

Theoretical growth rate of microalgae under high/low-flashing light

J. Ignacio Fierro U.¹, Liu-Di Lu³, Olivier Bernard^{1,2}

¹*INRIA Sophia Antipolis Méditerranée, BIOCORE Project-Team, Université Nice Côte d'Azur, 2004, Route des Lucioles - BP 93, 06902 Sophia-Antipolis Cedex, France*

²*Sorbonne Université, INSU-CNRS, Laboratoire d'Océanographie de Villefranche, 181 Chemin du Lazaret, 06230 Villefranche-sur-mer, France*

³*Section de mathématiques, Université de Genève, Rue du Conseil-Général 7-9, 1205 Genève, Switzerland*

Abstract

Light availability has a huge impact on the photosynthesis efficiency of the microalgae. Low light in the reactors leads to limited growth of the algae, whereas strong light may induce the damage to the photosynthetic reaction center, hence reduce the growth. Finding the optimal light regime is then a tricky problem, especially when the growth rate is inhibited by being overexposed to the light. In this paper, we study the theoretical microalgal growth rate using the Han model under the high/low flashing light regime, i.e., when two different light intensities are applied. Two approaches were considered depending on the period of the light pattern. For a large light period we show that, under some conditions, we can improve the average growth rate and get greater values than the ones that the PI-curve can achieve in the Han model. Although, these conditions change through the depth of a bioreactor. This theoretical improvement is due to a recover of photodamaged cells during the high light intensity phase. Considering flashing light, we give a minimal value of the duty cycle for which the optimal light intensity is perceived by the algae culture, we also give the value of the depth in which the algae perceives this optical light intensity.

Keywords: Microalgae, Flashing light, Growth rate, Han model

1 Introduction

Algal biomass has shown a great potential for the production of biofuels and bio-products, for instance food, pharmaceuticals and cosmetics [15]. The production

of a range of biofuels, such as biodiesel, biohydrogen, bio-oils, and biomethane, along with solid biochar and its application, has demonstrated the importance of microalgal research [13]. Mathematical modelling has become an important tool to make the leap from lab-scale observations towards the industrial-scale reality. The mathematical models can be used for monitoring, controlling and optimizing the production systems, meanwhile they could also drive the choice of a particular microalgae species which is best suited in local environment [6]. The algal growth is influenced by different factors such as temperature, light, pH, etc. Among all, light is a crucial factor for photosynthesis that will fuel the CO₂ uptake and further the growth of microalgae. Light is absorbed and scattered by the algae culture and cannot penetrate deeply into the liquid medium, especially for high-density microalgae culture systems [19].

For high light intensity, typically sunlight in summer afternoon, the reaction center can be damaged which then leads to the decrease in the photosynthesis efficiency [16], this is so-called photoinhibition. In this context, flashing light has appeared as a method to reduce photoinhibition and to increase the productivity in bioreactors. There has been a whelm of research on the benefit of supplying light by flashes, e.g., [2, 9, 1, 18]. The flashing light, however, rarely produces an enhancement on the algal production in comparison with the constant average light intensity [3]. This light regime consists of a light and dark phase, otherwise, in high/low-flashing light the dark period is replaced by a low light. This light regime can be more representative of real conditions [8].

Researches have been carried out to the understanding and the modelling of photosynthesis in response to light/dark cycles of various intensities, duration and duty cycles. The objective of this paper is to go beyond this light pattern to understand how alternating a low light (not necessarily zero) and a high light can affect the growth rate of the microalgae. We consider the Han model [11] that represents the dynamics of photon capture in the photosystems and takes into account the phenomenon of photoinhibition. We then study the theoretical growth rate under two different light regimes, namely the constant light regime and the high/low flashing light regime. We choose the constant light as the average of the high/low light intensities to guarantee the same amount of energy in the photosystem. We consider the local optical depth concept defined in [5] for our analysis to condense the concepts of depth and biomass concentration in a bioreactor. We show that the growth under the high/low flashing light regime can be enhanced compared with the growth under the constant light regime, meanwhile we also prove that for high frequencies (or short period of the light patron) the growth rate under the high/low flashing light regime is equal to the growth rate under the constant light regime.

This paper is organized as follows. In Section 2, we present the growth model and the light setting. In Section 3, we analyze what happened in the large period approach which will call *Large-T model* and how this case can improve the growth rate comparing to the continuous light regime. In Section 4, we study the small period approach called *Small-T model*, and we give an interval in which the algae culture perceives the optimal light if we consider the flashing light configuration. Section 5 justifies the approximations made and

confirms the obtained limits in the previous sections. Finally, in Section 6, we test numerically the results.

2 Description of the model

2.1 Han model

Han [11] has proposed a mechanistic model for algal photoinhibition induced by photodamage to photosystem-II (PSII). The reaction centers of PSII can take three states: open or reactive state A , closed or activated state B and inhibited state C . After absorbing photons, PSIIs move from state A to B at a rate proportional to σI , where σ is the *effective cross section* of the PSII and I is the light intensity. The minimal time required for an electron to transfer from water on the donor side of PSII to terminal electron acceptors is called *turnover time* and denoted by τ , so that τ^{-1} corresponds to the rate of state B passing to state A . Excessive absorption leads to photoinhibition of the PSII (C state) at a rate of $k_d\sigma I$ and has a recovery rate k_r . Figure 1 presents the relation between these three states. The dynamics of PSIIs at the three states can be described

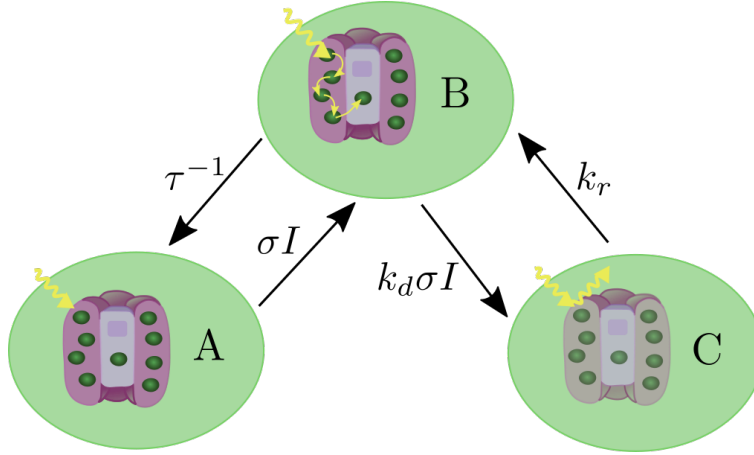


Figure 1: Illustration of the Han Model.

by the following differential equations describing the proportion of each state:

$$\begin{aligned} \frac{dA}{dt} &= -I\sigma A + \frac{B}{\tau}, \\ \frac{dB}{dt} &= I\sigma A - \frac{B}{\tau} + k_r C - k_d\sigma I B, \\ \frac{dC}{dt} &= -k_r C + k_d\sigma I B, \end{aligned} \quad (1)$$

and these three states satisfy that

$$A + B + C = 1. \quad (2)$$

Using Equation (2), we can eliminate B to reduce the system (1) into two equations:

$$\frac{d}{dt} \begin{pmatrix} A \\ C \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & k_d \end{pmatrix} \left[- \begin{pmatrix} \sigma I + \frac{1}{\tau} & \frac{1}{\tau} \\ \sigma I & \sigma I + \frac{k_r}{k_d} \end{pmatrix} \begin{pmatrix} A \\ C \end{pmatrix} + \begin{pmatrix} \frac{1}{\tau} \\ \sigma I \end{pmatrix} \right]. \quad (3)$$

The algal growth rate μ is proportional to $I\sigma A$, i.e.,

$$\mu := K\sigma IA, \quad (4)$$

where K corresponds to the growth rate coefficient.

At steady state of system (1), the growth rate for a constant light intensity I can be computed explicitly as

$$\mu_S(I) := \frac{K\sigma I}{1 + \tau\sigma I + \frac{k_d}{k_r}\tau(\sigma I)^2}. \quad (5)$$

Note that the maximum of this function is given by

$$\mu_{\max} = \frac{K}{\tau + 2\sqrt{\frac{k_d}{k_r}\tau}}, \quad (6)$$

which is achieved with the light intensity I_{opt} given by

$$I_{\text{opt}} = \frac{1}{\sigma\sqrt{\frac{k_d}{k_r}\tau}}. \quad (7)$$

System (3) has slow-fast time scales due to the presence of the factor k_d . For example, Table 1 present some values of the parameters in the literature, in [10, 14] k_d is on the order of 10^{-4} and the values of the entries of

$$\begin{pmatrix} \sigma I + \frac{1}{\tau} & \frac{1}{\tau} \\ \sigma I & \frac{k_r}{k_d} + \sigma I \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} \frac{1}{\tau} \\ \sigma I \end{pmatrix}$$

are greater than 0.1 when we consider a light intensity I of the order of 1000.

2.2 Light configurations and the two simplified models

Let us consider two light regimes, namely the constant regime and the high/low light regime. For the constant light regime, the reactor receives a constant light intensity at the surface. For high/low-flashing light regime, a periodic piece-wise constant light intensity is applied at the reactor surface. Let us denote by I_{\max} (resp. I_{\min}) the maximum (resp. minimum) light intensity and by $\eta \in (0, 1)$ the duty cycle. We can then define the average light intensity by

$$I_\eta := \eta I_{\max} + (1 - \eta) I_{\min}. \quad (8)$$

We will analyze the mean growth rate over a period T for these two light regimes. The reactor is assumed to be alimeted continuously by the light I_η for the

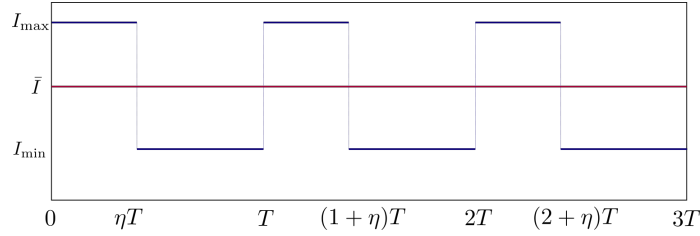


Figure 2: Illustration of the two light regime. The high/low regime (blue) in which the function I_s has a period T and switches from I_{\max} to I_{\min} for a time ηT and $(1 - \eta)T$ respectively. The constant light regime (red) which is considered as the weighted average between I_{\max} and I_{\min} .

constant light regime, whereas in the high/low light regime, we assume that the reactor is exposed regularly between a high light intensity I_{\max} for ηT and a low light intensity I_{\min} for $(1 - \eta)T$. See Figure 2.

