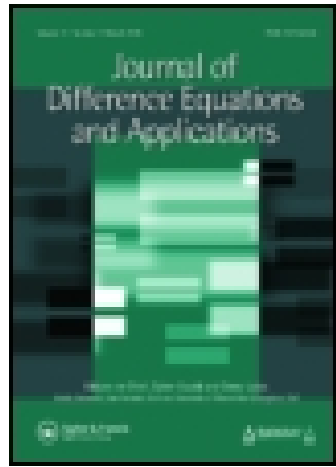


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# Global Asymptotic Behavior for a Discrete Model of Population Dynamics

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In this paper we investigate the global asymptotic behavior of the scalar delay difference equation

$$x(t) = f \left( \sum_{i=1}^n R_i x(t-i) \right), \quad \text{for all } t = 0, 1, 2, \dots$$

We give conditions under which there are periodic solutions and conditions under which the non negative solutions converge either to the non trivial fixed point of this equation or to one of the above periodic solutions.

**Keywords:** Global attractivity; population dynamics; difference equations

**Classification Categories:** 39A10, 92D25

## 1. INTRODUCTION

An important class of population dynamics models, which has applications in fisheries problems, is the class of density-dependent models. Such models were introduced in fisheries problems to understand intra-specific competition problems. Here, we consider the discrete time model employed by Beverton and Holt [1], Ricker [22], and Shepherd [25]. This model is also a particular case of the Liu and Cohen [19] model, which is obtained by discretizing a continuous time model of age structured populations.

We denote by  $x_i(t)$  the number of females with age in the interval  $[i-1, i]$  [at time  $t$ ,  $i = 1, 2, \dots, n$ . We will say that  $x_i(t)$  represents the number of females in the age class  $i$  at time  $t$ . For  $i = 1, 2, \dots, n-1$ , let  $p_i \in [0, 1]$  be the transition pro-

bability from age class  $i$  to age  $i + 1$ . Define  $b_i$  as the average number of offspring produced by females of age class  $i$ , and let  $p_0(t)$  be the fraction surviving to recruitment from time  $t$  to time  $t + 1$ . We assume that  $p_0(t)$  is of the form

$$p_0(t) = h \left( \sum_{i=1}^n b_i x_i(t) \right)$$

The function  $h$  is assumed to be a strictly decreasing continuous function with range, the interval  $]0, 1]$ , and domain  $[0, \infty[$  and we assume that

$$h(0) = 1, \quad \text{and} \quad \lim_{x \rightarrow +\infty} h(x) = 0.$$

The dynamics may then be completely described by the system for  $t = 0, 1, \dots$

$$\begin{cases} x_1(t+1) = \sum_{i=1}^n b_i x_i(t) h \left( \sum_{i=1}^n b_i x_i(t) \right) \\ x_2(t+1) = p_1 x_1(t) \\ x_3(t+1) = p_2 x_2(t) \\ \vdots \\ x_n(t+1) = p_{n-1} x_{n-1}(t) \end{cases} \quad (1)$$

with initial condition

$$x_i(0) = x_i \geq 0 \quad \forall i = 1, \dots, n$$

The local asymptotic behavior of this model has been investigated by Guckenheimer et al. [9], Levin and Goodyear [18], and Silva and Hallam [26]. Fisher and Goh [7] study the global stability of a special matrix model in which only individuals in the oldest age group are reproductive.

We need to introduce some notations. Throughout this paper, we denote by  $\mathbb{N}$  the set of all the non negative integers, by  $\mathbb{R}$  (resp:  $\mathbb{R}_+$ ) the set of all the real numbers (resp: non negative real numbers), and by  $\mathbb{R}^n$  (resp:  $M_n(\mathbb{R})$ ) the set of all the  $n$ -dimensional real vectors (resp:  $n$  by  $n$  real matrices). Moreover if  $V \in \mathbb{R}^n$ , we will denote by  $V_i$  (for  $1 \leq i \leq n$ ) the  $i^{\text{th}}$  component of  $V$ . We denote by

$$\mathbb{R}_+^n = \{V \in \mathbb{R}^n : V_i \geq 0 \quad \forall i = 1, \dots, n\},$$

and by

$$M_n(\mathbb{R}_+) = \{A = \{a_{ij}\} : a_{ij} \geq 0 \quad \forall i, j = 1, \dots, n\} \subset M_n(\mathbb{R}).$$

The set  $M_n(\mathbb{R}_+)$  is usually called the set of non negative matrices. Throughout this paper, we will use the classical notions and properties of non negative matrices. For this, we refer to the books by Gantmacher [8], by Horn and Johnson [11], and Minc [21].

### 1.1. Problem Transformation

Consider the system of equations (1), and remark that

$$x_1(t) = \sum_{i=1}^n b_i l_i x_1(t-i) h \left( \sum_{i=1}^n b_i l_i x_1(t-i) \right) \quad \forall t = n, n+1, n+2, \dots$$

So denoting  $x(t) = x_1(t+n)$  for all  $t \geq -n$ , the system of equations (1) can be rewritten as the following scalar delay difference equation

$$x(t) = \sum_{i=1}^n b_i l_i x(t-i) h \left( \sum_{i=1}^n b_i l_i x(t-i) \right) \quad \forall t = 0, 1, 2, \dots, \quad (2)$$

with initial condition

$$x(-i) = x_{-i} \geq 0 \quad \forall i = 1, \dots, n,$$

where

$$\begin{cases} l_1 = 1 \\ l_i = \prod_{j=1}^{i-1} p_j \quad \forall i = 2, \dots, n. \end{cases}$$

Denote by

$$R = \sum_{i=1}^n b_i l_i > 0.$$

Then, in the case where  $R \leq 1$ , since  $h$  is strictly decreasing and  $h(0) = 1$ , by using the lemma 5 in the paper by Magal and Pelletier [20], one has that all the non negative solutions of equation (2) converge to zero as  $t$  goes to infinity. Now, let  $R > 1$  be fixed, and denote by

$$f(x) = Rxh(Rx) \quad \forall x \geq 0, \quad (3)$$

and

$$R_i = \frac{b_i l_i}{R} \quad \forall i = 1, \dots, n.$$

Then, with these notations, equation (2) can be rewritten as

$$x(t) = f \left( \sum_{i=1}^n R_i x(t-i) \right), \quad \forall t \in \mathbb{N}, \quad (4)$$

with initial condition

$$x(-i) = x_{-i} \in \mathbb{R}_+, \quad \forall i = 1, \dots, n.$$

For convenience in the sequel, we introduce a system of equations, which is equivalent to the delay difference equation (4). This system is the following one

$$X(t+1) = F(X(t)), \forall t \in \mathbb{N} \quad (5)$$

with initial condition

$$X(0) = X_0 \in \mathbb{R}_+^n,$$

where  $F: \mathbb{R}_+^n \rightarrow \mathbb{R}_+^n$  is defined by

$$F(X) = \begin{bmatrix} f\left(\sum_{i=1}^n R_i X_i\right) \\ X_1 \\ X_2 \\ \vdots \\ X_{n-1} \end{bmatrix}, \forall X = (X_1, X_2, \dots, X_n)^T \in \mathbb{R}_+^n. \quad (6)$$

This system is connected with the delay equation (4) in the following manner,  $X_1(t) = x(t-1)$ ,  $X_2(t) = x(t-2)$ , ...,  $X_n(t) = x(t-n)$ , for  $t \geq 0$ .

