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Dynamics of the periodically forced light-limited Droop model

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Abstract :

The periodically forced light-limited Droop model represents microalgae growth under co-limitation by light and a single substrate, accounting for periodic fluctuations of factors such as light and temperature. In this paper, we describe the global dynamics of this model, considering general monotone growth and uptake rate functions. Our main result gives necessary and sufficient conditions for the existence of a positive periodic solution (i.e. a periodic solution characterized by the presence of microalgae) which is globally attractive. In our approach, we reduce the model to a cooperative planar periodic system. Using results on periodic Kolmogorov equations and on monotone sub-homogeneous dynamical systems, we describe the global dynamics of the reduced system. Then, using the theory of asymptotically periodic semiflows, we extend the results on the reduced system to the original model. To illustrate the applicability of the main result, we include an example considering a standard microalgae population model.

Keywords : Variable quota model, Positive periodic solution, Global stability, Microalgae, Cooperative System

1. Introduction

Microalgae are photosynthetic microorganisms, converting light energy into chemical energy [1]. Microalgae have many applications, among them biomass production for food and fine chemicals, biodiesel production, and wastewater treatment [1, 2]. For industrial applications, microalgae are grown in open ponds or photobioreactors [3]. In these systems, algae growth is mainly limited by the amount of nutrients and light availability. Different mathematical models have been developed to describe microalgae growth under these limitations. Under nutrient limitation, we find the Monod model and the Droop (or Cell Quota) model [4]. The former relates the growth rate to the nutrient concentration in the medium, while the latter relates the growth rate to an intracellular pool of nutrient known as cell quota. The applicability of the Monod model is limited to steady state condition [5]. The applicability of the Droop model is more widespread and has successfully described the growth rate even under fluctuations of the environmental conditions [4, 6, 7]. On the other hand, to describe the growth under light-limitation, Huisman and collaborators [8] introduced the theory of light-limited chemostat. Light-limitation differs considerably from nutrient-limitation. Light rapidly decreases as it passes through the microalgae culture due to absorption and scattering by algal cells. This results in a light gradient whose pattern depends on the microalgae concentration. As a consequence, the growth rate depends on the microalgae concentration. On top of that, the light source in microalgae cultures is not always constant along time. Outdoor cultures are subject to a light phase (day) and a dark phase (night) following a periodic pattern. Thus, the growth rate, that depends on light availability, becomes a periodic function in time. Periodicity on the models can also be induced by water temperature or nutrient supply fluctuations. Many theoretical works analyze single microalgae population growth with the Droop model [9, 10], or light limitation [11, 12, 13]. Models with both substrate and light limitations are studied in [13, 14, 15] with Monod approach, and in [16] with variable quota. Finally, a few studies deal with periodic forcing. Microalgae cultures under light limitation with a periodic light source are analyzed in [17, 18], and the Droop model with periodic nutrient supply is studied in [19]. But, to our knowledge, nothing has yet been done for both light and substrate limitations under periodic forcing.

In this work we study the asymptotic behavior of the periodically forced light-limited Droop model *i.e.* a model that results from combining the modelling approaches of Droop [4] and Huisman [8], when the growth rate, the uptake rate, the nutrient supply, and the dilution rate are periodic functions of time. We consider general monotone growth and uptake rate functions. In our approach, we reduce the model to a cooperative two-dimensional system to show that any solution approaches asymptotically to a periodic solution. Following results on Kolmogorov periodic equations [20], we find conditions such that any solution of the reduced system is asymptotic to a positive periodic solution *i.e.* a solution characterized by the presence of microalgae. This proves the existence of positive periodic solutions for the original system. Using results of the theory of subhomogeneous (or sublinear) dynamical systems [26], we give conditions for the uniqueness of positive periodic solutions. Finally, using the theory of asymptotically periodic semiflows [21] and classical results of the theory of differential equations such as the comparison method [22], we find a result on the global dynamics of the original model.

This article is organized as follows. In Section 2, we introduce the periodically forced light-limited Droop model and we state some basic results on the existence, uniqueness, and boundedness of solutions. In Section 3, we study a limiting two-dimensional periodic system of the model. We prove that any solution of this system is asymptotic to a periodic solution (Proposition 3.3), and we give conditions for the extinction (Proposition 3.5) and persistence (Theorem 3.6) of the population. We also determine conditions for the uniqueness of positive periodic solutions (Theorem 3.8). In Section 4, we present the main result (Theorem 4.1), a result on the global dynamics of the model. In Section

5, we apply our results to study a model describing microalgae growth under limitation by phosphorus and light. In Section 6, we discuss our results and some possible extensions. Finally, we include two appendices. In Appendix A we present some results on the asymptotic of scalar differential equations. In Appendix B we prove some properties of a growth rate function.

2. Model description and basic properties

2.1. Model description

Let us consider a well-mixed culture system with a biomass $x(t)$ of microalgae. Microalgae growth is only limited by light and a nutrient at concentration $s(t)$ in the medium. The light is provided by an external light source (artificial or natural) and its intensity can vary with time. The nutrient is supplied at variable concentration $s_{in}(t)$, from an external reservoir at the variable volumetric flow rate $Q_{in}(t)$. The dilution rate is the ratio $D(t) := F_{in}(t)/V(t)$ with $V(t)$ the volume of the culture. Following the Droop model [4], microalgae growth depends on the internal quota of nutrient $q(t)$. The quota increases with nutrient uptake and decreases with cell growth (by the effect of intracellular dilution). Following the theory of light-limited chemostats [8], the growth of microalgae affects their own light environment (self-shading). Then, the cell growth rate depends on the biomass concentration $x(t)$. Since the incident light may vary over time, the growth rate depends on time. The light-limited Droop model takes the following form:

$$\begin{aligned}\frac{dx}{dt} &= [\mu(t,x,q) - D(t)]x,\\ \frac{dq}{dt} &= \rho(t,q,s) - \mu(t,x,q)q,\\ \frac{ds}{dt} &= D(t)(s_{in}(t) - s) - \rho(t,q,s)x.\end{aligned} \tag{1}$$

The functions μ and ρ represent the growth rate of microalgae and the nutrient uptake rate respectively. Let $J = [q_0, \infty)$ with $q_0 > 0$. We assume that $\mu : \mathbb{R}_+^2 \times J \longrightarrow \mathbb{R}$, $\rho : \mathbb{R}_+ \times J \times \mathbb{R} \longrightarrow \mathbb{R}$, and D, $s_{in} : \mathbb{R}_+ \longrightarrow \mathbb{R}_+$ are continuous functions and satisfy the following set of assumptions:

H 2.1. *μ, ρ, D, and s_{in} are ω-periodic in t with $\omega > 0$.*

H 2.2. *$q \longmapsto \rho(t, q, s)$ is decreasing, $s \in [0, \infty) \longmapsto \rho(t, q, s)$ is increasing, and $\rho(t, q, s) = 0$ for all $s \leq 0$.*

H 2.3. *$\mu(t, x, q_0) \leq 0$ for any $t, x \geq 0$, and $q \longmapsto \mu(t, x, q)$ is increasing.*

H 2.4. *For any $q > q_0$, $x \longmapsto \mu(t, x, q)$ is decreasing.*

H 2.5. *$\lim_{q\to\infty} \rho(t, q, s) = 0$ and $\lim_{x\to\infty} \mu(t, x, q) \in (-\infty, 0]$, both uniformly for $t \in [0, \omega]$.*

H 2.6. *$\displaystyle\int_0^\omega D(t)dt > 0$ and $\displaystyle\int_0^\omega D(t)s_{in}(t)dt > 0$.*

H 2.7. *μ and ρ are locally Lipschitz uniformly for t in $[0, \omega]$.*

H 2.8. *There exists $q' > q_0$ such that $\displaystyle\int_0^\omega \mu(t, 0, q')dt > 0$.*

Remark 2.9. *(Subsistence quota) The parameter q_0 is known as the subsistence quota and represents the value of q at which growth ceases. H2.3 shows that there cannot be growth when $q = q_0$. In particular, this implies that the quota cannot be smaller than q_0. Indeed, the derivative of $q(t)$ is non-negative when $q = q_0$ (see the second equation in (1)).*

Remark 2.10. *In H2.5, the existence of the limits is given by the monotonicity of μ and ρ. The limit for μ is allowed to be $-\infty$.*

Remark 2.11. *(Respiration rate) In hypothesis H2.3, the growth rate is allowed to be negative. When microalgae is measured in terms of carbon biomass, μ corresponds to the carbon gain rate i.e. $\mu = p - m$, with p the photosynthesis (carbon uptake) rate and m the specific carbon loss rate. Thus, μ may be negative, especially in absence of light when $p = 0$.*

Remark 2.12. *From a biological point of view, H2.8 states that there is a quota such that a very small population can grow. Hypothesis H2.8 is necessary to avoid the extinction of the population and unbounded values of the cell quota (see Remarks 2.15 and 2.18).*

2.2. Existence, uniqueness, and boundedness of solutions

We define the total amount of limiting nutrient both in the substrate and in the biomass by means of $S = s + xq$. A simple calculation shows that S satisfies the differential equation:

$$\frac{dS}{dt} = D(t)(s_{in}(t) - S). \tag{2}$$

With respect to the solutions of (2), we have the following lemma.