Recall that I is a T -periodic function, and we have a slow/fast system (1). Depending on the scale of T , we can reduce the equation into one to simplify the calculations. We have two different cases. When T is small, compared to the Han model parameters ($T < \tau$), the order of magnitude is milliseconds, we will call *Small- T model* or high frequency model, and when T is large, for instance greater than $1/k_r$ (the order of magnitude is hours), we will call *Large- T model* or low frequency model. These reductions are given as follows:

Large- T model (or low frequency model) When light stays constant for a large enough time, the dynamic of A reaches its steady state much faster compared with that of C . One can then apply a fast-slow approximation by using the perturbation theory [12]. More precisely, we consider the slow manifold $A = \frac{1-C}{1+\tau\sigma I}$ (i.e. the pseudo steady state of A) to reduce the dynamics into one single equation on the photoinhibition state C :

$$\frac{dC}{dt} = -(\alpha(I) + k_r)C + \alpha(I), \quad (9)$$

with $\alpha(I) = \frac{k_d\tau(\sigma I)^2}{1+\tau\sigma I}$.

Small- T model (or high frequency model) When light varies very rapidly compared to the system dynamics, the dynamics of the photoinhibition state C stays approximately constant. We can then apply the Averaging Method [17] to simplify the system (3) into one equation on the open state A :

$$\frac{dA}{dt} = -\left(\sigma I + \frac{1}{\tau}\right)A + \frac{k_r - k_d\sigma\bar{I}A}{\tau(k_d\sigma\bar{I} + k_r)}, \quad (10)$$

with $\bar{I} = \frac{1}{T} \int_0^T I(t)dt$ and $\bar{I}A = \frac{1}{T} \int_0^T I(t)A(t)dt$.

2.3 Gradient of light intensity

Photobioreactors are illuminated at the surface. Then, light is attenuated along the depth z due to the light absorption and scattering. The Beer-Lambert law is chosen for modelling this phenomenon:

$$I(y) := I_s e^{-y}. \quad (11)$$

where $y := \varepsilon(X)z$, is the so-called local optical depth [5]. The vertical position is denoted by z . The light extinction coefficient $\varepsilon(X) > 0$ (m^{-1}) depends on the concentration of the microalgae X which, in our work, we will assume that the concentration does not change through the time.

Local optical depth is a concept that includes two factors of the light attenuation, the vertical position z (the depth) and the concentration. In our analysis, we are interested in the light attenuation, and not in the concentration of the medium or the size of the bioreactor, this leads us to use the concept of local optical depth. We will see that some results holds for small values of local optical depth ($y < 1$), yet this does not mean, necessarily, that the biomass concentration is low, or the vertical position is near to the surface. It can be true for a large value of the vertical position z with a low concentration or can be true for a small value of z considering a high concentration, as long as they share the same local optical depth which is smaller than 1. Nevertheless, when we consider $y = 0$ it always refers to the surface of the bioreactor.

From the definition of the light attenuation (11), we denote by $I_H(y) = I_{\max} e^{-y}$ (resp. $I_L(y) = I_{\min} e^{-y}$) the high light intensity (resp. the low light intensity) at local optical depth y .

Our objective is to compare the impact of the two light regimes on growth rate. When enlightened by a constant light intensity I_η , the light intensity perceived at local optical depth y is given by $I_M(y) = I_\eta e^{-y}$. By choosing I_η as (8), we guarantee that these two systems receive the same amount of energy. Our objective is to compare the growth rate for these two systems.

2.4 Exact asymptotic solution of the Han model

For every starting point of the Han model states (A and C), we prove in Lemma 2.1 that, for a periodic signal of light I , the solution of (3) converges to the periodic solution. For this reason, in all our analysis, we consider the periodic solution of this system and assume the periodic condition in the two models. Based on this assumption, we define the asymptotic exact T -averaged growth rate $\bar{\mu}^T$ by

$$\bar{\mu}^T(y) = \frac{1}{T} \int_0^T \mu(y, t) dt \quad (12)$$

where μ is defined in (4) and A is considered as the periodic solution of (1).

Lemma 2.1. *All solutions of (3) under the periodic high/low light regime converges to the periodic solution.*

Proof. Let us denote by

$$M(t) = \begin{pmatrix} \sigma I(t) + \frac{1}{\tau} & \\ k_d \sigma I(t) & k_d \sigma I(t) + k_r \end{pmatrix}, N(t) = \begin{pmatrix} \frac{1}{\tau} \\ k_d \sigma I(t) \end{pmatrix}.$$

The light regime is T -periodic, meaning that $I(t+T) = I(t)$ and $N(t+T) = N(t)$ and $M(t+T) = M(t)$. Let us set $x(t) = (A(t), C(t))^T$, then the periodic system of (3) reads

$$\frac{dx}{dt} = -M(t)x(t) + N(t). \quad (13)$$

This is a linear inhomogeneous system with periodic coefficients. Let $x(t)$ the solution of (13) for a given initial condition x_0 and $x_p(t)$ the periodic solution of (13) (i.e. $x_p(0) = x_p(T)$). Then $\xi(t) := x(t) - x_p(t)$ is the solution of the periodic system $\frac{d\xi}{dt} = -M(t)\xi(t)$. As $M(t)$ has positive eigenvalues (see Appendix A.4), then [7, Theorem 3, Section 10] asserts that $\xi(t)$ converges to zero as t approaches infinity. This concludes the proof. \square

We then assume (3) to be asymptotically T -periodic and only focus on the periodic solutions of this system i.e., $A(0) = A(T)$ and $C(0) = C(T)$. Solving (3) in periodic case and using the definition of the growth rate (4), it is possible to analytically compute the exact T -average growth rate in the high/low-flashing light as

$$\bar{\mu}^T(y) = \eta \mu_S(I_H(y)) + (1 - \eta) \mu_S(I_L(y)) - \frac{K\sigma}{T} \delta(y, T), \quad (14)$$

where the function μ_S is defined in (5), δ is the first component of the vector

$$\begin{aligned} \Delta = & \left[I_H(y) M_H^{-1}(y) \left(\text{Id} - e^{-\eta T M_H(y)} \right) \left(\text{Id} - e^{-(1-\eta) T M_L(y)} e^{-\eta T M_H(y)} \right)^{-1} \left(\text{Id} - e^{-(1-\eta) T M_L(y)} \right) \right. \\ & \left. - I_L(y) M_L^{-1}(y) \left(\text{Id} - e^{-(1-\eta) T M_L(y)} \right) \left(\text{Id} - e^{-\eta T M_H(y)} e^{-(1-\eta) T M_L(y)} \right)^{-1} \left(\text{Id} - e^{-\eta T M_H(y)} \right) \right] \\ & \cdot (M_H^{-1}(y) N_H(y) - M_L^{-1}(y) N_L(y)), \end{aligned} \quad (15)$$

with Id the identity matrix in $\mathbb{R}^{2 \times 2}$ and

$$M_H(y) = \begin{pmatrix} \sigma I_H(y) + \frac{1}{\tau} & \\ k_d \sigma I_H(y) & k_d \sigma I_H(y) + k_r \end{pmatrix}, \quad N_H(y) = \begin{pmatrix} \frac{1}{\tau} \\ k_d \sigma I_H(y) \end{pmatrix}, \quad (16)$$

$$M_L(y) = \begin{pmatrix} \sigma I_L(y) + \frac{1}{\tau} & \\ k_d \sigma I_L(y) & k_d \sigma I_L(y) + k_r \end{pmatrix}, \quad N_L(y) = \begin{pmatrix} \frac{1}{\tau} \\ k_d \sigma I_L(y) \end{pmatrix}. \quad (17)$$

The details of the computations are given in A.3. And we can give an explicit expression of the matrices:

$$\begin{aligned} M^{-1}(I) &= \frac{1}{k_d(\sigma I)^2 + k_r \sigma I + \frac{k_r}{\tau}} \begin{pmatrix} k_d \sigma I + k_r & -\frac{1}{\tau} \\ -k_d \sigma I & \sigma I + \frac{1}{\tau} \end{pmatrix}, \\ M^{-1}(I)N(I) &= \frac{1}{1 + \tau \sigma I + \frac{k_d}{k_r} \tau (\sigma I)^2} \begin{pmatrix} 1 \\ \tau \frac{k_d}{k_r} (\sigma I)^2 \end{pmatrix}. \end{aligned}$$

Note that the first component of the vector $M^{-1}(I)N(I)$ multiplied by $K\sigma I$ correspond to $\mu_S(I)$.

3 Analysis of the Large-T model

As mentioned in Section 2.2, depending on the scale of T , we can reduce (1) into one equation. In this section, we present an analysis based on the growth rate calculated using the large-T model. We show in particular that the average growth rate in this case can be greater than the values of the PI-curve of the Han model. This improvement happened at the surface when $y = 0$, and is due to the local convexity of the function μ_S . However, depending on the value of the local optical depth y , the average growth rate can be slower than the constant light regime.

