SINGLE PHYTOPLANKTON SPECIES GROWTH WITH LIGHT AND ADVECTION IN A WATER COLUMN

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Abstract. We investigate a nonlocal reaction-diffusion-advection equation which models the growth of a single phytoplankton species in a water column where the species depends solely on light for its metabolism. We study the combined effect of death rate, sinking or buoyant coefficient, water column depth and vertical turbulent diffusion rate on the persistence of a single phytoplankton species. Under a general reproductive rate which is an increasing function of light intensity, we establish the existence of a critical death rate; i.e., the phytoplankton survives if and only if its death rate is less than the critical death rate. The critical death rate is a strictly monotone decreasing function of sinking or buoyant coefficient and water column depth, and it is also a strictly monotone decreasing function of turbulent diffusion rate for buoyant species. In contrast to critical death rate, critical sinking or buoyant velocity, critical water column depth and critical turbulent diffusion rate may or may not exist. For instance, it is shown that if the death rate is suitably small with respect to the water column depth, the phytoplankton can persist for any sinking or buoyant velocity; i.e., there is no critical sinking or buoyant velocity under such situation. We further show that critical water column depth, critical sinking or buoyant velocity and critical turbulent diffusion rate for buoyant species can exist for some intermediate range of phytoplankton death rates and, whenever they exist, are always unique. In strong contrast, we show that there may exist two critical turbulent diffusion rates for sinking species. The phytoplankton forms a thin layer at the surface of the water column for sufficiently large buoyant rate, and it forms a thin layer at the bottom of the water column for sufficiently large sinking rate. Precise characterizations of these thin layers are also given.

1. Introduction

Phytoplankton are microscopic plant-like organisms that drift in the water column of lakes and oceans. They grow abundantly in oceans and lakes around the world, and they are the foundation of the marine food chain. Nutrient and light are the essential resources for the growth of phytoplankton. In phytoplankton communities species compete for nutrient and light in three possible ways. At one extreme, in oligotrophic ecosystems with an ample supply of light, species compete for limiting nutrients [15, 17]. At other extreme, in eutrophic ecosystem with ample nutrient supply, species compete for light [8, 10]. In some aquatic ecosystems the species compete for both nutrients and light which are complementary resources for their growth [5, 6, 12, 14, 20]. In the water column the phytoplankton are not only diffusing by the water turbulence but also sinking or buoyant. Most of phytoplankton are heavier than water, they have tendency to sink. On the other hand, some species like some cyanobacteria, green algae, have a lower density than water and they will float and will be called buoyant [8]. In this article we shall restrict our attentions to study the growth of a single species in a water column in eutrophic ecosystem where the species depends solely on light for its metabolism. The model equation is a nonlocal reaction-diffusion-advection equation proposed by Huisman et al. in [8, 9]. We study the combined effect of death rate, vertical turbulent diffusion coefficient, advection (sinking or buoyant) coefficient and water column depth on the survival of the single species (bloom development). Our approach is

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different from that in [8]. Under a general reproductive rate which is an increasing function of light intensity, we completely determine the necessary and sufficient conditions for the survival of the phytoplankton species in terms of turbulent diffusion coefficient, advection coefficient, water column depth and death rate of the phytoplankton species.

The rest of the paper is organized as follows: In Section 2, we present the mathematical model proposed in [8, 9] and discuss some previous related works. In Section 3, we state our main results which exclusively focus on the steady states of the model. In Section 4 we establish the existence and uniqueness of positive steady states in terms of the death rate of the phytoplankton species. Sections 5, 6, and 7 are devoted to studying qualitative properties of critical death rate and to determining critical water column depth, critical sinking or buoyant coefficient and critical turbulent diffusion rate, respectively. In Section 8, for large advection coefficients we show that the limiting profile of the steady state solution is a δ-function. Section 9 is the discussion section, where we focus on qualitative properties of critical water column depth, critical advection coefficient and critical turbulent diffusion rate.