Here, we will say that a fixed point (resp: an equilibrium solution) is non trivial, if it is not equal to zero. Now, since we have fixed  $R > 1$ , one can prove, by using the intermediate value theorem, that the map  $f$  in equation (3) has a unique non trivial fixed point, that we denote by

$$\bar{x} > 0.$$

This fixed point corresponds to the unique non trivial equilibrium solution of equation (4), which is

$$\bar{x}(t) = \bar{x} \forall t \geq -n.$$

Equivalently, this fixed point corresponds also to the unique non trivial equilibrium solution of equation (5), and to the unique non trivial fixed point  $\bar{X} \in \mathbb{R}_+^n$  of the map  $F$  in equation (6), which are

$$\bar{X}(t) = \bar{X} = (\bar{x}, \bar{x}, \dots, \bar{x})^T \in \mathbb{R}_+^n \quad \forall t \geq 0.$$

## 1.2. Problem Statement and Main Results

The goal of this paper is to describe the global asymptotic behavior of the difference equation (5) with  $F$  defined by (6). The main idea here is to divide the study into two parts: 1) the study of the nonlinear part, which corresponds to the following one dimensional difference equation

$$x(t+1) = f(x(t)) \quad \forall t \geq 0, \quad (7)$$

with initial condition

$$x(0) = x_0 \in \mathbb{R}_+,$$

and, 2) the study of the linear part, which corresponds to the linear difference equation

$$X(t+1) = LX(t) \quad \forall t \in \mathbb{N}. \quad (8)$$

with initial condition

$$X(0) = X_0 \in \mathbb{R}_+^n,$$

where

$$L = \begin{pmatrix} R_1 & R_2 & \cdots & \cdots & R_n \\ 1 & 0 & \cdots & \cdots & 0 \\ 0 & 1 & \ddots & & \vdots \\ \vdots & \ddots & \ddots & 0 & 0 \\ 0 & \cdots & 0 & 1 & 0 \end{pmatrix}. \quad (9)$$

Without loss of generality, we may assume that

$$R_n > 0.$$

Otherwise, we can always replace  $n$  by the largest integer  $n'$  in  $\{1, \dots, n\}$  such that  $R_{n'} > 0$ , and the problem is unchanged. Moreover, under this assumption the matrix  $L$  is irreducible. We refer to the book by Caswell [2] for this result.

Prior to stating the main results of the paper, a few definitions are in order. Throughout the paper, the topology in  $\mathbb{R}^n$  (resp:  $\mathbb{R}_+^n$  is the topology associated to an arbitrary norm on  $\mathbb{R}^n$ , denoted by  $\|\cdot\|$  (resp: to the metric defined by  $d(X, Y) = \|X - Y\|$  for all  $X, Y \in \mathbb{R}_+^n$ ).

Let  $G: \mathbb{R}_+^n \rightarrow \mathbb{R}_+^n$  ( $m \in \mathbb{N} - \{0\}$ ) be a map. In the sequel, we will denote by  $G^p$  for  $p \geq 0$ , the functions defined by

$$G^0 = Id, \quad \text{and} \quad G^p = G^{p-1} \circ G \quad \text{for all } p \geq 1.$$

We will say that  $\{V_1, V_2, \dots, V_k\}$  is a **k-periodic solution** ( $k \geq 1$ ) of  $G$  if

$$G(V_i) = V_{i+1} \quad \forall i = 1, \dots, k-1, \quad \text{and} \quad G(V_k) = V_1,$$

with

$$V_i \neq V_j \quad \forall i, j = 1, \dots, k \quad \text{with} \quad i \neq j.$$

The following definitions can be found in Hale [10]. A subset  $A$  of  $\mathbb{R}_+^n$  is said to be **stable** if for every neighborhood  $V$  of  $A$  in  $\mathbb{R}_+^n$ , there exists a neighborhood  $V' \subset V$  of  $A$  in  $\mathbb{R}_+^n$  such that  $G^m(V') \subset V \quad \forall m \geq 0$ . Moreover,  $A$  is said to **attract** a

subset  $B$  of  $\mathbb{R}_+^n$  under  $G$  if, for any  $\varepsilon > 0$ , there exists an  $m_0 = m_0(\varepsilon, A, B)$  such that  $G^m(B)$  belongs to the  $\varepsilon$ -neighborhood of  $A$  for  $m \geq m_0$ , that is

$$\delta(G^m(B), A) = \sup_{Y \in G^m(B)} \inf_{X \in A} \|X - Y\| \leq \varepsilon, \text{ for all } m \geq m_0.$$

Here, we investigate the case where the non trivial fixed point  $\bar{x}$  of  $f$  attracts the points of  $]0, +\infty[$  under  $f$ .

The case where the dimension  $n = 2$  is investigated by Fisher and Goh [7]. In their paper, the authors consider the case where the map  $f$  has a convex Liapunov function (i.e. there exists a continuous and convex map  $v: \mathbb{R}^+ \rightarrow \mathbb{R}^+$  such that  $v(f(x)) \leq v(x)$  for all  $x \in \mathbb{R}^+$  and  $v(f(x)) = v(x) \Rightarrow \bar{x} = x$  or  $0$ ), and the matrix  $L$  is primitive, that is when  $n = 2$  and

$$R_1 > 0, \text{ and } R_2 > 0.$$

With these assumptions, they show that the non trivial fixed point  $\bar{X}$  of  $F$  attracts the points of  $\mathbb{R}_+^2 - \{0\}$  under  $F$ . Here, we prove that the result holds only by supposing that the non trivial fixed point  $\bar{x}$  attracts the points of  $]0, +\infty[$  under  $f$ . In particular, this allows us to disregard the problem of existence of a convex Liapunov function.

In its generality, the problem is much more involved. Here, we present an attempt to extend the above results to a case where no obvious Liapunov function can be determined. As mentioned in the beginning, our approach is in two steps: first, we study a non linear scalar equation. This is done in section 2. Then, we turn our attention to a linear system equations. Finally, in section 4 putting together the results for the non linear and linear "parts" we determine the global asymptotic behavior of the  $n$  dimensional problems.

In section 2 of this paper, we will investigate the case where  $\bar{x}$  attract the points of the interval  $]0, +\infty[$  under  $f$ . This problem was already investigated by several authors Cull [3], [4], [5], Huang [12], [13], [14], [15], and Rosenkranz [23]. We also refer to the book by Kocic and Ladas [16] for a nice survey on this question.

We will make the following assumption on  $f$ :

$$(H1) \begin{cases} i) f \text{ is continous and satisfies } f(0) = 0, \text{ and } f(x) > 0 \forall x > 0. \\ ii) f \text{ has a non trivial fixed point } \bar{x} > 0. \end{cases}$$

The following Theorem is partially proved by Huang [14], except the stability of the nontrivial fixed point which was proved by Sharkovsky et al. [24]. Moreover, we also obtain the fact that the non trivial fixed point  $\bar{x}$  attracts the compact subset of  $]0, +\infty[$ . This last property will be essential in the proof of theorem 1.4. In section 2, we prove both results by using very elementary arguments and a very general result on dissipative systems.

**THEOREM 1.1** *Let  $f: \mathbb{R}_+ \rightarrow \mathbb{R}_+$  be a map, satisfying (H1). Then, the three following assertions are equivalent.*

a. *For each  $m = 1, 2, \dots$*

$$f^m(x) > x \text{ for all } 0 < x < \bar{x} \text{ and } f^m(x) < x \text{ for all } x > \bar{x}.$$

b.

$$f^2(x) > x \text{ for all } 0 < x < \bar{x} \text{ and } f^2(x) < x \text{ for all } x > \bar{x}.$$

c.  *$\bar{x}$  attracts the points of  $]0, +\infty[$  under  $f$ .*

*Moreover, under anyone of the three conditions,  $\bar{x}$  is stable and attracts the compact sets of  $]0, +\infty[$ ,*

*This theorem is a direct application of Theorem 2.4.2 p:17 in Hale [10], and Lemma 1 p:48 in Sharkovsky et al. [24].*

*Remark* If the assumptions made by Fisher and Goh [7] on equation (7) hold, then in particular  $\bar{x}$  attracts the points of  $]0, +\infty[$ . This remark is important because it shows that existence of a convex Liapunov function can be replaced by the condition (b) of Theorem 1.1 (see Corollary 1.5).

As a simple consequence of Theorem 1.1, we also have the following theorem.

**THEOREM 1.2** *Let  $f: \mathbb{R}_+ \rightarrow \mathbb{R}_+$  be a map satisfying (H1). If in addition we suppose that*

$$f(x) > x \text{ for all } 0 < x < \bar{x} \text{ and } f(x) < x \text{ for all } x > \bar{x},$$

*then if the nontrivial fixed point  $\bar{x}$  is unstable, or if the nontrivial fixed point  $\bar{x}$  does not attract the points of  $]0, +\infty[$  under  $f$ ,  $f$  has a non trivial 2-periodic solution.*

*Remark 1* We may observe that  $\bar{x}$  being unstable implies that  $\bar{x}$  does not attract the points of  $]0, +\infty[$  under  $f$ .