3.1 Average growth rate and analysis

In large-T model, the growth rate can be derived from (4) as

$$\mu = K\sigma IA = (1 - C)\gamma(I), \quad (18)$$

with $\gamma(I) = \frac{K\sigma I}{1 + \tau\sigma I}$ and C the periodic solution of (9). Since the light intensity I depends on the time t and the local optical depth y , the growth rate also depends on these two variables, i.e., $\mu = \mu(y, t)$. For a given local optical depth y , the T-average growth rate for the high/low light regime can be computed explicitly by

$$\bar{\mu}^T(y) = \frac{1}{T} \int_0^T \mu(y, t) dt = \eta\mu_S(I_H(y)) + (1 - \eta)\mu_S(I_L(y)) + \frac{\zeta_1(y, \eta, T)\zeta_2(y)}{Tk_r}, \quad (19)$$

with

$$\zeta_1(y, \eta, T) = \frac{(1 - e^{-(\alpha_L(y) + k_r)T(1-\eta)}) (1 - e^{-(\alpha_H(y) + k_r)T\eta})}{1 - e^{-(\alpha_L(y) + k_r)T(1-\eta)} - (\alpha_H(y) + k_r)T\eta},$$

$$\zeta_2(y) = \left(\frac{\alpha_H(y)}{\alpha_H(y) + k_r} - \frac{\alpha_L(y)}{\alpha_L(y) + k_r} \right) (\mu_S(I_H(y)) - \mu_S(I_L(y))),$$

$\alpha_H(y) := \alpha(I_H(y))$ and $\alpha_L(y) := \alpha(I_L(y))$. As for the constant light regime I_η , the T-average growth rate is obtained by $\mu_S(I_M(y))$. The details of the computations are presented in A.1. Let us denote by $\mu_S^\eta(y)$ the convex combination in (19):

$$\mu_S^\eta(y) := \eta\mu_S(I_H(y)) + (1 - \eta)\mu_S(I_L(y)), \quad (20)$$

When T is large enough, we can approximate the T-average growth rate by (20). Indeed, it is straightforward to see that $0 \leq \zeta_1(y, \eta, T) \leq 1$ and $0 \leq \frac{\alpha(I)}{\alpha(I) + k_r} \leq 1$, therefore, one has

$$|\bar{\mu}^T(y) - \mu_S^\eta(y)| = \left| \frac{\zeta_1(y, \eta, T)\zeta_2(y)}{Tk_r} \right| \leq \frac{|\mu_S(I_H(y)) - \mu_S(I_L(y))|}{Tk_r} \leq \frac{\mu_{\max}}{Tk_r}$$

where the last inequality is obtained by taking the maximum growth rate of the Han model given by (6). This leads to the following result.

Theorem 3.1. For large enough period T , for every local optical depth $y \geq 0$ we have $\lim_{T \rightarrow +\infty} \bar{\mu}^T(y) = \mu_S^\eta(y)$. Furthermore, the convergence is uniformly in y and $|\bar{\mu}^T(y) - \mu_S^\eta(y)| = \mathcal{O}(1/T)$.

3.2 Enhancing of the growth rate

Growth rate in high/low light regime can be enhanced or reduced compared to that of the constant light regime. More precisely, this relies on the local convexity of the function μ_S with respect to the light intensity I . Depending on the value of I , this can be either convex or concave. The next lemma clarifies the critical value of the light intensity.

Lemma 3.1. There exists a light intensity I_c , for which μ_S is a strictly convex function in $(I_c, +\infty)$ and strictly concave in $(0, I_c)$. This value only depends on the parameters (k_d, k_r, τ, σ) , i.e.,

$$I_c = \begin{cases} \frac{2}{\sigma \sqrt{\frac{k_d}{k_r}} \tau} \cos \left(\frac{1}{3} \arccos \left(\frac{\sqrt{\tau}}{2 \sqrt{\frac{k_d}{k_r}}} \right) \right) & \text{if } \tau < 4 \frac{k_d}{k_r} \\ \frac{2}{\sigma \sqrt{\frac{k_d}{k_r}} \tau} \cosh \left(\frac{1}{3} \operatorname{arccosh} \left(\frac{\sqrt{\tau}}{2 \sqrt{\frac{k_d}{k_r}}} \right) \right) & \text{if } \tau > 4 \frac{k_d}{k_r} \end{cases} \quad (21)$$

The proof is given in [B](#). This lemma enables us to state the next theorem, which is our main result. In this theorem, we provide conditions to enhance the growth rate, meaning that the average growth rate calculated in [\(19\)](#) is greater than the growth rate obtained for the continuous light regime I_η .

Theorem 3.2. Let I_c defined by [\(21\)](#). For every couple (I_{\max}, I_{\min}) , such that $I_{\max} > I_{\min} > I_c$, there exists $T > 0$ and $\eta \in (0, 1)$ such that

$$\bar{\mu}^T(0) \geq \mu_S(I_\eta) \quad (22)$$

where $I_\eta = \eta I_{\max} + (1 - \eta) I_{\min}$.

Proof. Setting $y = 0$ in [\(19\)](#) gives

$$\bar{\mu}^T(0) = \eta \mu_S(I_{\max}) + (1 - \eta) \mu_S(I_{\min}) + \frac{\zeta_1(0, \eta, T) \zeta_2(0)}{T k_r}.$$

Recall that

$$\begin{aligned} \zeta_2(0) &= \left(\frac{\alpha_H(0)}{\alpha_H(0) + k_r} - \frac{\alpha_L(0)}{\alpha_L(0) + k_r} \right) (\mu_S(I_H(0)) - \mu_S(I_L(0))) \\ &= \left(\frac{\alpha(I_{\max})}{\alpha(I_{\max}) + k_r} - \frac{\alpha(I_{\min})}{\alpha(I_{\min}) + k_r} \right) (\mu_S(I_{\max}) - \mu_S(I_{\min})). \end{aligned}$$

In $(I_c, +\infty)$ the function μ_S is decreasing, then $\mu_S(I_{\max}) - \mu_S(I_{\min}) < 0$. Moreover, the function $I \mapsto \frac{\alpha(I)}{\alpha(I) + k_r}$ is increasing, hence $\zeta_2(0) < 0$. On the other

hand, one has $0 \leq \zeta_1(0, \eta, T) \leq 1$ and $0 \leq \frac{\alpha(I)}{\alpha(I)+k_r} \leq 1$ for $I \geq 0$. All together implies that

$$\bar{\mu}^T(0) \geq \eta\mu_S(I_{\max}) + (1 - \eta)\mu_S(I_{\min}) + \frac{1}{Tk_r} (\mu_S(I_{\max}) - \mu_S(I_{\min})). \quad (23)$$

To conclude, we have to find T such that the right hand side of (23) is greater than $\mu_S(I_\eta)$ which is equivalent to the condition

$$\frac{1}{Tk_r} \leq \frac{\mu_S(I_\eta) - \eta\mu_S(I_{\max}) - (1 - \eta)\mu_S(I_{\min})}{\mu_S(I_{\max}) - \mu_S(I_{\min})}. \quad (24)$$

Since $\mu_S(I)$ is convex and decreasing on interval $(I_c, +\infty)$, the right hand side of (24) is always positive. Therefore, a couple (T, η) verifying condition (24) will ensure the inequality (22). This concludes the proof. \square

Biologically speaking, the previous theorem proves that for $I_{\max}, I_{\min} \in (I_c, +\infty)$ and $y = 0$ (i.e., at the surface), one can find a period T and a duty cycle η such that the T-average growth rate under the high/low light regime is greater than the constant average light regime. Based on the condition (24), if η is near to 0 or 1 we need larger T , since the right hand side of the inequality approaches to zero in this case. This improvement can be also valid for other choices of light (see Figure 5).

On the other hand, one can see that a condition between T and η is needed to give an interpretation of this improvement in the growth rate. Assume that the condition (24) holds for some T and η . Since $\mu_S(I_\eta) \geq \mu_S(I_{\max})$, then one has

$$\begin{aligned} \frac{1}{Tk_r} &\leq \frac{\mu_S(I_\eta) - \eta\mu_S(I_{\max}) - (1 - \eta)\mu_S(I_{\min})}{\mu_S(I_{\max}) - \mu_S(I_{\min})} \\ &\leq \frac{\mu_S(I_{\max}) - \eta\mu_S(I_{\max}) - (1 - \eta)\mu_S(I_{\min})}{\mu_S(I_{\max}) - \mu_S(I_{\min})} \\ &= 1 - \eta, \end{aligned}$$

or, in other words, $(1 - \eta)T \geq \frac{1}{k_r}$. Since k_r corresponds to the recovery rate of a photoinhibited PSU, then $\frac{1}{k_r}$ is the time needed for recovering a damaged PSU. Moreover, $(1 - \eta)T$ represents the time that the system is exposed under the low light. Therefore, by considering the exposed time under the low light which is larger than recovering time $\frac{1}{k_r}$, we could have an improvement on the average growth rate at the surface in the high/low light regime. Naturally, the best duty cycle η is investigated in this case. Assuming T large enough and we have the approximation

$$\bar{\mu}^T(y) = \mu_S^\eta(y). \quad (25)$$

Then we can state the next theorem.

Theorem 3.3. *For large T , choosing $I_{\max} > I_{\min} > I_c$, at the top of the bioreactor, there exists $\eta \in (0, 1)$ which maximizes the difference between the average growth rate in the high/low-flashing light regime, leading to a T-average growth rate larger than the one in continuous light regime.*

Proof. Setting $y = 0$. In the limit case of the large- T model, we approximate the average growth rate with (25). The optimum η_{opt} is defined as

$$\eta_{\text{opt}} := \operatorname{argmax}_{\eta \in (0,1)} \eta \mu_S(I_{\max}) + (1 - \eta) \mu_S(I_{\min}) - \mu_S(I_\eta)$$

which solution is such that

$$\frac{d}{dI} \mu_S(I_{\eta_{\text{opt}}}) = \frac{\mu_S(I_{\max}) - \mu_S(I_{\min})}{I_{\max} - I_{\min}} \quad (26)$$

and the existence is ensured by the mean value theorem. \square

This optimal η is actually the one which is capable of achieving the maximal difference between $\bar{\mu}^T(0)$ and $\mu_S(I_\eta)$. Moreover, (26) can be rewritten as

$$0 = \left[1 + \tau \sigma I_{\eta_{\text{opt}}} + \frac{k_d}{k_r} \tau (\sigma I_{\eta_{\text{opt}}})^2 \right]^2 \frac{\mu_S(I_{\max}) - \mu_S(I_{\min})}{K \sigma (I_{\max} - I_{\min})} + \frac{k_d}{k_r} \tau (\sigma I_{\eta_{\text{opt}}})^2 - 1.$$

Recall that $I_{\eta_{\text{opt}}} = \eta_{\text{opt}} I_{\max} + (1 - \eta_{\text{opt}}) I_{\min}$ where η_{opt} is the unknown optimal duty cycle.

