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Dynamics and productivity of microalgae in presence of predators ⋆

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Abstract: This paper is concerned with the dynamics and the productivity of biomass in a continuous microalgae culture contaminated by predators. We propose a general model describing a cultivation system where photolimited microalgae are grazed by zooplankton. We state necessary and sufficient conditions for the existence of a coexistence equilibrium. If this equilibrium exists, then microalgae and predators converge either to it or to a globally asymptotically stable periodic solution. In absence of the coexistence equilibrium, any solution approaches either an equilibrium characterized by the presence of algae and the absence of predators, or the washout equilibrium. This description of the dynamics allows to define the microalgae productivity in the long-term (*i.e.* when an attracting set is reached). With the help of numerical simulations, we show that operating the system at optimal (constant) dilution rate triggers the extinction of predators.

Keywords: Control; Biotechnology; Wastewater treatment; Microalgae; Predator–prey

1. INTRODUCTION

Microalgae are autotrophic unicellular organisms and a promising renewable source of chemical compounds, food, and biofuel (Mobin and Alam, 2017). Many factors affect the growth rate of microalgae, making mathematical modelling and production optimization a challenge. These factors range from physical constraints - light intensity and temperature - to biological constraints, e.g. the presence of invading species (Darvehei et al., 2018). Raceway ponds and closed photobioreactors are the two most common cultivation systems, raceways are cheaper and easier to maintain while photobioreactors might reach better productivities and are less prone to biological contamination (Schade and Meier, 2019). Despite all the different aspects influencing microalgae production, the presence of zooplankton grazers is one of the most dangerous. Some grazers might crash a cultivation of microalgae in few days, what might result in huge economical losses (Moreno-Garrido and Cañavate, 2001). Different operating conditions are associated with each cultivation method, e.g. different microalgae species and concentrations, also affecting how the system will respond to an invading species (Deruyck et al., 2019).

Zooplankton grazing microalgae includes ciliates, cladocerans, rotifers, and copepods.. In adverse conditions, some zooplankton might resort to sexual reproduction producing dormant eggs, which increases the complexity of the population dynamics (Montemezzani et al., 2015). The form of predation also varies between the species of grazers and the result of grazing will be highly dependent on the pair predator-prey. Microalgae also have defense mechanisms. For example, some microalgae might increase their presence as colonies constituting a defense structure against the attacks of grazers (Montemezzani et al., 2016). The life span of grazers and the time to get to the reproductive age play also a key role in their growth (Montemezzani et al., 2016). Furthermore, the growth rate of grazers is limited by their carrying capacity, meaning that after a certain concentration the population of grazers will no longer grow even if food is still available (Deruyck et al., 2019).

Different techniques have been assessed to deal with zooplankton invasion on microalgae cultures: Biological control, pesticides, extreme environment, pH control, filtration, etc. (Montemezzani et al., 2015). The success of the techniques depends on the microalgae and on the grazer species, therefore the monitoring of the organisms present in culture is necessary (McBride et al., 2014). Pesticides must eliminate the invading species, while they should only marginally affect the growth rate of microalgae or cause secondary environmental problems. Biological control is complicated to implement due to the diversity of grazers. It is difficult to design a system where all invading species will be adequately controlled. However, it has been observed that the increment in the retention time might greatly

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reduce the population of grazers (Montemezzani et al., 2016).

The dynamic interaction between microalgae and zooplankton grazers can be modeled by classic models of predator-prey systems. The growth rate of microalgae depends on many factors, and can be efficiently approximated by a function of one or two variables, such as light intensity and substrate concentration, on controlled environments (Darvehei et al., 2018). The grazer population might as well be divided to include the dynamics of eggs hatching and production (McNair et al., 1998). Then, analyzing the equilibrium of the system and the final productivity allows the determination of the best conditions to improve microalgal productivity in the presence of predators.

In this work, we analyze the microalgae productivity in a culture medium contaminated by predators. We analyze the asymptotic behavior of a chemostat model describing the growth of microalgae (e.g. *Chlorella Vulgaris*) in presence of predators (e.g. rotifer *Brachionus calyciflorus*). We show that the model admits a unique attracting set, that is, a set such that any solution starting in a neighborhood of it converges to it. Depending on the parameters of the model, this attracting set is either a limit cycle, a coexistence equilibrium, or an equilibrium without predators. This allows to define the microalgae productivity on the attracting set, which does not depend on the initial conditions and represents a natural extension of the classical steady state productivity in monocultures (Tang et al., 2012; Martínez et al., 2018a). With numerical simulations, we evaluate the impact of the dilution rate on productivity. Based on these results we propose a general guidance to optimize the microalgal vvproductivity in the presence of predators.