*Remark 2* From theorem 1.2, we also have the following equivalence. If  $f: \mathbb{R}_+ \rightarrow \mathbb{R}_+$  is a map satisfying (H1), if in addition we suppose that

$$f(x) > x \text{ for all } 0 < x < \bar{x} \text{ and } f(x) < x \text{ for all } x > \bar{x}.$$

then the assertion c) of theorem 1.1 is equivalent to the following assertion:

$$f^2(x) \neq x \text{ for all } x \in ]0, +\infty[ \setminus \{\bar{x}\}.$$

This equivalence was proved by Cull in [3], [4], and by Rosenkranz in [23].

In section 3, we investigate some properties of the linear part. This will lead us to the two following results, which are, as we will see in section 3, consequences



of some general results on irreducible non negative markovian matrices, see Theorem 3.1 and Lemma 3.2.

**PROPOSITION 1.3** *Suppose that assumption (H1) holds. Then, if the matrix  $L$  is non primitive, and has exactly  $p$  (with  $2 \leq p \leq n$ ) eigenvalues in the peripheral spectrum of  $L$  (i.e., of maximum modulus), equation (5) has at least one periodic solution with orbit  $C = \{C_1, C_2, \dots, C_p\}$  in the set*

$$E = \{X \in \mathbb{R}_+^n - \{0, \bar{X}\} : X_i = \bar{x} \text{ or } 0 \forall i = 1, \dots, n\}$$

and period  $k$ ,  $2 \leq k \leq p$ .

Moreover, every  $k$ -periodic solution of equation (5) in  $E$  satisfies

$$2 \leq k \leq p.$$

In section 3 corollary 3.4, we will prove a result, which gives a different argument for proving the main result of this paper. Corollary 3.4 says essentially that if  $\{X(t)\}_{t \in \mathbb{N}}$  is a solution of equation (5) with  $X(0) = X_0 \neq 0$ , then for all  $t \in \mathbb{N}$  large enough we have the following property:

If  $X_1(t+1) > 0$  then for each  $j = 1, \dots, n$  such that  $R_j > 0$  we have  $X_j(t) > 0$ .

This is in fact a direct consequence of a general result on irreducible non negative matrices, see Theorem 3.3.

Finally, in section 4, we will prove the following theorem, which is the main result of this paper.

**THEOREM 1.4** *Under assumption (H1), and suppose that*

$$f^2(x) > x \text{ for all } 0 < x < \bar{x} \text{ and } f^2(x) < x \text{ for all } x > \bar{x}.$$

Let  $\{X(t)\}_{t \in \mathbb{N}}$  be a solution of equation (5) with  $X(0) = X_0 \neq 0$ . Then, there are two cases.

Either, for some  $t_0 \in \mathbb{N}$ ,

$$X(t_0) \in \text{Int}(\mathbb{R}_+^n) = \{X \in \mathbb{R}_+^n : X_i > 0 \forall i = 1, \dots, n\}.$$

In this case,

$$X(t) \rightarrow \bar{X} \text{ as } t \rightarrow +\infty.$$

Or, the sequence  $\{X(t)\}_{t \in \mathbb{N}}$  takes its values in

$$\partial(\mathbb{R}_+^n) = \mathbb{R}_+^n - \text{Int}(\mathbb{R}_+^n).$$

Then, the solution  $\{X(t)\}_{t \in \mathbb{N}}$  is asymptotically  $k$ -periodic and approaches the orbit of a  $k$ -periodic solution  $C = \{C_1, C_2, \dots, C_p\}$  of equation (5), with

$$C \subset E = \{X \in \partial(\mathbb{R}_+^n) - \{0, \bar{X}\} : X_i = \bar{x} \text{ or } 0, \forall i = 1, \dots, n\}$$

and

$$2 \leq k \leq p \leq n,$$

where  $p$  is the number of eigenvalues in the peripheral spectrum of the matrix  $L$  (i.e., of maximum modulus).

*Remark* In the case where the matrix  $L$  is non primitive, one can see that the only  $k$ -periodic solutions of equation (5) are those described in proposition 1.3. Moreover, one can see from Theorem 1.4 that these periodic solutions are unstable, because all the solutions starting in  $\text{Int}(\mathbb{R}_+^n)$  converge to the non trivial fixed point  $X$ .

**COROLLARY 1.5** *With the same assumptions as in theorem 1.4,  $\bar{X}$  is stable and attracts the compact sets of  $\text{Int}(\mathbb{R}_+^n)$  under  $F$ . If, in addition,  $L$  is primitive, then  $X$  attracts the points of  $\mathbb{R}_+^n - \{0\}$  under  $F$ .*

*Remark* This corollary, with the remark following Theorem 1.1, yields a generalization of result by Fisher and Goh [7]. Because the result given by Fisher and Goh [7] is based on the existence of a convex Liapunov function, so with the remark following theorem 1.1, we know that the assumptions of theorem 1.4 hold.

*Examples* In order to apply Theorem 1.4 and Corollary 1.5 one must verify the following condition

$$f^2(x) > x \text{ for all } 0 < x < \bar{x} \text{ and } f^2(x) < x \text{ for all } x > \bar{x}.$$

A situation where this condition holds, is the Beverton and Holt [1] model which corresponds to

$$h(x) = \frac{1}{1 + \beta x}, \text{ for all } x \geq 0,$$

with  $\beta > 0$ .

In this case for all  $R > 1$ , the map  $f$  is defined by

$$f(x) = \frac{Rx}{1 + \beta Rx}, \text{ for all } x \geq 0,$$

and the condition is verify (because this map is monotone increasing). Another example where this condition holds, is the Ricker [22] model, which corresponds to

$$h(x) = \exp(-\beta x), \text{ for all } x \geq 0,$$

with  $\beta > 0$ .

In this case for all  $R > 1$ , the map  $f$  is defined by

$$f(x) = Rx \exp(-\beta Rx), \text{ for all } x \geq 0,$$

and it is proved (see appendix 2 p:154 in the paper by Fisher and Goh [7]) that if

$$1 < R \leq \exp(2),$$

then the non trivial fixed  $\bar{x}$  is stable and attracts the points of  $]0, +\infty[$  under  $f$ . So in this case, the condition hold.

In this two examples, when  $R > 1$  for the Beverton and Holt [1] model, and when  $1 < R < \exp(2)$  for the Ricker [22] model, theorem 1.4 and corollary 1.5 can be applied.

### Interpretation of the Results for the Population Model

Let us come back to the population model. First, we remark that, since we have supposed  $R_n > 0$  and  $R_n = 1 / R l_n b_n$ , we must have

$$p_i > 0 \forall i = 1, \dots, n-1, \quad (10)$$

(because  $l_n = p_1 p_2 \dots p_{n-1}$ ).

From this remark, we deduce that for all  $i = 1, \dots, n$

$$b_i > 0 \text{ if and only if } R_i > 0. \quad (11)$$

From (10) and (11) we deduce that the matrix  $L$  defined by (9) is primitive if and only if the Leslie matrix defined by

$$\begin{pmatrix} b_1 & b_2 & \cdots & \cdots & b_n \\ p_1 & 0 & \cdots & \cdots & 0 \\ 0 & p_2 & \ddots & & \vdots \\ \vdots & \ddots & \ddots & 0 & 0 \\ 0 & \cdots & 0 & p_{n-1} & 0 \end{pmatrix} \text{ is primitive.}$$

Moreover, the primitivity property of the matrix  $L$  defined by (9), depends only on the reproduction structure (i.e. on the strict positivity of the fertility rate  $b_i$ ). For example, the matrix  $L$  will be primitive, when two consecutive age classes have a positive fertility rate (i.e.  $b_i > 0$  and  $b_{i+1} > 0$  for some  $i \in \{1, \dots, n-1\}$ ), see Demetrius [6] for a proof of this result.

Now we can give an interpretation of the results for the population.

Let us first consider the case where only the first age class is reproductive, that is

$$x_1(t+1) = f(x_1(t)), \text{ for all } t = 0, 1, \dots$$

In this situation, we know that from the remark 2 following Theorem 1.2, that the condition

$$f^2(x) > x \text{ for all } 0 < x < \bar{x} \text{ and } f^2(x) < x \text{ for all } x > \bar{x}, \quad (12)$$

means that  $f$  has no 2-periodic solution, and under this condition the non trivial fixed point

$$\bar{x} = \frac{1}{R} h^{-1} \left( \frac{1}{R} \right),$$

is stable, and attracts the points of  $]0, +\infty[$ .

