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► **To cite this version:**

Pablo Amster, Gonzalo Robledo, Daniel Sepulveda. DYNAMICS OF A DISCRETE SIZE-STRUCTURED CHEMOSTAT WITH VARIABLE NUTRIENT SUPPLY. 2022. hal-03840654

**HAL Id: hal-03840654**

**<https://hal.science/hal-03840654>**

Preprint submitted on 5 Nov 2022

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# DYNAMICS OF A DISCRETE SIZE-STRUCTURED CHEMOSTAT WITH VARIABLE NUTRIENT SUPPLY

PABLO AMSTER, GONZALO ROBLEDO & DANIEL SEPÚLVEDA

ABSTRACT. This article revisits and extends to the nonautonomous framework the results about the dynamics of a discrete and nonlinear matrix model describing the growth of a size-structured single microbial population in an autonomous chemostat, which has been introduced by T.B. Gage et.al and H.L. Smith. The first and the second result provide a threshold determining either the extinction or the persistence of the total biomass. The main result establishes a set of sufficient conditions ensuring the existence, uniqueness and global attractiveness of an  $\omega$ -periodic solution.

## 1. INTRODUCTION

The mathematical modeling of the dynamics in a chemostat has an impressive amount of research on a wide scope of problems by using a plethora of approaches [14]. Nevertheless, in midst of that context, there exist topics sparingly treated. This is the case of the modeling of the dynamics of a single microbial biomass size-structured by using nonlinear matrix difference equations, which started with the seminal work of T. Gage et al. in [7], revisited by H.L. Smith in [15], both in the autonomous context. The main contribution of this article is to extend the above mentioned works to the nonautonomous framework, with specific focus on the periodic case.

**1.1. The chemostat.** The chemostat is a device where a microbial species is cultivated in a liquid medium containing nutrients to be consumed by the species. The nutrients are assumed to be in abundance with the exception of a specific one which is named *limiting substrate* or *nutrient*. The dynamics between the microbial biomass and the nutrient is described as follows: the nutrient is pumped into in with fixed rate at either fixed or variable concentration (input) while the mixture of microbial biomass and nutrient is removed to the exterior with fixed rate (washout). Moreover, we have to consider the consumption of the nutrient and the biomass growth.

In addition, we will take into account the following environmental, mechanical and biologic assumptions:

- The liquid medium is uniform in space.
- The substrate and the microorganisms are uniformly distributed in space.

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2020 *Mathematics Subject Classification.* 34K13, 34K60, 92D25.

*Key words and phrases.* Chemostat, Difference equations, Periodic solutions, Nonautonomous dynamics.

This research is partially supported by PROGRAMA REGIONAL MATH-AMSUD MATH2020006. The first author is supported by projects UBACyT 20020190100039BA and PIP 11220200100175CO, CONICET. The second author is supported by FONDECYT 1210733 and the third author is supported by FONDECYT 11190457.

- The input and the washout rate are similar.
- Respiration and mortality are negligible.
- The only organism-to-organism interaction is mediated by the nutrient concentration: the consumption of nutrient has a direct effect on the microbial species.

**1.2. The chemostat ODE models and its shortcomings.** The most known chemostat model satisfying the above assumptions is described by the system of ordinary differential equations

$$\begin{cases} s'(t) &= \overbrace{Ds^0(t)}^{\text{Input}} - \overbrace{Ds(t)}^{\text{Washout}} - \overbrace{\gamma^{-1}f(s(t))x(t)}^{\text{Nutrient consumption}} \\ x'(t) &= \underbrace{x(t)f(s(t))}_{\text{Microbial growth}} - \underbrace{Dx(t)}_{\text{Washout}}, \end{cases}$$

where  $s(t)$  and  $x(t)$  are the densities of the nutrient and the microbial biomass respectively. The nutrient is pumped into in with fixed rate  $D > 0$  at concentration described by  $t \mapsto s^0(t) > 0$ , which has been supposed constant, periodic, almost periodic or continuous in the literature and we refer to [1, Table 1] for a summary. Note that the work with ODE systems assumes implicitly the uniform distribution of nutrient and microbial biomass in the liquid medium. Moreover, the absence of mortality of the microbial species combined with the fact that the input and the washout rate are equal to  $D$  imply that the transformation  $v(t) = s(t) + \gamma^{-1}x(t)$  yields to

$$v'(t) = -Dv(t) + Ds^0(t),$$

and for any bounded and continuous inputs of nutrient  $t \mapsto s^0(t) > 0$  there exists a unique positive solution

$$v^*(t) = D \int_{-\infty}^t e^{-D(t-r)} s^0(r) dr$$

such that any solution  $t \mapsto v(t)$  verifies  $v(t) - v^*(t) \rightarrow 0$  when  $t \rightarrow +\infty$ .

The last assumption, namely, that the only organism-to-organism interaction is mediated by the nutrient concentration, is taken into account by considering that the consumption of substrate is proportional to the per capita growth rate of the biomass, that is

$$\frac{x'(t)}{x(t)} = f(s(t)).$$

As  $f(\cdot)$  describes the consumption of nutrient and its conversion in microbial biomass, the constant  $\gamma^{-1}$  is a yield coefficient reflecting this conversion. The modeling of  $f(\cdot)$  is dependent of the specific nutrient and microbial biomass but usually it is assumed that satisfies the following qualitative properties:

- (H1)** The function  $f: \mathbb{R}_+ \rightarrow \mathbb{R}$  satisfies: a)  $f \in C^1(\mathbb{R}_+, \mathbb{R})$  and  $f(0) = 0$ ; b)  $f'(S) > 0$  for any  $S \in \mathbb{R}_+$  and c)  $f'(S) \leq f'(0)$  for any  $S \in \mathbb{R}_+$ .

A serious shortcoming of the above model is the underlying assumption that the microbial cells have constant size and density, which only allows the description of the growth of the total microbial biomass while processes as DNA replication, unicellular growth and cellular division are not considered. This lack has been addressed in the seminal work of T. Gage et al. [7], which introduces a size-structured model of one species chemostat described by an autonomous and nonlinear system of  $r$  difference equations, where the modeling of the size structure of the microbial

cells is carried out by a matrix formalism reminiscent to the Leslie matrices. This formulation was improved by H.L. Smith in [15] who also considered two competing species in the reactor and proved that the competitive exclusion principle is verified.

The Gage-Smith model has been extended to  $n$  competitors in [16], where the competitive exclusion is verified. These results are also presented in [17, Ch.4]. Later, in [3], the hypotheses of homogeneity in the cell division assumed in the Gage-Smith model are reviewed and extended to the case where the division of cells can occur in several biomass classes. In the last years, the competitive model of Gage-Smith has been generalized in [18, 19] by considering  $f$  with inhibitory kinetics, namely, in **(H1)** it is assumed that  $f$  is a unimodal function.

**1.3. Novelty of this work.** We generalize the Gage-Smith model by considering a nonautonomous input of a nutrient. The importance and applications of considering bounded variable nutrient inputs has been addressed in the continuous framework by the authors in [1] and the conclusions are certainly valuable for the discrete case. In particular, we will focus on cases in which the input of nutrients are periodic.

The first results provide sufficient conditions ensuring either the washout (extinction) or the permanence of the microbial species. We point out the originality of these conditions and emphasize that can be understood in terms of the lower and upper Bohl exponents associated to a scalar linear difference equation. The main result is focused in the  $\omega$ -periodic case and gives a set of sufficient conditions ensuring the existence, uniqueness and attractiveness of a nontrivial  $\omega$ -periodic solution. The proof of this result emulates two steps of the autonomous case: i) the original  $r$ -dimensional system is reduced to a planar one, ii) The asymptotic behavior of the planar system allows to deduce asymptotic properties of the  $r$ -dimensional system by using the Golubitsky ergodic weak theorem. Nevertheless, we point out that our treatment is totally different. Firstly, the asymptotic behavior of the planar system is addressed by constructing a Poincaré map and then followed by the study of a non-homogeneous linear scalar equation, which is asymptotically equivalent to a  $\omega$ -periodic linear scalar equation. Finally, we adapt the use of the weak ergodic theorem for a sequence of maps defined with the use of Poincaré operators and Floquet Theory.

Last but not least, a formal novelty is our revisiting to the construction of the Gage-Smith model in order to contribute to a better understanding of a still little known model, which has been described only in [7],[15],[2] and [3]. This structured class model involves: size classes, cell growth and cell division. We shall try to make a clearer and detailed deduction of each of these topics, which, beyond the similarities, is not a mere repetition since it has original aspects mainly in the modeling of the cell growth. We trust that our exposition will be helpful for stimulating the study of this model.

## 2. THE DISCRETE TIME VARYING MODEL

**2.1. Basic assumptions.** To introduce a structure into the size of the cells, the microbial biomass is divided in  $r > 1$  size classes. The biomass of the cells at the  $j$ -th class size, with  $j \in \{1, \dots, r\}$ , at time  $t \in \mathbb{Z}$  is denoted by  $y_t^j$  while the amount of nutrient at time  $t$  is denoted by  $S_t$ . We also define the vectors  $\mathbf{x}_t = (y_t^1, y_t^2, \dots, y_t^r)^T \in \mathbb{R}^r$  and  $\mathbf{1} = (1, \dots, 1) \in \mathbb{R}^r$ .

The equation describing the nutrient dynamics is challenging in this class of models, since it needs to be consistent in the relative times of nutrient consumption

and pumping out over an iteration interval, see [15, pp.737]. We consider that, in a period of iteration, the nutrient is consumed first and then evacuated, in this way the evolution of the nutrient  $S_t$  in one unit of time is described as follows:

$$(2.1) \quad S_{t+1} = S_t - \underbrace{f(S_t)(\mathbf{1} \cdot \mathbf{x}_t)}_{\text{Nutrient consumption}} - \underbrace{E(S_t - f(S_t)(\mathbf{1} \cdot \mathbf{x}_t))}_{\text{Washout}} + \underbrace{E S_t^0}_{\text{Input}}.$$

That is, first, the nutrient is consumed by the biomass, second, the nutrient is pumped into in with fixed rate  $E \in (0, 1)$  at variable bounded concentration  $S_t^0$  with  $\inf_{t \in \mathbb{Z}} S_t^0 > 0$ , and the liquid medium inside the vessel is expelled with similar rate  $E$ . The consumption of nutrient is described by  $f(\cdot)$  which satisfies the assumptions **(H1)**, similarly as in the continuous case.

To describe the dynamics of the total biomass vector  $\mathbf{x}_t$ , we need to introduce additional assumptions and complementary descriptions:

**(SC1)** The microorganisms are born with a biomass  $b$  and grow to double in size.

**(SC2)** The reproduction of cells is given by the division of mature cells, with a mass equal to  $2b$ , into two cells of equal size.

**(SC3)** The size of organisms increases exponentially in an environment where the nutrient is abundant and constant.

**(SC4)** The average nutrient uptake rate per unit biomass is constant across all size classes.

More specifically, some consequences of **(SC1)**–**(SC4)** are:

- i) The growth of every microbial cell passes through  $r > 1$  size classes. The average mass of an individual cell at the  $i$ -th class will be assumed as  $2^{\frac{i-1}{r}} b = M^{i-1} b > 0$  where  $M = 2^{\frac{1}{r}}$ , then:

Class	Average biomass of cell
1	$2^{\frac{0}{r}} b = M^0 b$
2	$2^{\frac{1}{r}} b = M^1 b$
$\vdots$	$\vdots$
$r$	$2^{\frac{r-1}{r}} b = M^{r-1} b$

In absence of washout, the number of cells at the  $i$ -th class is given by

$$(2.2) \quad n_i(t) = \frac{y_i^t}{M^{i-1} b}.$$

- ii) In the  $i$ -th classes with  $i = 2, \dots, r-1$  there are neither birth of new cells nor division of cells. The cells only can either advance to the next size class or stay at the same one. Then,  $n_i(t)$  can be decomposed as follows:

$$(2.3) \quad n_i(t) = n_i^s(t) + n_i^p(t),$$

where  $n_i^s(t)$  is the number of cells that remain at the class  $i$  at the next unit time while  $n_i^p(t)$  is the number of cells reaching the  $i+1$ -th class at the next unit time.

- iii) The first class is named *birth class*. The cells can either stay at this class or advance to the second one in the next unit time. The decomposition (2.3) can be also applied for  $i = 1$ . We recall that there are no division of cells.
- iv) The  $r$ -th class will be called the *maximal size class*, where the cells reach a biomass  $2b$  and could divide in two cells of biomass  $b$ , which go back to the

birth class. In this context, the decomposition (2.3) is still valid but  $n_r^p(t)$  should be understood as the number of cells that are duplicated, then the number of cells that reach the birth class in the next time unit is  $2n_r^p(t)$ .

- v) The equation (2.3) combined with the above property allows an alternative description for  $n_i(t+1)$  as follows:

$$(2.4) \quad n_i(t+1) = \begin{cases} n_1^s(t) + 2n_r^p(t) & \text{for } i = 1 \\ n_i^s(t) + n_{i-1}^p(t) & \text{for } i = 2, \dots, r. \end{cases}$$

The equations (2.3)–(2.4) prompt to introduce the fraction of cells in the  $i$ -th class at time  $t$  that, in absence of washout, are transferred to the  $i+1$ -th class at the next unit time:

$$(2.5) \quad P_i(S_t) = \frac{n_i^p(t)}{n_i(t)} \quad \text{for any } t \geq 0.$$

A direct consequence of the above identity is

$$(2.6) \quad \frac{n_i^s(t)}{n_i(t)} = 1 - P_i(S_t).$$

To describe the dependence of the proportion  $P_i$  on the concentration of substrate at time  $t$ , we have to consider the difference of biomass  $y_{t+1}^{i+1} - y_t^i$  as follows

$$y_{t+1}^{i+1} - y_t^i = R_i(t) + \Delta_i(t),$$

where  $\Delta_i(t)$  is the amount of biomass from the  $i$ -th size class reaching the  $i+1$ -th size class after one iteration period. Moreover,  $R_i(t)$  is the amount of biomass remaining at the same class after one iteration period. By (2.3)–(2.4), we have

$$\begin{aligned} y_{t+1}^{i+1} - y_t^i &= M^i b n_{i+1}(t+1) - M^{i-1} b n_i(t) \\ &= M^i b [n_{i+1}^s(t) + n_i^p(t)] - M^{i-1} b [n_i^s(t) + n_i^p(t)] \\ &= \underbrace{M^i b n_{i+1}^s(t) - M^{i-1} b n_i^s(t)}_{= R_i(t)} + \underbrace{n_i^p(t) [M^i b - M^{i-1} b]}_{= \Delta_i(t)} \end{aligned}$$

and the transfert of biomass from the  $i$ -th size class to the  $i+1$ -th one after one iteration period is described by the term  $n_i^p(t)[M^i b - M^{i-1} b]$ .