2. MODEL DESCRIPTION

Let us consider the following predator-prey model describing the growth of microalgae in a chemostat contaminated by predators (see Figure 1):

$$\begin{aligned} \frac{dx}{dt} &= [\mu(x) - D]x - \frac{1}{\gamma}\nu(x)y \\ \frac{dy}{dt} &= [\nu(x) - m - D]y \end{aligned} \tag{1}$$

Here, x and y represent the population density of microalgae and predators respectively. D is the dilution rate, i.e.

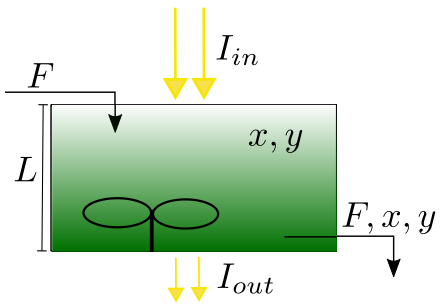

Fig. 1. Scheme of a continuous microalgae culture contaminated by predators.

inlet flow (F) divided by the reactor volume. The function $\nu(x)$ corresponds to the specific growth rate of predators, which depends on the microalgae concentration as follows:

$$\nu(x) = \nu_{max}\frac{x}{K_x + x}, \tag{2}$$

with ν_{max} the maximal growth rate and K_x a half saturation constant. The constant m represents the mortality rate of predators. The cosntant γ is a yield coefficient. The function $\mu(x)$ corresponds to the specific growth rate of microalgae. To describe μ, let L be the depth of the culture, which is illuminated from above as illustrated in Figure 1. We assume that light is attenuated exponentially according to the Lambert-Beer law i.e. at a distance $z \in [0, L]$ from the illuminated surface, the corresponding light intensity $I(x, z)$ satisfies

$$I(x, z) = I_{in}e^{-kxz},$$

with $k > 0$ the specific light attenuation coefficient of microalgae. Following the work of Huisman et al. (2002), the growth rate μ is given by

$$\mu(x) := \frac{1}{L}\int_0^L p(I(x, z))dz - r,$$

where $p(I)$ corresponds to the light response of microalgae and $r > 0$ is the respiration rate. $p(I)$ is described by a Monod model:

$$p(I) = p_{max}\frac{I}{K_I + I}, \tag{3}$$

where $K_I > 0$ is a half-saturation constant, and $p_{max} > 0$ is the maximal specific growth rate. A simple computation leads to

$$\mu(x) := \begin{cases} \dfrac{p_{max}}{kxL}\ln\left(\dfrac{K_I + I_{in}}{K_I + I_{out}(x)}\right) - r & if\ x > 0, \\ p(I_{in}) - r & if\ x = 0. \end{cases}$$

with $I_{out}(x) = I(x, L)$ the light intensity at the bottom of the culture.

3. MODEL ANALYSIS

In absence of predators ($y = 0$), the dynamics of microalgae is given by the following one-dimensional ODE

$$\frac{dx}{dt} = [\mu(x) - D]x. \tag{4}$$

Note that $x \longmapsto \mu(x)$ is strictly decreasing and that $\lim_{x\to\infty}\mu(x) = -r$ (see for example Proposition C.1 by Martínez et al. (2020)). Then, if $\mu(0) > D$, we have the existence of a unique x^* such that

$$\mu(x^*) = D. \tag{5}$$

Since $\mu'(x^*) < 0$, x^* is globally asymptotically stable (GAS) with respect to (4) on $(0, \infty)$. If $\mu(0) \leq D$, then any solution to (4) converges to 0. From now on, we will denote the equilibrium (of (1)) characterized by the presence of microalgae and the absence of predators, whenever exists, by

$$E^* = (x^*, 0). \tag{6}$$

The equilibrium characterized by the absence of both populations, which always exists, will be denoted by

$$E_0 = (0, 0). \tag{7}$$

Lemma 1. (Boundedness). Solutions to (1) are bounded.