2. **The mathematical model and previous works**

In [8, 9], Huisman et al. proposed and analyzed the following reaction-diffusion-advection equation which describes the population dynamics of a single phytoplankton species in a water column:

$$P_t = DP_{xx} - vP_x + P\left[g(I(x,t)) - d\right], \quad 0 < x < L, \quad t > 0, \tag{2.1}$$

with zero flux boundary conditions at $x = 0$ and $x = L$

$$\begin{aligned} DP_x(0,t) - vP(0,t) = 0, \\ DP_x(L,t) - vP(L,t) = 0, \end{aligned} \tag{2.2}$$

and with the initial condition

$$P(x,0) = P_0(x), \quad 0 \le x \le L, \tag{2.3}$$

where $P = P(x,t)$ is the population density of the phytoplankton species; $D > 0$ is the vertical turbulent diffusion coefficient; v is the sinking velocity ($v > 0$) or the buoyant velocity ($v < 0$); $L > 0$ is the depth of the water column; $d > 0$ is the death rate; by Lambert-Beer law the light intensity I is given by

$$I = I(x,t) = I_0 \exp(-k_0 x - k_1 \int_0^x P(s,t)ds), \tag{2.4}$$

where I_0 is the incident light intensity; k_0 is the background turbidity, k_1 is the absorption coefficient of phytoplankton. $g(I)$ is the specific growth rate of phytoplankton as a function of light intensity $I(x,t)$. Here we assume all nutrients are in amply supply so that only the light intensity limits the growth rate. We assume that $g(I)$ satisfies

$$g(0) = 0, \quad g'(I) > 0 \text{ for } I > 0, \quad g(I) \ge aI^\gamma \text{ for } I \in [0, I_0], \tag{2.5}$$

where $a > 0$ and $\gamma > 0$. The simplest example is

$$g(I) = aI^\gamma, \ 0 < \gamma \le 1. \tag{2.6}$$

The typical examples for the reproduction rate saturating for high light intensities are function of Monod type

$$g(I) = \frac{mI}{h + I}. \tag{2.7}$$

Or alternatively by

$$g(I) = m\frac{1 - e^{-cI}}{c}. \tag{2.8}$$

The self-shading model (i.e., $k_0 = 0$) was studied by Shigesada and Okubo in [19]. The existence, uniqueness and the global stability of the steady state for the infinite long water column ($L = \infty$) have been established in [13, 19]. More recently, among other things it is shown in [16] that the self-shading model has a unique positive steady state, which is also stable, for any finite water column depth. In particular, this means that the self-shading model has no critical water column depth beyond which the phytoplankton can not persist. This is very different from the case of $k_0 > 0$, where the critical depth exists for some intermediate range of phytoplankton death rate. See the next and last sections for more detailed discussions on the critical depth.

For the case $k_0 > 0$, it is shown in [8] that the conditions for phytoplankton bloom development can be characterized by critical water column depth and some critical values of the vertical turbulent diffusion coefficient. In [8] the authors also investigated the phase transition from bloom to no bloom extensively by numerical simulations. They also analyzed in depth the phase transition curve for the case $g(I) = aI^\gamma,\ 0 < \gamma \le 1$, by means of reducing the equation to a Bessel equation. In [7] the authors study both single species and two species competing for light in eutrophic ecosystem with no advections, and the dynamics of single species growth is also completely analyzed in [7]. In this paper, we will use several critical rates to give a complete classification of the phase transition from bloom to no bloom for the general single phytoplankton species model (2.1)-(2.5).

3. Main results

Consider the equation

$$\begin{cases} P_t = DP_{xx} - vP_x + P\left[g(I(x,t)) - d\right], & 0 < x < L,\ t > 0, \\ DP_x(0,t) - vP(0,t) = DP_x(L,t) - vP(L,t) = 0, \end{cases} \tag{3.1}$$

where $D > 0$, $v \in (-\infty, \infty)$, $g(I)$ satisfies (2.5), with typical examples (2.6)-(2.8) and $I(x,t)$ takes the form (2.4).