A key assumption will be that the biomass transfert  $\Delta_i(t)$  above described is directly proportional to the biomass  $y_t^i$  while the proportionality constant is dependent of the consumption of substrate as follows:

$$\Delta_i(t) = n_i^p(t)[M^i b - M^{i-1} b] = \underbrace{y_t^i \cdot f(S_t)}_{\text{Biomass} \cdot \text{Feed rate}} \quad \text{or equivalently} \quad \frac{\Delta_i(t)}{y_t^i} = f(S_t).$$

Now, it is observed that the number of cells reaching the  $i+1$ -th class after one iteration period can be obtained by dividing the increase in biomass of organisms of the  $i$ -th class by the difference of average size of both class, namely

$$(2.7) \quad n_i^p(t) = \frac{y_t^i f(S_t)}{M^{i+1} b - M^i b},$$

and by combining equations (2.5) and (2.7), it is deduced that

$$(2.8) \quad P_i(S_t) = \frac{1}{n_i(t)} \frac{y_t^i f(S_t)}{(M^{i+1} b - M^i b)} = \frac{f(S_t)}{M - 1}, \quad 1 \leq i \leq r.$$

Since the proportions  $P_i(S_t)$  are independent of the  $i$ -th class, from now on, will be denoted  $P(S_t)$ . Note that the proportion  $P(S_t)$  is not necessarily well defined and it is reasonable to introduce the additional assumption:

**(H2)** The function  $f$  is such that  $\lim_{u \rightarrow +\infty} f(u) := f_{\text{sup}} < M - 1$ .

A first regard to **(H2)** can give the wrong idea that it is an *ad-hoc* hypothesis. However, a better understanding of this assumption will be achieved by considering the duplication time of a newborn cell, which is the subject of the next subsection.

**2.2. Duplication time and well posedness of the problem.** To ensure the well posedness of the model, it will be necessary to take into account the minimal duplication time  $\mathcal{T}_{\text{min}}$  for a newborn cell and its relation with the length  $T$  of the iteration interval, the number  $r$  of classes and the uptake function  $f$ .

The minimal duplication time can be achieved in favorable conditions as: i) no outflow, namely  $E = 0$ , ii) infinite nutrient, namely,  $S_t$  large enough such that  $f(S_t) \simeq f_{\text{sup}}$  and iii) all the biomass from the  $i$ -th size class reaches the  $i + 1$ -th one after one iteration period, that is  $P(S_1) = 1$  or equivalently  $R_i(t) = 0$  and  $\Delta_i(t) = y_t^i f_{\text{sup}}$ . In addition to these assumptions, we consider that the duplication will be reached after  $r$  iterations. Namely, the number of cells at the  $i$ -th class on time is described by the equation  $y_{t+1}^{i+1} - y_t^i = \Delta_i(t)$  or equivalently

$$y_{t+1}^{i+1} = (1 + f_{\text{sup}})y_t^i \quad \text{with } y_0^1 = b,$$

and it follows that  $y_n^{n+1} = (1 + f_{\text{sup}})^n b$ . Since we know that  $y_{r-1}^r = 2^{\frac{r-1}{r}} b$ , it is deduced that  $(1 + f_{\text{sup}})^r = 2$ .

From the above equation, it is possible to obtain constraints on the iteration period  $T$  and the number of classes  $r$ , which depend on the minimum doubling time  $\mathcal{T}_{\text{min}}$  and the maximal growth rate  $\hat{\mu}_{\text{max}} := \ln(2)/\mathcal{T}_{\text{min}}$ . We observe that the duplication is obtained after passing through each of the  $r$  classes and given that the iteration period has a length of  $T$ , thus obtaining the equation  $rT = \mathcal{T}_{\text{min}}$ , it follows that in general  $rT \leq \mathcal{T}_{\text{min}}$  must be satisfied to ensure that cell duplication takes place in class  $r$ -th and not before.

It is worth mentioning that each species grown in the bioreactor has its own parameters, which cannot be adjusted, in particular the minimum doubling time and the maximum growth rate  $\hat{\mu}_{\text{max}}$ . We also observe that the maximum growth rate must be rescaled in time, considering  $f_{\text{sup}} := \hat{\mu}_{\text{max}}T$  to define the nutrient uptake function  $f(S)$  for the discrete model. In this way, the population's own parameters,  $\hat{\mu}_{\text{max}}$  and  $\mathcal{T}_{\text{min}}$ , constrain both the iteration period  $T$  and the number of classes  $r$  by means of **(H2)** and the inequality  $rT \leq \mathcal{T}_{\text{min}}$ . We conclude by mentioning that the imposition of upper bounds for  $f'(0)$  also has an impact on the iteration period.

**2.3. Deduction of the equations.** We represent the dynamics of biomass in the different size classes in Figure 1.

Notice that (2.8) says that the cellular growth at any size class is explicitly dependent of the consumption of limiting nutrient described by (2.1). On the other hand, the number of cells at the  $i$ -th class passing towards the next class at the next unit of time increases for bigger concentrations of limiting nutrient since, as stated in **(H1)**,  $f$  is an increasing function.

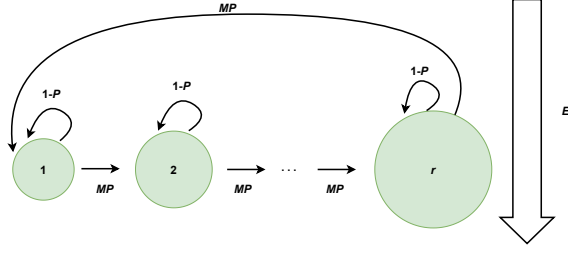


FIGURE 1. Scheme of dynamics in the different size classes.

Now, notice that the number of cells at the  $i$ -th class can be written as follows:

$$(2.9) \quad n_i(t+1) = \begin{cases} (1-E)n_i^s(t) + (1-E)2n_r^p(t) & \text{if } i = 1 \\ (1-E)n_i^s(t) + (1-E)n_{i-1}^p(t) & \text{if } i = 2, \dots, r. \end{cases}$$

The identities (2.5)–(2.6) allow to re-write (2.9) for  $i \in \{2, \dots, r\}$  as follows:

$$\begin{aligned} n_i(t+1) &= (1-E)n_i(t) \frac{n_i^s(t)}{n_i(t)} + (1-E)n_{i-1}(t) \frac{n_{i-1}^p(t)}{n_{i-1}(t)} \\ &= (1-E)n_i(t)[1 - P(S_t)] + (1-E)n_{i-1}(t)P(S_t). \end{aligned}$$

Let us multiply the above identity by  $M^{i-1}b$  to obtain

$$\underbrace{M^{i-1}bn_i(t+1)}_{y_{t+1}^i} = (1-E) \underbrace{M^{i-1}bn_i(t)}_{y_t^i} [1 - P(S_t)] + (1-E)M \underbrace{M^{i-2}bn_{i-1}(t)}_{y_t^{i-1}} P(S_t)$$

and, from (2.2), this is equivalent to

$$y_{t+1}^i = (1-E)[1 - P(S_t)]y_t^i + (1-E)MP(S_t)y_t^{i-1}.$$

Similarly, as  $2 = MM^{r-1}$  we multiply by  $b$  and for  $i = 1$  we deduce that

$$y_{t+1}^1 = (1-E)[1 - P(S_t)]y_t^1 + (1-E)MP(S_t)y_t^r,$$

and the dynamics of  $\mathbf{x}_t = (y_t^1, \dots, y_t^r)^T$  can be summarized as follows:

$$\begin{cases} y_{t+1}^1 &= (1-E)[1 - P(S_t)]y_t^1 + (1-E)MP(S_t)y_t^r \\ y_{t+1}^2 &= (1-E)MP(S_t)y_t^1 + (1-E)[1 - P(S_t)]y_t^2 \\ &\vdots \\ y_{t+1}^r &= (1-E)MP(S_t)y_t^{r-1} + (1-E)[1 - P(S_t)]y_t^r \end{cases}$$

or equivalently as

$$(2.10) \quad \mathbf{x}_{t+1} = A(S_t)\mathbf{x}_t - EA(S_t)\mathbf{x}_t,$$



where  $A(\cdot)$  is defined by

$$(2.11) \quad A(\cdot) = \begin{pmatrix} 1 - P(\cdot) & 0 & \dots & & & MP(\cdot) \\ MP(\cdot) & 1 - P(\cdot) & 0 & \dots & & 0 \\ 0 & MP(\cdot) & 1 - P(\cdot) & 0 & \dots & 0 \\ & & & \ddots & & 0 \\ 0 & \dots & & & MP(\cdot) & 1 - P(\cdot) \end{pmatrix},$$

The coupling of the equations (2.1) and (2.10) leads to

$$(2.12) \quad \begin{cases} S_{t+1} = \overbrace{E S_t^0 + S_t}^{\text{Input}} - \overbrace{f(S_t)(\mathbf{1} \cdot \mathbf{x}_t)}^{\text{Nutrient consumption}} - \overbrace{E(S_t - f(S_t)(\mathbf{1} \cdot \mathbf{x}_t))}^{\text{Washout}}, \\ \mathbf{x}_{t+1} = \underbrace{A(S_t)\mathbf{x}_t}_{\text{Biomass growth}} - \underbrace{EA(S_t)\mathbf{x}_t}_{\text{Washout}}. \end{cases}$$

Note that assumptions about uniform distribution of nutrient and biomass in the liquid medium are implicitly satisfied since (2.12) is a system of difference equations. Moreover, a careful reading of the deduction of Eqs. (2.12) shows that the mechanical and biologic assumptions stated in the introduction are also satisfied. In fact, the equations (2.1), (2.8) and (2.9) show that we are considering  $E \in (0, 1)$  as input and washout rate, the respiration and mortality are negligible and the species growth depends directly on its consumption of the nutrient.

**2.4. About the matrices  $A(S_t)$ .** The matrices  $A(S_t) \in M_r(\mathbb{R})$  have the following properties, which shall be useful to study the system (2.12):

1)  $A(S_t)$  are *nonnegative* for  $S_t > 0$ . This fact follows from the identity  $P(S_t) = f(S_t)/(M - 1)$  stated by (2.8) combined with **(H1)** and **(H2)**.

2)  $A(S_t)$  are *circulant* for any  $S_t > 0$ , namely, the  $i$ -th rows with  $i \in \{2, \dots, r\}$  are cyclic permutations of the first one. More precisely, given  $a_t = 1 - P(S_t)$  and  $b_t = MP(S_t)$ , we have  $A(S_t) = \text{Circ}(a_t, 0, \dots, 0, b_t)$ . In other words,

$$(2.13) \quad A(S_t) = a_t I_r + b_t C, \quad \text{where } C := \text{Circ}(0, \dots, 1).$$

In addition,  $A(S_t)$  are *semi-magic* matrices for  $S_t > 0$  since the sum of each row or column is equal to  $1 + (M - 1)P(S_t) = \{1 + f(S_t)\}$ .

3)  $A(S_t)$  are *irreducible* for  $S_t > 0$ : Let us recall (see [14]) that a matrix is irreducible if it cannot be put as a upper triangular block form with square diagonal blocks and nonzero upper block by reordering the standard basis vectors. A useful criterion for irreducibility is given by the study of the associated graph  $G_A$  of  $A(S_t) \in M_r(\mathbb{R})$ : Let  $P_1, P_2, \dots, P_r$  be  $r$  points in the plane. If  $A_{ij}(S_t) \neq 0$ , then there exists a line  $P_i P_j$  connecting  $P_i$  and  $P_j$  and  $A(S_t)$  is irreducible if for each pair  $(P_i, P_j)$  there exists a path  $P_i P_{k_1} P_{k_1} P_{k_2} \dots P_{s-1} P_j$  connecting  $P_i$  and  $P_j$ .

Observe that the lower diagonal terms given by  $A_{i,i-1}(S_t) = MP(S_t)$  for any  $i \in \{2, \dots, r\}$  also coincide with  $A_{1,r}(S_t)$  and the irreducibility of  $A(S_t)$  follows by studying its associated graph.

4)  $A(S_t)$  are *primitive* for any  $S_t > 0$ , i.e.  $A(S_t)^m$  is positive for some  $m$ . It is seen that positiveness holds for arbitrary  $m \geq r$ : indeed, from (2.13) we note that

$$A^m(S_t) = \sum_{k=0}^m \binom{m}{k} a_t^{m-k} b_t^k C^k$$

and it follows inductively that

$$C_{ij}^k = \begin{cases} 1 & \text{if } i \equiv j + k(r) \\ 0 & \text{otherwise.} \end{cases}$$

This means that for all  $i, j \in \{1, \dots, r\}$  there exists  $k \leq r$  such that  $C_{ij}^k = 1$  and, consequently,  $A^m(S_t)_{ij} > 0$  for all  $m \geq r$ . In addition, this condition (see e.g, [5, p.28]) is equivalent to the fact that the matrix has only one eigenvalue with modulus equal to its spectral radius.