Proof. Let (x, y) be a solution of (1) with $x(0), y(0) > 0$ and let $\bar{x}$ be such that

$$\frac{d\bar{x}}{dt} = (\mu(\bar{x}) - D)\bar{x}, \quad \bar{x}(0) = x(0).$$

It is clear that $\bar{x}(t) \leq b := \max\{x(0), x^*\}$ with x^* defined by (5). From a comparison argument, it follows that $x(t) \leq \bar{x}(t)$ for all $t \geq 0$, then $x(t)$ is bounded from above by b. Now, let us define the variable $z = \gamma x + y$. Then we have

$$\frac{dz}{dt} \leq \gamma\mu(x)x - Dz \leq \gamma\mu(0)b - Dz.$$

Then $z(t) \leq b' := \max\{z(0), \gamma\mu(0)b/D\}$ for all $t \geq 0$. It is clear that b' is an upper bound for y which completes the proof. □

The following proposition gives necessary and sufficient conditions for the survival in the long-term of both populations. In particular, it characterizes the existence of coexistence equilibrium.

Proposition 2. (Coexistence). Assume that $\mu(0) > 0$ and let M be such that

$$\mu(M) = 0. \tag{8}$$

If $\nu(M) > m$, then, there is a dilution rate $D_1 \in (0, \mu(0))$, such that

(a) If $0 < D < D_1$, then there is a unique coexistence equilibrum $E_c = (x_c, y_c)$, and any solution to (1) approaches asymptotically either E_c or a positive periodic solution.
(b) If $D_1 \leq D < \mu(0)$, then there is no coexistence equilibrium, and any solution to (1) approaches E^* asymptotically.

Proof. For any $D \geq 0$, let us define $x^*(D)$ by means of (5). Now define $\varphi(D) = \nu(x^*(D)) - m - D$. Note that φ is strictly decreasing, and that $\varphi(0) = \nu(M) - m > 0$ and $\varphi(\mu(0)) = -\mu(0) - m < 0$. Then, there is a unique $D_1 \in (0, \mu(0))$ such that $\varphi(D_1) = 0$. For the part (a), assume that $D < D_1$, then there is $x_c \in (0, x^*(D_1))$ such that $\nu(x_c) = D + m$. Since μ is strictly decreasing, we have that $\mu(x_c) > \mu(x^*(D_1)) = D_1 > D$. Consequently,

$$y_c := \gamma\frac{(\mu(x_c) - D)x_c}{\nu(x_c)} > 0.$$

Then the coexistence equilibrium is given by $E_c = (x_c, y_c)$. The uniqueness of E_c follows directly from the monotonicity of ν and μ.

The Jacobian matrix associated with (1) is given by

$$\begin{bmatrix} \mu(x) - D + \mu'(x)x - \frac{1}{\gamma}\nu'(x)y & -\frac{1}{\gamma}\nu(x) \\ \nu'(x)y & \nu(x) - D - m \end{bmatrix}. \tag{9}$$

It is straightforward to verify that E_0 (given by (7)) and E^* are saddle points. Using a stable manifold theorem argument, E_0 and E^* can only be reached by solutions starting on $(\{0\} \times \mathbb{R}_+) \cup (\mathbb{R}_+ \times \{0\})$. From Lemma 1, any solution to (1) is bounded. Thus, using the Poincaré-Bendixon Theorem, we conclude that any solution starting on the interior of $\mathbb{R}^2_+$ approaches asymptotically either E_c or a periodic cycle. For part (b), by contradiction, let $E_c = (x_c, y_c)$ be a coexistence equilibrium. Then

$$\mu(x_c) - \mu(x^*) = \frac{\nu(x_c)}{\gamma x_c}y_c > 0,$$

from where $x_c < x^*$. Now, since $D \geq D_1$ we have

$$0 = \nu(x_c) - m - D < \nu(x^*) - m - D = \varphi(D) \leq 0,$$

which is a contradiction. Then, there is no coexistence equilibrium. Hence, there is no limit cycle. Consequently, any solution with positive initial conditions approaches either E_0 or E^*. Again, since E_0 is a saddle point, using a stable manifold theorem argument, we conclude that E_0 can only be reached by solutions starting on $\{0\} \times \mathbb{R}_+$. Which completes the proof of (b). □

From now on, the coexistence equilibrium, whenever exists, will be denoted by

$$E_c = (x_c, y_c). \tag{10}$$

Lemma 3. (Stability of the coexistence equilibrium) Let us define the function $h : (0, \infty) \to \mathbb{R}$ by

$$h(x) := \frac{(\mu(x) - D)x}{\nu(x)}. \tag{11}$$

If the coexistence equilibrium E_c exists, then:

(a) if $h'(x_c) < 0$, then E_c is a sink (locally stable),
(b) if $h'(x_c) = 0$, then E_c is globally stable on $(0, \infty) \times (0, \infty)$
(c) if $h'(x_c) > 0$, then E_c is a source (unstable).