Our first main result concerns the existence and uniqueness of positive steady states of (3.1) in terms of the death rate d. Let $\lambda_1(a)$ denote the principal eigenvalue of

$$\begin{cases} -D\varphi_{xx} + v\varphi_x + a(x)\varphi = \lambda\varphi, & 0 < x < L, \\ D\varphi_x(0) = v\varphi(0), \quad D\varphi_x(L) = v\varphi(L). \end{cases} \tag{3.2}$$

It is well known that $\lambda_1(a)$ is real and can be characterized as

$$\lambda_1(a) = \inf_{\psi \in H^1(0,L)} \frac{\int_0^L e^{(v/D)x}(D\psi_x^2 + a\psi^2)dx}{\int_0^L e^{(v/D)x}\psi^2 dx}, \tag{3.3}$$

where $H^1(0,L)$ is the closure of $C^1[0,L]$ under the norm

$$\|u\| = \left(\int_0^L u^2\, dx\right)^{1/2} + \left(\int_0^L u_x^2\, dx\right)^{1/2}.$$

For every $v \in (-\infty, +\infty)$, $L > 0$ and $D > 0$, set

$$d_*(v, L, D) := -\lambda_1(-g(I_0 e^{-k_0 x})).$$

It is easy to show that $d_*(v, L, D)$ is positive. Our following result shows that d_* is the critical death rate; i.e., the phytoplankton survives if and only if its death rate is less than d_*.

Theorem 1. *If* $0 < d < d_*(v, L, D)$*, then* (3.1) *has a unique positive steady state; If* $d \geq d_*(v, L, D)$*, then zero is the only non-negative steady state of* (3.1)*.*

A natural question is whether there also exist critical water column depth, critical sinking/buoyant velocity and critical turbulent diffusion rate. To address these issues, we need to understand the dependence of d_* on the parameters D, v, L. The following result shows that d_* is monotone deceasing in v.

Theorem 2. *For any* $D > 0$ *and* $L > 0$*,* $d_*(v, L, D)$ *is strictly monotone decreasing for* $v \in (-\infty, \infty)$*. Moreover,*

$$\lim_{v\to-\infty} d_*(v, L, D) = g(I_0), \quad \lim_{v\to\infty} d_*(v, L, D) = g(I_0 e^{-k_0 L}).$$

We apply Theorem 2 to study the existence of critical sinking/buoyant velocity. By Theorem 2, for every $d \in (g(I_0 e^{-k_0 L}), g(I_0))$, there exists a unique $v_* := v_*(d, L, D)$ such that $d = d_*(v_*, L, D)$. Moreover,

$$v_* = \begin{cases} > 0, & \text{if } g(I_0 e^{-k_0 L}) < d < d_*(0, L, D), \\ = 0, & \text{if } d = d_*(0, L, D), \\ < 0, & \text{if } d_*(0, L, D) < d < g(I_0). \end{cases}$$

As a consequence of Theorems 1 and 2 and the definition of v_*, we have

Theorem 3. *Given any* $D > 0$ *and* $L > 0$*.*

(a) *If* $0 < d < g(I_0 e^{-k_0 L})$*,* (3.1) *has a unique positive steady state, denoted as* $P(x)$*, for any* $v \in (-\infty, \infty)$*. Moreover,*

$$\int_0^L P(x)\,dx > \frac{1}{k_1} \ln \frac{I_0 e^{-k_0 L}}{g^{-1}(d)} > 0. \tag{3.4}$$

(b) *If* $d \in (g(I_0 e^{-k_0 L}), g(I_0))$*,* (3.1) *has a unique positive steady state for every* $v \in (-\infty, v_*)$*; if* $v > v_*$*, zero is the only non-negative steady state of* (3.1)*.*

(c) *If* $d > g(I_0)$*, zero is the only non-negative steady state of* (3.1) *for* $v \in (-\infty, \infty)$*.*

Theorem 3 implies that critical sinking/buoyant velocity may or may not exist, and is unique whenever it exists. If d is suitably small, the phytoplankton can always bloom for any sinking/buoyant velocity; i.e., there is no critical sinking/buoyant velocity for this case. Only when the death rate falls into some intermediate range, there exists a critical sinking/buoyant velocity v_* such that the phytoplankton can bloom if and only if the sinking/buoyant velocity is smaller than v_*. For large death rates, the phytoplankton simply can not bloom.

We now turn to the existence of critical water column depth. First, we study how d_* qualitatively depend on L.