**Lemma 1.** *For  $S_t > 0$ , the spectral radius of  $(1 - E)A(S_t)$  is*

$$(2.14) \quad \rho((1 - E)A(S_t)) = (1 - E)\{1 + f(S_t)\}.$$

*Proof.* From the Perron–Frobenius Theorem for non negative irreducible matrices [14, p.257] we have that  $\rho((1 - E)A(S_t))$  is a real number and a simple eigenvalue. In addition, see e.g [11, p.141], the spectral radius satisfies the inequalities

$$\min_i \sum_{j=1}^r (1 - E)A_{ij}(S_t) \leq \rho((1 - E)A(S_t)) \leq \max_i \sum_{j=1}^r (1 - E)A_{ij}(S_t)$$

and the identity (2.14) follows from the fact that  $(1 - E)A(S_t)$  is semi-magic.  $\square$

**Corollary 1.** *For  $S_t > 0$  and any  $m > \ell \geq 0$  it follows that*

$$(2.15) \quad \rho \left( \prod_{t=\ell}^{\ell+m-1} (1 - E)A(S_t) \right) \leq (1 - E)^m \prod_{t=\ell}^{\ell+m-1} \{1 + f(S_t)\}$$

*Proof.* As the matrices  $(1 - E)A(S_t)$  are circulant, they are commutative [11, p.113] and a consequence of the Gelfand’s formula for the spectral radius is that

$$\rho \left( \prod_{t=\ell}^{\ell+m-1} (1 - E)A(S_t) \right) \leq \prod_{t=\ell}^{\ell+m-1} \rho((1 - E)A(S_t)).$$

Thus, the result follows from Lemma 1.  $\square$

### 3. BASIC RESULTS

**3.1. A reduced system.** Similarly as in the continuous case, **(B1)–(B2)** imply that the change of variables  $\Sigma_t = S_t + \mathbf{1} \cdot \mathbf{x}_t$ , where  $\mathbf{1} = (1, \dots, 1) \in \mathbb{R}^r$  leads to

$$(3.1) \quad \Sigma_{t+1} = (1 - E)\Sigma_t + ES_t^0, \quad t \geq 0.$$

Let us recall that in subsection 2.1 we assumed that  $\inf_{t \in \mathbb{Z}} S_t^0 > 0$  and  $S_t^0$  is bounded in  $\mathbb{Z}$ , which allows to define the solutions of (3.1) on  $\mathbb{Z}$ . Moreover, we can define

$$(3.2) \quad 0 < S_{\inf}^0 := \inf_{t \in \mathbb{Z}} S_t^0 \quad \text{and} \quad S_{\sup}^0 := \sup_{t \in \mathbb{Z}} S_t^0.$$

**Remark 1.** *Every solution of (3.1) with  $\Sigma_0 > 0$  verifies  $\Sigma_t > 0$  for any  $t \geq 0$ . Indeed, any solution has the form*

$$\Sigma_t = (1 - E)^t \Sigma_0 + \sum_{k=0}^{t-1} (1 - E)^{t-k-1} ES_k^0,$$

*and the positiveness follows from the fact that  $\Sigma_0 > 0$  and  $S_t^0 > 0$  for any  $t \geq 0$ .*

**Lemma 2.** Any solution  $\Sigma_t$  of (3.1) verifies

$$\lim_{t \rightarrow +\infty} (\Sigma_t - \Sigma_t^*) = 0, \quad \text{with } |\Sigma_t - \Sigma_t^*| = |\Sigma_0 - \Sigma_0^*|(1 - E)^t,$$

where  $t \mapsto \Sigma_t^*$  is defined by

$$(3.3) \quad \Sigma_t^* = E \sum_{j=-\infty}^{t-1} (1 - E)^{t-j-1} S_j^0$$

and is the unique  $\mathbb{Z}$ -bounded solution of (3.1). Moreover if  $\Sigma_0 < \Sigma_0^*$  (resp.  $\Sigma_0 > \Sigma_0^*$ ) then  $\Sigma_t < \Sigma_t^*$  (resp.  $\Sigma_t > \Sigma_t^*$ ) for any  $t \geq 0$ .

*Proof.* As  $S_t^0$  is a bounded sequence and  $E \in (0, 1)$ , it is easy to verify that (3.3) is well defined and is a bounded sequence. A direct computation shows that

$$\Sigma_{t+1}^* = E \sum_{j=-\infty}^t (1 - E)^{t-j} S_j^0 = (1 - E)E \sum_{j=-\infty}^{t-1} (1 - E)^{t-j-1} S_j^0 + ES_t^0$$

and we can deduce that  $t \mapsto \Sigma_t^*$  is a bounded solution of (3.1).

In order to prove that (3.3) is the unique bounded solution, let us consider a  $\mathbb{Z}$ -bounded solution  $t \mapsto \tilde{\Sigma}_t$  of (3.1) and note that

$$\tilde{\Sigma}_t - \Sigma_t^* = (1 - E)^t (\tilde{\Sigma}_0 - \Sigma_0^*),$$

is also bounded on  $\mathbb{Z}$ . Now, if  $\tilde{\Sigma}_0 \neq \Sigma_0^*$ , then the left hand side term diverges when  $t \rightarrow -\infty$ , obtaining a contradiction.

Finally, given any solution  $t \mapsto \Sigma_t$ , let  $e_t = \Sigma_t^* - \Sigma_t$  and notice that

$$(3.4) \quad e_{t+1} = (1 - E)e_t$$

has solutions  $e_t = (1 - E)^t (\Sigma_0^* - \Sigma_0)$  and we verify that  $\Sigma_t^*$  is the unique bounded solution and is attractive for  $t \rightarrow +\infty$  since  $e_t \rightarrow 0$  when  $t \rightarrow +\infty$ .  $\square$

**Remark 2.** The identity

$$E \sum_{j=-\infty}^{t-1} (1 - E)^{t-j-1} = E \sum_{k=0}^{\infty} (1 - E)^k = 1$$

implies the following properties:

- i) If  $S_t^0 \equiv S^0 > 0$ , then  $\Sigma_t^* = S^0$  for any  $t$ ,
- ii) As  $S_{\inf}^0 \leq S_t^0 \leq S_{\sup}^0$  for any  $t \in \mathbb{Z}$  then  $S_{\inf}^0 \leq \Sigma_t^* \leq S_{\sup}^0$  for any  $t \geq 0$ . In addition, the inequality is strict when  $S_t^0$  is not constant.
- iii) A direct consequence of the discrete Lebesgue dominated convergence Theorem is that if  $S_t^0 \rightarrow S^0$  when  $t \rightarrow \infty$  then  $\Sigma_t^* \rightarrow S^0$  when  $t \rightarrow \infty$ .

**Remark 3.** As  $\Sigma_t^*$  is a bounded sequence, the numbers  $\Sigma_{\inf}^*$  and  $\Sigma_{\sup}^*$  can be defined similarly as in (3.2) and by statement ii) from the previous remark we can see that

$$S_{\inf}^0 \leq \Sigma_{\inf}^* \leq \Sigma_{\sup}^* \leq S_{\sup}^0.$$

**Remark 4.** It is important to note that if  $t \mapsto S_t^0$  is  $\omega$ -periodic then  $t \mapsto \Sigma_t^*$  is also  $\omega$ -periodic. This property can be generalized to other function spaces and is due to the fact that (3.1) admits a unique  $\omega$ -periodic when  $S_t^0$  is  $\omega$ -periodic.

Since  $A(S_t)$  are semi-magic matrices we note that

$$\mathbf{1} \cdot A(S_t) = [1 + (M - 1)P_t]\mathbf{1} = [1 + f(S_t)]\mathbf{1},$$

and the total biomass  $U_t = \mathbf{1} \cdot \mathbf{x}_t$  has a behavior described by

$$U_{t+1} = (1 - E)[1 + f(S_t)]U_t,$$

which allows us to construct the reduced planar system

$$(3.5) \quad \begin{cases} U_{t+1} &= (1 - E)(1 + f(S_t))U_t, \\ S_{t+1} &= (1 - E)S_t - (1 - E)f(S_t)U_t + ES_t^0. \end{cases}$$

The next subsections study basic qualitative properties of (3.5) as boundedness and positiveness of the solutions. In addition, we will search sufficient conditions ensuring either the washout of the total biomass or its persistence.

**3.2. Boundedness and positiveness of solutions.** An accurate description of the biological context needs to consider new restrictions for the total biomass  $U_t$  since, otherwise, the total amount of nutrient consumed in the  $t$ -th iteration period, namely  $U_t f(S_t)$ , could exceed the concentration of the substrate available, which would imply  $S_{t+1} < 0$ . In consequence, additional work must be done to rule out this case and it will be useful to write the second equation of (3.5) as:

$$(3.6) \quad S_{t+1} = (1 - E)[S_t - f(S_t)U_t] + ES_t^0.$$

In the autonomous case, namely, when  $S_t^0 := S^0 = \Sigma_{\text{sup}}^*$  for any  $t$ , this positiveness problem has been addressed by finding sufficient conditions ensuring that  $S_t - f(S_t)U_t > 0$  for any  $t \geq 0$  which implies by (3.6) that  $S_{t+1} > 0$ . In fact, in [15, p.739] the authors assume that  $\frac{f(S)U}{S} < \eta$  for some  $\eta \in (0, 1)$ . Moreover, to verify this last property, in [3, p.322] the authors use  $f'(S_t) < f'(0)S_t$  combined with the concavity of  $f$  and prove that if there exists  $V > S^0$  and  $\eta \in (0, 1)$  such that  $f'(0)V < \eta$ , then  $S_t > 0$  for any  $t \geq 0$ . A careful reading of these results shows that the existence of a positively invariant and bounded set of initial conditions plays a key role.

In the non autonomous case, we will consider the following *invariance conditions* in order to address the positiveness problem:

**(I1)** The function  $f$  and the input of limiting substrate  $S_t^0$  are such that

$$f'(0)S_{\text{sup}}^0 \leq 1 + 2\sqrt{\frac{f'(0)ES_{\text{inf}}^0}{1 - E}}.$$

**(I2)** The function  $f$  and the unique bounded solution  $\Sigma_t^*$  of (3.1) are such that

$$f'(0)\Sigma_{\text{sup}}^* < 1.$$

While the condition **(I2)** is reminiscent to the conditions considered in [3] and [15] since  $S^0 = \Sigma_{\text{sup}}^*$  in the autonomous case. We remark that **(I1)** provides a new perspective since, instead of focusing on  $S_t - f(S_t)U_t$ , it sheds light on the positiveness of the right side of (3.6). Let us note that **(I1)** takes advantage of the fact that  $S_{\text{inf}}^0 > 0$  and can be verified even when **(I2)** is not.

**Remark 5.** We stress that conditions **(I1)** and **(I2)** are independent. For example, consider a 2-periodic function  $S^0$  with  $S_0^0 = 1$  and  $S_1^0 = S > 1$ , then

$$\Sigma_0^* = \frac{1 - E + S}{2 - E} > 1, \quad \Sigma_1^* = (1 - E)\Sigma_0^* + E < \Sigma_0^*.$$

Observe that, if  $E$  is small, then

$$\Sigma_{\max}^* = \Sigma_0^* \simeq (S+1)/2.$$

Given  $f$  such that **(H1)** and **(H2)** are satisfied and  $f'(0) < 1$ , we may choose  $S > 1$  such that

$$\frac{1}{S} < f'(0) < \frac{2}{S+1}.$$

Thus, taking  $E$  sufficiently small, condition **(I2)** is verified although **(I1)** does not hold. On the other hand, if the oscillation of  $S^0$  is not large, then **(I1)** is less restrictive than **(I2)**: in particular, observe that if  $S^0$  is constant then  $\Sigma^* \equiv S^0$ , so clearly **(I2)** implies **(I1)**.

As mentioned before, the positiveness of the substrate is strongly related with the boundedness of the solutions and the next results show that either **(I1)** or **(I2)** implies the existence of a bounded positively invariant set for the solutions. In fact, given  $W > 0$ , let us consider the set

$$\Omega_W := \{(U, S) : U, S > 0, U + S < W\}$$

**Lemma 3.** Assume that **(H1)**, **(H2)** and **(I1)** hold and let  $W := S_{\sup}^0$ . If  $(U, S) \in \bar{\Omega}_W$ , then  $G_t(U, S) \in \bar{\Omega}_W$ , where

$$G_t(U, S) := ((1-E)(1+f(S))U, (1-E)S - (1-E)f(S)U + ES_t^0).$$

*Proof.* Let  $(\tilde{U}, \tilde{S}) := G_t(U, S)$ . It is clear that  $\tilde{U} \geq 0$  and, moreover,

$$\tilde{U} + \tilde{S} = (1-E)(U+S) + ES_t^0 \leq (1-E)W + ES_{\sup}^0 \leq W.$$

Finally, observe that  $\tilde{S} \geq 0$  if and only if

$$f(S)U - S \leq \frac{E}{1-E}S_t^0.$$

Because  $f(S) \leq f'(0)S$  by **(H1)**, it suffices to verify that

$$(f'(0)U - 1)S \leq \frac{E}{1-E}S_{\inf}^0.$$

Next, observe that the absolute maximum value of the function

$$g(U, S) := (f'(0)U - 1)S$$

over the triangle  $\bar{\Omega}_W$  is achieved at its upper side; thus, it suffices to compute the absolute maximum of the parabola  $g(U, W - U) = (f'(0)U - 1)(W - U)$ , namely

$$g_{\max} = \frac{1}{4f'(0)}(Wf'(0) - 1)^2,$$

then  $g_{\max} < \frac{E}{1-E}S_{\inf}^0$  is equivalent to

$$|Wf'(0) - 1| < 2\sqrt{\frac{f'(0)ES_{\inf}^0}{1-E}},$$

which is always implied by **(I1)**.  $\square$

A careful reading of the last step in the preceding proof shows that we have to take into account the sign of  $S_{\sup}^0 f'(0) - 1$  and the distance between  $\Sigma_{\sup}^*$  and  $S_{\sup}^0$ , which leads to three possible cases when **(I1)** is verified:

- a) If  $S_{\sup}^0 f'(0) < 1$ , then **(I1)** implies **(I2)** since  $\Sigma_{\sup}^* \leq S_{\sup}^0$ ,

- b) If  $\Sigma_{\text{sup}}^* f'(0) < 1 < S_{\text{sup}}^0 f'(0) < 1 + 2\sqrt{\frac{f'(0)ES_{\text{inf}}^0}{1-E}}$ , then **(I1)** and **(I2)** are satisfied,
- c) If  $1 \leq \Sigma_{\text{sup}}^* f'(0) \leq S_{\text{sup}}^0 f'(0) < 1 + 2\sqrt{\frac{f'(0)ES_{\text{inf}}^0}{1-E}}$ , then **(I1)** is verified while **(I2)** is not.

**Lemma 4.** *Assume that **(H1)**, **(H2)** and **(I2)** hold and let  $W := \frac{1}{f'(0)}$ . Then there exists  $t^* \in \mathbb{Z}$  such that  $(U_t, S_t) \in \bar{\Omega}_W$  for all  $t > t^*$ , provided that  $(U_{t^*}, S_{t^*}) \in \bar{\Omega}_W$ . If furthermore  $U_{t^*} > 0$ , then  $(U_t, S_t) \in \Omega_W$  for all  $t > t^*$ .*

*Proof.* As  $\Sigma_{\text{sup}}^* < W$ , fix  $\varepsilon > 0$  such that  $\Sigma_{\text{sup}}^* + \frac{\varepsilon}{E} < W$  and set  $t^*$  such that  $\Sigma_{t^*}^* > \Sigma_{\text{sup}}^* - \varepsilon$ . Now, for  $(U_{t^*}, S_{t^*}) \in \bar{\Omega}_W$ , we have that  $U_{t^*} \geq 0$ ,  $S_{t^*} \geq 0$  and  $U_{t^*} + S_{t^*} \leq W$ . In order to prove that  $U_t + S_t \leq W$  for any  $t > t^*$ , we will consider  $\ell \mapsto \Sigma_t^W$  the solution of (3.1) such that  $\Sigma_{t^*}^W = W$ , then for  $t > t^*$  we have that

$$\Sigma_t^W - \Sigma_t^* = (1 - E)^{t-t^*} (W - \Sigma_{t^*}^*),$$

whence,

$$\Sigma_t^W \leq \Sigma_{\text{sup}}^* + (1 - E)(W - \Sigma_{t^*}^*) \leq W + \varepsilon - E(W - \Sigma_{t^*}^*) < W,$$

because  $\Sigma_{t^*}^* > \Sigma_{\text{sup}}^* - \varepsilon$  and  $E(W - \Sigma_{t^*}^*) \geq E(W - \Sigma_{\text{sup}}^*) > \varepsilon$ . As  $U_t + S_t$  satisfies the difference equation (3.1), the preceding inequality proves that  $\Sigma_t^W = U_t + S_t < W$  for all  $t > t^*$ . Now, since  $U_{t^*} + S_{t^*} \leq W = \Sigma_{t^*}^W$  it follows by comparison that  $U_t + S_t < \Sigma_t^W \leq W$  for any  $t \geq t^*$ .