Under the condition (12) on  $f$ , Theorem 1.4 and Corollary 1.5 extend the one dimensional case to the case where the number of reproducing age classes is arbitrary. More precisely, we see from Corollary 1.5 that, if the structure of the reproduction gives a Leslie matrix  $L$  which is primitive, then the population approaches the steady-state age distribution, which is given by

$$(l_1 \bar{x}, l_2 \bar{x}, \dots, l_n \bar{x})^T.$$

Let us now consider the case where the matrix  $L$  is non primitive. A model for this situation is the case where for all  $t = 0, 1, 2, \dots$

$$\begin{cases} x_1(t+1) = b_2 x_2(t) h(b_2 x_2(t)) \\ x_2(t+1) = p_1 x_1(t) \end{cases} \quad (13)$$

Then

$$\left\{ \left( \begin{array}{c} 0 \\ l_2 \bar{x} \end{array} \right), \left( \begin{array}{c} \bar{x} \\ 0 \end{array} \right) \right\}$$

is a 2-periodic solution of equation (13).

From Theorem 1.4 we see that even in the case where  $L$  is non primitive, if the age classes of the population become all positive for some finite time, then the population also approaches the steady-state age distribution.

Otherwise, the population becomes periodic, in the sense that the reproduction becomes periodic and the number of females of the class  $i$  (for  $i \in \{1, \dots, n\}$ ) approaches periodically either 0 or  $l_i \bar{x}$ .

## 2. ONE DIMENSIONAL CASE

In this section we will prove theorem 1.1 and 1.2. The next lemma provides a necessary condition for  $\bar{x}$  to attract the points of  $]0, +\infty[$ .

LEMMA 2.1 *Under (H1), assertion (c) of theorem 1.1 implies (a) of the same theorem.*

*Proof* We prove the result for  $m = 1$ , and as (H1) also holds for  $f^m$  with  $m \geq 1$  the lemma will follow. First we remark that, since  $\bar{x}$  attracts the points of  $]0, +\infty[$  under  $f$ ,  $\bar{x}$  must be the only fixed point of  $f$  in  $]0, +\infty[$ . Now suppose there exists  $y \in ]0, +\infty[ - \{\bar{x}\}$  such that

$$(f(y) < y \text{ and } 0 < y < \bar{x}) \text{ or } (f(y) > y \text{ and } y > \bar{x}).$$

Suppose for example that  $0 < y < \bar{x}$ , the case  $y > \bar{x}$  is similar. Since, we cannot have

$$f(x) < x \text{ for all } 0 < x < \bar{x},$$

because  $\bar{x}$  attract the points of  $]10, +\infty[$ , there must exist  $z$  such that

$$f(z) \geq z \text{ and } 0 < z < \bar{x}.$$

Now, by the intermediate value theorem, we have a contradiction, with the fact that  $\bar{x}$  is the only fixed point of  $f$  in  $]0, +\infty[$ .  $\square$

Lemma 2.1 proves  $(c) \Rightarrow (a)$ . On the other hand,  $(a) \Rightarrow (b)$  is trivial. Now we will prove the main part of the theorem 1.1, which is  $(b) \Rightarrow (c)$ . In fact, the principle of the proof is essentially the same as the proof of theorem 2.1 p:47 in Sharkovsky et al. [24]. The main difference here is that we obtain from a general result on dissipative systems (see theorem 2.4.2 p:17 in Hale [10]), first a global result, and also the stability of the non trivial fixed point, and the fact that the non trivial fixed point attracts the compact sets of  $]0, +\infty[$ . Here we state only the part of theorem 2.4.2 p:17 in Hale [10] that we are interested in.

THEOREM 2.2 (HALE [10]) *If  $T: X \rightarrow X$  is a continuous map on  $X$ , a complete metric space, and there is a non empty compact set  $K$  that attracts the compact sets of  $X$  and  $A = \bigcap_{m \geq 0} T^m K$ , then  $A$  is compact, invariant (i.e.  $A = T(A)$ ), stable, and attracts the compact sets of  $X$ .*

By using this theorem, we obtain the following lemma.

LEMMA 2.3 *Under (H1), and assertion (b) of theorem 1.1, there exists  $J = [a, b]$  (with  $0 < a \leq b$ ), a closed bounded interval which is invariant (i.e.,  $J = f(J)$ ), stable, and attracts the compact sets of  $]0, +\infty[$  in  $\mathbb{R}$ .*

*Proof* First under the assumptions made on  $f$ , it is not difficult to prove that we must have

$$(f(x) > x \text{ for all } 0 < x < \bar{x}) \text{ or } (f(x) < x \text{ for all } x > \bar{x}).$$

As each compact set in  $]0, +\infty[$  is included in some closed bounded interval of  $]0, +\infty[$ , to apply theorem 2.2 to  $f$ , we will find a closed bounded interval  $K = [c, d]$   $0 < c \leq d$ , such that

$$f(K) \subset K,$$

and for all closed bounded interval  $L \subset ]0, +\infty[$  there exists  $m \in \mathbb{N}$  such that

$$f^m(L) \subset K.$$

Then we will apply theorem 2.2 to  $f|_K$  and we will obtain the result. By continuity of  $f$ , and since  $f(0) = 0$ , there exists  $\epsilon \in ]0, \bar{x}[$  such that

$$f(x) < \bar{x} \quad \forall x \in [0, \epsilon].$$

Then, we take

$$c = \epsilon.$$

Now, denote by

$$b_0 = \max_{y \in [0, \bar{x}]} f(y) = \max_{y \in [\epsilon, \bar{x}]} f(y) \geq \bar{x}.$$

If  $b_0 = \bar{x}$ , then by continuity of  $f$ , and since  $f(\bar{x}) = \bar{x}$ , there exists  $\delta > 0$  such that

$$f(x) > \epsilon \quad \forall x \in [\bar{x}, \bar{x} + \delta].$$

Now we take

$$d = \bar{x} + \delta, \text{ and } K = [c, d].$$

Now by construction, we have

$$f(K) \subset K.$$

If  $b_0 > \bar{x}$ , we take

$$d = b_0, \text{ and } K = [c, d].$$

Then by construction we must have

$$f(K) \subset K.$$

Otherwise, there must exist some  $z_1 \in ]\bar{x}, \bar{x} + \delta[$  satisfying  $f(z_1) < \epsilon$ , and by construction of  $d$ , there must exist some  $z_0 \in ]\epsilon, \bar{x}[$  satisfying  $f(z_0) = z_1$ , but this contradicts the hypothesis, because then

$$f^2(z_0) < \epsilon \leq z_0 \text{ and } 0 < z_0 < \bar{x}.$$

Now we prove that  $K$  attracts the compact intervals of  $]0, +\infty[$ . Let  $L_1 = [a_1, b_1]$  (with  $0 < a_1 \leq b_1$ ) be a closed bounded interval of  $]0, +\infty[$ . If  $b_1 > d$ , let us consider the following sequence of intervals

$$L_m = [a_m, b_m] = f^m(L_1) \quad \forall m \geq 1.$$

And remark that, if  $b_m > d$  for some  $m \geq 1$  then by construction of  $K$

$$b_m = \max_{y \in L_{m-1}} f(y) = \max_{y \in L_{m-1} \text{ and } y > d} f(y),$$

(because  $f(x) < d \forall x \in [0, \bar{x}]$  and  $f(x) < x \forall x > \bar{x}$ ).