4 Analysis of the Small-T model

In this section we present the value of the T -average growth rate using the Small-T model, meaning that $T < \tau$. Recall that τ is the time during which one photon is processed in the PSU, thus T is in the order of milliseconds. We prove that the average growth rate, in the limit, corresponds to $\mu_S(I_\eta)$, i.e., the microalgae only perceives the average of the light in this case. We then provide an analysis in the flashing light regime and define the optimal local optical depth.

4.1 Average growth rate

Recall that, by definition (12), the T -average growth rate can be computed by $\bar{\mu}^T = \frac{1}{T} \int_0^T K \sigma I A dt = K \sigma \bar{I} A$. Then $\bar{\mu}^T$ is computed by

$$\bar{\mu}^T(y) = \frac{K \sigma k_r I_M(y) (1 + \xi_1(y) \xi_2(y, T))}{k_r + k_r \tau \sigma I_M(y) + k_d \tau (\sigma I_M(y))^2 + k_d \sigma I_M(y) \xi_1(y) \xi_2(y, T)},$$

where

$$\begin{aligned} \xi_1(y) &= \frac{\sigma (I_H(y) - I_L(y))^2 \eta (1 - \eta)}{\tau \beta_H(y) \beta_L(y)}, \\ \xi_2(y, T) &= \frac{(1 - e^{-\beta_H(y) \eta T})(1 - e^{-\beta_L(y) (1 - \eta) T})}{T(1 - e^{-\beta_H(y) \eta T - \beta_L(y) (1 - \eta) T})} \frac{\eta \beta_H(y) + (1 - \eta) \beta_L(y)}{\eta (1 - \eta) \beta_H(y) \beta_L(y)} - 1, \end{aligned}$$

$\beta_H(y) := \beta(I_H(y))$ and $\beta_L(y) := \beta(I_L(y))$. The details of the computation are given in A.2. Since

$$\lim_{T \rightarrow 0} \frac{(1 - e^{-\beta_H(y)\eta T})(1 - e^{-\beta_L(y)(1-\eta)T})}{T(1 - e^{-\beta_H(y)\eta T - \beta_L(y)(1-\eta)T})} = \frac{\eta(1-\eta)\beta_H(y)\beta_L(y)}{\beta_H(y) + \beta_L(y)},$$

one has $\lim_{T \rightarrow 0} \xi_2(y, T) = 0$. This leads to the following result.

Theorem 4.1. *For rapid light alternation, one has for every local optical depth $y > 0$ $\lim_{T \rightarrow 0} \bar{\mu}^T(y) = \mu_S(I_M(y))$.*

This theorem asserts that, in the limit, the growth rate of the high/low-flashing light is the same as the growth rate at steady state of A by considering the light intensity I_η . In this case, the algae perceives the average light intensity for growing and there is no possible gain in growth rate compared to continuous light.

4.2 Small-T flashing light

Flashing light corresponds to the particular case of the high/low-flashing light when $I_{\min} = 0$. Based on our previous analysis, we present the local optical depth at which the algae culture perceives the optimal light intensity for growing.

Assume that the approximation $\bar{\mu}^T(y) \sim \mu_S(I_\eta(y))$ holds. By Theorem 4.1, the light perceived by the algae at local optical depth y is $I_\eta(y) = \eta I_{\max} e^{-y}$. In this case, we can give an expression for the local optical depth at which the algae culture perceives the optimal light. This expression depends on the duty cycle η which, in practice, can be settled and then, we can choose the local optical depth in a certain range of values. We define *optimal local optical depth* as the local optical depth in which the average growth rate achieves the maximum of the growth rate.

Lemma 4.1. *Considering flashing light, let I_{\max} the maximum light intensity provided at the top of the bioreactor, η the duty cycle and σ, k_d, k_r, τ the parameters of the Han model. The optimal local optical depth is given by*

$$y_{opt} = \ln \left(I_{\max} \sigma \sqrt{\frac{k_d}{k_r}} \tau \eta \right) \quad (27)$$

Proof. The growth rate, considering flashing light and the limit case of the small-T model correspond to

$$\bar{\mu}^T(y) = \mu_S(\eta I_{\max} e^{-y}) = \mu_S(I_{\max} e^{-(y - \ln(\eta))}).$$

Matching the value of the optimal light of the function μ_S given by (7) and the growth rate calculated above, we obtain the equality

$$I_{\max} e^{-(y_{opt} - \ln \eta)} = \frac{1}{\sigma \sqrt{\frac{k_d}{k_r}} \tau}$$

and isolating y_{opt} we get the value (27). □

As η tends to zero, y_{opt} can take negative values. If y_{opt} take a negative value, the algae culture does not perceive the optimal light, meaning that all the culture is under a photo-limited condition. Hence, the election of the duty cycle η affects the productivity. For including the optimal light into the culture, we have to consider the inequality

$$\eta \geq \frac{1}{I_{\text{max}} \sigma \sqrt{\frac{k_d}{k_r} \tau}}.$$

Using the definition of I_{opt} , this is equivalent to the condition:

$$\eta \geq \frac{I_{\text{opt}}}{I_{\text{max}}}.$$

In conclusion, for every value of η in the range of $[I_{\text{opt}}/I_{\text{max}}, 1)$ the optimal light is perceived in the culture. By setting $\eta = I_{\text{opt}}/I_{\text{max}}$, the optimal light is then perceived at the top of the culture.

5 Junction between simplified models and the exact growth rate

We analyzed the large and the small- T model, then gave the limit of the T -averaged growth rate in Theorem 3.1 and Theorem 4.1 when $T \rightarrow +\infty$ and $T \rightarrow 0$ respectively. Meanwhile, we evaluated the T -average growth rate without considering the simplified models given in (14) named as the asymptotic exact growth rate. In this section, we show that the limits of (14) are the same as the results in Theorem 3.1 and Theorem 4.1.

Proposition 5.1. *The limit of the asymptotic exact growth rate coincides with the limit of Theorem 3.1 and Theorem 4.1 when $T \rightarrow +\infty$ and $T \rightarrow 0$ respectively.*

Proof. Let us first prove that when $T \rightarrow +\infty$, then $\bar{\mu}^T$ given by (14) converges to μ_S^η . The eigenvalues of the matrices M_H and M_L defined in (16)-(17) are positive (see Appendix A.4) and then, the exponential matrices

$$e^{-\eta T M_H(y)} \quad \text{and} \quad e^{-(1-\eta) T M_L(y)}$$

converges to the zero matrix as $T \rightarrow +\infty$ for every local optical depth y . Thus,

$$\lim_{T \rightarrow +\infty} \Delta = [I_H(y) M_H^{-1}(y) - I_L(y) M_L^{-1}(y)] (M_H^{-1}(y) N_H(y) - M_L^{-1}(y) N_L(y)),$$

where Δ is defined in (15). From the exact growth rate given by (14), we can also conclude that

$$\lim_{T \rightarrow +\infty} \bar{\mu}^T(y) = \eta \mu_s(I_H(y)) + (1 - \eta) \mu_s(I_L(y)) = \mu_S^\eta(y),$$

which is the result of Theorem 3.1. Now, for the other case, we have that

$$\lim_{T \rightarrow 0} \frac{\Delta}{T} = \eta(1 - \eta)M_\eta^{-1}(y)(I_H(y)M_L(y) - I_L M_H(y)) \\ \cdot [(M_H^{-1}(y)N_H(y) - M_L^{-1}(y)N_L(y))],$$

where $M_\eta(y) = \eta M_H(y) + (1 - \eta)M_L(y)$. We can manipulate this term and get that

$$\lim_{T \rightarrow 0} \frac{\Delta}{T} = M_\eta^{-1} [-I_\eta N_\eta + \eta I_H M_\eta M_H^{-1} N_H + (1 - \eta)I_L M_\eta M_L^{-1} N_L] (y) \\ = -I_\eta(y)M_\eta^{-1}(y)N_\eta(y) + \eta I_H(y)M_H^{-1}(y)N_H(y) \\ + (1 - \eta)I_L(y)M_L^{-1}(y)N_L(y).$$

Replacing this limit in (14), we conclude that

$$\lim_{T \rightarrow 0} \bar{\mu}^T(y) = \mu_S(I_\eta(y)).$$

This corroborates the behavior of the mean of the growth rate in the large-T and small-T models. \square

6 Illustration with simulation studies

6.1 Parameter settings

The Han model parameters can be different depending on the authors and the studied species. Here we consider the values taken from [10, 14, 4] and recalled in Table 1. For these parameters, the critical value I_c defined in Lemma 3.1

	[10]	[14]	[4]	Unit
k_r	$6.8 \cdot 10^{-3}$	$4.8 \cdot 10^{-4}$	$2.6 \cdot 10^{-4}$	s^{-1}
k_d	$2.99 \cdot 10^{-4}$	$2.99 \cdot 10^{-4}$	$4.5 \cdot 10^{-8}$	-
τ	0.25	6.8493	5.6	s
σ	0.047	0.0029	3.3127	$m^2 \mu\text{mol}^{-1}$
K	$8.7 \cdot 10^{-6}$	$3.6467 \cdot 10^{-4}$		-
I_{opt}	202.93	166.94	9.69	$\mu\text{molm}^{-2}\text{s}^{-1}$
I_c	414.29	356.24	56.45	$\mu\text{molm}^{-2}\text{s}^{-1}$

Table 1: Parameter values for Han Model.

is computed together with the optimal light intensity I_{opt} and indicated in the table.