The proof of the fact that  $S_t$  and  $U_t$  are nonnegative for any  $t \geq t^*$  shall proceed by induction. Assume that  $U_t, S_t \geq 0$ , then the inequality  $U_{t+1} \geq 0$  can be proved easily. Moreover, by **(H1)** we have that

$$f(S_t)U_t \leq f'(0)S_tU_t \leq S_t$$

which, in turn, implies  $S_{t+1} \geq 0$  by (3.6).  $\square$

From now on, we may assume for simplicity that  $t^* = 0$ .

**Corollary 2.** *Assume that **(H1)**, **(H2)** and either **(I1)** or **(I2)** hold and set  $W := S_{\text{sup}}^0$  or  $W := \frac{1}{f'(0)}$  respectively. Then  $\bar{\Omega}_W$  is positively invariant.*

**3.3. Washout of the total cellular biomass.** In order to obtain sufficient conditions ensuring the washout of the biomass in the system (3.5), we will study the boundedness properties of the following sequences:

$$(3.7) \quad \pi_{c_0}(t, t_0) := (1 - E)^{t-t_0} \prod_{j=t_0}^{t-1} \{1 + f(\Sigma_j^*) + c_0\} \quad \text{where } c_0 \in \mathbb{R} \text{ and } t_0 \in \mathbb{Z}_0^+.$$

For convenience, we shall always assume  $c_0 \geq -1$ . This is not strictly necessary but will ensure the positiveness of the factors. In addition, it will be useful to introduce a technical result:

**Lemma 5.** *If the bounded sequences of nonnegative numbers  $\{c_j\}_j$ ,  $\{A_j\}_j$  and  $\{b_j\}_j$  verify  $A_j - b_j \geq c$  for some constant  $c > 0$ , then*

$$(3.8) \quad \left( \prod_{j=t_0}^t c_j A_j \right) e^{-\frac{1}{(A-b)_{\text{inf}}} \sum_{j=t_0}^t b_j} \leq \prod_{j=t_0}^t c_j \{A_j - b_j\} \leq \left( \prod_{j=t_0}^t c_j A_j \right) e^{-\frac{1}{A_{\text{sup}}} \sum_{j=t_0}^t b_j},$$

where  $A_{\text{sup}} := \sup_{j \geq t_0} A_j > 0$  and  $(A - b)_{\text{inf}} := \inf_{j \geq t_0} \{A_j - b_j\} > 0$ .

*Proof.* By using the mean value Theorem, we write

$$\ln(A_j - b_j) = \ln(A_j) - \frac{b_j}{\xi_j}$$

with  $\xi_j$  between  $A_j - b_j$  and  $A_j$ , then it can be deduced that

$$\sum_{j=t_0}^t [\ln(c_j) + \ln(A_j)] \leq \sum_{j=t_0}^t [\ln(c_j) + \ln(A_j - b_j)] + \frac{1}{(A - b)_{\inf}} \sum_{j=t_0}^t b_j$$

which is equivalent to the left inequality of (3.8). Similarly, we can deduce that

$$\sum_{j=t_0}^t [\ln(c_j) + \ln(A_j - b_j)] \leq \sum_{j=t_0}^t [\ln(c_j) + \ln(A_j)] - \frac{1}{A_{\sup}} \sum_{j=t_0}^t b_j,$$

which is equivalent to the right inequality of (3.8).  $\square$

**Theorem 1.** *Let us consider the system (3.5) with initial conditions  $(U_0, S_0) \in \Omega_W$  and the sequences (3.7):*

- i) *If  $\{\pi_0(t, 0)\}_{t \geq 0}$  is bounded, then  $\lim_{t \rightarrow \infty} (U_t, \Sigma_t^* - S_t) = (0, 0)$ .*
- ii) *If  $\{\pi_{c_0}(t, 0)\}_{t \geq 0}$  is bounded for some  $c_0 > 0$ , then the above convergence is exponential.*
- iii) *If  $\{\pi_{c_0}(t+m, m)\}_{t \geq 0}$  is uniformly bounded for some  $c_0 > 0$  and any  $m \in \mathbb{N}_0$ , then the above exponential convergence is uniform with respect to the initial time. Namely, there exist two constants  $K > 0$  and  $\alpha > 0$  such that*

$$(3.9) \quad U_t \leq K e^{-\alpha(t-t_0)} U_0 \quad \text{for } t \geq t_0,$$

with  $K$  and  $\alpha$  independent of  $t_0$ .

*Proof.* The proof will be divided in several steps:

*Step 1: The case  $S_t > \Sigma_t^*$  for any  $t \geq 0$ .* In this case, we can deduce the inequality  $S_{t+1} - \Sigma_{t+1}^* < S_t - \Sigma_t^*$  and, consequently that  $\{S_t - \Sigma_t^*\}_t$  is a decreasing and nonnegative sequence convergent to  $C \geq 0$ . Moreover, by Lemma 2 we have that

$$U_t = \Sigma_t - S_t = \Sigma_t - \Sigma_t^* + \Sigma_t^* - S_t,$$

is convergent to  $-C$ . Thus, the positiveness of  $U_t$  implies that  $C = 0$  and the statement i) is verified in this case.

*Step 2: The case  $S_{T_0} \leq \Sigma_{T_0}^*$  for some  $T_0$ .* In this case, it is easy to see that  $S_t < \Sigma_t^*$  for any  $t \geq T_0$ . Now, we can see that, for any  $t > T_0$ , the sequence  $U_t$  verifies

$$\begin{aligned} \frac{U_t}{U_0} &= (1 - E)^t \prod_{j=0}^{t-1} \{1 + f(S_j)\} \leq (1 - E)^t \prod_{j=0}^{T_0-1} \{1 + f(S_j)\} \prod_{j=T_0}^{t-1} \{1 + f(\Sigma_j^*)\} \\ &= (1 - E)^t \left( \frac{\prod_{j=0}^{T_0-1} \{1 + f(S_j)\}}{\prod_{j=0}^{T_0-1} \{1 + f(\Sigma_j^*)\}} \right) \prod_{j=0}^{t-1} \{1 + f(\Sigma_j^*)\} = C_{T_0} \pi_0(t, 0), \end{aligned}$$

and is bounded since we assume the boundedness of  $\{\pi_0(t, 0)\}_{t \geq 0}$ . We claim that

$$(3.10) \quad \limsup_{t \rightarrow \infty} U_t = 0.$$

Indeed, otherwise, there exists a subsequence  $\{U_{t_j}\}_j$  verifying

$$\lim_{j \rightarrow \infty} U_{t_j} = \tilde{U} > 0, \quad \text{or equivalently} \quad \lim_{j \rightarrow \infty} \Sigma_{t_j}^* - S_{t_j} = \tilde{U},$$

and we can assume that  $\Sigma_{t_j}^* - S_{t_j} \geq c > 0$  for any  $j$ . Consequently,

$$f(\Sigma_{t_j}^*) - f(\Sigma_{t_j}^* - c) = f'(\xi_j)c \geq b > 0,$$

for some  $b \in (0, 1 + f(\Sigma_{\min}^*))$ . In addition, define the sequence

$$b_k := \begin{cases} b & \text{si } k \in \{t_j\} \\ 0 & \text{si } k \notin \{t_j\}, \end{cases}$$

and note that

$$\begin{aligned} \frac{U_t}{U_0} &= (1 - E)^t \left( \frac{\prod_{j=0}^{T_0-1} \{1 + f(S_j)\}}{\prod_{j=0}^{T_0-1} \{1 + f(\Sigma_j^*) - b_j\}} \right)^{T_0-1} \prod_{j=0}^{T_0-1} \{1 + f(\Sigma_j^*) - b_j\} \prod_{j=T_0}^{t-1} \{1 + f(S_j)\} \\ &= K_{T_0} (1 - E)^t \prod_{j=0}^{T_0-1} \{1 + f(\Sigma_j^*) - b_j\} \prod_{j=T_0}^{t-1} \{1 + f(S_j)\}. \end{aligned}$$

In order to estimate the above identity, we will consider two cases when  $t \geq T_0$ : If  $t \notin \{t_j\}_j$ , we have that  $f(S_t) \leq f(\Sigma_t^*)$ . On the other hand, if  $t \in \{t_j\}_j$  then  $f(S_t) \leq f(\Sigma_t^* - c) \leq f(\Sigma_t^*) - b$  and it follows that

$$\frac{U_t}{U_0} \leq K_{T_0} (1 - E)^t \prod_{j=0}^{t-1} \{1 + f(\Sigma_j^*) - b_j\}.$$

By Lemma 5, and considering  $c_j = 1$ ,  $A_j = 1 + f(\Sigma_k^*) > b_j$  and  $A_{\sup} := 1 + f(\Sigma_{\sup}^*)$ , we have the inequality

$$\frac{U_t}{U_0} \leq K_{T_0} \left( (1 - E)^t \prod_{j=0}^{t-1} \{1 + f(\Sigma_j^*)\} \right) e^{-\frac{1}{A_{\sup}} \sum_{j=0}^{t-1} b_j},$$

where the right term is convergent to zero, obtaining a contradiction and (3.10) is verified. This fact combined with the positiveness of  $U_t$  and Lemma 2 leads to the asymptotic behavior  $\lim_{t \rightarrow \infty} (U_t, \Sigma_t^* - S_t) = (0, 0)$  and the statement i) is proved.

*Step 3: The convergence is exponential when  $\pi_{c_0}(t, 0)$  is bounded for some  $c_0 > 0$ .* If  $\pi_{c_0}(t, 0)$  is bounded, then  $\pi_0(t, 0)$  is also bounded and by the previous steps we know that  $\Sigma_t^* - S_t$  converges to 0. Then, we can fix  $T_0$  large enough such that  $f(S_t) < f(\Sigma_t^*) + c_0/2$  for  $t > T_0$ , and, as in the previous step, we can deduce

$$\frac{U_t}{U_0} \leq K_{T_0} (1 - E)^t \prod_{j=0}^{t-1} \{1 + f(\Sigma_j^*) + c_0/2\}.$$

By using again Lemma 5 with  $A_j = 1 + f(\Sigma_j^*) + c_0$  and  $b_j = c_0/2$ , combined with the boundedness of  $\pi_{c_0}(t, 0)$ , it follows that

$$\frac{U_t}{U_0} \leq K_{T_0} \left( (1 - E)^t \prod_{j=0}^{t-1} \{1 + f(\Sigma_j^*) + c_0\} \right) e^{-\frac{c_0}{2(A_{\sup} + c_0)} t} \leq K_1 e^{-\frac{c_0}{2(A_{\sup} + c_0)} t},$$



and the statement ii) follows.

*Step 4: End of proof.* The statement iii) assumes the existence of a constant  $M > 0$  such that

$$(3.11) \quad (1 - E)^\ell \prod_{k=m}^{m+\ell-1} \{1 + f(\Sigma_k^*) + c_0\} \leq M$$

for some  $c_0 > 0$  and for any couple of positive integers  $m$  and  $\ell$ . Now, by using Lemma 2 combined with the positiveness of  $c_0$ , we can deduce the existence of  $T > 0$  such that

$$(3.12) \quad f(S_j) < f(\Sigma_j^*) + c_0/2 \quad \text{for any } j \geq T.$$

Now, we will prove the property (3.9) by considering three cases.

*Case a):*  $T \leq t_0 < t$ . In this case, the inequality (3.12) implies that

$$\begin{aligned} \frac{U_t}{U_{t_0}} &= (1 - E)^{t-t_0} \prod_{j=t_0}^{t-1} \{1 + f(S_j)\} \\ &\leq (1 - E)^{t-t_0} \prod_{j=t_0}^{t-1} \{1 + f(\Sigma_j^*) + c_0 - c_0/2\}. \end{aligned}$$

Now, by using Lemma 5 with  $A_j = 1 + f(\Sigma_j^*) + c_0$  and  $b_j = c_0/2$  followed by the inequality (3.11) with  $m = t_0$  and  $\ell = t - t_0$ , we can deduce that

$$\frac{U_t}{U_{t_0}} \leq (1 - E)^\ell \prod_{j=t_0}^{t_0+\ell-1} \{1 + f(\Sigma_j^*) + c_0\} e^{-\alpha(t-t_0)} \leq M e^{-\alpha(t-t_0)},$$

where  $\alpha := \frac{c_0}{2(1+f(\Sigma_{\max}^*)+c_0)}$ . Then, we have that

$$U_t \leq M e^{-\alpha(t-t_0)} U_{t_0} \quad \text{for any } T \leq t_0 \leq t.$$

Given  $t \mapsto S_t$ , let us denote

$$X(t) := (1 - E)^t \prod_{j=0}^{t-1} \{1 + f(S_j)\}.$$

Then, notice that  $\frac{U_t}{U_{t_0}} = X(t)X^{-1}(t_0)$ , and the above inequality is equivalent to

$$(3.13) \quad X(t)X^{-1}(t_0) \leq M e^{-\alpha(t-t_0)} \quad \text{for any } T \leq t_0 \leq t.$$

*Case b):*  $t_0 < T \leq t$ . In this case, let us define

$$N = \sup_{0 \leq \sigma, \tau \leq T} X(\tau)X^{-1}(\sigma)$$

and by using  $\frac{U_t}{U_{t_0}} = X(t)X^{-1}(t_0)$  combined with (3.13), we have that

$$\begin{aligned} \frac{U_t}{U_{t_0}} &= X(t)X^{-1}(T)X(T)X^{-1}(t_0) \\ &\leq NX(t)X^{-1}(T) \\ &\leq MN e^{-\alpha(t-T)} \\ &\leq MN e^{\alpha T} e^{-\alpha(t-t_0)}, \end{aligned}$$

then, we conclude that

$$U_t \leq MN e^{\alpha T} e^{-\alpha(t-t_0)} U_{t_0} \quad \text{for any } t_0 < T \leq t.$$

*Case c):*  $t_0 \leq t \leq T$ . In this case, note that  $t - t_0 < T$ , which implies that  $e^{\alpha T} e^{-\alpha(t-t_0)} \geq 1$ . Moreover, by using the definition of  $N$  and the inequality (3.13), we can see that

$$\begin{aligned} \frac{U_t}{U_{t_0}} &= X(t)X^{-1}(0)X(0)X^{-1}(t_0)X(T)X^{-1}(T) \\ &\leq N^2 M e^{\alpha T} e^{-\alpha(t-t_0)}, \end{aligned}$$

and we conclude that

$$U_t \leq M N^2 e^{\alpha T} e^{-\alpha(t-t_0)} U_0 \quad \text{for any } 0 \leq t_0 \leq t \leq T.$$

In consequence, the inequality (3.9) is satisfied with  $K = M \max\{1, N e^{\alpha T}, N^2 e^{\alpha T}\}$  and  $\alpha$  defined as in the case a).  $\square$

The previous theorem provides sufficient conditions ensuring the washout of the microbial biomass, which are described in terms of the boundedness of the sequences  $\{\pi_{c_0}(t, 0)\}_t$  and  $\{\pi_{c_0}(t+m, n)\}_t$ . In this context, it is important to emphasize that these properties are related to the *upper Bohl exponent* (see [4] for details) of the scalar difference equation

$$(3.14) \quad z_{t+1} = (1 - E)[1 + f(\Sigma_t^*)]z_t,$$

which is defined by

$$(3.15) \quad \bar{\beta} := \limsup_{n-m, m \rightarrow +\infty} \left( \prod_{j=m}^{n-1} (1 - E)\{1 + f(\Sigma_j^*)\} \right)^{\frac{1}{n-m}} = \limsup_{n-m, m \rightarrow +\infty} \pi_0(n, m)^{\frac{1}{n-m}}.$$

The following results describe the relation between the upper Bohl exponent of (3.14) and the statement of Theorem 1.