Lemma 2.13. *Equation (2) admits a unique ω-periodic solution $s_*(t)$ which is positive and globally attractive.*

Proof. From a direct calculation we have that:

$$S(t) = (S(0) + f(t))e^{-d(t)}, \tag{3}$$

and that $s_*(t)$ is given by:

$$s_*(t) = e^{-d(t)} \left(\frac{f(\omega)}{e^{d(\omega)} - 1} + f(t) \right), \tag{4}$$

with $d(t) = \int_0^\omega D(t)dt$ and $f(t) = \int_0^t e^{d(\tau)} s_{in}(\tau) D(\tau) d\tau$. Since s_{in} and D are non-negative, we have that f is a non-negative function. Since $\int_0^\omega D(t)s_{in}(t)dt > 0$ (see H2.6), we have that $f(\omega) > 0$. Thus, $s_*(t)$ is positive. For the global stability, it easily follows that $|S(t) - s_*(t)| \to 0$ as $t \to \infty$. □

Now we state the existence and uniqueness of solutions for system (1).

Lemma 2.14. *System (1) admits a unique global solution for any initial condition on $\mathbb{R}_+ \times J \times \mathbb{R}_+$.*

Proof. The existence and uniqueness of solutions is given by hypothesis H2.7. Let (x, q, s) be a solution of (1) such that $x(0), s(0) \geq 0$ and $q(0) \geq q_0$, with Δ the maximal interval of existence. We have $(x(t), q(t), s(t)) \in \mathbb{R}_+ \times J \times \mathbb{R}_+$ for any $t \in \Delta$. Since the variable $S = xq + z$ satisfies the differential equation (2) and (x, q, s) is non-negative, by Lemma 2.13, xq and s cannot be unbounded in a finite interval of time. Now we note that $x(t)q(t) \geq x(t)q_0$, then $x(t) \leq S(t)/q_0$ for all $t \in \Delta$. Finally, since $dq/dt \leq \rho(t, q_0, S(t)) - \mu(t, S(t)/q_0, q_0)q$, we conclude that q cannot be unbounded in a finite interval of time. Thus, $\Delta = [0, \infty)$. $\square$

Remark 2.15. *Let (x, q, s) be a solution of (1). If H2.8 does not hold, then $x(t) \to 0$ as $t \to \infty$. Indeed, since μ is decreasing in x we have that:*

$$\frac{dx(t)}{dt} \leq x(t)[\mu(t, 0, q(t)) - D(t)]. \tag{5}$$

Since H2.8 does not hold, $\int_0^{n\omega} \mu(t, 0, q(t))dt < 0$ for any integer $n \geq 1$. Thus, applying Gronwall's inequality to (5) on the interval $[t - \omega[t/\omega], t]$ we obtain:

$$x(t) \leq x(t - \omega[t/\omega])e^{-\alpha[t/\omega]}, \tag{6}$$

where $[t/\omega]$ is the greatest integer less than or equal to t/ω and $\alpha = \int_0^\omega D(\tau)d\tau > 0$. Letting $t \to \infty$ in (6) we obtain that $x(t) \to 0$.

The following lemma will be repeatedly used in the rest of the paper.

Lemma 2.16. *For any non-negative continuous function σ there is $Q > 0$ such that:*

$$\int_0^\omega \left(\frac{\rho(t, Q, \sigma(t))}{Q} - \mu(t, 0, Q) \right) dt < 0.$$

Proof. From H2.5 we have that $\lim_{q\to\infty} \int_0^\omega \rho(t, q, s)dt = 0$ for any $s \geq 0$. Then there exists $Q > q'$, with q' given by H2.8, such that:

$$\int_0^\omega \rho(t, Q, \max_{t\in[0,\omega]} \sigma(t))dt < \epsilon := q' \int_0^\omega \mu(t, 0, q')dt. \tag{7}$$

From the monotonicity of μ and ρ as functions of q (see H2.2 and H2.3), we have that:

$$Q \int_0^\omega \mu(t, 0, Q)dt > q' \int_0^\omega \mu(t, 0, q')dt = \epsilon \geq \int_0^\omega \rho(t, Q, \sigma(t))dt,$$

from where we complete the proof. $\square$

Lemma 2.17. *Solutions of (1) starting on $\mathbb{R}_+ \times J \times \mathbb{R}_+$ are uniformly bounded.*

Proof. From Theorem 8.5 in [23], the ultimate boundedness of solutions of a periodic system implies the uniform boundedness of solutions. Thus, we prove that solutions of (1) starting on $\mathbb{R}_+ \times J \times \mathbb{R}_+$ are ultimately bounded. Let $(\bar{x}, \bar{q}, \bar{s})$ be a solution of (1) with $\bar{x}(0), \bar{s}(0), \bar{q}(0) - q_0 \geq 0$. We have that $\bar{S}(t) = \bar{x}(t)\bar{q}(t) + \bar{s}(t)$ satisfies the differential equation (2). From Lemma 2.13, there is $t' > 0$ such that $\bar{S}(t) \leq s'$ for all $t \geq t'$, with $s' := 1 + \max s_*(t)$. By similar arguments as in Proof of Lemma 2.14, we have $\bar{x}(t) \leq s'/q_0$ and $\bar{s}(t) \leq s'$ for all $t > t'$. It remains to prove the existence of a constant β, not depending on initial conditions, such that $\limsup_{t\to\infty} \bar{q}(t) \leq \beta$. For this purpose, let us define $h(t,q) := \frac{\rho(t,q,s')}{q} - \mu(t,0,q)$ and $g(t,q) = \frac{\rho(t,q,s')}{q} - D(t)$. From Lemma 2.16 and H2.5, there exists $Q > \bar{q}(0)$ such that:

$$\int_0^\omega h(t,Q)dt < 0 \text{ and } \int_0^\omega g(t,Q)dt < 0. \tag{8}$$

Now, if $\bar{q}(t) \leq Q$ for all $t \geq t'$, then the proof is ready. Then, let us assume that $\bar{q}(t_1) = Q$ for some $t_1 > t'$ and that $q(t) \geq Q$ for all $t \geq t_1$. Then we have that $\bar{x}_s(t) := \bar{x}(t)\bar{q}(t)$ satisfies the following equation for all $t \geq t_1$:

$$\frac{dx_s}{dt} = \left(\frac{\rho(t,\bar{q}(t),\bar{s}(t))}{\bar{q}(t)} - D(t)\right) x_s \leq g(t,Q)x_s. \tag{9}$$

Using Gronwall's inequality on the interval $[t_1, t_1+t], t > 0$ gives:

$$\bar{x}_s(t_1+t) \leq \bar{x}_s(t_1 + t - \omega[t/\omega])e^{-\alpha[t/\omega]},$$

where $[t/\omega]$ is the greatest integer less than or equal to t/ω and $\alpha = -\int_0^\omega g(\tau,Q)d\tau > 0$. Since s' is an upper bound for $\bar{x}_s$ and q_0 is a lower bound for $\bar{q}$, we obtain:

$$\bar{x}(t_1+t) \leq \frac{s'}{q_0}e^{-\alpha[t/\omega]}. \tag{10}$$

Now, from H2.7, there exists $\delta_0 > 0$ such that:

$$|\mu(t,x,Q) - \mu(t,0,Q)| \leq l|x|, \tag{11}$$

for all $t \in [0,\omega]$ and $x \in [-\delta_0, \delta_0]$, with l the Lipschitz constant of μ. Let $\epsilon := -\frac{1}{2}\int_0^\omega h(t,Q)dt$ and let us choose $t_2 > t_1$ such that $\frac{s'}{q_0}e^{-[(t_2-t_1)/\omega]\alpha} <$

$\min\{\delta_0, \epsilon/l\}$. Thus, from (10) and (11), we obtain that $|\mu(t, \bar{x}(t), Q) - \mu(t, 0, Q)| < \epsilon$ for all $t \geq t_2$, and consequently:

$$\frac{d\bar{q}(t)}{dt} \leq \bar{q}(t) \left(h(t, Q) + \epsilon \right). \tag{12}$$

using Gronwall's inequality on the interval $[t_2, t_2 + n\omega]$ gives $\bar{q}(t_2 + n\omega) \leq \bar{q}(t_2)e^{-n\epsilon}$. Let $\gamma := \max_{t\in[0,\omega]} \frac{\rho(t,q_0,s')}{q_0} - \mu(t, s'/q_0, q_0)$. Then $d\bar{q}(t)/dt \leq \gamma\bar{q}(t)$. Applying Gronwall's inequality on the interval $[t_1, t_2]$ gives $\bar{q}(t_2) \leq Qe^{\gamma(t_2-t_1)}$. Consequently $\bar{q}(t_2 + n\omega) \leq Qe^{\gamma(t_2-t_1)+n\epsilon}$. Thus, for $n > \gamma(t_2 - t_1)/\epsilon$, we have that $\bar{q}(t_2 + n\omega) < Q$. Therefore $\bar{q}$ must return to Q in a finite time smaller than $T := t_2 - t_1 + n\omega$. Since T does not depends on initial conditions, we conclude that q is ultimately bounded by $Qe^{T\gamma}$. □

Remark 2.18. *If H2.8 does not hold, then solutions of (1) are not bounded. Indeed, let* (x, q, s) *be a solution of (1) with* $x(0), s(0) \geq 0$ *and* $q(0) \geq q_0$. *Let us assume that* q *is bounded from above by* $Q > 0$. *Since* ρ *is non-negative and* μ *is decreasing in* x, *we have* $\frac{dq(t)}{dt} \geq -\mu(t, 0, Q)q$. *Applying Gronwall's inequality on the interval* $[0, n\omega]$ *with* $n \geq 1$ *an integer, we obtain:*

$$q(n\omega) = q(0)e^{-n\int_0^\omega \mu(t,0,Q)dt}. \tag{13}$$

If H2.8 does not hold, then $\int_0^\omega \mu(t, 0, Q)dt < 0$. *Thus, letting* $n \to \infty$ *in (13), we conclude that* q *is not bounded which is a contradiction.*

A solution (x, q, s) of (1) will be called an ω-periodic solution provided each component is ω-periodic. An ω-periodic solution with absence of microalgae is called washout periodic solution. The following proposition shows that (1) has a washout periodic solution.