Theorem 4. *For any* $D > 0$ *and* $v \in (-\infty, \infty)$*,* $d_*(v, L, D)$ *is strictly monotone decreasing for* $L \in (0, \infty)$*. Moreover,*

$$\lim_{L\to 0+} d_*(v, L, D) = g(I_0), \quad \lim_{L\to\infty} d_*(v, L, D) = d_\infty(v, D),$$

where $d_\infty(v, D)$ *is a non-negative monotone decreasing function of* $v \in (-\infty, \infty)$*, and there exists some* $v_0 > 0$ *such that* $d_\infty(v, D) > 0$ *for* $v < v_0$*.*

We now apply Theorem 4 to study the existence of critical water column depth. By Theorem 4, given any $v \in R^1$ and $D > 0$, for every $d \in (d_\infty(v, D), g(I_0))$, there exists a unique $L_* := L_*(d, v, D) > 0$ such that $d = d_*(v, L_*, D)$. As a consequence of Theorems 1 and 4 and the definition of L_*, we have

Theorem 5. *Given any $v \in (-\infty, \infty)$ and $D > 0$.*

(a) *If $0 < d < d_\infty(v, D)$,* (3.1) *has a unique positive steady state for any $L > 0$.*

(b) *If $d \in (d_\infty(v, D), g(I_0))$,* (3.1) *has a unique positive steady state for every $L \in (0, L_*)$; if $L > L_*$, zero is the only non-negative steady state.*

(c) *If $d > g(I_0)$, zero is the only non-negative steady state of* (3.1) *for any $L > 0$.*

Theorem 5 also implies that critical water column depth may or may not exist, and is unique whenever it exists. If d is suitably small, there may be no critical water column depth as the phytoplankton can bloom for any water column depth. For some intermediate range of death rates, there exists a critical water column depth L_* such that the phytoplankton can persist if and only if the water column depth is less than L_*. We do not know whether $d_\infty(v, D)$ is positive for every $v \in (-\infty, \infty)$ and $D > 0$ and it will be of interest to further understand $d_\infty(v, D)$.

Finally, we address the existence of critical turbulent diffusion coefficient. This case is much more subtle as the numerical simulations in [8] suggest that there may exist two critical turbulent diffusion coefficients for sinking species. Similar as before, we first study how the critical death rate d_* depends on turbulent diffusion coefficient D. It turns out that the sinking case ($v > 0$) is indeed more subtle than the buoyant case ($v < 0$):

Theorem 6. *For any $v \in (-\infty, \infty)$ and $L > 0$,*

$$\lim_{D\to\infty} d_*(v, L, D) = \frac{1}{L}\int_0^L g(I_0 e^{-k_0 x})\, dx;$$

(a) *For any $v \le 0$ and $L > 0$, $d_*(v, L, D)$ is strictly monotone decreasing for $D > 0$, and* $\lim_{D\to 0+} d_*(v, L, D) = g(I_0)$.

(b) *For any $v > 0$ and $L > 0$,* $\lim_{D\to 0+} d_*(v, L, D) = g(I_0 e^{-k_0 L})$; *Moreover, given any $L > 0$, there exists some $v_1 > 0$ such that for every $0 < v < v_1$,*

$$\sup_{0<D<\infty} d_*(v, L, D) > \lim_{D\to\infty} d_*(v, L, D) > \lim_{D\to 0+} d_*(v, L, D); \tag{3.5}$$

In particular, for $L > 0$ and $0 < v < v_1$, $d_*(v, L, D)$ is not monotone in D.

We do not know whether (3.5) holds for general $v > 0$ and $L > 0$. By Theorem 6, given any $v \le 0$ and $L > 0$, for every $d \in (\frac{1}{L}\int_0^L g(I_0 e^{-k_0 x}), g(I_0))$, there exists a unique $D_* := D_*(d, v, L) > 0$ such that $d = d_*(v, L, D_*)$. By Theorems 1 and 6 and the definition of D_*, we have

Theorem 7. *Given any $v \le 0$ and $L > 0$.*

(a) *If $0 < d < \frac{1}{L}\int_0^L g(I_0 e^{-k_0 x})$,* (3.1) *has a unique positive steady state for any $D > 0$.*

(b) *If $d \in (\frac{1}{L}\int_0^L g(I_0 e^{-k_0 x}), g(I_0))$,* (3.1) *has a unique positive steady state for every $D \in (0, D_*)$; if $D > D_*$, zero is the only non-negative steady state.*

(c) *If $d > g(I_0)$, zero is the only non-negative steady state of* (3.1).