**Lemma 6.** *If  $\bar{\beta} < 1$ , then there exists  $c_0 > 0$  such that  $\{\pi_{c_0}(t, 0)\}_t$  is bounded.*

*Proof.* The definition of upper limit implies the existence of  $\varepsilon > 0$  and  $n_0 \in \mathbb{N}$  such that

$$\prod_{j=0}^{n-1} (1 - E)\{1 + f(\Sigma_j^*)\} < (1 - 2\varepsilon)^n \quad n \geq n_0$$

Now, we can prove the existence of  $\alpha > 1$  such that

$$\prod_{j=0}^{n-1} (1 - E)\{1 + f(\Sigma_j^*)\} \alpha < (1 - \varepsilon)^n \quad n \geq n_0.$$

The boundedness of  $\pi_{c_0}(t, 0)$  with  $c_0 = \alpha - 1$  is obtained by noticing that

$$\{1 + f(\Sigma_j^*)\} \alpha > 1 + f(\Sigma_j^*) + \alpha - 1.$$

$\square$

**Remark 6.** *It is easy to see that the converse statement of the above result is false, in fact, it may happen that  $\pi_{c_0}(t, 0)$  is bounded but  $\bar{\beta} = 1$ .*

**Lemma 7.** *The sequence  $\{\pi_{c_0}(t+m, m)\}_{t \geq 0}$  is uniformly bounded for some  $c_0 > 0$  and any  $m \in \mathbb{N}_0$  if and only if  $\bar{\beta} < 1$*

Firstly, if we assume the existence of  $c_0$  ensuring the uniform boundedness of the sequence  $\{\pi_{c_0}(t+m, m)\}_{t \geq 0}$ , then condition (3.11) holds. This fact, combined with Lemma 5 implies that

$$\begin{aligned} \pi_0(t+m, m) &= (1-E)^t \prod_{j=m}^{t+m-1} \{1 + f(\Sigma_j^*) + c_0 - c_0\} \\ &\leq (1-E)^t \prod_{j=m}^{t+m-1} \{1 + f(\Sigma_j^*) + c_0\} e^{-\frac{c_0 t}{1+f(\Sigma_{\max}^*)}} \\ &\leq M e^{-\frac{c_0 t}{1+f(\Sigma_{\max}^*)}} \end{aligned}$$

Now, if  $t = n - m$ , we have that

$$\bar{\beta} = \limsup_{m, n-m \rightarrow \infty} \pi_0(n, m) \leq \lim_{n-m \rightarrow \infty} M^{\frac{1}{n-m}} e^{-\frac{c_0}{1+f(\Sigma_{\max}^*)}} = e^{-\frac{c_0}{1+f(\Sigma_{\max}^*)}} < 1.$$

Secondly, if the Bohl exponent is lower than 1, we can rewrite (3.15) as

$$\limsup_{m, t \rightarrow \infty} (1-E)^t \prod_{k=m}^{m+t-1} \{1 + f(\Sigma_k^*)\} = \bar{\beta} < 1$$

by the change of variables  $n = t + m$ . Now, we can proceed as in the proof of the previous Lemma. In fact, the definition of upper limit implies the existence of  $\varepsilon > 0$ ,  $m_0$  and  $t_0$  such that

$$(1-E)^t \prod_{k=m}^{m+t-1} [1 + f(\Sigma_k^*)] < (1-2\varepsilon)^{t-1}$$

for any  $m > m_0$  and  $t > t_0$ . As before, this also implies that, for some values  $c_0 > 0$ ,  $m > m_0$  and  $t > t_0$ ,

$$(1-E)^t \prod_{k=m}^{m+t-1} [1 + f(\Sigma_k^*) + c] < (1-\varepsilon)^{t-1}.$$

Finally, for  $m \leq m_0$  and  $t \leq t_0$  it is verified that

$$(1-E)^t \prod_{k=m}^{m+t-1} [1 + f(\Sigma_k^*) + c_0] \leq (1-E)^t [1 + f(\Sigma_{\sup}^*) + c_0]^t \leq K_0$$

for some constant  $K_0$ .

**Corollary 3.** *Assume that (H1), (H2) and either (I1) or (I2) hold. If  $t \mapsto S_t^0$  is  $\omega$ -periodic and  $E$  is such that*

$$(3.16) \quad (1-E) \left( \prod_{j=0}^{\omega-1} \{1 + f(\Sigma_j^*)\} \right)^{\frac{1}{\omega}} < 1,$$

then  $\lim_{t \rightarrow +\infty} (U_t, \Sigma_t^* - S_t) = (0, 0)$  and the convergence is uniformly exponential.

*Proof.* If  $t \mapsto S_t^0$  is  $\omega$ -periodic, then we know from Remark 4 that  $t \mapsto \Sigma_t^*$  and  $t \mapsto 1 + f(\Sigma_t^*)$  are  $\omega$ -periodic. Thus, the result follows since  $\bar{\beta}$  coincides with the left-hand side of (3.16) in the  $\omega$ -periodic case.  $\square$

**3.4. Persistence of the total biomass.** Usually, it is said that the total biomass  $U_t$  described in (3.5) is *persistent* if  $\liminf_{t \rightarrow +\infty} U_t > 0$  whenever  $U_0 > 0$ . In order to obtain sufficient conditions ensuring persistence, it will be useful to introduce the following result:

**Lemma 8.** *The following assumptions are equivalent:*

a) *There exists  $c_0 < 0$  such that*

$$(3.17) \quad \liminf_{t-t_0, t_0 \rightarrow \infty} \pi_{c_0}(t, t_0) > 0,$$

b) *There exists  $c_1 < 0$  such that*

$$\lim_{t-t_0, t_0 \rightarrow +\infty} \pi_{c_1}(t, t_0) = \infty.$$

c) *There exists  $c_0 < 0$  and  $T, \varepsilon > 0$  such that  $\pi_{c_0}(t, t_0) > \varepsilon$  for  $t - T \geq t_0 \geq T$ .*

d) *For each  $M > 0$  there exists  $c_1 < 0$  and  $T > 0$  such that  $\pi_{c_1}(t, t_0) > M$  for  $t - T \geq t_0 \geq T$ .*

*Proof.* a)  $\iff$  b): As the implication b)  $\Rightarrow$  a) is direct, we shall only prove a)  $\Rightarrow$  b). Choose  $c_1 < 0$  and  $\Delta > 0$  such that

$$c_0 < c_1 - \Delta < 0 \quad \text{and} \quad 1 + f(\Sigma_{\text{inf}}^*) + c_1 > \Delta,$$

which combined with Lemma 5 allows us to deduce

$$\begin{aligned} \pi_{c_0}(t, t_0) &\leq (1 - E)^{t-t_0} \prod_{j=t_0}^{t-1} \{1 + f(\Sigma_j^*) + c_1 - \Delta\} \\ &\leq \pi_{c_1}(t, t_0) e^{-r(t-t_0)}, \end{aligned}$$

where  $r = \Delta / (1 + f(\Sigma_{\text{inf}}) + c_1)$ . Thus,  $\pi_{c_1}(t, t_0) \geq \pi_{c_0}(t, t_0) e^{r(t-t_0)}$  and the implication follows.

Let us recall that  $\liminf_{t-t_0, t_0 \rightarrow +\infty} \pi_{c_0}(t, t_0) = \ell > 0$  if and only if for any  $\delta > 0$  there exists  $T > 0$  such that  $\pi_{c_0}(t, t_0) \geq \ell - \delta$  for any  $t - t_0 > T$  and  $t_0 > T$ .

If we assume a), let us consider  $\delta \in (0, \ell)$  and define  $\varepsilon = \ell - \delta$ . Then there exists  $c_0 < 0$  and  $T, \varepsilon > 0$  such that  $\pi_{c_0}(t, t_0) \geq \varepsilon$  for any  $T < t_0 < t - T$ , and c) is verified. On the other hand, the implication c)  $\Rightarrow$  a) is straightforward.

Finally, note that b)  $\iff$  d) is clear from the definition of limit. In fact, let us recall that the property  $\lim_{t-t_0, t_0 \rightarrow +\infty} \pi_{c_1}(t, t_0) = \infty$  is equivalent to:

For all  $M > 0$  there exists  $T > 0$  such that  $t - t_0 > T, t_0 > T \Rightarrow \pi_{c_1}(t, t_0) > M$ . □

**Theorem 2.** *For any initial condition  $(U_0, S_0) \in \Omega_W$  with  $U_0 > 0$ , the total biomass is persistent if and only if there exists  $c_0 < 0$  such that (3.17) is verified.*

*Proof.* Let us assume that  $\liminf_{t \rightarrow \infty} U_t > 0$ . Then, there exists  $\varepsilon > 0$  and  $T > 0$  such that  $U_t > \varepsilon$  for any  $t \geq T$ . Now, if  $t \geq t_0 \geq T$ , then

$$\frac{U_t}{U_{t_0}} > \frac{\varepsilon}{U_{t_0}} \geq \frac{\varepsilon}{W},$$

and we can deduce that

$$\frac{\varepsilon}{W} \leq \prod_{j=t_0}^{t-1} (1 - E) \{1 + f(\Sigma_j^*) - f'(\xi_j)(\Sigma_j^* - \Sigma_j + U_j)\},$$

where  $\xi_j$  is a number between  $\Sigma_j^*$  and  $S_j = \Sigma_j - U_j$ . By using Lemma 2 and considering  $T$  large enough, we obtain the estimation:

$$\frac{\varepsilon}{W} \leq \prod_{j=t_0}^{t-1} (1-E)\{1+f(\Sigma_j^*)-\eta\varepsilon\}$$

for some constant  $\eta > 0$  and the condition (3.17) is verified with  $c_0 := -\eta\varepsilon < 0$ .

Now, let us assume that the condition (3.17) is verified for some  $c_0 < 0$ . Firstly, we claim the existence of  $t_0 \geq 0$  such that  $S_t < \Sigma_t^*$  for any  $t \geq t_0$ . Indeed, otherwise, assume that  $S_t > \Sigma_t^*$  for any  $t \geq 0$ , then it follows trivially that

$$\pi_0(t, 0) < \prod_{j=0}^{t-1} (1-E)\{1+f(S_t)\} = \frac{U_t}{U_0},$$

which is bounded. Moreover, by using Lemma 5 and writing  $c_0 = -|c_0|$ , it is seen that

$$\pi_{c_0}(t, 0) = \prod_{j=0}^{t-1} (1-E)\{1+f(\Sigma_t^*)-|c_0|\} \leq \prod_{j=0}^{t-1} (1-E)\{1+f(\Sigma_t^*)\} e^{\frac{-|c_0|}{A_{\text{sup}}}} t = \pi_0(t, 0) e^{\frac{c_0}{A_{\text{sup}}}} t,$$

with  $A_{\text{sup}} =: 1+f(\Sigma_{\text{sup}}^*)$ , obtaining a contradiction with the boundedness of  $\pi_0(t, 0)$ .

Secondly, we will see that  $U_t$  cannot converge to 0. Indeed, otherwise, note that there exists  $\xi_t$  between  $\Sigma_t^*$  and  $S_t$  such that

$$f(\Sigma_t^*) - f(S_t) = f'(\xi_t)(\Sigma_t^* - S_t) = f'(\xi_t)(\Sigma_t^* - \Sigma_t + U_t).$$

Hence, there exists  $T_0 > t_0$  large enough such that if  $t \geq T_0$  then

$$f(\Sigma_t^*) - f(S_t) \leq -c_0,$$

which implies that  $1 + f(\Sigma_t^*) + c_0 \leq 1 + f(S_t)$  for any  $t \geq t_0$ . Then

$$\pi_{c_0}(t, t_0) \leq \prod_{j=t_0}^{t-1} (1-E)[1+f(S_t)] = \frac{U_t}{U_{t_0}},$$

and the convergence of  $U_t$  towards zero leads a contradiction with (3.17).