In this section, we provide some numerical tests to illustrate the two approximations and the exact solution of the Han system.

6.2 Quality of the approximated solution

First, we study the quality of the solutions given by the two approximations. More precisely, we compare the solution of the approximation (9) and (10) with the exact solutions of (3). In Figure 3 the dynamics of the states A and C are plotted for $T = 0.5$ s and $T = 3600$ s. 0.5 s is considered for the small-T model, in which the large-T model is not a good approximation. As for $T = 3600$ s we need to drop the assumption of C constant. In this case, the small-T model is far from the real solution. We observe that A and C change between two values, these values correspond to the steady states considering I_{\max} and I_{\min} .

As expected, one can see that (10) provides a good approximation for small period (in this case for $T = 0.5$ s) and (9) provides a good approximation for large period ($T = 3600$ s). On the other hand, the quality of the approximation depends on the time period T . We refer to hereafter a small period as $T < \tau$ and a large period as $T > 1/k_r$.

6.3 Connection between two approximations

Here we study the connection of the average growth rate between the one obtained from the large-T model (9), the small-T model (10) and the exact model (3). More precisely, we compute the T-average growth rate at surface $\bar{\mu}^T(0)$ by varying the period T from $T = 0.01$ s to $T = 36\,000$ s, and the results are shown in Figure 4. As $T \rightarrow 0$ the average growth rate converges to the value $\mu_S(I_\eta(0))$, whereas $\bar{\mu}^T \rightarrow \mu_\eta(0)$ when $T \rightarrow +\infty$. Moreover, the inequality (22) holds for $T \geq 174$ s as shown in Figure 4 (Top), which is not the case in Figure 4 (Bottom). Note that the time needed to process a photon (τ) and the time needed to recover a PSU ($1/k_r$) are also given in Figure 4.

Small Period For $T \in (0, \tau]$ Small-T model gives a good approximation. As the light change in a time scale lower than the time of processing photons, in this case, the algae perceives the average of the light (i.e, I_η at the top).

Transition Period For $T \in (\tau, \frac{1}{k_r})$ the small period started to fail, and consider the large-T model is more accurate.

Large Period For $T \in [\frac{1}{k_r}, \infty)$ Large-T model fits. If a high light is combined with a low light, then some damaged PSU can be recovered and we can get an improvement of the T-average growth rate compared to the continuous light regime.

6.4 Improvement of the growth rate

As shown in Theorem 3.2, that there exists an improvement the growth rate for some configurations exists. Figure 5 (Top left) presents a case where I_{\min} and I_{\max} are greater than I_c defined in (21). The improvement occurs when we consider the local optical depth equal to zero, this corresponds to the surface of the bioreactor. Moreover, we observe that for some values of y in Figure 5

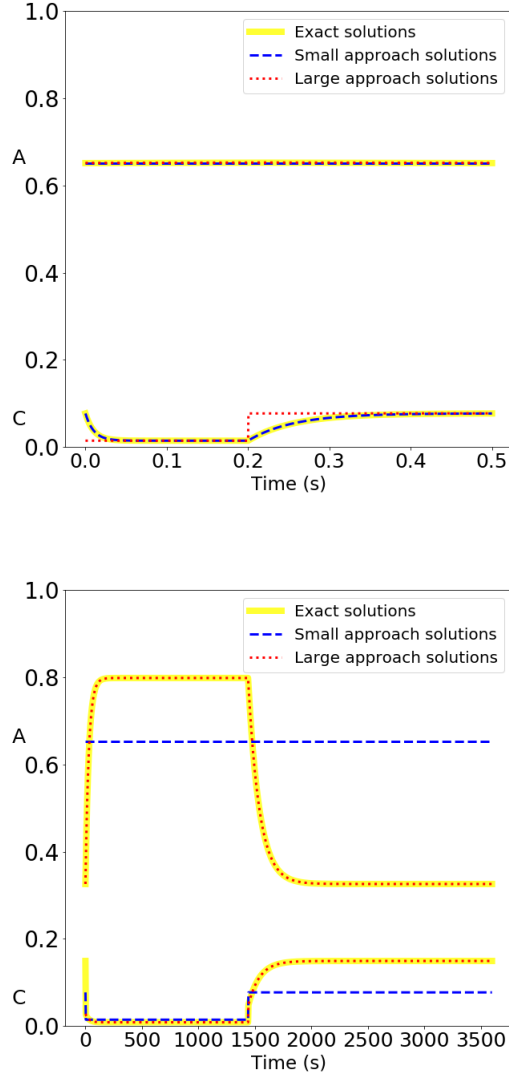


Figure 3: Comparison of the two modelling approximations with the exact solution of the states of the Han model. Top: $T = 0.5\text{s}$. Bottom: $T = 3600\text{s}$ The state A and C of the exact solutions (3) (continuous yellow line), of the small-T model (10) (segmented blue line) and of the large-T model (9) (segmented red line) are provided for $I_{\max} = 2000 \mu\text{mol m}^{-2} \text{s}^{-1}$, $I_{\min} = 300 \mu\text{mol m}^{-2} \text{s}^{-1}$, $\eta = 0.4$, $y = 0$ and four different values of T . The Han parameters is taken from [10] in Table 1.

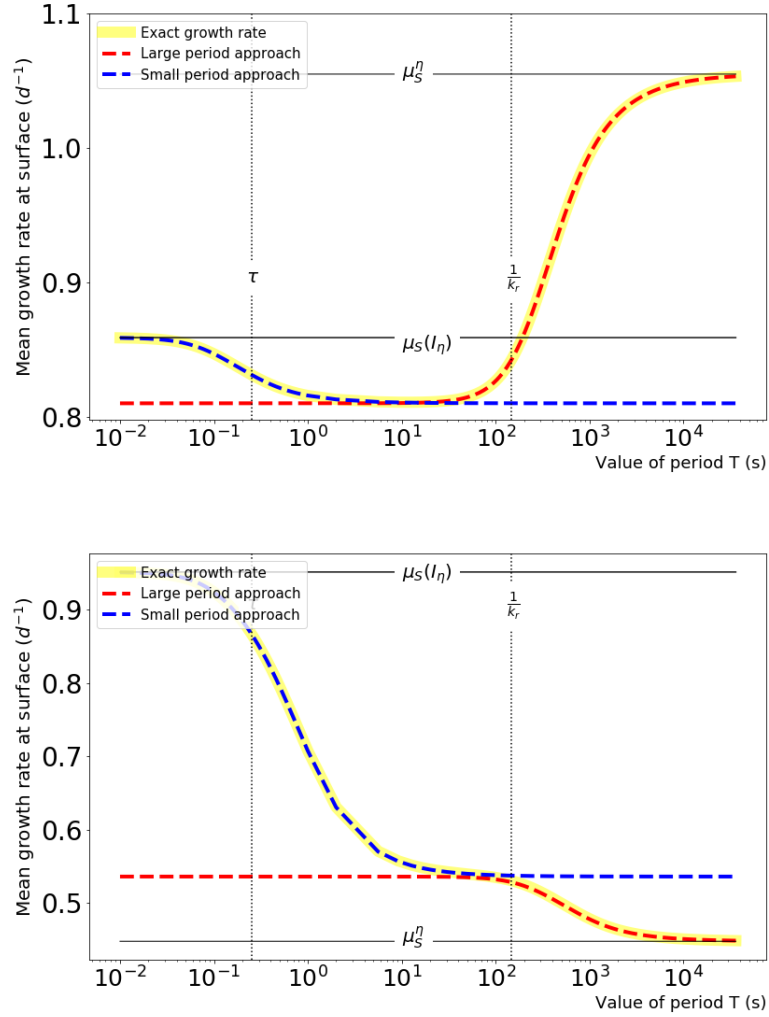


Figure 4: Average growth rate at surface $\bar{\mu}^T$ for the two simplified models. Top: $I_{\max} = 2000 \mu\text{molm}^{-2}\text{s}^{-1}$ and $I_{\min} = 350 \mu\text{molm}^{-2}\text{s}^{-1}$. Bottom: $I_{\max} = 2000 \mu\text{molm}^{-2}\text{s}^{-1}$ and $I_{\min} = 10 \mu\text{molm}^{-2}\text{s}^{-1}$. The period T is plotted in log scale. The Han parameters of [10] are considered with and $\eta = 0.5$.

(Bottom right), the T-average growth rate (black curve) has greater values than the PI-curve of the Han model (blue curve). This means that the improvement perceived at the surface can go further into the culture. Although, for greater values of y the T-average growth rate is smaller than the PI-curve.

Note that I_{\max} and I_{\min} are assumed to be larger than I_c in Theorem 3.2. Figure 5 (Top right) illustrates that this assumption can be relaxed especially for I_{\min} , meaning that I_{\min} can be lower than I_c and the T -average growth rate can still be greater than the growth rate in continuous light regime. Note that η should be chosen wisely to guarantee the improvement in this case, for instance here the value of $\mu_S(I_\eta)$ is lower than $\mu_S(I_\eta)$ for η_1 , whereas an improvement is obtained for η_2 .

On the other hand, some selections for I_{\min} can only give lower values of the T-average growth rate comparing with the PI-curve as we can see in Figure 5 (Bottom left). In this case, every selection of η provides a T -average growth rate lower than the PI-curve.

Figure 6 summarizes the behavior of the two simplified models. The exact growth rate is plotted in form of polygon. We can see that, for greater values of T , the exact growth rate coincides with the T-averaged growth rate of the large-T model. In this case, the hypotheses of Theorem 3.2 holds. The red polygon corresponds to the surface of the bioreactor ($y = 0$) where the curve of the T-average growth rate of the large-T model is greater to the T-average growth rate of the small-T model due to Theorem 3.2. Note that in the small-T model, the average growth rate matches $\mu_S(I_\eta)$, which corresponds to the continuous light regime with the same average light intensity. As y becomes larger, the growth rate in large approach is lower than the continuous light regime, as shown in the green and blue polygon.