Similar to other critical rates, critical turbulent diffusion rate depth may or may not exist for buoyant species and whenever it exists, it is unique. However, the story is quite different for sinking species. Let v_1 be as given in Theorem 6 such that (3.5) holds for $0 < v < v_1$. Set

$$\overline{d} = \sup_{0<D<\infty} d_*(v, D, L), \quad \underline{d} = \inf_{0<D<\infty} d_*(v, D, L).$$

By Theorem 6, we see that $\underline{d} \in (0, g(I_0 e^{-k_0 L})]$ and $\overline{d} > \frac{1}{L}\int_0^L g(I_0 e^{-k_0 x})$. The following result shows that, in strong contrast to buoyant species, there may exist two or more critical turbulent diffusion rate for sinking species:

Theorem 8. *Given $L > 0$ and $0 < v < v_1$.*

(a) *If $0 < d < \underline{d}$, (3.1) has a unique positive steady state for any $D > 0$.*

(b) *If $d \in (\frac{1}{L}\int_0^L g(I_0e^{-k_0x}), \overline{d})$, there exist $0 < D_{min} < \underline{D} \le \overline{D} < D_{max}$ such that (3.1) has no positive steady state for any $D \in (0, D_{min}) \cup (D_{max}, \infty)$, and (3.1) has a unique positive steady state for any $D \in (D_{min}, \underline{D}) \cup (\overline{D}, D_{max})$.*

(c) *If $d > \overline{d}$, zero is the only non-negative steady state of (3.1).*

From these results we can conclude that critical death rate always exists and is unique. In contrast, there are either zero or one critical water column depth, zero or one critical sinking/buoyant velocity, and zero or one critical turbulent diffusion rate for buoyant species. Interestingly, there may exist two critical turbulent diffusion rates for sinking species which was first shown numerically in [8]. These theoretical findings may shed some new insight into the combined effects of death rate, water column depth, sinking/buoyant velocity and turbulent diffusion rate in the persistence of single phytoplankton species.

The rest of this section concerns qualitative properties of the unique positive steady state $P(x; v)$ of (2.1)-(2.2) when the advection coefficient v varies, assuming that other parameters D, d, L, k_0, k_1 are all fixed. For the simplicity of notation and the clarity of the presentation, we perform the following scaling for the equation (2.1)-(2.2). Let

$$\begin{aligned} &\tilde{x} = \frac{x}{L},\ \tilde{t} = \frac{D}{L^2}t,\ \tilde{k}_0 = k_0L,\ \tilde{k}_1 = k_1L,\ \tilde{d} = \frac{L^2}{D}d,\ \tilde{v} = \frac{v}{D}L,\\ &\tilde{P}(\tilde{x},\tilde{t}) = P(x,t),\ \tilde{I}(\tilde{x},\tilde{t}) = I(x,t) = I_0e^{-\tilde{k}_0\tilde{x}}\exp(-\tilde{k}_1\int_0^{\tilde{x}}\tilde{P}(s,\tilde{t})ds),\\ &\tilde{g}(\tilde{I})(\tilde{x},\tilde{t}) = \frac{L^2}{D}g(I(x,t)). \end{aligned} \tag{3.6}$$

Then equation (2.1)-(2.2) becomes

$$\begin{cases} \tilde{P}_{\tilde{t}} = \tilde{P}_{\tilde{x}\tilde{x}} - \tilde{v}\tilde{P}_{\tilde{x}} + \left(\tilde{g}(\tilde{I}) - \tilde{d}\right)\tilde{P}, \quad 0 < \tilde{x} < 1,\\ \tilde{P}_{\tilde{x}}(0,\tilde{t}) - \tilde{v}\tilde{P}(0,\tilde{t}) = 0, \quad \tilde{P}_{\tilde{x}}(1,\tilde{t}) - \tilde{v}\tilde{P}(1,\tilde{t}) = 0. \end{cases} \tag{3.7}$$

If we drop the $\sim$ sign, equation (3.7) becomes

$$\begin{cases} P_t = P_{xx} - vP_x + (g(I) - d)P, \quad 0 < x < 1,\ t > 0,\\ P_x(0,t) - vP(0,t) = 0, \quad P_x(1,t) - vP(1,t) = 0, \end{cases} \tag{3.8}$$

where I is still given by (2.4).