Finally, let us verify that  $\liminf_{t \rightarrow +\infty} U_t > 0$  for arbitrary  $U_0 > 0$ . Indeed, otherwise there exists a divergent sequence  $\{t_j\}_j$  such that  $\lim_{j \rightarrow \infty} U_{t_j} = 0$ . Without loss of generality, we will also assume that  $U_{t_j} \leq U_t$  for any  $t \leq t_j$ . According to Lemma 8, condition (3.17) is verified for some  $c_0 < 0$  if and only if d) holds; hence, let us fix  $T > 0$  and  $c < 0$  such that  $\pi_c(t, t_0) > 1$  for  $t - T \geq t_0 \geq T$  and observe that if  $t_j - T \leq k < t_j$ , then

$$\frac{U_{t_j}}{U_k} \geq (1-E)^{t_j-k} \geq (1-E)^T,$$

which allows us to see that

$$\begin{aligned}
1 \geq \frac{U_{t_j}}{U_{t_j-T}} &= \prod_{k=t_j-T}^{t_j-1} (1-E)\{1+f(S_k)\} \\
&= \prod_{k=t_j-T}^{t_j-1} (1-E)\{1+f(\Sigma_k^*) - f'(\xi_k)[\Sigma_k^* - \Sigma_k + U_k]\} \\
&\geq \prod_{k=t_j-T}^{t_j-1} (1-E)\{1+f(\Sigma_k^*) - f'(\xi_k)[\Sigma_k^* - \Sigma_k + U_{t_j}(1-E)^{-T}]\}.
\end{aligned}$$

Thus, for  $j$  large enough such that  $f'(\xi_k)[\Sigma_k^* - \Sigma_k + U_{t_j}(1-E)^{-T}] < -c$  we deduce

$$1 \geq \prod_{k=t_j-T}^{t_j-1} (1-E)\{1+f(\Sigma_k^*) - f'(\xi_k)[\Sigma_k^* - \Sigma_k + U_k]\} > \pi_c(t_j, t_j - T).$$

This contradiction proves that  $\liminf_{t \rightarrow \infty} U_t > 0$ .  $\square$

Similarly as in the washout study, the condition (3.17) is related to the *inferior Bohl exponent*  $\underline{\beta}$  associated to the difference equation (3.14), which is defined by

$$\underline{\beta} := \liminf_{n-m, m \rightarrow +\infty} \left( \prod_{j=m}^{n-1} (1-E)[1+f(\Sigma_j^*)] \right)^{\frac{1}{n-m}} = \liminf_{n-m, m \rightarrow +\infty} \pi_0(n, m)^{\frac{1}{n-m}}.$$

**Lemma 9.** *If  $\underline{\beta} > 1$ , then there exists  $c_0 < 0$  such that (3.17) is verified.*

*Proof.* Assume  $\underline{\beta} > 1$ , then there exists  $\varepsilon \in (0, e^{f(\Sigma_{\text{inf}}^*)} - 1)$  such that if  $t - t_0$ , is large enough, then

$$\prod_{j=t_0}^{t-1} (1-E)[1+f(\Sigma_j^*)] > (1+\varepsilon)^{t-t_0}.$$

By using Lemma 5 with  $c_0 := -\ln(1+\varepsilon) < 0$ , we can verify that

$$\pi_{c_0}(t, t_0) \geq \prod_{j=t_0}^{t-1} (1-E)[1+f(\Sigma_j^*)](1+\varepsilon)^{-(t-t_0)} > 1$$

for  $t - t_0$  and  $t_0$  large enough and (3.17) follows.  $\square$

**Corollary 4.** *If  $t \mapsto S_t^0$  is  $\omega$ -periodic and there exists  $E_0 \in (0, 1)$  such that  $t \mapsto \Sigma_t^*(E_0)$  verifies*

$$(3.18) \quad (1-E_0) \left( \prod_{j=0}^{\omega-1} \{1+f(\Sigma_j^*)\} \right)^{\frac{1}{\omega}} > 1,$$

*then the total biomass of the system (3.5) with  $E = E_0$  is persistent.*

*Proof.* As done in the proof of Corollary 3, the periodicity implies that  $\underline{\beta}$  is equal to the left side of (3.18). The result is a direct consequence of Lemma 9 and Theorem 2  $\square$

## 4. STUDY OF THE PERIODIC CASE

In this section, we address the existence and attractiveness of positive  $\omega$ -periodic solutions for (2.12) whenever the input  $t \mapsto S_t^0$  is positive and  $\omega$ -periodic. To this end, we consider the planar system (3.5) with  $f$  satisfying **(H1)**, **(H2)** and **(I2)**. As noticed in Remark 4, these assumptions imply that  $\Sigma_t^*$  is the unique  $\omega$ -periodic positive solution of (3.1). In this framework, it will be useful to define

$$0 < S_{\min}^0 := \min_{t \in \{0, \dots, \omega-1\}} S_t^0 \quad \text{and} \quad S_{\max}^0 := \max_{t \in \{0, \dots, \omega-1\}} S_t^0.$$

**4.1. Study of a reduced system.** The change of variables  $\Sigma_t = S_t + U_t$  combined with the positiveness of  $S_t$  also leads to the decoupled system

$$(4.1) \quad \begin{cases} \Sigma_{t+1} &= (1 - E)\Sigma_t + ES_t^0 \\ U_{t+1} &= (1 - E)(1 + f(\Sigma_t - U_t))U_t. \end{cases}$$

Note that the initial conditions of (3.5) lie in  $\Omega_W$  with  $W = 1/f'(0)$  if and only if the initial conditions of (4.1) belong to the set

$$(4.2) \quad X_0 = \{(\Sigma, U) \in \mathbb{R}^2 : 0 < \Sigma \leq W \quad \text{and} \quad 0 < U < \Sigma\}.$$

Now, under the assumption that **(H1)**, **(H2)**, **(I2)** are verified, we can see that if  $(\Sigma_t, U_t)$  is a solution of (4.1) passing through  $(\Sigma_0, U_0) \in X_0$  at  $t = t_0 = t^* = 0$ , by Lemma 4, it follows that  $(\Sigma_t, U_t) \in X_0$  for any forward solution of (4.1) passing through  $(\Sigma_0, U_0)$  at initial time  $t_0 = 0$ .

The study of (4.1) will be a complementary and useful tool. In fact, by Lemma 2, it follows that the biomass equation is asymptotically equivalent to

$$(4.3) \quad U_{t+1} = (1 - E)(1 + f(\Sigma_t^* - U_t))U_t, \quad U_0 = a \geq 0.$$

Note that (4.3) is well defined when **(I2)** is satisfied. In fact, as we already know that  $S_t = \Sigma_t^* - U_t$  verifies

$$S_{t+1} = (1 - E)[S_t - f(S_t)U_t] + ES_t^0$$

and by **(I2)**, the positiveness of  $S_t$  implies that  $\Sigma_t^* > U_t$ . For simplicity, we may extend  $f$  to the whole line by setting  $f(\Sigma_t^* - U_t) = 0$  if  $\Sigma_t^* \leq U_t$ , so the solutions are globally defined and it is clear that  $U_t > 0$ , provided that  $a > 0$ . This defines the Poincaré mapping  $\mathcal{P} : [0, \Sigma_0^*] \rightarrow [0, +\infty)$  given by  $\mathcal{P}(a) := U_\omega$ .

**Theorem 3.** *Assume that **(H1)**, **(H2)**, **(I2)** hold and condition (3.18) is satisfied for some  $E \in (0, 1)$ . Then (4.3) has a unique positive  $\omega$ -periodic solution  $t \mapsto U_t^*$ , and any other solution of (4.3) with initial condition  $0 < U_0 \leq \Sigma_0^*$  has the asymptotic behavior  $\lim_{t \rightarrow +\infty} |U_t - U_t^*| = 0$ .*

*Proof.* The proof will be divided in two steps.

*Step 1: Existence and uniqueness.* Using Lemma 4 it is seen, for  $a > 0$ , that  $S_t > 0$  for all  $t$  and consequently  $\mathcal{P}(a) < \Sigma_\omega^* = \Sigma_0^*$ . On the other hand, notice that  $\mathcal{P}(0) = 0$  and, moreover, since  $f$  is of class  $C^1$ , it follows that  $\mathcal{P}$  is continuously differentiable, see [9]. Direct computation shows that

$$\mathcal{P}'(a) = \lim_{h \rightarrow 0} \frac{U(\omega, 0, a+h) - U(\omega, 0, a)}{h} = \frac{\partial U}{\partial \xi}(\omega, 0, \xi) \Big|_{\xi=a} := v_\omega,$$

where  $v_t$  is the solution of the initial value problem

$$v_{t+1} = (1 - E)[1 + f(\Sigma_t^* - U_t) - f'(\Sigma_t^* - U_t)U_t]v_t \quad \text{with} \quad v_0 = 1.$$

Then

$$v_t = (1 - E)^t \prod_{j=0}^{t-1} [1 + f(\Sigma_j^* - U_j) - f'(\Sigma_j^* - U_j)U_j]$$

and therefore

$$(4.4) \quad \mathcal{P}'(a) = v_\omega = (1 - E)^\omega \prod_{t=0}^{\omega-1} [1 + f(\Sigma_t^* - U_t) - f'(\Sigma_t^* - U_t)U_t].$$

In particular, using (3.18) it is seen that

$$\mathcal{P}'(0) = (1 - E)^\omega \prod_{j=0}^{\omega-1} [1 + f(\Sigma_j^*)] > 1.$$

Thus, if we set  $q(a) := a - \mathcal{P}(a)$  it follows that  $q(0) = 0$ ,  $q'(0) < 0$  and  $q(\Sigma_0^*) > 0$ , which leads to the existence of  $a \in (0, \Sigma_0^*)$  such that  $q(a) = 0$ , that is,  $\mathcal{P}(a) = a$ . Furthermore, observe that if  $a > 0$  is a fixed point of  $\mathcal{P}$  and  $U_t$  is the corresponding solution with  $U_0 = a$ , then  $U_t$  is  $\omega$ -periodic. Hence, the equality

$$\frac{U_{t+1}}{U_t} = (1 - E)(1 + f(\Sigma_t^* - U_t)),$$

implies that

$$(4.5) \quad 1 = \frac{U_\omega}{U_0} = (1 - E)^\omega \prod_{j=0}^{\omega-1} (1 + f(\Sigma_j^* - U_j)).$$

Now, from (4.4) and (4.5) we obtain:

$$(4.6) \quad \mathcal{P}'(a) = (1 - E)^\omega \prod_{j=0}^{\omega-1} [1 + f(\Sigma_j^* - U_j) - f'(\Sigma_j^* - U_j)U_j] < 1.$$

In other words, if  $a \in (0, \Sigma_0^*)$  is such that  $q(a) = 0$ , then  $q'(a) > 0$  and we conclude that  $\mathcal{P}$  has a unique nontrivial fixed point  $a_0$ .

*Step 2: Asymptotic stability.* By **(H1)** and **(I2)** he have  $f'(\Sigma_t^* - U_t)U_t \leq f'(0)U_t < 1$ ; as a consequence, it follows from (4.4) that  $\mathcal{P}'(a) > 0$  for all  $a \in [0, \Sigma_0^*]$ .

As  $\mathcal{P}(\Sigma_0^*) < \Sigma_0^*$ , we know that  $\mathcal{P}([0, \Sigma_0^*]) \subset [0, \Sigma_0^*]$ . Let  $b \in (0, \Sigma_0^*) \setminus \{a_0\}$ , and define  $\{\mathcal{P}^n(b)\}_{n \in \mathbb{N}} \subset (0, \Sigma_0^*]$ . For  $\mathcal{P}(b) > b$ , the sequence  $\{\mathcal{P}^n(b)\}_{n \in \mathbb{N}}$  is strictly increasing and converges to  $b_0 \in (0, \Sigma_0^*]$  which is a fixed point of  $\mathcal{P}$ , so  $b_0 = a_0$ . Similarly, if  $\mathcal{P}(b) < b$  then  $\{\mathcal{P}^n(b)\}_{n \in \mathbb{N}}$  is strictly decreasing and converges to  $b^0 \in [0, \Sigma_0^*]$  which is a fixed point of  $\mathcal{P}$ . Since  $\mathcal{P}'(0) > 1$ , we know that  $\mathcal{P}(x) > x$  for  $0 < x < a_0$ ; thus,  $b > a_0$  and  $\mathcal{P}^n(b) > a_0$  for all  $n$ , whence  $b^0 = a_0$ . We conclude that every orbit of  $\mathcal{P}$  starting in  $(0, \Sigma_0^*]$  converges to  $a_0$ . So, from the continuous dependence on initial conditions, see [9], it follows that  $|U_t - U_t^*| \rightarrow 0$  as  $t \rightarrow \infty$ , where  $U_0 = b \in (0, \Sigma_0^*]$  and  $U_0^* = a_0$ . Indeed, given  $\varepsilon > 0$ , fix  $\delta > 0$  such that if  $|U_0 - a_0| < \delta$  then  $|U_t - U_t^*| < \varepsilon$  for  $0 \leq t \leq \omega$ . Since  $\mathcal{P}^n(b) = U_{n\omega}$ , fix  $n_0$  such that  $|U_{n_0\omega} - a_0| < \delta$  for  $n \geq n_0$ . The function  $W_t := U_{n_0\omega+t}$  is solution of (4.3) with  $W_0 = U_{n_0\omega}$  and  $|U_{n_0\omega+t} - U_{n_0\omega+t}^*| = |W_t - U_t^*| < \varepsilon$  for  $n \geq n_0$  and  $0 \leq t \leq \omega$ .  $\square$

**Remark 7.** *The first step in the previous proof is valid if **(I1)** is assumed instead of **(I2)**: indeed, it suffices to observe that the map  $\mathcal{P}$  is still well defined, in virtue of Lemma 3. This yields the existence of a unique periodic solution. However, the asymptotic stability may fail, because the monotonicity of  $\mathcal{P}$  is not guaranteed. A*



simple example of this reads as follows: as in Remark 5 let  $S^0$  be 2-periodic with  $S_0^0 = 1$  and  $S_1^0 = S > 1$ , then both values  $\Sigma_0^* = \Sigma_{\max}^*$  and  $\Sigma_1$  tend to 1 as  $S \rightarrow 1$ . Next, consider  $f$  such that  $f' \equiv c$  in  $[0, \Sigma_0^*]$ , where  $c$  is the (unique) value such that

$$1 < cS = 1 + 2\sqrt{\frac{Ec}{1-E}}.$$

Thus, **(I1)** is satisfied although, when  $S \sim 1$ , we seen  $c\Sigma_0^* > 1$  and **(I2)** is not fulfilled. Observe, moreover, for simplicity fix  $E = 1/2$  and  $U_0 = a \in [0, \Sigma_0^*]$  then

$$U_1 = \frac{1}{2}(1 + c(\Sigma_0^* - a))a, \quad U_2 = \frac{1}{2}(1 + c(\Sigma_1^* - U_1))U_1.$$

Notice that  $U_1$  is a parabola whose maximum value is attained at  $a = \frac{1}{2c} + \frac{\Sigma_0^*}{2} < \Sigma_0^*$  which, in turn, implies  $U_1'(\Sigma_0^*) < 0$ . Furthermore,

$$\mathcal{P}'(a) = U_2'(a) = \frac{1}{2}[1 + c\Sigma_1^* - 2cU_1(a)]U_1'(a)$$

and, note that the definitions of  $c, \Sigma_0^*$  and  $\Sigma_1^*$  allow us to conclude that the positivity of the term in the bracket is equivalent

$$1 + 2\sqrt{c} < 3 + c$$

and, because the latter inequality holds for all  $c > 0$ , it is deduced that  $\mathcal{P}'(\Sigma_0^*) < 0$ .