7 Conclusions

We calculate the T-averaged growth rate in two simplified models: for large period T and small period T . In the small-T model, we can simply approximate the T-average growth rate by considering $\mu_S(\eta I_H + (1 - \eta)I_L)$, and for the large period T , we can approximate the T-average growth rate by considering $\eta\mu_S(I_H) + (1 - \eta)\mu_S(I_L)$. In terms of growth rate, there is no distinction between the constant regime with light I_η and switching the light quickly between I_H and I_L in the time ηT and $(1 - \eta)T$ respectively. In contrast, in the large-T model we can improve the growth rate if we consider a low local optical depth (for example, a very diluted environment). Although, for higher local optical depth, the growth rate is lower than the constant light regime. Our assumptions were simpler, and a mixing device was not considered, which can be a very interesting extension.

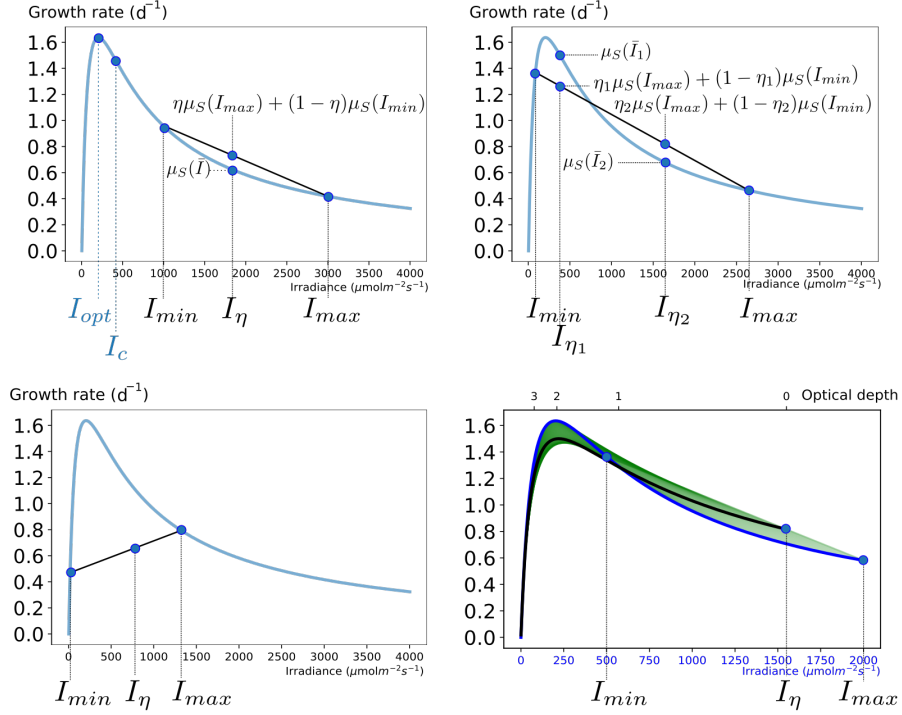


Figure 5: Different combinations of I_{max} , I_{min} and η . Top left: Diagram of the Theorem 3.2 in which I_{max} and I_{min} are greater than I_c . In this configuration, for each $\eta \in (0,1)$ we can find T for which $\bar{\mu}^T(0) > \mu_S(I_\eta)$. Top right: For $I_{min} < I_c$, $\bar{\mu}^T(0) > \mu_S(I_\eta)$ for η_2 and $\bar{\mu}^T(0) < \mu_S(I_\eta)$ for η_1 . Bottom left: For some configurations, it is impossible to find a fraction η and a period T for which $\bar{\mu}^T(0) > \mu_S(I_\eta)$. Bottom right: The green area represents all the possible values for μ_S^η if we vary the local optical depth and η for a given I_{max} and I_{min} . The black line correspond to the values of μ_S^η for a fixed value of η . The growth rate at steady state μ_S is plotted in blue using the parameters in [10].

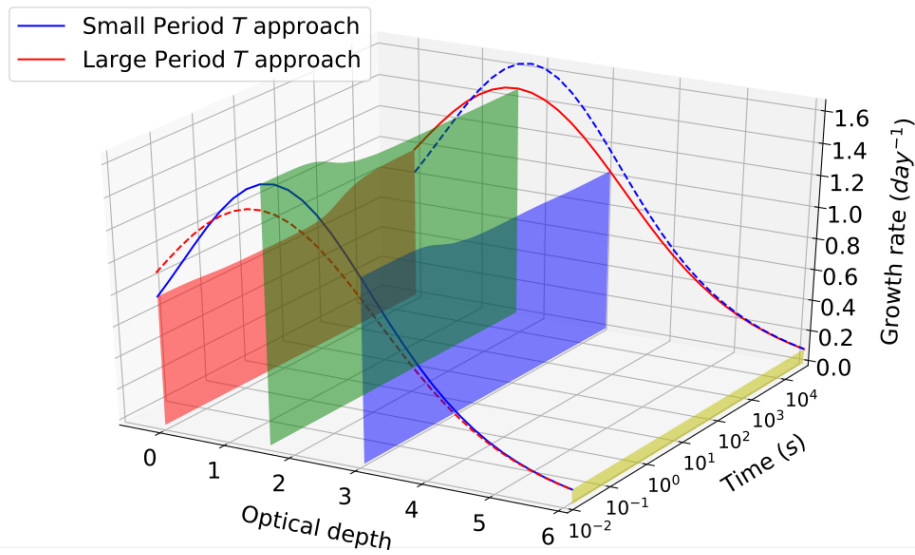


Figure 6: Average growth rate as a function of period T for four different local optical depths. We set $I_{\max} = 2000 \mu\text{mol m}^{-2} \text{s}^{-1}$, $I_{\min} = 500 \mu\text{mol m}^{-2} \text{s}^{-1}$, $\eta = 0.5$ and the Han parameters from [10]. The average growth rate in limit case for small- T model (blue curve) and for large- T model (red curve). For small values of the time we plotted in the continuous line the small- T model and analogous for the larger values of T .

References

- [1] S. Abu-Ghosh, D. Fixler, Z. Dubinsky, and D. Iluz. Continuous background light significantly increases flashing-light enhancement of photosynthesis and growth of microalgae. *Bioresource technology*, 187:144–148, 2015.
- [2] S. Abu-Ghosh, D. Fixler, Z. Dubinsky, and D. Iluz. Flashing light in microalgae biotechnology. *Bioresource Technology*, 203:357–363, 2016.
- [3] S. Abu-Ghosh, D. Fixler, Z. Dubinsky, A. Solovchenko, M. Zigman, Y. Yehoshua, and D. Iluz. Flashing light enhancement of photosynthesis and growth occurs when photochemistry and photoprotection are balanced in *dunaliella salina*. *European Journal of Phycology*, 50(4):469–480, 2015.
- [4] M. Baklouti, V. Faure, L. Pawlowski, and A. Sciandra. Investigation and sensitivity analysis of a mechanistic phytoplankton model implemented in a new modular numerical tool (Eco3M) dedicated to biogeochemical modelling. *Progress in Oceanography*, 71:34–58, 2006.
- [5] O. Bernard and L.-D. Lu. Optimal optical conditions for Microalgal production in photobioreactors. To appear in *Journal of Process Control*, 8 2021.
- [6] O. Bernard, F. Mairet, and B. Chachuat. Modelling of microalgae culture systems with applications to control and optimization. *Microalgae Biotechnology*, pages 59–87, 2015.
- [7] R.W. Brockett. *Finite dimensional linear systems*. SIAM, 2015.
- [8] D. Demory, C. Combe, P. Hartmann, A. Talec, E. Pruvost, R. Hamouda, F. Souillé, P.-O. Lamare, M.-O. Bristeau, J. Sainte-Marie, S. Rabouille, F. Mairet, A. Sciandra, and O. Bernard. How do microalgae perceive light in a high-rate pond? towards more realistic lagrangian experiments. *The Royal Society*, May 2018.
- [9] J.M. Fernández-Sevilla, C. Brindley, N. Jiménez-Ruiz, and F.G. Acién. A simple equation to quantify the effect of frequency of light/dark cycles on the photosynthetic response of microalgae under intermittent light. *Algal Research*, 35:479–487, 2018.
- [10] J. Grenier, F. Lopes, H. Bonnefond, and O. Bernard. Worldwide perspectives of rotating algal biofilm up-scaling. Submitted paper, 2020.
- [11] B.-P. Han. A mechanistic model of algal photoinhibition induced by photo-damage to photosystem-ii. *Journal of Theoretical Biology*, 214(4):519–527, 2002.
- [12] H.K. Khalil. *Nonlinear Systems*. Pearson Education. Prentice Hall, 2002.

- [13] M. Kumar, Y. Sun, R. Rathour, A. Pandey, I.S. Thakur, and D.C.W. Tsang. Algae as potential feedstock for the production of biofuels and value-added products: Opportunities and challenges. *Science of The Total Environment*, 716:137116, 2020.
- [14] P.-O. Lamare, N. Aguilon, J. Sainte-Marie, J. Grenier, H. Bonnefond, and O. Bernard. Gradient-based optimization of a rotating algal biofilm process. *Automatica*, 105:80–88, 2019.
- [15] J.J. Milledge. Commercial application of microalgae other than as biofuels: a brief review. *Reviews in Environmental Science and Bio/Technology*, 10(1):31–41, 2011.
- [16] J.A. Raven. The cost of photoinhibition. *Physiologia plantarum*, 142(1):87–104, 2011.
- [17] J.A. Sanders, F. Verhulst, and J. Murdock. *Averaging Methods in Nonlinear Dynamical Systems*. Applied Mathematical Sciences. Springer-Verlag New York, 2 edition, 2007.
- [18] P.S.C. Schulze, C. Brindley, J.M. Fernández, R. Rautenberger, H. Pereira, R.H. Wijffels, and V. Kiron. Flashing light does not improve photosynthetic performance and growth of green microalgae. *Bioresource Technology Reports*, 9:100367, 2020.
- [19] D. Stramski, A. Sciandra, and H. Claustre. Effects of temperature, nitrogen, and light limitation on the optical properties of the marine diatom *Thalassiosira pseudonana*. *Limnology and Oceanography*, 47(2):392–403, 2002.