Proposition 2.19. *The system (1) has at least one washout periodic solution.*

Proof. It is not difficult to see that any washout periodic solution must be of the form $(0, q(t), s_*(t))$ with $s_*(t)$ the periodic solution of (2). Thus, putting $x = 0$ and $s = s_*(t)$ in the second equation of (1) results in:

$$\frac{dq}{dt} = \rho(t, q, s_*(t)) - \mu(t, 0, q)q. \tag{14}$$

Let us define:

$$F_0(t,q) = \frac{\rho(t,q,s_*(t))}{q} - \mu(t,0,q). \tag{15}$$

From Lemma 2.16, there exists $Q > 0$ such that $\int_0^\omega F_0(t,Q)dt < 0$. From H2.3 we have that $F_0(t,q_0) \geq 0$ for all $t \geq 0$. Thus, the proof follows from a direct application of Proposition 6.4 in Appendix A. □

Remark 2.20. *(Uniqueness of the washout) The uniqueness of the washout can be stated under additional assumptions over the monotonicity of ρ and μ. For example, consider F_0 defined in (15). If for some t the function $q \longmapsto F_0(t,q)$ is strictly decreasing, then we have the uniqueness of the washout.*

3. Reduced system

Dropping the equation for s and replacing s in (1) by $s = s_*(t) - xq$ results in the following reduced ω-periodic system for (x,q):

$$\begin{array}{rcl} \dfrac{dx}{dt} & = & [\mu(t,x,q) - D(t)]x, \\ & & \\ \dfrac{dq}{dt} & = & \rho(t,q,s_*(t) - xq) - \mu(t,x,q)q. \end{array} \tag{16}$$

In the following we study the asymptotic behavior of the reduced system (16). We are interested in solutions of (16) starting with a positive initial microalgae concentration and an internal quota not lower than q_0 *i.e.* solutions with initial conditions on the set:

$$P := \{(x,q) \; ; \; x > 0, \, q \geq q_0\}.$$

Our first lemma states a basic property of solutions of (16).

Lemma 3.1. *For any solution (x,q) of (16) starting on P we have that $x(t) > 0$, $q(t) \geq q_0$ for all $t > 0$. Moreover, there is $t' \geq 0$ such that $s_*(t) \geq x(t)q(t)$ for all $t \geq t'$.*

Proof. Since $\frac{dq}{dt}|_{q=q_0} \geq 0$, if $q(0) \geq q_0$ then $q(t) \geq q_0$ for all $t \geq 0$. If $x(0) > 0$, x cannot reach $x = 0$ in a finite time by the uniqueness of solutions of initial value problems. Then $x(t) > 0$ for all $t \geq 0$. The variable $x_s := xq$ satisfies the differential equation:

$$\frac{dx_s}{dt} = x_s \left(\frac{\rho(t, q, s_*(t) - x_s)}{q} - D(t) \right). \tag{17}$$

Thus, the variable $y(t) = s_*(t) - x_s(t)$ satisfies:

$$\frac{dy}{dt} = D(t)(s_{in}(t) - y) + (y - s_*(t)) \frac{\rho(t, q, y)}{q}. \tag{18}$$

We note that $\frac{dy}{dt}|_{y=0} = s_{in}(t)D(t) \geq 0$, therefore if $y(t') \geq 0$ for some $t' \geq 0$ then $y(t) \geq 0$ for all $t \geq t'$ and the proof is completed. Then we have to prove the existence of $t' > 0$ such that $y(t') \geq 0$. By contradiction, let us assume that $y(t) < 0$ for all $t \geq 0$. From (18) and H2.2 we have $dy/dt = D(t)(s_{in}(t) - y)$. From Lemma 2.13, y approaches asymptotically to s_*, which is a contradiction because s^* is positive. □

The following convergence results for the reduced system need the uniqueness of the washout periodic solution.

Proposition 3.2. *Let us assume that (16) admits a unique washout periodic solution* $(0, q_*)$. *Then, for any solution* (x, q) *of (16) satisfying* $\lim_{t\to\infty} x(t) = 0$, *we have that* $\lim_{t\to\infty} |q(t) - q_*(t)| = 0$.

Proof. Let $(\bar{x}, \bar{q})$ a solution of (16). Following the proof of Proposition 2.19, we define $F(t, q) = \rho(t, q, s_*(t) - q\bar{x}(t))/q - \mu(t, \bar{x}(t), q)$. From H2.3 we have that $F(t, q_0) \geq 0$ for all $t \geq 0$. Since $\lim_{t\to\infty} \bar{x}(t) = 0$, we have that $\lim_{t\to\infty} |F_0(t, q) - F(t, q)| = 0$. Thus, the proof follows from a direct application of Proposition 6.4b) in Appendix A. □

Now we prove that any solution of (16) is asymptotic to an ω-periodic solution. The heart of the proof lies in the fact that the change of variables $x_s = xq$ leads the reduced system to a cooperative system.

Proposition 3.3. *If (16) admits a unique washout periodic solution, then any solution of (16) starting on* P *approaches asymptotically to an* ω*-periodic solution.*

Proof. Let $(\bar{x}, \bar{q})$ be a solution of (16) with $\bar{x}(0) > 0$ and $\bar{q}(0) \geq q_0$. Let $\bar{x}_s(t) := \bar{x}(t)\bar{q}(t)$. From Lemma 3.1, it easily follows that $\bar{x}_s(t)$ and $\bar{x}(t)$ are bounded. Considering the change of variables $x_s := qx$, we have that $(\bar{x}(t), \bar{x}_s(t))$ is a solution of the following system:

$$\begin{aligned} dx/dt &= f_1(t, x, x_s) := [\mu(t, x, x_s/x) - D(t)]x, \\ dx_s/dt &= f_2(t, x, x_s) := \rho(t, x_s/x, s_*(t) - x_s)x - D(t)x_s. \end{aligned} \tag{19}$$

The system (19) is cooperative *i.e.* f_1 and f_2 are increasing in x_s and x respectively. Following the proof of Theorem 4.2 in Chapter 7 in the Book [24], we have that the sequences $\bar{x}_n := \bar{x}(n\omega)$ and $\bar{x}_{sn} := \bar{x}_s(n\omega)$ are convergent. Let $l := \lim_{n\to\infty} \bar{x}_n$ and $l' := \lim_{n\to\infty} \bar{x}_{sn}$. If $l > 0$, then $l' > 0$ and consequently $\bar{q}_n := \bar{q}(n\omega) = \bar{x}_{sn}/\bar{x}_n \to l/l'$ as $n \to \infty$. Thus, $(\bar{x}, \bar{q})$ approaches asymptotically an ω-periodic solution of (16) with initial conditions $(l, l'/l)$. Let us assume now that $l = 0$ and let $g(t) := \mu(t, \bar{x}(t), \bar{q}(t)) - D(t)$. We can write $\bar{x}(t) = \bar{x}(0)e^{\alpha(t)+\beta(t)}$, with:

$$\alpha(t) = \int_0^{\omega[t/\omega]} g(\tau)d\tau, \text{ and } \beta(t) = \int_{\omega[t/\omega]}^{t} g(\tau)d\tau.$$

Let Q be an upper bound for $\bar{q}$ given by Lemma 2.17, then we have $g(t) \leq \mu(t, 0, Q)$. Thus, $\beta(t) \leq b := \omega \max_{t\in[0,\omega]} \mu(t, 0, Q)$. We have that $\bar{x}_n = \bar{x}(0)e^{\alpha(n\omega)}$. Since $\bar{x}_n \to 0$, we conclude that $\alpha(n\omega) \to -\infty$. Then, it is trivial that $\alpha(t) \to -\infty$ as $t \to \infty$. Thus, we conclude that $\bar{x}(t) \leq \bar{x}(0)e^{\alpha(t)+b} \to 0$ as $t \to \infty$. From Proposition 2.19, we conclude that $(\bar{x}, \bar{q})$ is asymptotic to the washout periodic solution. □

Remark 3.4. *The monotonicity of μ as a function of x is not essential in the proof of Proposition 3.3. Indeed, the system (19) does not lose the property of being cooperative.*

The following proposition states conditions for the extinction of the population.