Proof. The Jacobian matrix associated to (1) evaluated at E_c is given by (see (9))

$$J(E_c) = \begin{bmatrix} \mu(x_c) - D + \mu'(x_c)x_c - \frac{1}{\gamma}\nu'(x_c)y & -\frac{1}{\gamma}\nu(x_c) \\ \nu'(x_c)y_c & 0 \end{bmatrix}.$$

Then the trace of $J(E_c)$, denoted τ, and the determinant of $J(E_c)$, denoted δ, are given by

$$\tau = \mu(x_c) - D + \mu'(x_c)x_c - \frac{1}{\gamma}\nu'(x_c)y \quad \text{and}$$
$$\delta = \frac{1}{\gamma}y_c\nu(x_c)\nu'(x_c) > 0.$$

Thus, if $\tau < 0$, E_c is a sink, if $\tau > 0$, then E_c is a source. If $\tau = 0$, then E_c is a center for the linear system $\frac{d}{dt}(x, y)^T = J(E_c)(x, y)^T$. Then, according to Theorem 5 in Chapter 2.10 in the book of Perko (2013), E_c is either a focus, a center, or a center-focus for (1). Choosing appropriately b in Theorem 2.1 by Hwang (1999), we conclude that there are no limit cycles when $\tau = 0$. Hence, E_c is focus, and consequently stable. From Proposition 2, we conclude the global stability of E_c. Finally, it is straightforward to prove that τ and $h'(x_c)$ have the same sign. This completes the proof. □

According to Proposition 2, any solution to (1) that is not attracted by E_c approaches a limit cycle. The following lemma gives necessary conditions for the uniqueness and the stability of this limit cycle.

Lemma 4. Let h be the function defined in (11) and define:

$$q(x) := [K_x h'(x) + x(x + K_x)h''(x)](\nu(x) - D - m) - K_x\nu(x)h'(x).$$

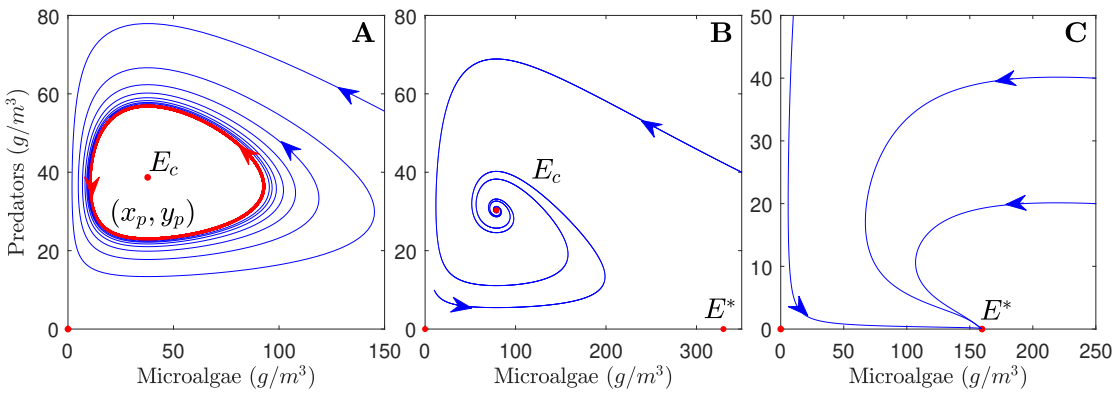

Fig. 2. Three different situations taken into account in the definition of the long-term productivity given by (17). **A**. The coexistence equilibrium E_c exists and is unstable ($D = 0.1\,d^{-1}$). **B**. The coexistence equilibrium E_c exists and is stable ($D = 0.3\,d^{-1}$). **C**. There is no coexistence equilibrium ($D = 0.7\,d^{-1}$)

Assume that the coexistence equilibrium E_c exists. If $h'(x_c) > 0$ and the following inequality holds for every $x \in [0, x^*]$:

$$q(x) \leq 0, \tag{12}$$

then (1) admits a unique limit cycle which is globally stable on $(0, \infty) \times (0, \infty)$.

