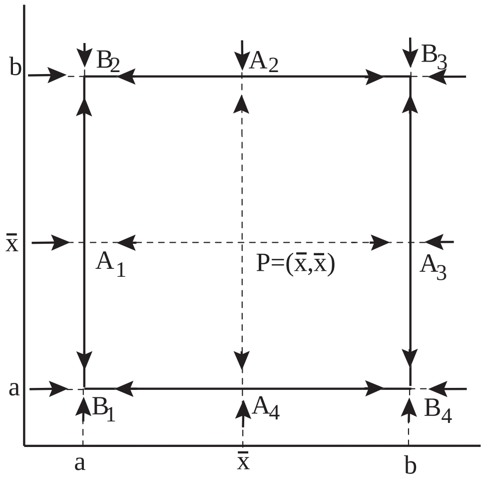

Figure 1: Saddle-Node configuration for $\alpha = 0$.

For $k = 1$ in (1.2), we can state the following analogous of Theorem 4.1:

Theorem 4.2. *Assume that $k = 1$ and the conditions of Theorem 4.1 hold. Then, one of the following occurs:*

(a) If $|h'(\bar{x})| \le 1$, then $\bar{x}$ is the global attractor of all positive solutions of (1.2).

(b) If $|h'(\bar{x})| > 1$, then Eq. (1.2) has exactly two solutions of minimal period four (up to shifts): one node and one saddle. Moreover, they attract all solutions with initial condition $(x_{-1}, x_0) \neq (\bar{x}, \bar{x})$.

It is easy to see that the node is defined by the sequence $\{a, a, b, b, \dots\}$, where $\{a, b\}$ is the unique cycle of the map h with minimal period two, and the saddle is defined by $\{a, \bar{x}, b, \bar{x}, \dots\}$. Thus, if we consider the associated map $H = H_0 : \mathbb{R}^2_+ \to \mathbb{R}^2_+$ defined by $H(x, y) = (y, h(x))$, then the fixed point $P = (\bar{x}, \bar{x})$ is a repeller, the attracting cycle of period four is $P_1 = \{B_1, B_2, B_3, B_4\}$, where $B_1 = (a, a)$, $B_2 = (a, b)$, $B_3 = (b, b)$, $B_4 = (b, a)$, and the saddle is $P_2 = \{A_1, A_2, A_3, A_4\}$, where $A_1 = (a, \bar{x})$, $A_2 = (\bar{x}, b)$, $A_3 = (b, \bar{x})$, $A_4 = (\bar{x}, a)$. This cycle attracts the set

$$W = \{(x, y) \in \mathbb{R}^2_+ \,:\, (x - \bar{x})(y - \bar{x}) = 0\} \setminus \{P\}.$$

The set W is formed by the union of the stable manifolds of the points A_i $(i = 1, 2, 3, 4)$ under the 4^{th} iterate of H. The remainder points are attracted by P_1. Figure 1 shows the dynamics of the fourth iteration of H. Notice that the square with vertices B_1, B_2, B_3, B_4 is invariant and attracts $\mathbb{R}^2_+ \setminus \{P\}$. This type of attractor is usually called "resonance circle" (see, e.g., [1] and [22, Chapter 15]).

According to Theorem 8 in [13], the conclusions of Theorem 4.2 remain valid for Eq. (1.1) with $k = 1$ for all small enough values of $\alpha \geq 0$. It would be interesting to investigate whether or not the resonance circle also persists for small enough α.

We notice that a similar situation holds for Eq. (1.1) when $k \geq 2$. The main difference is that multistability is possible, that is, there are coexisting attracting periodic solutions of different periods. For example, for $k = 2$ and small α, almost all points are attracted by a cycle of period 2 and other of period 6 (see [13, 14] for a detailed example).

Assuming that h has an attracting 2-cycle $\{a, b\}$, it is worth mentioning that in the semelparous case ($\alpha = 0$), there is always an attracting cycle of period $2(k+1)$ corresponding to the initial vector $(a, a, \ldots, a) \in \mathbb{R}^{k+1}$. As mentioned by Mertz and Myers [34], Ricker was the first one to notice long-period endogenous population fluctuations in his simulations of an age-structured fish stock. He estimated that the natural period of these oscillations (called *Ricker oscillations* in [34]) is twice the median time from oviposition to oviposition. The same authors claim that there is some empirical evidence of oscillations of period two. In [13], it was proved that Equation (1.1) has a cycle of minimal period 2 if and only if k is even and the one-dimensional map

$$h_\alpha(x) := \alpha x + (1 - \alpha)h(x) \tag{4.2}$$

has a cycle of minimal period 2 (see [13, Proposition 6]). Thus, if h meets the conditions of Theorem 4.1 and k is even then Eq. (1.1) has always two coexisting attracting periodic solutions of minimal periods 2 and $2(k + 1)$ for small enough α.