Proposition 3.5. *Let us assume that (16) admits a unique washout periodic solution $(0, q_*)$. If one of the following conditions holds:*

a) $\int_0^\omega [\mu(t, 0, q_*(t)) - D(t)]dt < 0$*;*

b) $\int_0^\omega [\mu(t, 0, q_*(t)) - D(t)]dt = 0$ *and the function* $x \longmapsto \mu(t, x, q_*(t))$ *is strictly decreasing for some* $t \in [0, \omega]$*;*

then, any solution of (16) starting on P *approaches asymptotically* $(0, q_*(t))$*.*

Proof. Let (x, q) be a solution of (16) starting on P, and let $x_s = xq$. Following the proof of Lemma 2.3 in [25], we define $\bar{x}(t)$ to be the unique solution of:

$$\frac{d\bar{x}}{dt} = [\mu(t, \bar{x}, q_*(t)) - D(t)]\bar{x}, \tag{20}$$

with $\bar{x}(0) := \max\{x(0), x_s(0)/q_*(0)\}$. We also define $\bar{x}_s(t) := \bar{x}(t)q_*(t)$. It is easy to verify that:

$$\frac{d\bar{x}_s}{dt} = \rho(t, \bar{x}_s/\bar{x}, s_*(t))\bar{x} - D(t)\bar{x}_s.$$

Let us consider the functions $f_i, i = 1, 2$ defined in (19). We have the following inequality:

$$\begin{aligned} \frac{d\bar{x}}{dt} &\geq f_1(t, \bar{x}, \bar{x}_s), \\ \frac{d\bar{x}_s}{dt} &\geq f_2(t, \bar{x}, \bar{x}_s), \end{aligned} \tag{21}$$

with $\bar{x}(0) \geq x(0)$ and $\bar{x}_s(0) \geq x_s(0)$. Applying Theorem B.1 from Appendix B in [24], we conclude that $x(t) \leq \bar{x}(t)$ and $x_s(t) \leq \bar{x}_s(t)$.

Now, let us define the sequence $\bar{x}_n = \bar{x}(n\omega)$, $n \in \mathbb{N}$. Since μ is decreasing in x and $\int_0^\omega [\mu(t, 0, q_*(t)) - D(t)]dt \leq 0$ (in a) and b)), we have:

$$\begin{aligned} \bar{x}_{n+1} &= \bar{x}_n \exp\left(\int_0^\omega [\mu(t, \bar{x}, q_*(t)) - D(t)]dt\right) \\ &\leq \bar{x}_n \exp\left(\int_0^\omega [\mu(t, 0, q_*(t)) - D(t)]dt\right) \\ &\leq \bar{x}_n, \end{aligned}$$

hence $\bar{x}_n$ is a decreasing sequence. Since $\bar{x}_n \geq 0$ for all $n \in \mathbb{N}$, we conclude that $\bar{x}_n$ is convergent and therefore $\bar{x}$ approaches asymptotically an ω-periodic solution of (20). We prove now that in both cases, a) and b), $x = 0$ is the unique periodic solution. By contradiction, let $\bar{x}_p$ be a positive periodic solution. Then we have

$$\int_0^\omega [\mu(t, \bar{x}_p(t), q_*(t)) - D(t)]dt = 0. \tag{22}$$

However, in case a):

$$\int_0^\omega [\mu(t, \bar{x}_p(t), q_*(t)) - D(t)]dt \leq \int_0^\omega [\mu(t, 0, q_*(t)) - D(t)]dt < 0,$$

which contradicts (22). In case b):

$$\int_0^\omega [\mu(t, \bar{x}_p(t), q_*(t)) - D(t)]dt < \int_0^\omega [\mu(t, 0, q_*(t)) - D(t)]dt = 0,$$

which again contradicts (22). Hence $x = 0$ is the unique periodic solution of (20) and we have that $\lim_{t\to 0} \bar{x}(t) = 0$. This implies $\lim_{t\to\infty} x(t) = 0$. By Lemma 3.2, we conclude that $\lim_{t\to\infty} |q(t) - q_*(t)| = 0$. □

An ω-periodic solution (x, q) of (16) will be called **positive ω-periodic solution**, if $x(t) > 0$, $q(t) \geq q_0$, and $x(t)q(t) \leq s_*(t)$ for all $t \in [0, \omega]$. The following theorem gives conditions to ensure that any solution of (16) approaches a positive ω-periodic solution.

Theorem 3.6. *Let us assume that (16) admits a unique washout periodic solution $(0, q_*)$ and that $\int_0^\omega [\mu(t, 0, q_*(t)) - D(t)]dt > 0$. Then, (16) admits at least one positive ω-periodic solution and any solution of (16) starting in P approaches asymptotically a positive ω-periodic solution.*

Proof. Along the proof we will write $u = (x, q)$. Let us define $G = (G_1, G_2) : \mathbb{R}_+^2 \times J \times \mathbb{R}_+ \longrightarrow \mathbb{R}^2$ by:

$$G_1(t, u, v) = \mu(t, u) - D(t) \text{ and } G_2(t, u, v) = \hat{\rho}(t, u_2, v - u_1 u_2)/u_2 - \mu(t, u), \tag{23}$$

with $\hat{\rho}$ a continuous extension of ρ on $\mathbb{R}_+ \times J \times \mathbb{R}$ to $\mathbb{R}_+^2 \times \mathbb{R}$ such that $\hat{\rho}$ is ω-periodic in t and locally Lipschitz in u uniformly in t. Consider the Kolmogorov periodic system:

$$\frac{du_i}{dt} = u_i G_i(t, u, s_*(t)), \ i = 1, 2, \tag{24}$$

For initial conditions on $\mathbb{R}_+ \times [0, q_0]$, solutions of (24) stay on $\mathbb{R}_+ \times [0, q_0]$ or they intersect the set $\mathbb{R}_+ \times J$ for some $t > 0$. Thus, solutions of (24) exist for any initial condition on $\mathbb{R}^2_+$ and they are uniformly bounded. Let $\phi_0(t, u)$ be the unique solution of (24) with $\phi_0(0, u) = u \in \mathbb{R}^2_+$ and let $\varphi := \phi(\omega, \cdot) : \mathbb{R}^2_+ \longrightarrow \mathbb{R}^2_+$ be the Poincaré map associated to (24). From Lemma 1 in the appendix of [20], we conclude that there is $\delta > 0$ such that $\lim_{n\to\infty} d(\varphi^n(u), (0, q_*(0))) \geq \delta$ for all $u \in int(\mathbb{R}^2_+)$. This implies that for any $u \in (0, \infty) \times J$, $\phi_0(t, u)$ is not asymptotic to the washout periodic solution. From Proposition 3.3, we conclude that $\phi(t, u)$ approaches an ω-periodic solution (x^*, q^*) different from the washout periodic solution. From Lemma 3.1, we have that $x^*(t)q^*(t) \leq s_*(t)$ for all $t \geq 0$. Thus (x^*, q^*) is a positive periodic solution and the proof is completed. □

The following result that states an order of the positive periodic solutions of (16).

Lemma 3.7. *For any two periodic solutions* (x^*_i, q^*_i)*,* $i = 1, 2$ *of (16) with* $x^*_i(0) > 0$*, we have that either*

- $x^*_1(t) \leq x^*_2(t)$ *and* $x^*_1(t)q^*_1(t) \leq x^*_2(t)q^*_2(t)$ *for all* $t \in [0, \omega]$*, or*
- $x^*_1(t) \geq x^*_2(t)$ *and* $x^*_1(t)q^*_1(t) \geq x^*_2(t)q^*_2(t)$ *for all* $t \in [0, \omega]$*.*

Proof. We write $x^*_{si} = x^*_i(t)q^*_i(t)$, $i = 1, 2$. Then, we have that $(x^*_i, x^*_{si}), i = 1, 2$ are periodic solutions of (19). We claim that either (a) $x^*_{1s}(t) \leq x^*_{2s}(t)$ for all $t \in [0, \omega]$ or (b) $x^*_{1s}(t) \geq x^*_{2s}(t)$ for all $t \in [0, \omega]$. Indeed, let us assume that there is $t_0 \in [0, \omega]$ such that $x^*_{1s}(t_0) = x^*_{2s}(t_0)$, otherwise the claim is trivial. Then either (I) $x^*_1(t_0) < x^*_2(t_0)$ or (II) $x^*_2(t_0) > x^*_1(t_0)$, otherwise both periodic solutions are the same. If (I) holds, then by a Kamke's Theorem argument, we have that $x^*_{1s}(t) \leq x^*_{2s}(t)$ for all $t \geq t_0$, and by the periodicity of x^*_{1s} and x^*_{2s} we conclude that (a) holds. In the same way, if (II) holds then (b) holds. Thus, the claim is proved. Now, since f_1 (see (19)) is increasing in x_s, we conclude that (a) implies $x_1^*(t) \leq x_2^*(t)$, and (b) implies $x_1^*(t) \geq x_2^*(t)$. This completes the proof. $\square$

We end this section with a theorem that gives conditions for the uniqueness of positive ω-periodic solutions of (16). For an interpretation of the hypotheses in the following theorem, see the remarks at the end of this section.