**Remark 8.** *H.L. Smith and P. Waltman proved an analogous version of the above result for a continuous-time chemostat model with periodic dilution rate, see [14, Ch. 7, Prop. 3.2]. Our proof of Theorem 3 deserves some comments:*

*i) The identity  $\Sigma_t = S_t + U_t$  allows to define  $S_t^* := \Sigma_t^* - U_t^*$ , where as before  $U_t^*$  is the unique  $\omega$ -periodic solution of (4.3). Then, we can easily deduce that  $t \mapsto (U_t^*, S_t^*)$  is the unique  $\omega$ -periodic solution of the system (3.5).*

*ii) In the same way as in (4.5), it follows from the above identity that*

$$(4.7) \quad (1 - E)^\omega \prod_{t=0}^{\omega-1} (1 + f(S_t^*)) = 1.$$

**Theorem 4.** *Assume that **(H1)**, **(H2)**, **(I2)** and condition (3.18) are satisfied for some  $E \in (0, 1)$ , then the  $\omega$ -periodic solution  $t \mapsto (\Sigma_t^*, U_t^*)$  of (4.1) is globally attractive for any positive solution, namely, any solution  $t \mapsto (\Sigma_t, U_t)$  of (4.1) with initial condition  $(\Sigma_0, U_0) \in X_0$  (where  $W = \frac{1}{f'(0)}$ ) verifies the asymptotic behavior*

$$\lim_{t \rightarrow +\infty} |\Sigma_t - \Sigma_t^*| + |U_t - U_t^*| = 0.$$

*Proof.* Note that  $(\Sigma_0, U_0) \in X_0$  if and only if  $(U_0, S_0) \in \Omega_W$ . Then, by Lemma 4 it follows that  $(\Sigma_t, U_t) \in X_0$  for any forward solution of (4.1) passing through  $(\Sigma_0, U_0)$  at initial time  $t_0 = t^* = 0$ .

By Lemma 2, we know that  $\lim_{t \rightarrow +\infty} |\Sigma_t - \Sigma_t^*| = 0$ . In consequence, we will only verify that  $\lim_{t \rightarrow +\infty} |U_t - U_t^*| = 0$ .

By Theorem 3 and statement i) from Remark 8, there exists a unique  $\omega$ -periodic solution  $(U_t^*, S_t^*)$  with  $U_t^* + S_t^* = \Sigma_t^*$ . Moreover, if  $(U_t, S_t)$  is another positive solution of (4.1), then the function  $\Sigma_t = U_t + S_t$  verifies the identity  $\Sigma_t - \Sigma_t^* =$

$(1 - E)^{t-t_0}[\Sigma_{t_0} - \Sigma_{t_0}^*]$ , as proved by Lemma 2. Now, let us define  $W_t := U_t - U_t^*$  and

$$A_t := \begin{cases} \frac{f(S_t) - f(S_t^*)}{S_t - S_t^*} & S_t \neq S_t^* \\ f'(S_t^*) & S_t = S_t^*, \end{cases}$$

which allows us to write

$$W_{t+1} = C_t W_t + D_t,$$

where  $C_t$  and  $D_t$  are defined by:

$$C_t := (1 - E)[1 + f(S_t^*) - A_t U_t] \quad \text{and} \quad D_t := (1 - E)A_t U_t (\Sigma_t - \Sigma_t^*).$$

By variation of parameters we have that, for any  $t_0 \geq 0$ ,

$$(4.8) \quad W_{t_0+k+1} = \left( \prod_{j=t_0}^{t_0+k} C_j \right) W_{t_0} + \sum_{j=t_0}^{t_0+k} D_j \prod_{s=j+1}^{t_0+k} C_s$$

where, as usual, we assume that  $\prod_{s=t_0+k+1}^{t_0+k} C_s = 1$ . Let us recall that  $\{S_t\}_t$  is bounded since  $(\Sigma_0, U_0) \in X_0$ , then we can write  $A_t = f'(\xi_t)$  with  $\xi_t$  between  $S_t$  and  $S_t^*$  such that  $\xi_t \in [0, W]$  since  $0 < S_t \leq S_t + U_t \leq W$ . From **(H1)** it may be concluded that there exists a constant  $a := \min_{r \in [0, W]} f'(r) > 0$  such that

$a \leq A_t \leq f'(0)$ . Moreover, by **(I2)** and the positiveness of  $S_t$ , it follows that

$$\begin{aligned} 1 - U_t f'(0) &= 1 - (\Sigma_t^* - S_t) f'(0) + (\Sigma_t^* - \Sigma_t) f'(0) \\ &= 1 - \Sigma_t^* f'(0) + S_t f'(0) + (\Sigma_t^* - \Sigma_t) f'(0) \\ &\geq (\Sigma_t^* - \Sigma_t) f'(0). \end{aligned}$$

Next, we can deduce that

$$S_{t+1} \geq (1 - E)[1 - U_t f'(0)] S_t + E S_t^0 \geq (1 - E)(\Sigma_t^* - \Sigma_t) f'(0) S_t + E S_t^0 \geq c > 0$$

for some  $c \in (0, E S_{\min}^0)$ , when considering  $t$  large enough.

Now, as  $U_t = \Sigma_t - S_t$ , and by using again **(I2)** combined with the fact that  $\Sigma_t$  and  $\Sigma_t^*$  are asymptotically equivalent, it is verified that

$$A_t U_t \leq f'(0)[\Sigma_t - c] < f'(0) \Sigma_t^* \leq 1,$$

which implies that  $C_t > 0$  for  $t$  large enough.

As  $U_t$  is also bounded, for any initial time  $t_0$  we have

$$|D_t| \leq c_1 |\Sigma_{t_0} - \Sigma_{t_0}^*| (1 - E)^{t-t_0}$$

for some  $c_1$  and any  $t > t_0$ . In order to estimate (4.8), we observe that

$$\prod_{s=j+1}^{t_0+k} C_s \leq \prod_{s=j+1}^{t_0+k} (1 - E) \{1 + f(S_s^*)\},$$

which is bounded since  $S_t^*$  is  $\omega$ -periodic and  $\prod_{s=0}^{\omega-1} (1 - E) \{1 + f(S_s^*)\} = 1$ . Then, there exists a constant  $K$  such that

$$(4.9) \quad \left| \sum_{j=t_0}^{t_0+k} D_j \prod_{s=j+1}^{t_0+k} C_s \right| \leq K |\Sigma_{t_0} - \Sigma_{t_0}^*| \sum_{j=t_0}^{t_0+k} (1 - E)^{j-t_0} \leq \frac{K}{E} |\Sigma_{t_0} - \Sigma_{t_0}^*|,$$

is arbitrarily small for  $t_0 > T_1$ , where  $T_1$  is large enough. Now, let us write

$$\prod_{j=t_0}^{t_0+k} C_j = \prod_{j=t_0}^{t_0+k} (1 - E) \{1 + f(S_j^*)\} \prod_{j=t_0}^{t_0+k} \left( 1 - \frac{A_j U_j}{1 + f(S_j^*)} \right),$$

where, as we have seen, the first factor is bounded. On the other hand, note that the second factor converges towards 0. Indeed, as  $0 < \frac{A_j U_j}{1+f(S_j^*)} < 1$  for large values of  $j$ , the convergence follows from the fact that  $A_j U_j$  cannot be convergent to 0 since  $A_j \geq a > 0$  and  $U_j$  is persistent by (3.18). In consequence,  $\lim_{k \rightarrow \infty} \prod_{j=t_0}^{t_0+k} C_j = 0$ .

Now, given  $\varepsilon > 0$ , from (4.8) and (4.9) we may fix  $t_0$  such that

$$\left| W_{t_0+k+1} - \prod_{j=t_0}^{t_0+k} C_j W_{t_0} \right| < \varepsilon,$$

and, by letting  $k \rightarrow \infty$ , we obtain  $\limsup_{j \rightarrow \infty} |W_j| \leq \varepsilon$  and  $\liminf_{j \rightarrow \infty} |W_j| \geq -\varepsilon$ . Finally, as the above limits hold for any  $\varepsilon > 0$  we conclude that  $\lim_{j \rightarrow \infty} U_j - U_j^* = 0$  and the result follows.  $\square$

**4.2. Existence and attractiveness of a periodic solution of the original system (2.12).** In this subsection, we will assume that the hypotheses of Theorem 4 are satisfied. Now, let  $t \mapsto (S_t, \mathbf{x}_t)$  be a solution of (2.12) such that  $(\mathbf{1} \cdot \mathbf{x}_0, S_0) \in \Omega_W$  with  $W = 1/f'(0)$  at initial time  $t_0 = 0$ . Moreover, let us recall that  $\mathbf{1} \cdot \mathbf{x}_t = U_t$ . By Theorem 4 and the asymptotical equivalence between  $S_t = \Sigma_t - U_t$  and  $S_t^* = \Sigma_t^* - U_t^*$ , we can deduce that  $t \mapsto (\mathbf{1} \cdot \mathbf{x}_t, S_t)$  is a solution of the system (3.5) such that

$$\lim_{t \rightarrow \infty} |S_t - S_t^*| = 0 \quad \text{and} \quad \lim_{t \rightarrow \infty} |\mathbf{1} \cdot \mathbf{x}_t - U_t^*| = 0,$$

where  $t \mapsto (U_t^*, S_t^*)$  is the unique  $\omega$ -periodic solution of (3.5).

Now, for any initial condition  $(\mathbf{1} \cdot \mathbf{x}_0, S_0) \in \Omega_W$  at initial time  $t_0 = 0$ , it follows that the linear system

$$(4.10) \quad \mathbf{x}_{t+1} = (1 - E)A(S_t)\mathbf{x}_t,$$

is  $\omega$ -asymptotically periodic with limit

$$(4.11) \quad \mathbf{x}_{t+1} = (1 - E)A(S_t^*)\mathbf{x}_t,$$

where  $A(\cdot)$  is described by (2.11). The Floquet theory for linear difference  $\omega$ -periodic systems (see *e.g.* [12, Ch.3]) allows a deep study of the system (4.11).

**Lemma 10.** *If (H1), (H2), (I2), hold and condition (3.18) is satisfied for some  $E \in (0, 1)$ , then any basis of solutions of the  $\omega$ -periodic system (4.11) is composed by one  $\omega$ -periodic solution and  $r - 1$  uniformly exponentially stable solutions.*

*Proof.* The evolution operator associated to the system (4.11) is defined by

$$\Phi(k, \ell) = (1 - E)^{k-1-\ell} A(S_{k-1}^*) \cdots A(S_\ell^*) \quad \text{for all } k \geq \ell.$$

The Floquet multipliers of (4.11) are the eigenvalues of  $\Phi_\omega := \Phi(\omega - 1, 0)$  and consequently, a basis of solutions can be constructed in terms of its associated eigenvectors. By Proposition 3.2.3 from [12] it follows that if  $\lambda = 1$  is a Floquet multiplier, then there exists an  $\omega$ -periodic solution.

A first step to deduce the existence of a Floquet multiplier  $\lambda = 1$ , is to prove that  $\rho(\Phi_\omega)$ , the spectral radius of  $\Phi_\omega$ , verifies  $\rho(\Phi_\omega) = 1$ . By using the Corollary 1 combined with the identity (4.7) we have that

$$\rho(\Phi_\omega) \leq (1 - E)^\omega \prod_{t=0}^{\omega-1} \{1 + f(S_t^*)\} = 1.$$

Now, we will see that the above inequality is, in fact, an identity. Indeed, otherwise we will have that  $\rho(\Phi_\omega) < 1$ , that is, all the Floquet multipliers are inside the unit circle, which implies that the linear  $\omega$ -periodic system (4.11) is uniformly exponentially stable. Then for any non trivial solution  $t \mapsto \mathbf{x}_t$  of (4.11) it follows that  $t \mapsto \mathbf{1} \cdot \mathbf{x}_t$  is a solution of  $U_{t+1} = (1 - E)\{1 + f(S_t^*)\}U_t$ , which is convergent to zero, but we obtain a contradiction with (4.7) and we conclude that  $\rho(\Phi_\omega) = 1$ .

As  $(1 - E)A(S_t^*)$  are primitive, nonnegative and commutative, it follows that  $\Phi_\omega$  is irreducible and nonnegative [5, p.28] and also primitive [11, p.268]. By Perron–Frobenius Theorem for irreducible nonnegative matrices [14, p.257], we have that  $1 = \rho(\Phi_\omega)$  is a simple eigenvalue having a strictly positive eigenvector  $v^*$ , namely,

$$\Phi_\omega v^* = \Phi(\omega - 1, 0)v^* = v^*,$$

and it follows that  $t \mapsto \Phi(t - 1, 0)v^*$  is an  $\omega$ -periodic solution of (4.11).

The Floquet multiplier  $\lambda = 1$  is also called the Perron–Frobenius eigenvalue and the one dimensional subspace of its right eigenvectors will be denoted by  $\langle v^* \rangle$ . Any vector  $e \in \langle v^* \rangle$  is called a Perron–Frobenius eigenvector and it follows clearly that  $\Phi_\omega e = e$ .