A Analytical Computations

A.1 Large period T

For large period case, the evolution system (3) can be approximated by (9) which can be solved explicitly for a constant light intensity I as

$$C(y, t) = \frac{\alpha(I(y))}{\alpha(I(y)) + k_r} (1 - e^{-(\alpha(I(y)) + k_r)t}) + e^{-(\alpha(I(y)) + k_r)t} C(y, 0), \quad t \in (0, T).$$

Moreover, the system is assumed to be periodic (i.e. $C(y, 0) = C(y, T)$). For the constant light regime $I_M(y)$, one has $C(y, t) = \frac{\alpha(I_M(y))}{\alpha(I_M(y)) + k_r}$, $\forall t \in [0, T]$. Using (18), the T-average growth rate is given by $(1 - C)\gamma(I_M(y)) = \frac{K\sigma I_M(y)}{1 + \tau\sigma I_M(y) + \frac{k_d}{k_r}\tau(\sigma I_M(y))^2} = \mu_S(I_M(y))$. For the high/low light regime, one has

$$C(y, t) = \begin{cases} \frac{\alpha_H(y)}{\alpha_H(y) + k_r} (1 - e^{-(\alpha_H(y) + k_r)t}) + e^{-(\alpha_H(y) + k_r)t} C(y, 0), & t \in (0, \eta T) \\ \frac{\alpha_L(y)}{\alpha_L(y) + k_r} (1 - e^{-(\alpha_L(y) + k_r)(t - \eta T)}) + e^{-(\alpha_L(y) + k_r)(t - \eta T)} C(y, \eta T), & t \in (\eta T, T) \end{cases}$$

Using the periodic border condition of C , one has

$$C(y, 0) = \frac{\frac{\alpha_L(y)}{\alpha_L(y)+k_r} \left(1 - e^{-(\alpha_L(y)+k_r)T(1-\eta)}\right) + e^{-(\alpha_L(y)+k_r)T(1-\eta)} \frac{\alpha_H(y)}{\alpha_H(y)+k_r} \left(1 - e^{-(\alpha_H(y)+k_r)T\eta}\right)}{1 - e^{-(\alpha_L(y)+k_r)T(1-\eta)} - (\alpha_H(y)+k_r)T\eta}.$$

For a given local optical depth y , the T-average growth rate is given by

$$\begin{aligned} \bar{\mu}^T(y) &= \frac{1}{T} \left(\int_0^{\eta T} \mu(y, t) dt + \int_{\eta T}^T \mu(y, t) dt \right) \\ &= \eta \frac{\gamma_H(y) k_r}{\alpha_H(y) + k_r} + (1 - \eta) \frac{\gamma_L(y) k_r}{\alpha_L(y) + k_r} \\ &\quad + \frac{\gamma_H(y)}{T(\alpha_H(y) + k_r)} \left(\frac{\alpha_H(y)}{\alpha_H(y) + k_r} - C(y, 0) \right) \left(1 - e^{-(\alpha_H(y)+k_r)T\eta} \right) \\ &\quad + \frac{\gamma_L(y)}{T(\alpha_L(y) + k_r)} \left(\frac{\alpha_L(y)}{\alpha_L(y) + k_r} - C(y, T\eta) \right) \left(1 - e^{-(\alpha_L(y)+k_r)T(1-\eta)} \right) \\ &= \eta \mu_S(I_H(y)) + (1 - \eta) \mu_S(I_L(y)) + \frac{\zeta_1(y, \eta, T) \zeta_2(y)}{T k_r}, \end{aligned}$$

where $\gamma_H(y) := \gamma(I_H(y))$ and $\gamma_L(y) := \gamma(I_L(y))$.

A.2 Small period T

For small period case, the dynamics of C is negligible (i.e. C is a constant). Integrating (3) from 0 to T gives

$$0 = \int_0^T \dot{C} dt = -k_r T C - k_d \sigma C \int_0^T I dt + k_d \sigma \int_0^T I dt - k_d \sigma \int_0^T I A dt.$$

Let us denote by $\bar{I} := \frac{1}{T} \int_0^T I dt$ and by $\overline{IA} := \frac{1}{T} \int_0^T I A dt$, then one finds the constant value for C as

$$C = \frac{k_d \sigma (\bar{I} - \overline{IA})}{k_d \sigma \bar{I} + k_r}. \quad (28)$$

For high/low light regime, one has

$$A(y, t) = \begin{cases} e^{-\beta_H(y)t} A(0) + \frac{1-C}{\tau \beta_H(y)} (1 - e^{-\beta_H(y)t}), & t \in [0, \eta T], \\ e^{-\beta_L(y)(t-\eta T)} A(\eta T) + \frac{1-C}{\tau \beta_L(y)} (1 - e^{-\beta_L(y)(t-\eta T)}), & t \in [\eta T, T]. \end{cases}$$

The periodicity on A gives

$$A(y, 0) = \frac{e^{-\beta_L(y)(1-\eta)T} \frac{1-C}{\tau \beta_H(y)} (1 - e^{-\beta_H(y)\eta T}) + \frac{1-C}{\tau \beta_L(y)} (1 - e^{-\beta_L(y)(1-\eta)T})}{1 - e^{-\beta_L(y)(1-\eta)T - \beta_H(y)\eta T}}. \quad (29)$$

On the other hand, the average of IA can be computed by

$$\begin{aligned}
T\overline{IA} &= \int_0^{\eta T} I_H(y)A(y, t)dt + \int_{\eta T}^T I_L(y)A(y, t)dt \\
&= A(y, 0)I_H(y)\frac{1 - e^{-\beta_H(y)\eta T}}{\beta_H(y)} + I_H(y)\frac{1 - C}{\tau\beta_H(y)}\left(\eta T - \frac{1 - e^{-\beta_H(y)\eta T}}{\beta_H(y)}\right) \\
&\quad + A(y, \eta T)I_L(y)\frac{1 - e^{-\beta_L(y)(1-\eta)T}}{\beta_L(y)} + I_L(y)\frac{1 - C}{\tau\beta_L(y)}\left((1 - \eta)T - \frac{1 - e^{-\beta_L(y)(1-\eta)T}}{\beta_L(y)}\right).
\end{aligned}$$

Using (29) and simplifying the latter, one finds

$$\begin{aligned}
T\overline{IA} &= \frac{1 - C}{\tau\beta_L^2(y)\beta_H^2(y)}\frac{(1 - e^{-(\sigma I_{\max} + \frac{1}{\tau})\eta T})(1 - e^{-(\sigma I_{\min} + \frac{1}{\tau})(1-\eta)T})}{1 - e^{-(\sigma I_{\max} + \frac{1}{\tau})\eta T - (\sigma I_{\min} + \frac{1}{\tau})(1-\eta)T}}(I_H(y)\beta_L(y) \\
&\quad - I_L(y)\beta_H(y))(\beta_H(y) - \beta_L(y)) + \frac{1 - C}{\tau\beta_H(y)\beta_L(y)}(I_L(y)\beta_L(y)\eta T \\
&\quad + I_H(y)\beta_H(y)(1 - \eta)T).
\end{aligned}$$

By using the definition of $I_H(y)$, $I_L(y)$, $\beta_H(y)$, $\beta_L(y)$ and replacing C by (28) in the previous equation, one has

$$T\overline{IA} = \frac{k_d\sigma\overline{IA} + k_r}{\tau\beta_H^2(y)\beta_L^2(y)(k_d\sigma I_\eta + k_r)}\left(\Delta(y, T)\frac{\sigma}{\tau}(I_{\max} - I_{\min})^2 + \left(\frac{I_\eta}{\tau} + \sigma I_{\max}I_{\min}\right)\beta_H(y)\beta_L(y)T\right),$$

where $\Delta(y, T) = \frac{(1 - e^{-(\sigma I_{\max} + \frac{1}{\tau})\eta T})(1 - e^{-(\sigma I_{\min} + \frac{1}{\tau})(1-\eta)T})}{1 - e^{-(\sigma I_{\max} + \frac{1}{\tau})\eta T - (\sigma I_{\min} + \frac{1}{\tau})(1-\eta)T}}$. In other words

$$\overline{IA} = \frac{k_r\left(\frac{\Delta(y, T)}{T\beta_H(y)\beta_L(y)}\frac{\sigma}{\tau}(I_{\max} - I_{\min})^2 + \frac{I_\eta}{\tau} + \sigma I_{\max}I_{\min}\right)}{\tau\beta_H(y)\beta_L(y)(k_d\sigma I_\eta + k_r) - k_d\sigma\left(\frac{\Delta(y, T)}{T\beta_H(y)\beta_L(y)}\frac{\sigma}{\tau}(I_{\max} - I_{\min})^2 + \frac{I_\eta}{\tau} + \sigma I_{\max}I_{\min}\right)}.$$

Finally, the T -average growth rate is given by

$$\bar{\mu}^T(y) = \frac{K\sigma k_r I_M(y)(1 + \xi_1(y)\xi_2(y, T))}{k_r + k_r\tau\sigma I_M(y) + k_d\tau(\sigma I_M(y))^2 + k_d\sigma I_M(y)\xi_1(y)\xi_2(y, T)}, \quad (30)$$

where

$$\begin{aligned}
\xi_1(y) &= \frac{\sigma(I_H(y) - I_L(y))^2\eta(1 - \eta)}{\tau\beta_H(y)\beta_L(y)}, \\
\xi_2(y, T) &= \frac{(1 - e^{-\beta_H(y)\eta T})(1 - e^{-\beta_L(y)(1-\eta)T})}{T(1 - e^{-\beta_H(y)\eta T - \beta_L(y)(1-\eta)T})} \frac{\eta\beta_H(y) + (1 - \eta)\beta_L(y)}{\eta(1 - \eta)\beta_H(y)\beta_L(y)} - 1.
\end{aligned}$$