Theorem 3.8. *We recall the subsistence quota q_0 introduced in Section 2. Assume that:*

I) $\rho(t, q_0, s) > 0$ for all $t \in [0, \omega]$, $s > 0$,

and that for any continuous function q on $[0, \omega]$, satisfying $q(t) > q_0$ for all $t \in [0, \omega]$, we have:

II) the function $x \longmapsto \mu(t, x, q(t))$ is strictly decreasing for some $t \in [0, \omega]$, and

III) the function $s \longmapsto \rho(t, q(t), s)$ is either strictly increasing or equal to zero for all $s \geq 0$.

Then, (16) admits at most one ω-periodic solution (x^*, q^*) with $x^*(0) > 0$ and $q^*(0) \geq q_0$.

Proof. Let $\phi(t, v)$ be the unique solution of (19) satisfying $\phi(0, v) = v$, let $K := int(\mathbb{R}_+^2)$ and $\varphi = \phi(\omega, \cdot) : K \longrightarrow K$ be the Poincaré map associated to (19). Let u be a positive fixed point of φ and let $\alpha \in (0, 1)$. We define the variables $y(t) := \alpha\phi(t, u)$ and $z(t) := \phi(t, \alpha u)$. Let us consider the functions f_i, $i = 1, 2$ defined in (19). We can easily verify that for all $t \in [0, \omega]$:

$$\begin{aligned} \frac{dy_i(t)}{dt} &= \alpha f_i(t, y_1(t)/\alpha, y_2(t)/\alpha) \leq f_i(t, y_1(t), y_2(t)), i = 1, 2, \\ y(0) &= \alpha u, \end{aligned} \tag{25}$$

and that:

$$\begin{aligned} \frac{dz_i(t)}{dt} &= f_i(t, z_1(t), z_2(t)),\ i = 1, 2, \\ z(0) &= \alpha u. \end{aligned} \tag{26}$$

Applying Theorem B.1 from Appendix B in [24], we conclude that $y_i(t) \leq z_i(t)$ for all $t \in [0, \omega]$, $i = 1, 2$.

Let $q_y(t) := y_2(t)/y_1(t)$. Since $y(t)/\alpha$ corresponds to an ω-periodic solution of (19), $(y_1(t)/\alpha, q_y(t))$ corresponds to an ω-periodic solution of (16). We claim that $q_y(t) > q_0$ for all $t \in [0, \omega]$. Indeed, from Lemma 3.1, we know that $q_y(t)$ cannot be lower than q_0. Thus, by contradiction, if $q_y(t') = q_0$ for some t', then q_y reaches a minimum at $t = t'$. Hence, $dq_y(t')/dt = 0$. However, from hypothesis I), we have that $dq_y(t')/dt > 0$ which is a contradiction. Therefore our claim is true. From hypothesis II), we conclude that $x \longmapsto \mu(t', x, q_y(t'))$ is strictly decreasing for some $t' \in [0, \omega]$. Consequently, for $i = 1$, the inequality in (25) is strict for t'. Again, since $y(t)/\alpha$ is an ω-periodic solution of (19), we have:

$$\int_0^\omega \rho(t, y_2(t)/y_1(t), s_*(t) - y_2(t)/\alpha) = \int_0^\omega D(t)dt > 0,$$

from where there exists an interval of time t'' such that:

$$\rho(t'', y_2(t'')/y_1(t''), s_*(t'') - y_2(t'')/\alpha) > 0$$

From hypothesis III), we conclude that for $i = 2$, the inequality in (25) is strict for some t''. Since inequalities in (25) are strict at some moment and f_1 and f_2 are continuous, we obtain that for $i = 1, 2$:

$$0 = \alpha \int_0^\omega f_i(t, y_1(t)/\alpha, y_2(t)/\alpha)dt < \int_0^\omega f_i(t, y_1(t), y_2(t))dt. \qquad (27)$$

We prove now that $y_i(t) < z_i(t)$, $i = 1, 2$ for some $t \in [0, \omega]$. Without loss of generality, we do it for $i = 1$. By contradiction, if $z_1(t) = y_1(t)$ for all $t \in [0, \omega]$, then we have:

$$\begin{aligned} z_1(\omega) - z_1(0) &= \int_0^\omega f_1(t, z_1(t), z_2(t))dt \\ &= \int_0^\omega f_1(t, y_1(t), z_2(t))dt \\ &\geq \int_0^\omega f_1(t, y_1(t), y_2(t))dt. \\ &> 0 \ \text{(see (27))}. \end{aligned}$$

Thus, we conclude that $z_1(0) \neq z_1(\omega)$ which is a contradiction because $y_1(0) = y_1(\omega)$. Therefore there exists t_0 such that $z_1(t_0) > y_1(t_0)$. Let us consider $\underline{z}_1$ defined by:

$$\frac{d\underline{z}_1}{dt} = f_1(t, \underline{z}_1, z_2(t)), \ \underline{z}_1(t_0) = y_1(t_0). \tag{28}$$

Since $\frac{dy_1}{dt} \leq f_1(t, y_1, z_2(t))$, by a comparison argument, we have that $y_1(\omega) \leq \underline{z}_1(\omega)$. By an uniqueness argument, we have that $\underline{z}_1(\omega) < z_1(\omega)$. Hence, we conclude that $y_1(\omega) < z_1(\omega)$. Similarly, we can argue that $y_2(\omega) < z_2(\omega)$.

Since $\alpha\varphi(u) = y(\omega)$ and $z(\omega) = \varphi(\alpha u)$, and due to arbitrary choice of α and u, we conclude that for any $\alpha \in (0, 1)$ and $u \in K$:

$$\alpha\varphi(u) < \varphi(\alpha u). \tag{29}$$

Now, let us assume that φ admits two different fixed points $u, u' \in K$. From a Kamke's Theorem argument, it follows that φ is monotone. Thus, following the same arguments as in the proof of Lemma 2.3.1 in Chapter 2 in [26], we obtain the existence of $\sigma > 0$ such that $u = \sigma u'$. From Lemma 3.7 we can assume that $u \leq u'$ (component-wise inequality). Therefore, $\sigma \in (0, 1)$. Thus, $u = \varphi(u) = \varphi(\sigma u') > \sigma\varphi(u') = \sigma u' = u$, which is a contradiction. Therefore, φ admits at most one fixed point and the proof is completed. □

Remark 3.9. *(Interpretation of hypotheses in Theorem 3.8) Hypothesis I) simply says that at any moment of the day, if microalgae reach their minimal quota* *(subsistence quota q_0), they will absorb nutrients from the medium. To interpret hypothesis II), first we must consider that any increase of the microalgae population is expected to reduce the light availability in the medium (self-shading). Thus, hypothesis II) states the existence of a moment at which any decrease of the light availability reduces the specific growth rate, in other words, there is a moment of the day at which the culture is light limited. Hypothesis III) is inspired by the fact that for high values of the quota microalgae stop absorbing nutrients, independent of the concentration of nutrients in the medium. Thus, hypothesis III) says that at any moment of the day, if there is absorption of nutrients (low values of quota), then increasing the nutrient concentration in the medium will increase the absorption rate. However, if there is no absorption of nutrients (high values of quota), then it is impossible to initiate the consumption of nutrients by increasing their concentration in the medium.*

4. Main result

An ω-periodic solution (x^*, q^*, s^*) of (1) is known as **positive ω-periodic solution** if $x^*(t) > 0$, $q^*(t) \geq q_0$, and $s^*(t) \geq 0$. The following theorem states a threshold type result on the global asymptotics of (1). In particular, it gives necessary and sufficient conditions for the existence of a globally attractive positive periodic solution.

Theorem 4.1. *Let us assume that (1) admits a unique washout periodic solution $(0, q_*, s_*)$ and that assumptions of Theorem 3.8 hold. Let (x, q, s) be a solution of (1) with $x(0) > 0, q(0) \geq q_0$, and $s(0) \geq 0$. We have:*

a) If $\int_0^\omega [\mu(t, 0, q_*(t)) - D(t)]dt > 0$, (1) admits a unique positive ω-periodic solution (x^*, q^*, s^*), and

$$\lim_{t\to\infty} |(x(t), q(t), s(t)) - (x^*(t), q^*(t), s^*(t))| = 0.$$

b) If $\int_0^\omega [\mu(t, 0, q_*(t)) - D(t)]dt \leq 0$, then

$$\lim_{t\to\infty} |(x(t), q(t), s(t)) - (0, q_*(t), s_*(t))| = 0.$$

Proof. As in the proof of Theorem 3.6, we write $u = (x, q)$ and we consider the functions G_i, $i = 1, 2$ defined in (23). Consider the Kolmogorov non-autonomous system:

$$\frac{du_i}{dt} = u_i G_i(t, u, S(t)), \ i = 1, 2, \tag{30}$$

where $S(t)$ is the unique solution of (2) with $S(0) \geq u_1(0)u_2(0)$. Recalling the proof of Theorem 3.6, solutions of (24) and (30) exist for any initial condition on $\mathbb{R}^2_+$ and they are uniformly bounded. Let $\phi_0(t, s, u)$ and $\phi(t, s, u)$ be the unique solutions of (24) and (30) respectively with $\phi(s, s, u) = \phi_0(s, s, u) = u \in \mathbb{R}^2_+$. We note that for initial conditions on $\mathbb{R}_+ \times J$, (1) is equivalent to (30) (take $s(0) = S(0) - u_1(0)u_2(0)$). From Theorems 3.6 and 3.8 and Proposition 3.5 we obtain the following result on the global asymptotics of (24).