Proof. Using Theorem 2.2 by Hwang (1999), it suffices to verify that under the hypotheses of the lemma we have that for all $x \in (0, x^*) - \{x_c\}$:

$$\frac{d}{dx}\left(\frac{\nu(x)h'(x)}{\nu(x) - m - D}\right) \leq 0. \tag{13}$$

□

Remark 5. Condition (12) can be evaluated for a given set of parameters. A way of doing this is studying the following optimization problem

$$\begin{array}{lllll} \max & q(x) & & & \\ s.t. & I_{in,min} & \leq I_{in} & \leq I_{in,max}, & \\ & 0 & \leq D & \leq D_1(I_{in}), & \\ & 0 & \leq x & \leq x^*(D, I_{in}), & \\ & 0 & \leq h'(x_c(D, I_{in})). & & \end{array} \tag{14}$$

If the coexistence equilibrium exists and is unstable, and if the maximum of $q(x)$ is negative, then for all $I_{in} \in [I_{in,min}, I_{in,max}]$, the conclusion of Lemma 4 follows. Note that the constraints in (14) are well defined only if all the values of I_{in} satisfy $\mu(0; I_{in}) \geq 0$. Using the parameters of Table 1 and taking $I_{in} \in [4, 2000]\,\mu\,mol\,m^{-2}\,s^{-1}$, the maximum of $q(x)$ is -67.8. This result was obtained using the solver *fmincon* of MATLAB.

4. PRODUCTIVITY OPTIMIZATION

In absence of predators, the steady-state (areal) microalgae productivity is defined by

$$P(D) = LDx^*, \tag{15}$$

with x^* defined by (5). P represents the quantity of microalgae that is produced per unit of area and time when the system reaches its steady state. Note that x^* depends on the dilution rate. It is well known that P is maximal if

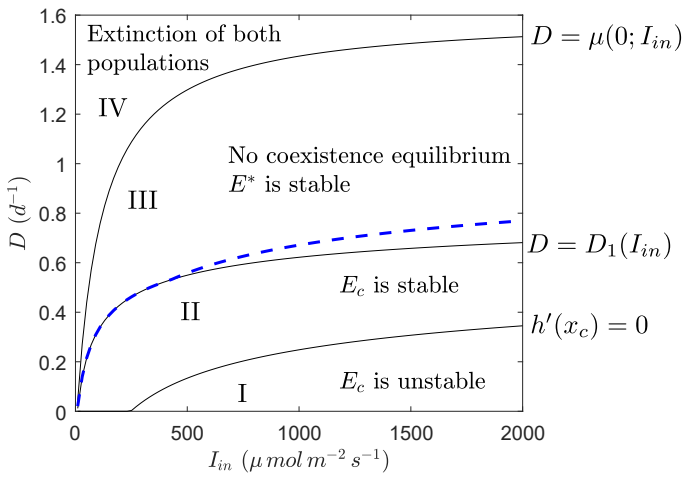

Fig. 3. Two dimensional bifurcation diagram. In region I solutions approach a limit cycle. In region II, the coexistence equilibrium, E_c, is stable. In region III, there is no coexistence equilibrium, and solutions approach to E^*. In region IV both populations go extinct. The dashed line is defined as $D = \max\{D_1, D^*_{opt}\}$.

the following compensation condition holds (see the work of Mairet et al. (2015)):

$$p(I_{out}(x^*)) = r. \tag{16}$$

We will denote by D^*_{opt} the dilution rate verifying (16). Now, we extend the definition of productivity, which represents the microalgae productivity in the long-term, to a culture contaminated by predators.

According to Proposition 2, there is a dilution rate $D_1 > 0$ such that for any $D < D_1$ microalgae and predators survive in the long-term. Moreover, they either settle in the coexistence equilibrium E_c or they approach a periodic solution of (1) (see Figure 2). If E_c is unstable, then any solution with positive initial conditions, different from E_c, approach a periodic solution. Following Lemma 4 and Remark 5, we assume that this periodic solution is unique and its trajectory and period will be denoted by (x_p, y_p) and T respectively (see Figure 2A).