Another approach to study the dynamics of (1.1) consists in considering it as a one parameter family of maps of $\mathbb{R}^{k+1}_+$, in the line of Aronson *et al.* [1]. Thus, we should investigate the bifurcations occurring in this family when the parameter α ranges between 1 and 0.

Since the positive equilibrium is asymptotically stable when $-1 \leq h'(\bar{x}) < 0$, we assume $c = -h'(\bar{x}) > 1$. Looking at the characteristic equation (3.1), we know that $\bar{x}$ is locally asymptotically stable for α close to one. For the asymptotical stability to be lost, (3.1) must have a root crossing the unit circle of the complex plane in the increasing direction of its modulus. It is easy to check that the characteristic polynomial $p(\lambda) = \lambda^{k+1} - \alpha\lambda^k - (1 - \alpha)h'(\bar{x})$ cannot have a root $\lambda = 1$ for $\alpha \in [0, 1)$, and $\lambda = -1$ is only possible for even k and $\alpha = \alpha_0 = (c-1)/(c+1)$. This coincides with the border of the asymptotic stability region in the plane (c, α) for $k = 0$. If $k > 0$, the asymptotic stability of the equilibrium is lost for a critical value $\alpha = \alpha_k > \alpha_0$. (We notice that, for $k = 0$, a supercritical period-doubling bifurcation for Eq. (1.1) occurs at $\alpha = \alpha_0$ if $(Sh_\alpha)(\bar{x}) < 0$, see [13, Theorem 5].) Thus, for $k \geq 1$, the typical situation in which the roots of $p(\lambda)$ cross the unit circle is by a couple of conjugate complex zeros, giving place to the born of an attracting invariant circle via a Naimark-Sacker bifurcation (also called Hopf bifurcation for maps, see, e.g, [41]). This fact was also observed in [4], where some discussions were made considering a Ricker recruitment function.

Numerical experiments for $k = 1, 2$, and a recruitment function as in Example 3.1 show that the invariant curve is smooth for values of α close to the bifurcation point α_k and it losses its differentiability in some intervals giving place to attracting periodic points of different minimal periods. This typically occurs through saddle-node bifurcations for different iterations H_α^q of the map H_α defined in (4.1). The latest one occurs for α close to zero and $q = 2(k+1)$, giving place to the attracting cycle which persists until $\alpha = 0$. A very interesting discussion of this type of bifurcations can be seen in [1] for the difference equation

$$x_{n+1} = \alpha x_n(1 - x_{n-1})$$

proposed by Maynard Smith as a discrete model in population dynamics.

We finish considering again the two-dimensional model defined by Equation (3.10) in Example 3.1. For a discussion of the corresponding three-dimensional model, see [13].

Example 4.1. Let us state again Equation (3.10):

$$x_{n+1} = \alpha x_n + (1-\alpha)2e^{2-x_{n-1}}. \tag{4.3}$$

The characteristic equation associated to the linearization at $\bar{x}$ is

$$\lambda^2 - \alpha\lambda + 2(1-\alpha) = 0.$$

The roots $\lambda_\pm = (\alpha \pm (\alpha^2 - 8(1-\alpha))^{1/2})/2$ satisfy $|\lambda_\pm|^2 = 2 - 2\alpha$, and it is easy to check that at $\alpha_1 = 0.5$ they cross transversally the unit circle. An application of the Naimark-Sacker bifurcation theorem for two-dimensional maps (see, e.g., [22, Theorem 15.31]) ensures the existence of an attracting closed C^1 invariant circle for α in a neighbourhood $(0.5 - \delta, 0.5)$, $\delta > 0$, of the bifurcation point $\alpha_1 = 0.5$.