I) If $\displaystyle\int_0^\omega [\mu(t, 0, q_*(t)) - D(t)]dt > 0$, (24) admits a unique positive ω-periodic solution (x^*, q^*), and for any $u \in (0, \infty) \times J$ we have $\lim_{t\to\infty} |\phi_0(t, 0, u) - (x^*(t), q^*(t))| = 0$.

II) If $\displaystyle\int_0^\omega [\mu(t, 0, q_*(t)) - D(t)]dt \leq 0$, for any $u \in [0, \infty) \times J$, $\lim_{t\to\infty} |\phi_0(t, 0, u) - (0, q_*(t))| = 0$.

From Theorem 3.6, $x^*(t)q^*(t) \leq s_*(t)$ for all $t \in [0, \omega]$. Then, $(x^*, q^*, s_* - x^*q^*)$ is the unique positive ω-periodic solution of (1). Given the equivalence between (30) and (1), we have to prove that I) and II) remain valid when replacing ϕ_0 by ϕ.

From Lemma 2.13, $\lim_{t\to\infty} |S(t) - s_*(t)| = 0$, and hence $\lim_{t\to\infty} |G(t, u, S(t)) - G(t, u, s_*(t))| = 0$. By Proposition 3.2 in [21], $\phi(t, s, u)$ is asymptotic to the ω-periodic semiflow $T(t) := \phi_0(t, 0, \cdot) : \mathbb{R}^2_+ \longrightarrow \mathbb{R}^2_+$, and hence $T_n(u) = \phi(n\omega, 0, u)$, $n \geq 0$, is an asymptotically autonomous discrete dynamical process with limit discrete semiflow $\varphi^n : \mathbb{R}^2_+ \longrightarrow \mathbb{R}^2_+, n \geq 0$, where $\varphi = T(\omega)$ is the Poincaré map associated to (24). By Theorem 3.1 in [21], it suffices to prove in case a) that $\lim_{n\to\infty} T_n(u) = u^* := (x^*(0), q^*(0))$ for any $u \in (0, \infty) \times J$, and in case b) that

$\lim_{n\to\infty} T_n(u) = u_* := (0, q_*(0))$ for any $u \in \mathbb{R}_+ \times J$

In case a), by conclusion I), u^* is a globally attractive fixed point of φ in $(0,\infty)\times\mathbb{R}_+$. Thus, the only fixed points of φ are u^* and the washout u_*. By Theorem 2.4 in [21], the ω-limit of u is a fixed point of φ. By Lemma 2 (with $n = 2$) in [20], we have:

$$\{u \in \mathbb{R}^2_+ \, ; \lim_{n\to\infty} T_n(u) = (0, q_*(0))\} \cap int(\mathbb{R}^2_+) = \phi.$$

Thus, $\lim_{n\to\infty} T_n(u) = u^*$ for any $u \in int(\mathbb{R}^2_+)$, which proves a).

In case b), by conclusion II), u_* is a globally attractive fixed point of φ in $\mathbb{R}_+ \times \mathbb{R}_+$. Thus, the only fixed point of φ is u_*. By Theorem 2.4 in [21], the ω-limit of u is a fixed point of φ, hence u_*. This proves b). □

5. Application: Microalgae growth under phosphorus and light limitation.

Here we consider a periodic version of the light-limited Droop model proposed by Passarge and collaborators in [27] for describing microalgae growth under light and phosphorus limitation. The model reads:

$$\begin{aligned} dx/dt &= [\min\{\mu_I(t,x), \mu_P(q)\} - D]x, \\ dq/dt &= \rho(q,s) - \min\{\mu_I(t,x), \mu_P(q)\}\, q, \\ ds/dt &= D(s_{in} - s) - \rho(q,s)x, \end{aligned} \tag{31}$$

with s_{in} and D constant and positive, and the functions μ_I, μ_P defined as follows. $\mu_P(q) = \mu_{max}\left(1 - \frac{q_0}{q}\right)$ is the specific growth rate as described by Droop [4] under nutrient limitation, and $\mu_I(t,x) = \frac{1}{L}\int_0^L p(I(t,x,z))dz$ is the vertical average of the local specific growth rate $p(I) = \mu_{max}\frac{I}{K_I + I}$ when microalgae is only limited by light. $I(t,x,z)$ is the light intensity perceived by microalgae at a distance z from the surface of the culture vessel and is determined from the Lambert-Beer law:

$$I(t,x,z) = I_{in}(t)e^{-(kx+K_{bg})z}, \quad z \in [0, L], \tag{32}$$

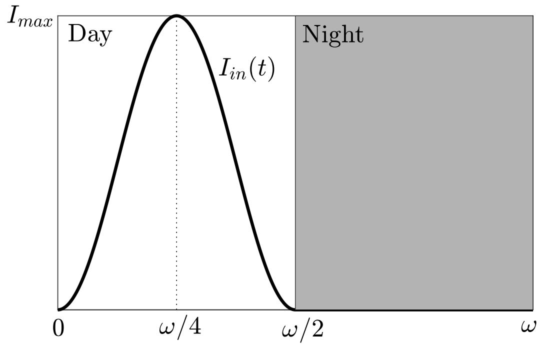

Figure 1: I_{in} as a function of t.

with $I_{in}(t)$ the incident light intensity, $k > 0$ the specific light extinction coefficient of microalgae, and $K_{bg} \geq 0$ the background turbidity. A direct integration shows that:

$$\mu_I(t,x) = \frac{\mu_{max}}{(kx + K_{bg})L} \ln\left(\frac{K_I + I_{in}(t)}{K_I + I_{out}(t,x)}\right), \tag{33}$$

with $I_{out}(t,x) = I(t,x,L)$ the light intensity at the bottom of the culture. The incident light intensity varies periodically according to

$$I_{in}(t) = I_{max} \max\{0, \sin(2\pi t/\omega)\}^2, \tag{34}$$

with $\omega > 0$ the length of a day and I_{max} the maximal incident light (at midday). Figure 1 illustrates the function I_{in}.

The uptake rate function is:

$$\rho(q,s) = \begin{cases} \rho_{max} \frac{s}{K_s+s} \frac{q_L-q}{q_L-q_0} & if \quad q \leq q_L, \\ 0 & if \quad q > q_L, \end{cases} \tag{35}$$

where ρ_{max} is the maximal uptake rate of phosphorus, q_L is the hypothetical maximal quota, and K_s is a half-saturation constant.

It is not difficult to see that (31) satisfies the hypotheses H2.1-H2.8 presented in section 2 (see Appendix B for the properties of μ_I). Thus, we can apply Theorem 4.1 to obtain the following result.

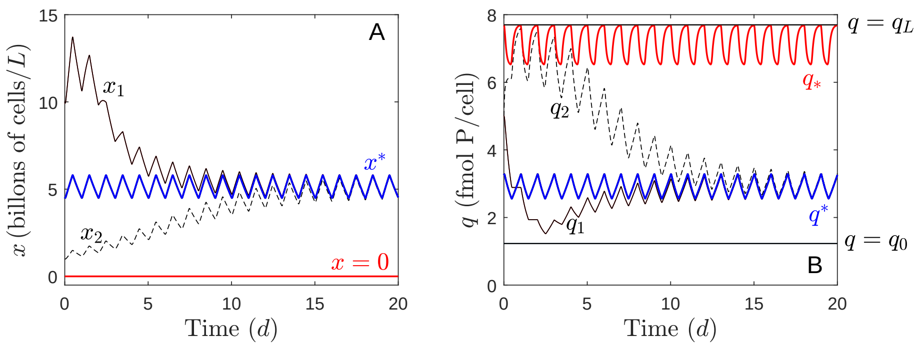

Figure 2: Periodic solutions of (31) and their asymptotic behavior. System (31) admits only two periodic solutions, the ω periodic solution represented by $x = 0$ and q_*, and a positive ω-periodic solution represented by $x^* > 0$ and q^*. Any solution starting with a positive microalgae concentration approaches the positive ω-periodic solution. In this case, x_1, q_1 and x_2, q_2 correspond to two different solutions of (31) with $x_1(0), x_2(0) > 0$ and $q_1(0) = q_2(0)$. We note that the cell quota remains between q_0 and q_L. A. Microalgae population density. B. Cell quota.