Table 1. Kinetic parameters and yield coefficients

Parameter	Value	Unit	Reference
p_{max}	1.68	d^{-1}	(Huisman et al., 2002)
K_I	108	$\mu mol\, m^{-2}\, s^{-1}$	(Huisman et al., 2002)
r	0.1	d^{-1}	
k	0.2	$m^2\, g^{-1}$	(Deruyck et al., 2019)
ν_{max}	1.4	d^{-1}	(Deruyck et al., 2019)
K_x	219	gm^{-3}	(Deruyck et al., 2019)
m	0.15	d^{-1}	(Deruyck et al., 2019)
γ	0.21		(Deruyck et al., 2019)
L	0.15	m	

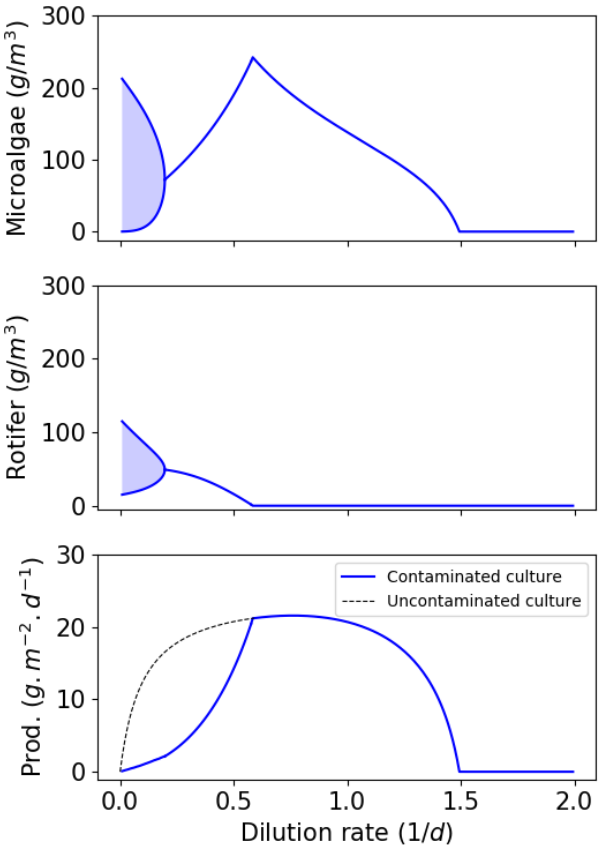

Fig. 4. Bifurcation diagram, limit cycles, and productivity. $I_{in} = 2000\, \mu mol\, m^{-2}\, s^{-1}$

We define the areal long-term productivity, denoted by $Q(D)$, as

$$\begin{cases} \dfrac{1}{T}\displaystyle\int_0^T LDx_p(t)dt, & if\ E_c \text{ exists and is unstable,} \\ LDx_c, & if\ E_c \text{ exists and is stable,} \\ LDx^*, & if\ D_1 \leq D < \mu(0). \end{cases} \tag{17}$$

Figure 2 shows the three possible cases that are considered in the definition of Q. The following lemma, which is intuitive, shows that in presence of predators the long-term productivity cannot be higher than P.

Lemma 6. Let $P(D)$ and $Q(D)$ be defined by (15) and (17) respectively. For any $D \in (0, \mu(0))$ we have that $Q(D) \leq P(D)$.

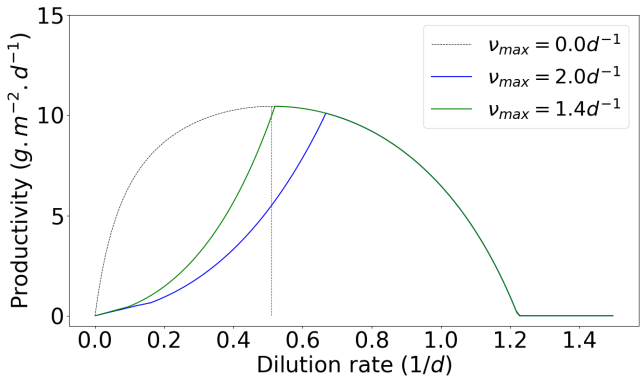

Fig. 5. Productivity comparison under different grazing rates of predators. The vertical dashed line shows the optimal productivity for the uncontaminated culture. $I_{in} = 400\, \mu mol\, m^{-2}\, s^{-1}$

.