A.3 Exact growth rate

We split equation (3) in the high/low-flashing light configuration

$$\begin{cases} \frac{d}{dt} \begin{pmatrix} A(y, t) \\ C(y, t) \end{pmatrix} = -M_H(y) \begin{pmatrix} A(y, t) \\ C(y, t) \end{pmatrix} + N_H(y), & \text{if } t < \eta T, \\ \frac{d}{dt} \begin{pmatrix} A(y, t) \\ C(y, t) \end{pmatrix} = -M_L(y) \begin{pmatrix} A(y, t) \\ C(y, t) \end{pmatrix} + N_L(y), & \text{if } t > \eta T. \end{cases}$$

Using the variation of parameters method, one can solve explicitly the previous system for the case $t < \eta T$

$$\begin{pmatrix} A(y, t) \\ C(y, t) \end{pmatrix} = (\text{Id} - e^{-tM_H(y)})M_H^{-1}(y)N_H(y) + e^{-tM_H(y)} \begin{pmatrix} A(y, 0) \\ C(y, 0) \end{pmatrix},$$

and for the case $t > \eta T$

$$\begin{pmatrix} A(y, t) \\ C(y, t) \end{pmatrix} = (\text{Id} - e^{-(t-\eta T)M_L(y)})M_L^{-1}(y)N_L(y) + e^{-(t-\eta T)M_L(y)} \begin{pmatrix} A(y, \eta T) \\ C(y, \eta T) \end{pmatrix},$$

where Id denotes the identity matrix in $\mathbb{R}^{2 \times 2}$. Imposing periodic conditions (i.e., $(A(y, 0), C(y, 0)) = (A(y, T), C(y, T))$), one can then compute the values of $(A(y, 0), C(y, 0))$ and the values of $(A(y, \eta T), C(y, \eta T))$

$$\begin{aligned} \begin{pmatrix} A(y, \eta T) \\ C(y, \eta T) \end{pmatrix} &= (\text{Id} - e^{-\eta TM_H(y)})M_H^{-1}(y)N_H(y) + e^{-\eta TM_H(y)} \begin{pmatrix} A(y, 0) \\ C(y, 0) \end{pmatrix}, \\ \begin{pmatrix} A(y, 0) \\ C(y, 0) \end{pmatrix} &= (\text{Id} - e^{-(1-\eta)TM_L(y)})M_L^{-1}(y)N_L(y) + e^{-(1-\eta)TM_L(y)} \begin{pmatrix} A(y, \eta T) \\ C(y, \eta T) \end{pmatrix}. \end{aligned}$$

Replacing one in another, we then have

$$\begin{aligned} \begin{pmatrix} A(y, \eta T) \\ C(y, \eta T) \end{pmatrix} &= (\text{Id} - e^{-\eta TM_H(y)} e^{-(1-\eta)TM_L(y)})^{-1} \\ &\cdot \left[(\text{Id} - e^{-\eta TM_H(y)})M_H^{-1}(y)N_H(y) \right. \\ &\quad \left. + e^{-\eta TM_H(y)} (\text{Id} - e^{-(1-\eta)TM_L(y)})M_L^{-1}(y)N_L(y) \right], \end{aligned} \tag{31}$$

$$\begin{aligned} \begin{pmatrix} A(y, 0) \\ C(y, 0) \end{pmatrix} &= (\text{Id} - e^{-(1-\eta)TM_L(y)} e^{-\eta TM_H(y)})^{-1} \\ &\cdot \left[(\text{Id} - e^{-(1-\eta)TM_L(y)})M_L^{-1}(y)N_L(y) \right. \\ &\quad \left. + e^{-(1-\eta)TM_L(y)} (\text{Id} - e^{-\eta TM_H(y)})M_H^{-1}(y)N_H(y) \right]. \end{aligned} \tag{32}$$

On the other hand, the T-average of the growth rate is given by calculating the following integral:

$$\begin{aligned}
\int_0^T I(y, t) \begin{pmatrix} A(y, t) \\ C(y, t) \end{pmatrix} dt &= I_H(y) \int_0^{\eta T} \begin{pmatrix} A(y, t) \\ C(y, t) \end{pmatrix} dt + I_L(y) \int_{\eta T}^T \begin{pmatrix} A(y, t) \\ C(y, t) \end{pmatrix} dt \\
&= \eta T I_H(y) M_H^{-1}(y) N_H(y) \\
&\quad - I_H(y) M_H^{-1}(y) \left(\text{Id} - e^{-\eta T M_H(y)} \right) \left[M_H^{-1}(y) N_H(y) - \begin{pmatrix} A(y, 0) \\ C(y, 0) \end{pmatrix} \right] \\
&\quad + I_L(y) (1 - \eta) T M_L^{-1}(y) N_L(y) \\
&\quad - I_L(y) M_L^{-1}(y) \left(\text{Id} - e^{-(1-\eta) T M_L(y)} \right) \left[M_L^{-1}(y) N_L(y) - \begin{pmatrix} A(y, \eta T) \\ C(y, \eta T) \end{pmatrix} \right].
\end{aligned}$$

Implementing then (31) and (32) into (33), one finds

$$\begin{aligned}
\int_0^T I(y, t) \begin{pmatrix} A(y, t) \\ C(y, t) \end{pmatrix} dt &= \eta T I_H(y) M_H^{-1}(y) N_H(y) \\
&\quad + (1 - \eta) T I_L(y) M_L^{-1}(y) N_L(y) + \Delta,
\end{aligned}$$

where

$$\begin{aligned}
\Delta &= \left[I_H(y) M_H^{-1}(y) \left(\text{Id} - e^{-\eta T M_H(y)} \right) \left(\text{Id} - e^{-(1-\eta) T M_L(y)} e^{-\eta T M_H(y)} \right)^{-1} \right. \\
&\quad \cdot \left. \left(\text{Id} - e^{-(1-\eta) T M_L(y)} - I_L(y) M_L^{-1}(y) \left(\text{Id} - e^{-(1-\eta) T M_L(y)} \right) \right) \right. \\
&\quad \cdot \left. \left(\text{Id} - e^{-\eta T M_H(y)} e^{-(1-\eta) T M_L(y)} \right)^{-1} \left(\text{Id} - e^{-\eta T M_H(y)} \right) \right] \\
&\quad \cdot \left(M_H^{-1}(y) N_H(y) - M_L^{-1}(y) N_L(y) \right).
\end{aligned}$$

The average growth rate $\frac{1}{T} \int_0^T K \sigma I A dt$ is proportional to the first coordinate of (A.3) multiplied by $\frac{K \sigma}{T}$. Denote by δ the first coordinate of Δ and using the following two identities

$$M_H^{-1}(y) N_H(y) = \begin{pmatrix} \frac{k_r}{\tau k_d (\sigma I_H(y))^2 + \tau k_r \sigma I_H(y) + k_r} \\ \frac{\tau k_d (\sigma I_H(y))^2}{\tau k_d (\sigma I_H(y))^2 + \tau k_r \sigma I_H(y) + k_r} \end{pmatrix}, \quad (33)$$

$$M_L^{-1}(y) N_L(y) = \begin{pmatrix} \frac{k_r}{\tau k_d (\sigma I_L(y))^2 + \tau k_r \sigma I_L(y) + k_r} \\ \frac{\tau k_d (\sigma I_L(y))^2}{\tau k_d (\sigma I_L(y))^2 + \tau k_r \sigma I_L(y) + k_r} \end{pmatrix}. \quad (34)$$

Then $\mu_S(I_H(y))$ (resp. $\mu_S(I_L(y))$) is the first coordinate of (33) (resp. of (34)) multiplied by $K \sigma$. Hence, the T-average of the growth rate is

$$\bar{\mu}^T(y) = \eta \mu_S(I_H(y)) + (1 - \eta) \mu_S(I_L(y)) - \frac{K \sigma}{T} \delta(y, T).$$

A.4 Eigenvalues of matrix M

We will condense the analysis of the eigenvalues of M_H and M_L in the matrix

$$M(I) = \begin{pmatrix} \sigma I + \frac{1}{\tau} & \frac{1}{\tau} \\ k_d \sigma I & k_d \sigma I + k_r \end{pmatrix}.$$

Denoting λ_1 and λ_2 the eigenvalues, then we have

$$\text{Tr}(M(I)) = \lambda_1 + \lambda_2 = \sigma I + \frac{1}{\tau} + k_d \sigma I + k_r, \quad (35)$$

$$\text{Det}(M(I)) = \lambda_1 \lambda_2 = k_d (\sigma I)^2 + k_r \sigma I + \frac{k_r}{\tau}. \quad (36)$$

From (36), λ_1 and λ_2 has the same sign, and since (35) holds, the two eigenvalues are positive.

B Proof of Lemma 3.1

The second derivative of the function μ_S is

$$\frac{d^2}{dI^2} \mu_S(I) = - \frac{2K\sigma \left[\tau\sigma + \frac{k_d}{k_r} \tau\sigma^2 I \left(3 - \frac{k_d}{k_r} \tau\sigma^2 I^2 \right) \right]}{\left(1 + \tau\sigma I + \frac{k_d}{k_r} \tau(\sigma I)^2 \right)^3},$$

and it is zero in the point I_c which satisfies

$$\left(\frac{k_d}{k_r} \tau \right)^2 \sigma^3 I_c^3 - 3 \frac{k_d}{k_r} \tau \sigma^2 - \tau \sigma = 0.$$

This is a depressed cubic equation that can be solved explicitly and its solution corresponds to (21).