Theorem 5.1. *System (31) admits a unique washout ω-periodic solution, $(0, q_*(t), s_{in})$. Moreover, for*

$$\Delta := \frac{1}{\omega}\int_0^{\omega} \min\{\mu_I(t,0), \mu_P(q_*(t))\}dt - D,$$

we have:

a) if $\Delta > 0$, then (31) admits a unique positive ω-periodic solution $(x^*(t), q^*(t), s^*(t))$ and any solution to (31) with a positive initial population density approaches it asymptotically,

b) if $\Delta \leq 0$, then any solution to (31) asymptotically approaches the washout ω-periodic solution.

Proof. We recall equation (14) to study the uniqueness of the washout periodic solution. We note that $\int_0^{\omega} F_0(t, q(t))dt < 0$ for any function $q(t) \in [q_L, \infty)$. Thus, the quota associated to any washout must intersect the set $[q_0, q_L]$. Since $\mu(t, x, q) := \min\{\mu_I(t, x), \mu_P(q)\} \geq 0$, we have that $[q_0, q_L]$ is positively invariant with respect to (14). Thus, the quota associated to any washout stays on

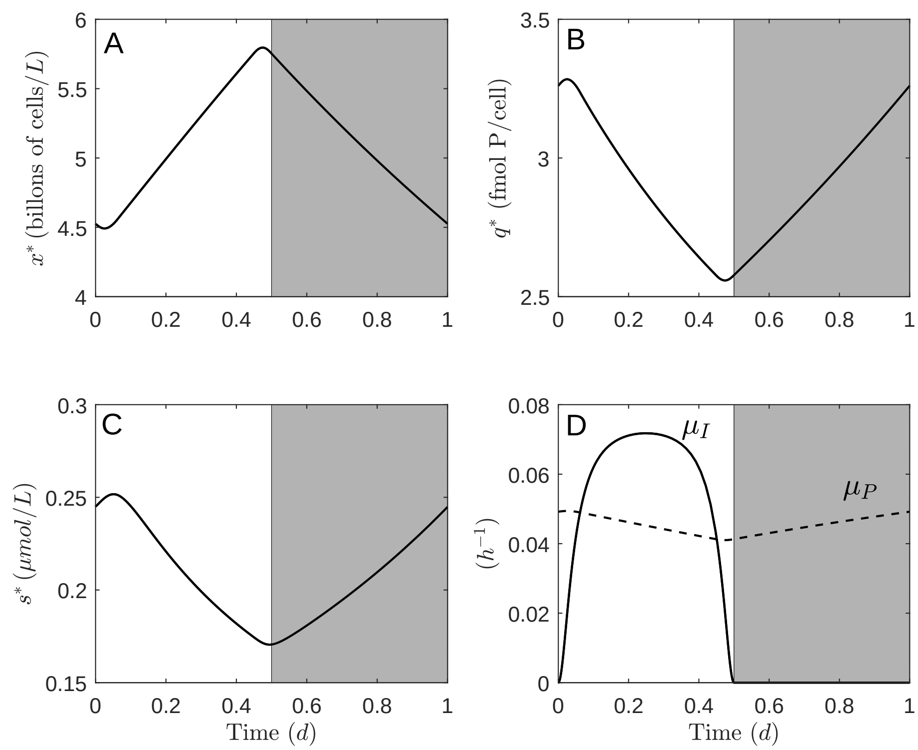

Figure 3: Unique positive periodic solution of (31). A. Population density. B. Intracellular phosphorus content. C. External phosphorus concentration. D. Light and phosphorus limitation.

$[q_0, q_L]$. Since $q \longmapsto \rho(q, s_{in})$ is strictly decreasing on $[q_0, q_L]$, we have that $q \longmapsto F_0(t, q)/q$ is also strictly decreasing on $[q_0, q_L]$. This implies the uniqueness of the washout and part a) is proved.

Let $q : [0, \omega] \longrightarrow (q_0, \infty)$ be a continuous function and $q_m := \min_{t\in[0,\omega]} q(t)$. Since $q_m > q_0$, we have $\mu_P(q_m) > 0$. Now, we note that

$$\mu_I(t, x) \leq \nu(t) := \begin{cases} \mu_{max} \frac{I_{in}(t)}{K_I + I_{in}(t)} & if \quad K_{bg} = 0, \\ \frac{\mu_{max}}{K_{bg} L} \ln\left(1 + \frac{I_{in}(t)}{K_I}\right) & if \quad K_{bg} > 0. \end{cases}$$

Thus, from the definition of $I_{in}(t)$, it is clear that we can choose $t' \in [0, \omega]$ such that $I_{in}(t') > 0$ and $\mu_I(t', x) \leq \nu(t') \leq \mu_P(q_m) \leq \mu_P(q(t'))$ for all $x \geq 0$ *i.e.* $\mu(t', x, q(t')) = \mu_I(t', x)$ for all $x \geq 0$. Then we have that $x \longmapsto \mu(t', x, q(t'))$ is strictly decreasing (see Proposition 6.5 in Appendix B). We note now that $s \longmapsto \rho(q, s)$ is strictly increasing for any $q \in [q_0, q_L]$ and that $\rho(q_0, s) > 0$ for any $s > 0$. Thus, applying Theorem 4.1 we conclude the proof. $\square$

Remark 5.2. *A crucial fact to ensure the uniqueness of positive periodic solutions of (31) is that the incident light intensity $I_{in}(t)$ is continuous, and zero during some time (night period). Indeed, this implies that $I_{in}(t)$ can take values as close to zero as we want. Hence, for any evolution of the quota $q(t)$ (greater than q_0), it is possible to find a time t' at which $\mu_I(t', x) \leq \mu_P(q(t'))$ for all $x \geq 0$ (details are in the proof of Theorem 5.1). In other words, there is a moment during the day at which limitation by light is predominant. This implies hypothesis II) in Theorem 3.8 (see Remark 3.9).*

To illustrate Theorem 5.1, let us consider the kinetic parameters for *Chlorella vulgaris* provided in [27]. The rest of parameters are chosen as $D = 0.02\, h^{-1}$, $K_{bg} = 6\, m^{-1}$, $s_{in} = 15\, \mu mol\,/L$, $L = 0.4\, m$, and $I_{max} = 2000\, \mu mol\, m^{-2}\, s^{-1}$. Figure 2 illustrates the microalgae population density and the cell quota associated to the periodic solutions of (31) and their attractiveness property. Figure 3 illustrates the positive periodic solution (x^*, q^*, s^*) and its evolution during one day. The shaded area corresponds to the night (*i.e.* $I_{in}(t) = 0$). Figure

3D shows that during the day ($t \in [0, 0.5]$) microalgae growth is mainly limited by phosphorus, while during the night ($t \in [0.5, 1]$), there is no growth due to the absence of light. Thus, microalgae population only grows during the day (see Figure 3A), and consequently the internal cell quota and external nutrient concentration decrease during the day (see Figures 3B and 3C).

6. Discussion and conclusions

In this work, we studied the asymptotic behavior of a single microalgae model accounting for nutrient and light limitation. We found conditions such that prolonged continuous periodic culture operation (periodic dilution rate and nutrient supply) under periodic fluctuations of environmental conditions (such as the light source or the medium temperature) allows periodic concentrations to be maintained in the culture. More precisely, if (1) admits only one washout periodic solution $(0, q_*, s_*)$, then the following condition:

$$\int_0^\omega D(t)dt < \int_0^\omega \mu(t, 0, q_*(t))dt, \tag{36}$$

is sufficient and necessary for the existence of a unique positive periodic solution. This solution is globally attractive (Theorem 4.1).

As an application of our results, we gave necessary and sufficient conditions for the existence of a unique positive globally attractive periodic solution for a periodic version of the model proposed by Passarge and collaborators [27] (see Theorem 5.1). In this model, the specific growth rate is represented by the law of minimum. If in (31) the specific growth rate is a multiplicative function *i.e.* $\mu_I(t, x)(1 - q_0/q)$, a new version of Theorem 5.1 can be readily stated.

A possible extension of this work consist in allowing the function μ not to be monotone as a function of x. In [28] it is shown that when microalgae suffer from photoinhibiton (*i.e.* a decrease of the photosynthetic rate due to an excess of light), then an Allee effect may occurs *i.e.* μ in (1) is increasing as a function of x for small values of x. In such a case, the cooperativity of the reduced system (16) is not lost (see Remark 3.4). Thus, a similar result to Proposition 3.3 could be obtain for this new model.

Appendix A

Consider the non-autonomous Kolmogorov equation:

$$\frac{du}{dt} = uF(t,u), \quad u \in \mathbb{R}_+ = [0,\infty), \tag{37}$$

and the ω-periodic Kolmogorov equation:

$$\frac{du}{dt} = uF_0(t,u), \quad u \in \mathbb{R}_+, \tag{38}$$

where $F(t,u) : \mathbb{R}_+^2 \longrightarrow \mathbb{R}$ is continuous, decreasing in u and locally Lipschitz in u, and $F_0(t,u) : \mathbb{R}_+^2 \longrightarrow \mathbb{R}$ is continuous, ω-periodic in t ($\omega > 0$), decreasing in u and locally Lipschitz in u uniformly in $t \in [0,\omega]$. Consider the following assumptions:

A 6.1. $\lim_{t\to\infty} |F(t,u) - F_0(t,u)| = 0$ *uniformly for* u *in any bounded subset of* $\mathbb{R}_+$.