Now, suppose that

$$b_m > d \forall m \in \mathbb{N} - \{0\}.$$

Then for each  $m \in \mathbb{N}$  there exists  $x(m) \in ]d, b_1]$  such that

$$b_m = f^{m-1}(x(m)) < f^{m-2}(x(m)) < \dots < x(m).$$

By compactness of  $[d, b_1]$ , we can always suppose that

$$x(m) \rightarrow \bar{x} \text{ as } m \rightarrow +\infty.$$

Now, by using the continuity of  $f$  we must have

$$d \leq f^{m+1}(\bar{x}) \leq f^m(\bar{x}) \text{ for all } m \in \mathbb{N}.$$

So  $f^m(\bar{x}) \rightarrow \gamma$  as  $m \rightarrow +\infty$ , with

$$f(\gamma) = \gamma \text{ and } \gamma \geq d > \bar{x}.$$

This is a contradiction, so there exists  $m_0 \in \mathbb{N}$  such that

$$b_m \leq d \forall m \geq m_0.$$

Now, by applying the same method one can show that, if  $a_{m_0} < \varepsilon$  there exists  $m_1 \geq m_0$  such that

$$\varepsilon \leq a_{m_1} \forall m \geq m_1.$$

And, finally,  $\forall m \geq m_1$

$$f^m(L) \subset K.$$

Now, one can apply theorem 2.2, and we deduce that, then the set  $J = \bigcap_{m \geq 0} f^m(K)$  is compact, invariant (i.e.  $f(J) = J$ ), stable and attract the compact set of  $]0, +\infty[$ . It remains to prove that  $J$  is an interval, but this is clear because  $J = \bigcap_{m \geq 0} f^m(K)$  is the intersection of a non increasing sequence of intervals.  $\square$

Now to complete the proof of (b)  $\Rightarrow$  (c), it remains to show that  $J = \{\bar{x}\}$ . For this, we will apply the following lemma, which can be found in Sharkovsky et al. [24] (Lemma 1 p:48).

**LEMMA 2.4 (SHARKOVSKY ET AL. [24])** *Let  $K \subset \mathbb{R}$  be a closed bounded interval distinct from a point and let  $f: K \rightarrow K$  be a continuous map with  $f(K) = K$ . Then the interval  $K$  contains at least two fixed points or a fixed point and a 2-periodic solution.*

From this lemma, we see that under assertion (b) of theorem 1.1, the closed bounded invariant interval  $J$  determined in lemma 2.3 is necessarily reduced to  $J = \{\bar{x}\}$ . This completes the proof of theorem 1.1.

*Proof (of theorem 1.2)* From theorem 1.1 we see that, if the nontrivial fixed point  $\bar{x}$  is unstable, or does not attract the points of  $]0, +\infty[$  (that is to say, (c) is not satisfied), then by using the assertion (b) there exists  $y_0 \in ]0, +\infty[ - \{\bar{x}\}$  such that

$$(f^2(y_0) \leq y_0 \text{ and } 0 < y_0 < \bar{x}) \text{ or } (f^2(y_0) \geq y_0 \text{ and } \bar{x} < y_0).$$

Now by using the fact that  $f(0) = 0$  and continuity of  $f$ , it is not difficult to prove that for  $y_1 \in ]0, \bar{x}[$  small enough we have

$$f^2(y_1) > y_1$$

(because  $f(0) = 0$  and by assumption of theorem 1.2,  $f(y) > y$  for all  $y \in ]0, \bar{x}[$ ). By denoting

$$M = \sup_{x \in ]0, \bar{x}[} f(x)$$

we have for all  $y_2 \in ]M, +\infty[$

$$f^2(y_2) < y_2,$$

(because  $f(y) > y$  for all  $y \in ]\bar{x}, +\infty[$ ).

Finally, by applying the intermediate value theorem either between  $y_0$  and  $y_1$  (if  $y_0 < \bar{x}$ ), or between  $y_0$  and  $y_2$  (if  $y_0 > \bar{x}$ ), we obtain a non trivial 2-periodic solution of  $f$ . Theorem 1.2 is proved.  $\square$

### 3. STUDY OF THE LINEAR PART

We start this section by some notations.

Let  $A \in M_n(\mathbb{R})$  be a real matrix, we denote by  $\sigma(A)$  the spectrum of  $A$ ,  $r(A)$  the spectral radius of  $A$  (i.e. the maximum modulus of all the eigenvalues of  $A$ ), and by  $\sigma_0(A)$  the peripheral spectrum of  $A$  (i.e. the set of all the eigenvalues of  $A$  with modulus equal to  $r(A)$ ). We also denote by

$$1_{R^k} = (1, 1, \dots, 1)^T \in \mathbb{R}^k \text{ (for } k \geq 1).$$

With these notations,  $A \in M_n(\mathbb{R}_+)$  a non negative matrix is said to be **markovian** if

$$A 1_{R^n} = 1_{R^n}.$$

Now, we state a result on irreducible non negative matrices, from which we will deduce all the results of this section.

**THEOREM 3.1** *Let  $A \in M_n(\mathbb{R}_+)$  be an irreducible non negative matrix.*

*If there are precisely  $p \in \{1, \dots, n\}$  eigenvalues of  $A$  in  $\sigma_0(A)$  (i.e., of maximum*



modulus) counting the algebraic multiplicity, then there exists a permutation of the canonical basis of  $\mathbb{R}^n$ , such that:

$$A^P = \begin{bmatrix} A_{11} & 0 & 0 & \cdots & 0 \\ 0 & A_{22} & 0 & & \vdots \\ 0 & 0 & \ddots & \ddots & \vdots \\ \vdots & & \ddots & \ddots & 0 \\ 0 & \cdots & \cdots & 0 & A_{pp} \end{bmatrix} \in M_n(\mathbb{R}_+)$$

in the permuted basis, where for all  $i = 1, \dots, p$  the block-matrix  $A_{ii} \in M_{n_i}(\mathbb{R}_+)$  is primitive.

*Proof* To prove this result one can use the Frobenius form of the irreducible non negative matrix (see the book by Minc [21] theorem 3.1 p:51 for this result). By computing the  $p^{\text{th}}$  power of the matrix under this form theorem 3.1 is obtained. We will not detail further the proof of this result.  $\square$

LEMMA 3.2 Let  $A = \{a_{ij}\} \in M_n(\mathbb{R}_+)$  be an irreducible non negative markovian matrix, and let  $V \in \mathbb{R}_+^n$  be a vector satisfying

$$0 \leq V_j \leq 1; \forall j = 1, \dots, n$$

and suppose there exists  $j_0 \in \{1, \dots, n\}$  such that

$$0 < V_{j_0} < 1.$$

Then for all  $m \in \mathbb{N} - \{0\}$  there exists  $j_m \in \{1, \dots, n\}$  such that

$$0 < (A^m V)_{j_m} < 1.$$

*Proof* Let  $V \in \mathbb{R}_+^n$  be a non negative vector satisfying the assumptions of lemma 3.2 and let  $j_0 \in \{1, \dots, n\}$  be an integer such that

$$0 < V_{j_0} < 1.$$

Since  $A$  is irreducible for all  $j \in \{1, \dots, n\}$  there exists  $i \in \{1, \dots, n\}$  such that

$$a_{ij} > 0.$$

So, for  $j = j_0$  there exists  $i_0 \in \{1, \dots, n\}$  satisfying

$$a_{i_0 j_0} > 0.$$

This implies that, with the fact that  $A$  is markovian,

$$0 < (AV)_{i_0} = \sum_{j=1}^n a_{i_0 j} V_j = \sum_{j=1 \text{ and } j \neq j_0}^n a_{i_0 j} V_j + a_{i_0 j_0} V_{j_0} < 1.$$

Moreover, by using again the fact that  $A$  is markovian, we obtain:

$$0 \leq (AV)_j \leq 1 \forall j = 1, \dots, n.$$

Now, introduce the sequence

$$V^{(m)} = A^m V.$$

By repeating the above argument, one can see that

$$0 \leq V_i^{(m)} \leq 1 \quad \forall i = 1, \dots, n,$$

and for some  $j \in \{1, \dots, n\}$

$$0 \leq V_j^{(m)} \leq 1.$$

Lemma 3.2 is proved. □

From theorem 3.1, and lemma 3.2, we now can prove proposition 1.3.