Proof. We only consider the case when E_c is unstable. Since, $x_c < x^*$ and E_c is in the interior of any periodic orbit, we conclude that $x_p(t) \leq x^*$ for some $t \in [0, T]$. Note that the set $[0, x^*] \times [0, \infty)$ is positively invariant, then $x_p(t) \leq x^*$ for all $t \in [0, T]$. From where the proof follows directly. □

To determine the existence of a dilution rate maximizing $Q(D)$ is not trivial, due to the possible presence of periodic orbits. The following proposition considers the case when for any dilution rate there are no limit cycles involved in the definition of Q. This occurs for low values of the incident light intensity for example (see Figure 3).

Proposition 7. Let D_1 be the dilution rate given by Proposition 2 and let D^*_{opt} be the dilution rate maximizing P. Assume that for any $D < D_1$ the coexistence equilibrium, which exists according to Proposition 2, is stable. Then, Q is maximal when

$$D = \max\{D_1, D^*_{opt}\}. \tag{18}$$

Proof. For any $D \in (0, \mu(0))$, we have that

$$Q := \begin{cases} Dx_c, & if\ D < D_1, \\ Dx^*, & if\ D_1 \leq D < \mu(0). \end{cases} \tag{19}$$

Since x_c is defined through $\nu(x_c) = D + m$, and ν is strictly increasing, it is clear that Q is strictly increasing with respect to D on $[0, D_1)$. From the definition of D_1 (see proof of Proposition 2), we have that Q is continuous at D_1. Finally, note that $Q = P$ for all $D \in [D_1, \mu(0))$. Thus, if $D^*_{opt} \leq D_1$, then Q is strictly decreasing on $[D_1, \mu(0))$, hence Q is maximal at $D = D_1$. If $D^*_{opt} \geq D_1$, then Q is strictly increasing on $[0, D^*_{opt}]$ and strictly decreasing on $[D^*_{opt}, \mu(0))$. Hence, Q is maximal at $D = D^*_{opt}$. □

Conjecture 8. Let D_1 be the dilution rate given by Proposition 2. Then, Q is maximal when (18) holds.

To support Conjecture 8, with the help of the toolbox Matcont for MATLAB developed by Dhooge et al. (2003), we evaluate numerically the productivity Q (defined by (17)) as a function of the dilution rate. Figure 4 shows that Q is strictly increasing on $[0, D_1]$, even in presence of limit cycles. In this case, $D_1 < D^*_{opt}$. In accordance with Conjecture 8, Q is maximal at $D = D^*_{opt}$. In this

situation, the optimal dilution rate in the contaminated culture coincides with that of a culture without predators. However, this is not always the case. Figure 5 shows that for a lower incident light intensity, Q is maximal at $D = D_1$ and this situation becomes clearer if we consider a predator that grows faster.

5. DISCUSSION AND CONCLUSIONS

We proposed a definition of long-term productivity, which is based on the existence of a unique attracting set, in a continuous microalgae culture contaminated by predators. We conjecture that the optimal dilution rate is the maximal dilution rate between that at which coexistence is lost (D_1 in Proposition 2) and that at which the productivity is maximal in absence of predators (D^*_{opt} defined through (16)). Thus, according to our conjecture, optimal operation of the culture leads predators to extinction. These theoretical results are in accordance with experimental findings by Montemezzani et al. (2016), where shorter retention times (i.e. higher dilution rates) resulted in a productivity gain and control of the population of grazers.

Not representing the dynamics of the grazer population might lead to very unfavorable operational conditions. As shown in Figures 4 and 5, there is an important loss of productivity by operating the culture at small dilution rates in presence of predators. Operating under the optimal dilution rate, that is determined in absence of predators (D^*_{opt}), can also be a bad strategy. As shown in Figure 5, there could be a loss of about half of the productivity. This high lost due to predation can be reduced to 4% increasing the dilution rate from $0.50d^{-1}$ to $0.66d^{-1}$. Since outdoor cultivation is very susceptible to contamination, it would be recommended to operate at dilution rates higher than the calculated optimal rate for an uncontaminated culture.

An appropriate control strategy can drastically minimize the impact of predation and eventually reach productivities that are not significantly lower than without predation. This option is not straightforward since often the operators decrease the dilution rate after a threat for the culture has been detected.

This work represents a first theoretical approach to the impact of predators on microalgae cultivation. More realistic models must be developped to consider the attachment of predators to the reactor walls and microalgae agglomeration to protect themselves. Including photoinhibition of the algae in the model can also strongly increase complexity, especially if a contamination occurs decreasing the biomass concentration below the Allee threshold as defined by Martínez et al. (2018b).

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