A 6.2. $\int_0^\omega F_0(t,R)dt < 0$ *for some* $R > 0$.

Lemma 6.3. *Assume that A6.1 and A6.2 hold. Then, solutions of (37) are ultimately bounded.*

Proof. Let $\phi(t,s,u), t \geq s \geq 0$, be the unique solution of (37) with $\phi(s,s,u) = u$. From 6.1, there is $t_0 > 0$ such that $|F(t,0) - F_0(t,0)| < 1$ for all $t \geq t_0$. Since F is decreasing in u, we have that

$$F(t,u) \leq F(t,0) < 1 + \max_{t\in[0,\omega]} F_0(t,0), \text{ for all } t \in [t_0,\infty), u \in \mathbb{R}_+$$

and

$$F(t,u) \leq \max_{t\in[0,t_0]} F(t,0), \text{ for all } t \in [0,t_0), u \in \mathbb{R}_+.$$

From these inequalities we conclude that $F(t,u)$ is bounded from above, and consequently $\phi(t,s,u)$ exists for all $t \geq s \geq 0$.

Let $R > 0$ be according to 6.2 and let $\epsilon > 0$ be such that $\epsilon < -\frac{1}{\omega}\int_0^\omega F_0(t,R)dt$. From 6.1, there is t^* such that $|F(t,R) - F_0(t,R)| < \epsilon$ for all $t \geq t^*$. Then, for all $t \geq t^*$ we have

$$\int_t^{t+\omega} F(\tau,R)d\tau < -\epsilon_1 := \epsilon\omega + \int_0^\omega F_0(t,R)dt < 0. \tag{39}$$

If $u = 0$ then $\phi(t,0,u) = 0$ for all $t \geq 0$, hence suppose that $u > 0$. In that case $\phi(t,0,u) > 0$ for all $t \in \mathbb{R}_+$. For the rest of the proof we need the following claim:

Claim 1: If there is $t_1 \geq t^*$ such that $\phi(t,0,u) \geq R$ for all $t \in [t_1, t_1+\omega]$ then $\phi(t_1+\omega,0,u) < \phi(t_1,0,u)e^{-\epsilon_1}$.

The proof of the claim follows directly from the following inequality:

$$ln\left(\frac{\phi(t_1+\omega,0,u)}{\phi(t_1,0,u)}\right) = \int_{t_1}^{t_1+\omega} F(t,\phi(t,0,u))dt \leq \int_{t_1}^{t_1+\omega} F(t,R)dt < -\epsilon_1.$$

Let us assume that $\phi(t,0,u) \geq R$ for all $t \geq t^*$. Using Claim 1 we obtain that

$$\phi(t^*+k\omega,0,u) < \phi(t^*,0,u)exp(-k\epsilon_1), \text{ for any } k \in \mathbb{N}$$

and a contradiction is achieved letting $k \to \infty$. We may therefore assume without loss of generality that $\phi(t^*,0,u) < R$.

Now suppose that there is $t_1 > t^*$ such that $\phi(t_1,0,u) = R$. Let us define $\Delta := \max\{\delta \geq 0\,;\, \phi(t_1+\delta,0,u) \geq R\}$ and $\mathcal{I} := [t_1, t_1+\Delta]$. From the Claim 1 we have that $\phi(t_1+\omega,u) < Re^{-k\epsilon_1} < R$, therefore Δ is well defined and smaller than ω. For each $t \in \mathcal{I}$ we have:

$$ln\left(\frac{\phi(t,0,u)}{\phi(t_1,0,u)}\right) = \int_{t_1}^{t} F(t,\phi(\tau,0,u))d\tau \leq (t-t_1)M \leq \omega M, \tag{40}$$

with M an upper bound for $F(t,u)$. From 40, we conclude that $\phi(t,0,u) \leq Re^{M\omega}$ for all $t \in \mathcal{I}$. This implies that $\phi(t,0,u) \leq \beta = Re^{M\omega}$ for all $t \geq t^*$, and consequently $\limsup_{t\to\infty} \phi(t,0,u) \leq \beta$. $\square$

The following proposition is inspired by part b) of Theorem 2.1 in [20].

Proposition 6.4. *Assume that A6.1-A6.2 hold. Let $a > 0$ and $J = [a,\infty)$. If $F_0(a,t) \geq 0$ for all $t \geq 0$, then:*

a) The periodic equation (38) admits an ω-periodic solution u^* satisfying $u^*(t) \geq a$ for all $t \in [0,\omega]$.

b) Assume that $F(t,a) \geq 0$ for all $t \geq 0$. If (38) admits a unique ω-periodic solution u^* satisfying $u^*(t) \geq a$, then any solution to (37) with initial condition on J approaches asymptotically to u^*.

Proof. Let $\phi(t,s,u)$ and $\phi_0(t,s,u)$ be the unique solutions of (37) and (38) respectively with $\phi(s,s,u) = \phi_0(s,s,u) = u \in \mathbb{R}_+$. From Lemma 6.3, solutions of (38) and (37) are ultimately bounded, and hence, uniformly bounded. Let $S : J \longrightarrow J$ be the Poincaré map associated to (38). We note that J is positively invariant with respect to (38), then S is well defined. Let $u \in J$. Since $S^n(u)$ is monotone and bounded, $S^n(u)$ is convergent. Since J is positively invariant with respect to (38), $u_0 = \lim_{n\to\infty} S^n(u) \in J$. Thus, $u^*(t) = \phi_0(t,s,u_0)$ is an ω-periodic solution satisfying $u^*(t) \in J$, and the part a) is proved.

For the part b), let u^* be the unique ω-periodic solution with $u^*(0) \in J$. By Proposition 3.2 in [21], $\phi(t,s,u)$ is asymptotic to the ω-periodic semiflow $T(t) := \phi_0(t,0,\cdot) : \mathbb{R}_+ \longrightarrow \mathbb{R}_+$, and hence $T_n(u) = \phi(n\omega,0,u), n \geq 0$, is an asymptotically autonomous discrete dynamical process with limit discrete semiflow $S^n : \mathbb{R}_+ \longrightarrow \mathbb{R}_+, n \geq 0$. Since $u^*(0)$ is the unique globally stable fixed point of S, by Theorem 2.4 in [21], we conclude that $\lim_{n\to\infty} T_n(u) = u^*(0)$ for any $u \in J$. Applying Theorem 3.1 in [21], we conclude the proof. $\square$

Appendix B

Here, we state some properties of the function μ_I defined in (33).

Proposition 6.5. *Let us consider μ_I given in (33). Then*

a) $\lim_{x\to\infty} \mu_I(t,x) = 0$ *uniformly for $t \in [0,\omega]$.*

b) $x \longmapsto \mu_I(t,x)$ is strictly decreasing for all $t \in (0,\omega/2)$ and $\mu_I(t,x) = 0$ for all $t \in [\omega/2,\omega]$.

c) μ_I is Lipschitz in x uniformly in t.

Proof. We recall that $\mu_I(t,x) = \int_0^L p(I(t,x,z))dz$. By doing the change of variable $I = I(t,x,z)$, we rewrite μ_I as:

$$\mu_I(t,x) = \frac{g(q)}{(kx+K_{bg})L}\int_{I_{out}(t,x)}^{I_{in}(t)} \frac{p(I)}{I}dI \tag{41}$$

where $I_{out}(t,x) = I(t,x,L)$. We can easily verify that:

$$0 \leq \mu_I(t,x) \leq \frac{1}{kxL} I_{max}\mu_{max}. \tag{42}$$

Letting $x \to \infty$ in (42), we prove a). For b), if $I_{in}(t) > 0$ we have:

$$\frac{\partial \mu_I(t,x)}{\partial x} = \frac{g(q)kL}{(kx+K_{bg})^2L^2}\int_{I_{out}(t,x)}^{I_{in}(t)} \frac{p(I_{out}(t,x)) - p(I)}{I}dI. \tag{43}$$

Since p is strictly increasing and $I_{out}(t,x) < I$ for all $I \in (I_{out}(t,x), I_{in}(t)]$ and $x > 0$, we conclude that $\frac{\partial\mu(t,x,q)}{\partial x} < 0$ for all $x > 0$, and consequently μ is strictly decreasing in x. For c), let us define $\theta = (kx + K_{bg})L$. Let l be a Lipschitz constant of p, then we have:

$$\begin{aligned}
\left|\frac{\partial \mu_I(t,x)}{\partial x}\right| &\leq \frac{kL}{\theta^2}\int_{I_{out}(t,x)}^{I_{in}(t)} \frac{|p(I) - p(I_{out}(t,x))|}{I}dI \\
&\leq \frac{klL}{\theta^2}\int_{I_{out}(t,x)}^{I_{in}(t)} \frac{|I - I_{out}(t,x)|}{I}dI \\
&\leq lkLI_{max}\frac{1-e^{-\theta}}{\theta} \leq lkLI_{max}.
\end{aligned}$$

Thus μ_I is Lipschitz in x uniformly in t and c) is proved. ∎

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