*Proof (of proposition 1.3)* Since (H1) holds, and since we consider the  $k$ -periodic solutions in  $E$ , we can always replace the map  $F$  in equation (6) by the matrix  $L$  of equation (8), and look for the periodic solutions in  $E$  of the following equation

$$X(t + 1) = LX(t) \quad \forall t \in \mathbb{N} \tag{14}$$

with initial condition

$$X(t) = X_0 \in \mathbb{R}_+^n.$$

Now, we show existence of such periodic solutions. Since  $L$  is an irreducible non negative matrix, we can apply theorem 3.1. So, there exists a permutation of the canonical basis of  $\mathbb{R}^n$  and  $p \in \{1, \dots, n\}$  such that

$$L^p = \begin{bmatrix} A_{11} & 0 & 0 & \dots & 0 \\ 0 & A_{22} & 0 & & \vdots \\ 0 & 0 & \ddots & \ddots & \vdots \\ \vdots & & \ddots & \ddots & 0 \\ 0 & \dots & \dots & 0 & A_{pp} \end{bmatrix} \in M_n(\mathbb{R}_+)$$

in the permuted basis, where the block matrices  $A_{ii} \in M_{n_i}(\mathbb{R}_+)$  are primitive for all  $i = 1, \dots, p$ , and  $p$  is the number of eigenvalues of  $L$  in  $\sigma_0(L)$ . Denote for all  $j \in \{1, \dots, n\}$

$$V(j) = \begin{bmatrix} 0_{R^{n_1}} \\ \vdots \\ 0_{R^{n_{j-1}}} \\ 1_{R^n} \\ 0_{R^{n_{j+1}}} \\ \vdots \\ 0_{R^{n_p}} \end{bmatrix}.$$

Since  $L$  is markovian,  $L^p$  is also markovian and we have for all  $j \in \{1, \dots, n\}$

$$L^p V(j) = V(j).$$

Moreover  $p > 1$  because  $L$  is non primitive. Thus for all  $j \in \{1, \dots, p\}$  the finite sequence  $\{V(j), LV(j), \dots, L^{p-1}V(j)\}$  contains a  $k$ -periodic solution of equation (14) with  $1 \leq k \leq p$ . Now, from the fact that  $L$  is irreducible and markovian, we must have

$$LV = V \Leftrightarrow V = \lambda 1_{\mathbb{R}^n} \quad (\lambda \in \mathbb{R}),$$

and so  $k > 1$ . Moreover, if there exists  $j_0 \in \{1, \dots, p\}$  such that  $\{V(j_0), LV(j_0), \dots, L^{p-1}V(j_0)\}$  is not contained in

$$\{X \in \mathbb{R}_+^n : \forall i = 1, \dots, n \ X_i = 1 \text{ or } 0\}.$$

then, there exists  $\tilde{p} \in \{0, \dots, p-1\}$  and  $i_0 \in \{1, \dots, n\}$  such that

$$0 < (L^{\tilde{p}}V(j_0))_{i_0} < 1,$$

and by applying lemma 3.2, we obtain a contradiction with the fact that

$$L^{2p-\tilde{p}}L^{\tilde{p}}V(j_0) = V(j_0).$$

Now, denote by

$$X(j) = \bar{x}V(j) \text{ for all } j \in \{1, \dots, p\}.$$

Then, for each  $j \in \{1, \dots, p\}$   $C_j = \{X(j_0), LX(j_0), \dots, L^{p-1}X(j_0)\}$  contains a  $k$ -periodic solution of equation (5) in  $E$  with  $1 < k \leq p$ .

Now we show that every  $k$ -periodic solution of equation (5) in  $E$ , satisfies  $1 < k \leq p$ . Let  $C = \{C_1, \dots, C_k\}$  be the orbit of a  $k$ -periodic solution of equation (5) in  $E$ .

Since for all  $l = 1, 2, \dots$

$$L^{klp} = \begin{bmatrix} A_{11}^{kl} & 0 & 0 & \dots & 0 \\ 0 & A_{22}^{kl} & 0 & & \vdots \\ 0 & 0 & \ddots & \ddots & \vdots \\ \vdots & & \ddots & \ddots & 0 \\ 0 & \dots & \dots & 0 & A_{pp}^{kl} \end{bmatrix} \in M_n(\mathbb{R}_+)$$

and

$$C_i = L^{klp}C_i \quad \forall i = 1, \dots, k,$$

then for  $l$  large enough

$$A_{ii}^{kl} \gg 0 \quad \forall i = 1, \dots, p,$$

that is all the components of  $A_{ii}^{kl}$  are positive.

We deduce from this fact that for each  $i \in \{1, \dots, k\}$

$$C_i = \sum_{j \in J_i} X(j)$$

for some  $J_i \subset \{1, \dots, p\}$ ,  $J_i \neq \emptyset$ , and  $X(j) = \bar{x} V(j)$

Now from the first part of the proof, we know that  $1 \leq k \leq p$ . Moreover, since  $L$  is irreducible, if  $k = 1$  the periodic solution must be  $X$ , which is impossible because  $X \notin E = \{X \in \mathbb{R}_+^n - \{0, X\} : X_i = \bar{x} \text{ or } 0 \forall i = 1, \dots, n\}$ . Thus, we must have  $k > 1$ .

Proposition 1.3 is proved. □

Now we give a general result on irreducible non negative markovian matrices, from which we will deduce corollary 1.3.

**THEOREM 3.3** *Let  $A = \{a_{ij}\} \in M_n(\mathbb{R}_+)$  be an irreducible non negative matrix.*

*Then, there exists  $m_1 \in \mathbb{N} - \{0\}$  a positive integer such that*

*for all  $X \in \mathbb{R}_+^n - \{0\}$ ,  $m \geq m_1$ ,*

*If  $((A^{m+1}X)_i > 0$  and  $a_{ij} > 0$ ) then  $(A^m X)_j > 0$ .*

*Proof* Without loss of generality, since the matrix  $A$  is irreducible, by making the change of variable as in the beginning of the proof of theorem 3.1, we can always assume that  $A$  is markovian. Denote by  $p \in \{1, \dots, n\}$  the number of eigenvalues of  $\sigma_0(A)$  (i.e., of modulus one). Since the matrix  $A$  is irreducible, we can apply theorem 3.1, and we deduce that there exists a permutation on the canonical basis of  $\mathbb{R}^n$  such that

$$A^P = \begin{bmatrix} A_{11} & 0 & 0 & \dots & 0 \\ 0 & A_{22} & 0 & & \vdots \\ 0 & 0 & \ddots & \ddots & \vdots \\ \vdots & & \ddots & \ddots & 0 \\ 0 & \dots & \dots & 0 & A_{pp} \end{bmatrix} \in M_n(\mathbb{R}_+),$$

in the permuted basis, where the block matrices  $A_{ii} \in M_{n_i}(\mathbb{R}_+)$  are primitive for all  $i = 1, \dots, p$ .

Without loss of generality, we can always assume that  $A$  is as above.

Now, since the non negative matrices  $A_{ii}$  are primitive, there exists  $m_0 \in \mathbb{N}$  such that, for all  $i = 1, \dots, p$

$$A_{ii}^{m_0} \gg 0$$

This means that all the component of  $A_{ii}^{m_0}$  are positive. Let  $X \in \mathbb{R}_+^n - \{0\}$  be a non negative vector, we have to show that for all  $m > m_1 = m_0 p$ , for all  $i = 1, \dots, n$ , and for all  $j = 1, \dots, n$  if

$$(A^{m+1}X)_i > 0 \text{ and } a_{ij} > 0 \text{ then } (A^m X)_j > 0.$$

As before we denote by

$$V(j) = \begin{bmatrix} 0_{R^{n_1}} \\ \vdots \\ 0_{R^{n_{j-1}}} \\ 1_{R^{n_j}} \\ 0_{R^{n_{j+1}}} \\ \vdots \\ 0_{R^{n_p}} \end{bmatrix} \quad \forall j = 1, \dots, p$$

Let  $m \geq m_1$  and  $i_0 \in \{1, \dots, n\}$  such that  $(A^{m+1}X)_{i_0} > 0$ . Then, there exists at least one  $j_0 \in \{1, \dots, p\}$  such that

$$a_{i_0 j_0} < 0 \text{ and } (A^m X)_{j_0} > 0.$$

But then, there exists  $l_0 \in \{1, \dots, p\}$  such that

$$V(l_0)_{j_0} > 0$$

(because  $\sum_{j=1}^p V(j) = 1_{R^n}$ ), and

$$A^m X = A^{m_0 p} A^{m-m_0 p} X = \begin{bmatrix} A_{11}^{m_0} & 0 & 0 & \dots & 0 \\ 0 & A_{22}^{m_0} & 0 & & \vdots \\ 0 & 0 & \ddots & \ddots & \vdots \\ \vdots & & \ddots & \ddots & 0 \\ 0 & \dots & \dots & 0 & A_{pp}^{m_0} \end{bmatrix} A^{m-m_0 p} X$$