Finally, as  $\Phi_\omega$  is a primitive matrix and because  $1 = \rho(\Phi_\omega)$  is simple, it follows that –see subsection 2.4 for details– any other Floquet multiplier  $\lambda$  verifies  $|\lambda| < 1$ .  $\square$

To prove the existence and attractiveness of an  $\omega$ -periodic solution of (2.12) it will be useful to recall a byproduct of the weak ergodic theorem of Golubitsky [8]:

**Proposition 1.** [3, Th.2.4] *Suppose that  $T_n$  is a sequence of nonnegative and primitive matrices, and that  $T_n \rightarrow T$  as  $n \rightarrow \infty$  where  $T$  is also nonnegative and primitive. If  $e$  is the Perron–Frobenius eigenvector of  $T$  satisfying  $\mathbf{1} \cdot e = 1$  and  $\xi_{n+1} = T_n \xi_n$  is a sequence with  $\xi_0 > 0$  then*

$$\lim_{n \rightarrow \infty} \frac{T_{n-1} \xi_{n-1}}{\mathbf{1} \cdot \xi_{n-1}} = e.$$

**Theorem 5.** *If (H1), (H2), (I2), hold and (3.18) is satisfied for some  $E \in (0, 1)$ , then (2.12) has an  $\omega$ -periodic solution  $(S_t^*, \mathbf{x}_t^*)$  such that  $\lim_{t \rightarrow \infty} |S_t - S_t^*| + |\mathbf{x}_t - \mathbf{x}_t^*| = 0$  for any solution  $(S_t, \mathbf{x}_t)$  with  $(\mathbf{1} \cdot \mathbf{x}_0, S_0) \in \Omega_W$  (with  $W = \frac{1}{f(0)}$ ) at  $t_0 = 0$ .*

*Proof. Existence:* Let  $\mathbf{x}_t^*$  be an  $\omega$ -periodic solution of (4.11) with initial condition  $\mathbf{x}_0^* \in \langle v^* \rangle$  and  $S_t^*$  be the nutrient coordinate of the unique  $\omega$ -periodic solution of (3.5). Now, let us construct the family of systems:

$$(4.12) \quad S_{t+1} = (1 - E)S_t + (1 - E)f(S_t^*)\mathbf{1} \cdot \mathbf{x}_t^* + ES_t^0.$$

From now on, we will consider the equation (4.12) where  $\mathbf{x}_t^*$  is an  $\omega$ -periodic solution of (4.11) verifying  $\mathbf{x}_0^* = \frac{U_0^*}{\mathbf{1} \cdot v^*} v^*$ , which implies that  $\mathbf{1} \cdot \mathbf{x}_t^* = U_t^*$  is the unique  $\omega$ -periodic solution of

$$U_{t+1} = (1 - E)[1 + f(S_t^*)]U_t \quad \text{with} \quad U_0 = U_0^*$$

and we restrict our interest to

$$(4.13) \quad S_{t+1} = (1 - E)S_t + (1 - E)f(S_t^*)U_t^* + ES_t^0.$$

As in Remark 1, it can be proved that (4.13) has a unique  $\omega$ -periodic solution denoted by  $\tilde{S}_t^*$ . To prove that  $\tilde{S}_t^* = S_t^*$ , let  $\eta_t = \tilde{S}_t^* - S_t^*$ , satisfying  $\eta_{t+1} = (1-E)\eta_t$  and its unique  $\mathbb{Z}$ -bounded solution is  $\eta_t = 0$ , then the identity  $\tilde{S}_t^* = S_t^*$  follows.

When summarizing the above facts, we deduce that if  $\mathbf{x}_t^*$  is an  $\omega$ -periodic solution of (4.11) with  $\mathbf{x}_0^* = \frac{U_0^*}{\mathbf{1} \cdot v^*} v^*$  then  $S_t^*$  is an  $\omega$ -periodic solution of (4.12) coincident with the unique  $\omega$ -periodic solution of (4.13). Then by coupling (4.11) and (4.12), it follows that  $(S_t^*, \mathbf{x}_t^*)$  is an  $\omega$ -periodic solution of (2.12).

*Attractiveness:* Let us recall that  $\Sigma_t - \Sigma_t^* \rightarrow 0$ ,  $U_t - U_t^* \rightarrow 0$  and  $S_t - S_t^* \rightarrow 0$  when  $t \rightarrow \infty$ . In consequence, we only need to verify that  $\mathbf{x}_t - \mathbf{x}_t^* \rightarrow 0$ .

We consider the Poincaré operator  $\mathcal{P}: \mathbb{R}_+^r \rightarrow \mathbb{R}_+^r$  related to (4.10). If  $\mathbf{x}_0 \neq 0$  is the biomass of an initial condition of (2.12), then let  $\mathbf{x}_{n\omega} := x_n$  for  $n \in \mathbb{Z}_0^+$ . Thus,

$$x_1 = \mathcal{P}x_0 = (1-E)^\omega A(S_{\omega-1}) \cdots A(S_0)x_0$$

and we can define the recursion

$$x_n = \mathcal{P}x_{n-1} = \underbrace{(1-E)^\omega A(S_{n\omega-1}) \cdots A(S_{(n-1)\omega})}_{=T_{n-1}} x_{n-1},$$

or equivalently  $x_n = T_{n-1}x_{n-1}$ . By using the properties of  $A(S_t)$  stated in the subsection 2.4 we can prove that  $T_n$  is a sequence of primitive, nonnegative and commutative matrices. Moreover, Theorem 4 also ensures that  $T_n \rightarrow \Phi_\omega$  when  $n \rightarrow \infty$ . Note that  $\Phi_\omega$  is also nonnegative, primitive and commutative as we observed in the proof of Lemma 10. Now, the weak ergodic theorem of Golubitsky states that if  $e$  is a Perron–Frobenius eigenvector of  $\Phi_\omega$  satisfying  $\mathbf{1} \cdot e = 1$ , then

$$(4.14) \quad \lim_{n \rightarrow \infty} \frac{x_n}{\mathbf{1} \cdot x_{n-1}} = e.$$

As we know that  $\lim_{n \rightarrow \infty} U_{n\omega-1} = U_{n\omega-1}^* = U_j^*$  for some  $j \in \{0, \dots, \omega-1\}$ , the identities  $\mathbf{1} \cdot x_{n-1} = \mathbf{1} \cdot \mathbf{x}_{n\omega-1} = U_{n\omega-1}$  allow us to deduce that  $\lim_{n \rightarrow \infty} \mathbf{1} \cdot x_{n-1} = U_j^*$  and by (4.14) it follows that

$$(4.15) \quad \lim_{n \rightarrow \infty} x_n = U_j^* e = \frac{U_j^* e}{\mathbf{1} \cdot e} \in \langle v^* \rangle.$$

As we see at the beginning of the proof of this theorem, the above vector  $U_j^* e$  can be seen as a initial condition of the linear periodic system (4.11), that is, we have the identity  $U_j^* e = x_0^* = x_{n\omega}^*$ .

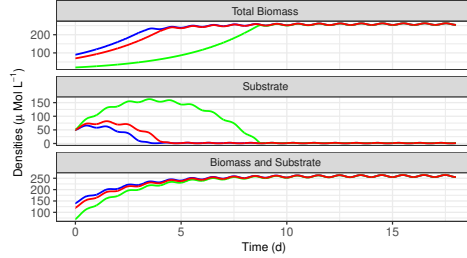
Let us note that (4.15) is equivalent to  $\mathcal{P}^n \mathbf{x}_0 \rightarrow \mathbf{x}_{n\omega}^* \in \langle v^* \rangle$  when  $n \rightarrow \infty$ , which implies that  $\mathbf{x}_{n\omega} - \mathbf{x}_{n\omega}^* \rightarrow 0$ . We emphasize that it can be proved that  $\mathbf{x}_t - \mathbf{x}_t^* \rightarrow 0$  in a similar way as in the proof of Theorem 3.

□

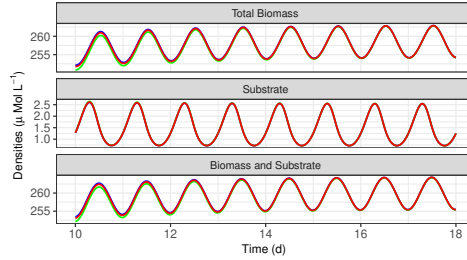
## 5. NUMERICAL SIMULATIONS

To illustrate our results and allow a comparison with previous ones, we carry out numerical simulations for the cultivation of microalgae of the *Cryptomonas* species, as was done by Arino et al. [3]. The genus *Cryptomonas* was established by C.G. Ehrenberg in 1831, and this kind of algae can be found in both fresh and saltwater sources around the world. Two aspects that have been investigated about *Cryptomonas* are the identification of new species that belong to this genus [6], and

how these unicellular algae regulate their internal protein reserve to optimize their growth rate under nitrogen- and light-limited conditions [13].



(A) Dynamics with transient phase.



(B) Dynamics without transient phase.

FIGURE 2. Dynamic of the total biomass and substrate. The initial conditions are:  $(U, S) = (90, 50)$  (blue curve),  $(U, S) = (20, 50)$  (green curve), and  $(U, S) = (70, 50)$  (red curve).

We consider the growth of the microalgae *Cryptomonas sp* with nitrate as limiting substrate and a Monod or Michaelis–Menten type growth function  $\mu(S) = \hat{\mu}_{\max} \frac{S}{K+S}$  and the periodic input rate of nitrate

$$S_t^0 = 260 + 70 \sin\left(\frac{2\pi t}{1000}\right) \mu \text{ Mol } L^{-1}.$$

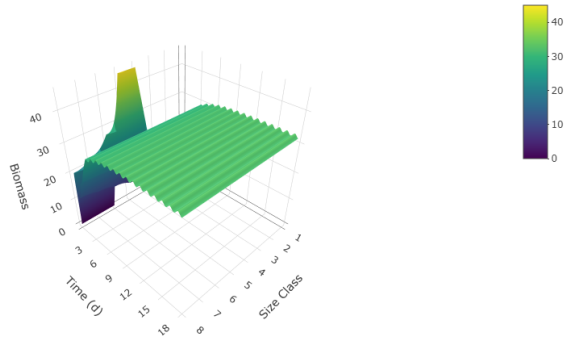
For the convenience of the reader, the culture conditions are presented in Table 1. By considering  $E = DT$ ,  $f(S) = \frac{f_{\text{sup}} S}{K+S}$  where  $f_{\text{sup}} = \hat{\mu}_{\max} T$ , the hypotheses **(H2)**, **(I1)**, **(I2)** and the inequality for the minimum doubling time, then the constraints for the number of size classes,  $r$ , and the iteration period,  $T$ , are:

$$f_{\text{sup}} \leq 2^{1/r} - 1, \quad rT \leq \mathcal{T}_{\min}, \quad f'(0)S_{\text{sup}}^0 \leq 1 + 2\sqrt{\frac{f'(0)ES_{\text{inf}}^0}{1-E}}, \quad f'(0)\Sigma_{\text{sup}}^* < 1.$$

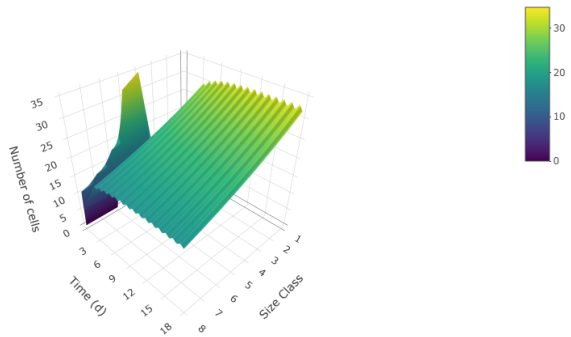
Then we set the number of size classes in (2.12) to eight, that is,  $r = 8$ . Consequently, we consider  $T = 0.001$  and it is possible to determine  $f$  and  $D$ . We carried out our numerical simulations in the software R version 4.0.2 and use libraries GGPlot2, Reshape2, Latex2exp and Plotly to build Figures 2 and 3.

## REFERENCES

- [1] Amster P, Robledo G, Sepúlveda D (2020) Dynamics of a chemostat with periodic nutrient supply and delay in the growth. *Nonlinearity* 33:5839–5860.



(A) Dynamics of biomass.



(B) Dynamics of number of cells.

FIGURE 3. Dynamics with null initial condition in all classes, except for classes 4 and 5 with  $45 \mu \text{ Mol } L^{-1}$  units of biomass.

Parameter	Value	Unit	Meaning	Source
$\hat{\mu}_{\max}$	0.7	$d^{-1}$	maximum growth rate	[3]
$K$	1	$\mu \text{ Mol } L^{-1}$	half-saturation constant	[3]
$D$	0.4	$d^{-1}$	dilution rate	[3]
$\mathcal{T}_{\min}$	1	$d$	minimal duplication time	[3]

TABLE 1. Cryptomonas culture conditions growing with nitrate as a limiting substrate.

- [2] Arino J (2001) Modélisation structurée de la croissance du phytoplancton en chemostat. Université Joseph Fourier, Grenoble (Ph.D Thesis).
- [3] Arino J, Gouzé JL, Sciandra A (2002) A discrete, size-structured model of phytoplankton growth in the chemostat. J Math Biol 45:313–336.
- [4] Babiarz A, Czornik A, Niezabitowski M (2015) On the number of upper Bohl exponents for diagonal discrete time-varying linear system. J Math Anal Appl 429:337–353.
- [5] Berman A, Plemmons RJ (1994) Nonnegative Matrices in the Mathematical Sciences, SIAM, Philadelphia

- [6] Choi B, Son M, Kim JI, Shin W (2013) Taxonomy and phylogeny of the genus *Cryptomonas* (Cryptophyceae, Cryptophyta) from Korea. *Algae* 28:307–330.
- [7] Gage T, Williams FM, Horton JB (1984) Division synchrony and the dynamics of microbial populations: a size-specific model. *Th Pop Biol.* 26:296–314
- [8] Golubitsky M, Keeler EB, Rothschild M (1975) Convergence on the age structure: applications of the projective metric. *Th Pop Biol.* 7:84–93.
- [9] Henderson J, Lee L (1991) Continuous dependence and differentiation of solutions of finite difference equations. *Int J Math Math Sci.* 14:747–756
- [10] Hinrichsen D, Pritchard AJ (2005) *Mathematical Systems Theory I.* Springer-Verlag, Berlin-Heidelberg
- [11] Lütkepohl H (1996) *Handbook of Matrices.* Wiley, Chichester
- [12] Pötzsche C (2010) *Geometric Theory of Discrete Nonautonomous Dynamical Systems.* Springer, New York
- [13] Sciandra A, Lazzara L, Claustre H, Babin M (2000) Responses of growth rate, pigment composition and optical properties of *Cryptomonas* sp. to light and nitrogen stresses. *Mar Ecol Prog Ser.* 201:107–120.
- [14] Smith HL, Waltman P (1995) *The Theory of the Chemostat, Dynamics of the Microbial Competition.* Cambridge University Press, Cambridge
- [15] Smith HL (1996) A discrete, size-structured model of microbial growth and competition in the chemostat. *J Math Biol.* 34:734–754
- [16] Smith HL, Zhao XQ (2001) Competitive exclusion in a discrete size-structured chemostat model. *Discrete Contin Dyn Syst Ser B.* 1:183–191
- [17] Zhao XQ (2005) *Dynamical Systems in Population Biology.* Springer, New York
- [18] Zhang D, Wang L (2019) Multistability driven by inhibitory kinetics in a discrete-time size-structured chemostat model. *Chaos* 29 063112
- [19] Zhang D, Cai X, Wang L (2019) Complex dynamics in a discrete-time size-structured chemostat model with inhibitory kinetics. *Discrete Contin Dyn Syst Ser B.* 24:3439–3451.

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