Numerical simulations show that, during small ranges of values of the parameter α, an attracting cycle is observed instead of the invariant circle; for example, a period 9 cycle between $\alpha = 0.223$ and $\alpha = 0.235$ or a period 13 cycle between $\alpha = 0.137$ and $\alpha = 0.144$. These cycles appear in successive saddle-node bifurcations for the corresponding iterate of the planar map $H_\alpha(x, y) = (y, \alpha y + (1-\alpha)2e^{2-x})$. For example, it can be shown that for $\alpha = \alpha_* \approx 0.0772$, there is a fixed point $P_0 = (1.26, 0.09)$ of map $H_{\alpha_*}^4$ such that the Jacobian matrix $D(H_{\alpha_*}^4)_{P_0}$ of the linearization at P_0 has two eigenvalues $\lambda_1 = 1$, $\lambda_2 \in (0, 1)$. Direct computations show that the Saddle-Node Bifurcation Theorem for 2-dimensional maps can be applied to H_α^4 (see, e.g., [37, Theorem VII.2.2]). This means that it is possible to parametrize $\alpha = m(s)$, $(x, y) = q(s)$ such that $m(0) = \alpha_*$, $q(0) = P_0$, $H_{m(s)}^4(q(s)) = q(s)$. Numerical continuation methods show that the fixed point exists for $\alpha \in [0, \alpha_*]$. Moreover, $\lambda_2 < 1$ for $\alpha \in [0, \alpha_*]$, and hence there exist two fixed points of H_α^4: a stable node and a saddle. Thus, the dynamics described in Theorem 4.2 (b) holds for α between 0 and α_*.

In Figure 2 we plotted the bifurcation diagram for $\mu := 1 - \alpha$ ranging between $\mu = 0$ and $\mu = 1$. We can observe several periodic windows; in particular, the latest

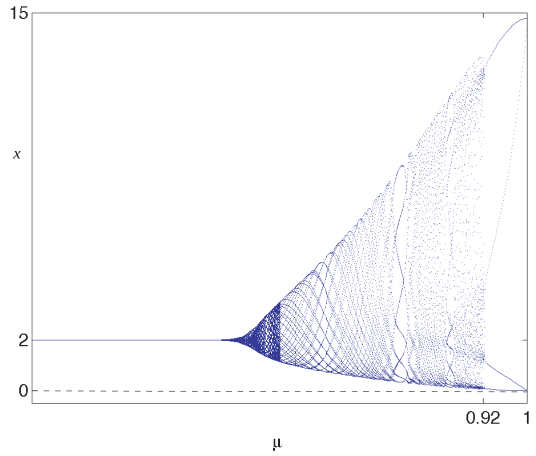

Figure 2: Bifurcation diagram for $\mu = 1 - \alpha$.

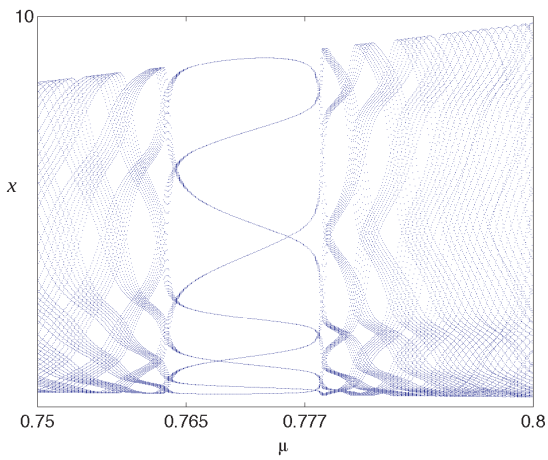

Figure 3: A magnification of the bifurcation diagram for $0.75 \leq \mu \leq 0.8$.

one corresponds to the attracting orbit of period four. The right-hand side part of this diagram reveals an important fact: although for $\mu = 1$ (semelparous case) there is a 4-periodic solution, it behaves as an orbit of period 2, since the population oscillates only between two values (the lowest one close to 0 and the highest one close to 15). For α small enough but positive, there is a real period four orbit; the approximate values for $\alpha = \alpha_*$ are $0.09, 1.26, 3.87$ and 12.76.

In Figure 3 we plotted a magnification of the bifurcation diagram for $\mu \in [0.75, 08]$ (that is, $\alpha \in [0.2, 0.25]$). This picture shows clearly the window corresponding to a period 9 attracting cycle for the values of α between 0.223 and 0.235 mentioned before.

Remark 4.1. *Since we performed simple numerical experiments, we notice that the observed invariant curve or periodic orbit might hide a more complicated attractor for some values of the parameter. See [1] for further discussions on this topic.*

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