From this we deduce that for all  $i = 1, \dots, n$  such that  $V(l_0)_i > 0$  we have  $(A^m X)_i > 0$ . But now by using lemma 3.2, we must have for each  $j = 1, \dots, p$  such that  $a_{i_0 j} > 0$  then  $V(l_0)_j > 0$  (because  $A^p V(l_0) = V(l_0)$ , so by using the lemma 3.2 we must have  $(AV(l_0))_{i_0} = 1$ ). Theorem 3.3 is proved, with  $m_1 = m_0 p$ .  $\square$

**COROLLARY 3.4** *Under assumption i) of (H1), we have the following statement.*

*There exists  $t_1 \in \mathbb{N}$  a non negative integer such that, for each  $X_0 \in \mathbb{R}_+^n$ , if we denote by  $\{X(t)\}_{t \in \mathbb{N}}$  the solution of equation (5) with initial value  $X_0 \in \mathbb{R}_+^n - \{0\}$ , we have for  $t \geq t_1$ ,*

$$\text{if } X_j(t+1) > 0 \text{ and } R_j > 0 \text{ then } X_j(t) > 0.$$

*Proof* By using i) of (H1) (i.e.,  $f(0) = 0$  and  $f(x) > 0$  for all  $x > 0$ ) we can always replace  $F$  by  $L$  in equation (5), and by applying theorem 3.3 to this new equation we obtain the result.  $\square$

#### 4. PROOF OF THEOREM 1.4 AND COROLLARY 1.5

We start this section by proving a result on the delay difference equation (4), from which we will deduce the asymptotic behavior of the solutions of equation (5). We recall that the equilibrium solution

$$\bar{x}(t) = \bar{x} \quad \forall t \geq -n,$$

of equation (4) is said to be stable, if for all  $\epsilon > 0$  there exists  $\eta \in ]0, \min(\epsilon, \bar{x})[$  such that, all the solution  $\{x(t)\}_{t \geq -n}$  of equation (4) starting with an initial value

$$x(-i) = x_{-i} \in ]\bar{x} - \eta, \bar{x} + \eta[, \quad \forall i = 1, \dots, n$$

satisfies

$$x(t) \in ]\bar{x} - \epsilon, \bar{x} + \epsilon[ \quad \forall t \geq -n.$$

**PROPOSITION 4.1** *Suppose assumption (H1) holds, and consider  $\{x(t)\}_{t \geq -n}$  a solution of the delay difference equation (4).*

*Then, if we denote by  $\{x(t)\}_{p \in \mathbb{N}}$  the sequence of the positive elements of  $\{x(t)\}_{t \geq -n}$  we have*

$$x(t_p) \rightarrow \bar{x} \text{ as } p \rightarrow +\infty.$$

*Moreover, the only non trivial constant solution of equation (4)*

$$\bar{x}(t) = \bar{x} \quad \forall t \geq -n,$$

*is stable.*

*Proof* Let  $(x_{-n}, x_{-n+1}, \dots, x_{-1}) \in \mathbb{R}_+^n - \{0\}$ , if we denote by  $\{x(t)\}_{t \geq -n}$  the solution of equation (4) with initial condition

$$x(-i) = x_{-i} \quad \forall i = 1, \dots, n,$$

then by the corollary 3.4, there exists  $t_0 \in \mathbb{N}$  such that

$$\forall t \geq t_0 \quad \forall i = 1, \dots, n \text{ if } x(t) > 0 \text{ and } p_i > 0 \text{ then } x(t-i) > 0.$$

Without loss of generality we can always suppose that  $t_0 = 0$ , by taking the initial condition

$$(x(t_0 - n), x(t_0 - n + 1), \dots, x(t_0 - 1)).$$

Now, from (H1) one can easily prove that

$\forall M, m > 0$  with  $0 < m \leq M$  there exist  $a, b > 0$  with  $a < b$  such that

$$[m, M] \subset [a, b] \text{ and } f([a, b]) \subset [a, b].$$

Now, denote by

$$m = \min_{i=1, \dots, n \text{ and } x(-i) > 0} (x(-i)) \text{ and } M = \max_{i=1, \dots, n} (x(-i)),$$

and choose  $a, b > 0$  with  $a < b$  such that

$$[m, M] \subset [a, b] \text{ and } f([a, b]) \subset [a, b].$$

Then, if  $x(0) > 0$  we have

$$x(0) \in f([a, b])$$

because  $p_i > 0$  implies  $x(-i) > 0$  and so  $\sum_{i=1}^n p_i x(-i) \in [a, b]$ .

But  $f([a, b]) \subset [a, b]$  so we have also

$$x(0) \in [a, b].$$

If  $x(1) > 0$  then we have  $x(0) = 0$  or  $x(0) \in [a, b]$ , so by using the arguments as previously we have

$$x(1) \in f([a, b]) \text{ and } x(1) \in [a, b].$$

Thus by induction we have

$$\forall t \in \mathbb{N} \text{ if } x(t) > 0 \text{ then } x(t) \in f([a, b]) \text{ and } x(t) \in [a, b].$$

Now consider  $x(t)$  for  $t \geq n$ .

If  $x(n) > 0$  we have

$$x(n) = f\left(\sum_{i=1}^n p_i x(n-i)\right)$$

and

$$\sum_{i=1}^n p_i x(n-i) \in f([a, b])$$

because  $f([a, b])$  is an interval and  $p_i > 0$  implies  $x(n-i) > 0$ . So,

$$x(n) \in f^2([a, b]),$$

and by induction we have

$$\forall t \geq n \text{ if } x(t) > 0$$

$$\forall t \geq n \text{ if } x(t) > 0 \text{ then } x(t) \in f^i([a, b]) \forall i = 0, 1, 2.$$

Finally, by induction arguments on  $k$ , we obtain

$$\forall k \in \mathbb{N}, \forall t \geq kn, \text{ if } x(t) > 0 \text{ then } x(t) \in f^{k+1}([a, b]).$$

Now, from theorem 1.1, we know that under (H1)  $\bar{x}$  attracts the compact sets of  $\mathbb{R} - \{0\}$  under  $f$ , and in particular  $\bar{x}$  attracts  $[a, b]$  under  $f$ .

Thus if we denote by  $\{x(t_p)\}_{p \in \mathbb{N}}$  the sequence of all the positive elements of  $\{x(t)\}_{t \geq -n}$ , one has

$$x(t_p) \rightarrow \bar{x} \text{ as } p \rightarrow +\infty.$$

(because  $f^k([a, b]) \rightarrow \{\bar{x}\}$  as  $k \rightarrow +\infty$ ).

This proves the first part of proposition 4.1.

Now, we prove that the equilibrium solution of equation (4),  $\{\bar{x}(t)\}_{t \geq -n}$  defined by

$$\bar{x}(t) = \bar{x} \forall t \geq -n,$$

is stable.

Let  $\varepsilon > 0$  and  $\eta^* \in ]0, \min(\varepsilon, \bar{x})[$ . Then, from theorem 1.1 we know that  $\bar{x}$  is a stable fixed point of  $f$ . So, there exists  $\eta \in ]0, \min(\varepsilon - \eta^*, \bar{x})[$  such that

$$f^m([\bar{x} - \eta, \bar{x} + \eta]) \subset ]\bar{x} - \varepsilon + \eta^*, \bar{x} + \varepsilon - \eta^* [ \forall m \geq 0.$$

By taking

$$a = \min \left( \min_{x \in [\bar{x}, \bar{x} + \eta]} f(x), \bar{x} - \eta \right)$$

and

$$b = \max \left( \max_{x \in [\bar{x} - \eta, \bar{x}]} f(x), \bar{x} + \eta \right)$$

we have

$$f([a, b]) \subset [a, b] \subset [\bar{x} - \varepsilon + \eta^*, \bar{x} + \varepsilon - \eta^*] \subset ]\bar{x} - \varepsilon, \bar{x} + \varepsilon [$$

Now, it is clear that if we denote by  $\{x(t)\}_{t \geq -n}$  a solution of equation (4) with initial value satisfying

$$x(-i) = x_{-i} \in ]a, b[ \forall i = 1, \dots, n.$$

Then

$$x(0) \in [a, b] \subset ]\bar{x} - \varepsilon, \bar{x} + \varepsilon [$$

and by induction argument,

$$x(t) \in [a, b] \subset ]\bar{x} - \varepsilon, \bar{x} + \varepsilon [ \forall t \geq -n.$$

So  $\{\bar{x}(t)\}_{t \geq -n}$  is stable.

The proposition is proved.  $\square$

Now, we will give the proof of theorem 1.4. In the proof we will use the classical notions of omega-limit sets for an orbit of a difference equation. For this we refer to the paper by La Salle [17] for definitions and properties.



*Proof (of theorem 1.4)* Let  $X_0 \in \mathbb{R}_+^n - \{0\}$  and denote by  $\{X(t)\}_{t \in \mathbb{N}}$  the solution of equation (5) with initial value

$$X(0) = X_0.$$

If there exists  $t_0 \in \mathbb{N}$  such that

$$X(t_0) \in \{X \in \mathbb{R}_+^n : X_i > 0 \forall i = 1, \dots, n\},$$

then, since  $L$  is irreducible, we must have

$$X(t) \in \{X \in \mathbb{R}_+^n : X_i > 0 \forall i = 1, \dots, n\} \forall t \geq t_0,$$

so  $\{X(t)\}_{t \in \mathbb{N}}$  is eventually strongly positive, and from proposition 4.1, we must have

$$X(t) \rightarrow \bar{X} \text{ as } t \rightarrow +\infty.$$

If, on the other hand,  $\{X(t)\}_{t \in \mathbb{N}}$  is not eventually strongly positive, then, from the proposition 4.1, we deduce that

$$(\omega X_0) \subset E = \{X \in \mathbb{R}_+^n - \{0, \bar{X}\} : \forall i = 1, \dots, n X_i = \bar{x} \text{ or } 0\},$$

where  $\omega(X_0)$  denotes the omega-limit set of the solution of equation (5) with initial value  $X_0$ .

But, by using the fact that  $E$  is a finite set,  $\omega(X_0)$  is invariant by  $F$  (i.e.,  $F(\omega(X_0)) = \omega(X_0)$ ), and is connected-invariant (see La Salle [17] for the definition), we must have

$$\Omega(X_0) = \{C_1, \dots, C_k\}$$

where  $\{C_1, \dots, C_k\}$  is the orbite of a  $k$ -periodic solution of equation (5) which is include in  $E$ .

Now by using the proposition 1.2 on the  $k$ -periodic solutions of equation (5) in  $E$ , we know that if  $p$  is the number of eigenvalues of  $L$  in its peripheral spectrum, we must have

$$2 \leq k \leq p.$$

Theorem 1.4 is proved. □

*Proof (of corollary 1.5)* First, it is clear that from the proposition 4.1 the fixed point  $\bar{X}$  of  $F$  is stable. Now, it remains to remark that, since  $\bar{X}$  is stable and attracts the point of

$$\text{Int}(\mathbb{R}_+^n) = \{X \in \mathbb{R}_+^n : X_i > 0 \forall i = 1, \dots, n\},$$

$\bar{X}$  attracts the compact sets of  $\text{Int}(\mathbb{R}_+^n)$  because  $\text{Int}(\mathbb{R}_+^n)$  is an open subset of  $\mathbb{R}^n$ .

To conclude the proof the corollary 1.5, it is sufficient to remark that, if the matrix is primitive then every solution  $\{X(t)\}_{t \in \mathbb{N}}$  of equation (5) with initial value  $X_0$  in  $\mathbb{R}_+^n - \{0\}$  is eventually strongly positive, i.e. there exists  $t_0 \in \mathbb{N}$  such that

$$X(t) \in \{X \in \mathbb{R}_+^n : X_i > 0 \forall i = 1, \dots, n\} \forall t \geq t_0.$$

Thus by application of the theorem 1.4, we obtain the corollary 1.5.  $\square$

## 5. CONCLUSION

In this work, we have given a global description of the asymptotic behavior of equation (5), under essentially the hypothesis that  $\bar{x}$  attracts the points of  $]0, +\infty[$  under  $f$ .

Under this assumption, we have studied the change in the asymptotic behavior due to changes in the structure of the "linear part" (i.e. the passage from the irreducible primitive case to the irreducible non primitive case, and conversely) of the model. We have seen that the changes do not affect the asymptotic behavior in the interior of  $\mathbb{R}_+^n$  (i.e. we obtain the convergence of the solutions starting in the interior of  $\mathbb{R}_+^n$  to the non trivial fixed point). On the other hand, the passage from the irreducible primitive case to the irreducible non primitive case, give rise to periodic solutions on the border of  $\mathbb{R}_+^n$ , and these periodic solutions attract the solutions staying on the border of  $\mathbb{R}_+^n$ .

Many related results were obtained by several authors. We refer to the book by Kocic and Ladas [16] where many results and examples can be found.

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### References

- [1] R. J. H. Beverton and S.J. Holt, On the dynamics of exploited fish populations. U.K. Min. Agric. Fish Food, *Fishery Investigations (Ser. 2)*, **19**, (1957), p. 533.
- [2] H. Caswell, *Matrix population models*, Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts, 1989.
- [3] P. Cull, Global stability of population models, *Bull. Math. Biol.* **43**, (1981), p. 47-58.
- [4] P. Cull, Local and global stability of population models, *Biol. Cybern.* **54**, (1986), p. 141-149.
- [5] P. Cull, Stability of discrete one-dimensional population models, *Bull. Math. Biol.* **50**, (1988), p. 67-75.
- [6] L. Demetrius, Primitivity conditions for growth matrices, *Math. Biosci.* **4**, (1971), p. 129-136.
- [7] M. E. Fisher and B.S. Goh, Stability results for delayed-recruitment models in population dynamics, *J. Math. Biol.* **4**, (1984), p. 147-156.
- [8] F. R. Gantmacher, *Theory of matrices*. Vol. 2, Chelsea Publishing Company, New York, 1959.
- [9] J. Guckenheimer, G. Oster and A. Paktchi, The dynamics of density dependent population models, *J. Math. Biol.* **4**, (1977), p. 101-147.

- [10] J. K. Hale, *Asymptotic behavior of dissipative systems. Mathematical surveys and monographs*, Amer. Math. Soc. Providence, Rhode Island, 1988.
- [11] F. R. Horn and C.R. Johnson, *Matrix analysis*, Cambridge University Press, 1985.
- [12] Y. N. Huang, A counterexample of P. Cull's theorem, *Kexue Tonbao*, **31**, (1986), p. 1002-1003.
- [13] Y. N. Huang, A theorem on global stability of discrete population models, *Math. Theory. Pract.*, **1**, (1987), p. 42-43.
- [14] Y. N. Huang, A note on stability of discrete population models, *Math. Biosciences* **95**, (1989), p. 189-198.
- [15] Y. N. Huang, A note on global stability of discrete one-dimensional population models, *Math. Biosciences* **102**, (1990), p. 121-124.
- [16] V. L. Kocic and G. Ladas, *Global behavior of nonlinear difference equations of higher order with applications*, Kulwer Academic Publishers group, Dordrecht, 1993.
- [17] J. P. La Salle, The stability of dynamical systems, *SIAM*, Philadelphia, 1976.
- [18] S. A. Levin and C.P. Goodyear, Analysis of an age-structured fishery model, *J. Math. Biol.* **9**, (1980), p. 245-274.
- [19] L. Liu and J.E. Cohen, Equilibrium and local stability in a logistic matrix model for age-structured populations, *J. Math. Biol.* **25**, (1987), p. 73-88.
- [20] P. Magal and D. Pelletier, *A fixed point theorem applied to a model of population dynamics*, 1995. (To appear)
- [21] H. Minc, *Nonnegative Matrices*. John Wiley and Sons, New York, 1988.
- [22] W. E. Ricker, Stock and recruitment, *J. Fish. Res. Board Can.* **11**, (1954), p. 559.
- [23] G. Rosenkranz, On global stability of discrete population models. *Math. Biosciences* **64**, (1983), p. 227-231.
- [24] A. N. Sharkovsky, Yu. L. Maistrenko and E. Yu. Romanenko, *Difference Equations and Their Applications*, Kluwer Academic Publishers, 1985.
- [25] J. G. Shepherd, A family of general production curves for exploited populations, *Math. Biosciences* **59**, (1982), p. 77-93.
- [26] J. A. L. Silva and T. G. Hallam, Effects of delay, truncations and dependence reproduction schedules on stability of non linear Leslie matrix models, *J. Math. Biol.* **31**, (1993), p. 367-395.