Let $P(x; v)$ denote the unique positive steady state of (3.8). By Theorem 3, if $0 < d < g(I_0e^{-k_0})$, $P(x; v)$ exists for any $v \in (-\infty, \infty)$. The following result describes the asymptotic profiles of $P(x; v)$ for large positive v.

Theorem 9. *Suppose that $0 < d < g(I_0e^{-k_0})$.*

(a) *If $v \ge 2\sqrt{g(I_0) - d}$, then $P(x; v)$ is strictly increasing in $[0, 1]$;*

(b) *As $v \to \infty$, $P(x; v) \to 0$ uniformly in any compact subset of $[0, 1)$, $P(1; v)/v \to \kappa^*$, $P(\cdot; v) \to \kappa^*\delta(1)$, where $\kappa^* > 0$ is uniquely determined by*

$$\int_0^1 g(I_0e^{-k_0-k_1\kappa^*z})\,dz = d. \tag{3.9}$$

Moreover,

$$\lim_{v\to\infty}\left\|P(x; v) - P(1; v)e^{-v(1-x)}\right\|_{L^\infty(0,1)} = 0 \tag{3.10}$$

and

$$\lim_{v\to\infty}\left\|\frac{P(x;v)}{ve^{-v(1-x)}}-\kappa^*\right\|_{L^\infty(0,1)}=0. \tag{3.11}$$

Remark 3.1. *$\delta(1)$ denotes the Dirac measure at $x=1$, and $P(\cdot;v)\to\kappa^*\delta(1)$ as $v\to\infty$ means that for any continuous function f in $[0,1]$,*

$$\lim_{v\to\infty}\int_0^1 f(x)P(x;v)\,dx=\kappa^*f(1).$$

Similarly, the asymptotic profiles of $P(x;v)$ for large negative v can be characterized as follows:

Theorem 10. *Suppose that $0<d<g(I_0)$.*

(a) *If $v\le 0$, then $P(x;v)$ is strictly decreasing in $[0,1]$;*

(b) *As $v\to-\infty$, $P(x;v)\to 0$ uniformly in any compact subset of $(0,1]$, $P(0;v)/v\to\kappa_*$, $P(\cdot;v)\to-\kappa_*\delta(0)$, where $\kappa_*<0$ is uniquely determined by*

$$\int_0^1 g(I_0e^{k_1\kappa_*(1-z)})\,dz=d. \tag{3.12}$$

Moreover,

$$\lim_{v\to-\infty}\|P(x;v)-P(0;v)e^{vx}\|_{L^\infty(0,1)}=0 \tag{3.13}$$

and

$$\lim_{v\to-\infty}\left\|\frac{P(x;v)}{ve^{vx}}-\kappa_*\right\|_{L^\infty(0,1)}=0. \tag{3.14}$$

By Theorem 10, the buoyant species is always monotone decreasingly distributed in the water column, and the phytoplankton forms a thin layer at the surface of the water column when the buoyant coefficient is sufficiently large. On the other end, by Theorem 9, $P(x;v)$ is monotone increasing in the water column when the sinking velocity is suitably large, and the phytoplankton forms a thin layer at the bottom of the water column.

4. Proof of Theorem 1

Consider the steady state equation

$$\begin{cases} DP_{xx}-vP_x+P\,[g(I)-d]=0, & 0<x<L,\\ DP_x(0)-vP(0)=0, & DP_x(L)-vP(L)=0,\end{cases} \tag{4.1}$$

where

$$I=I(x)=I_0e^{-k_0x}\exp(-k_1\int_0^x P(s)ds). \tag{4.2}$$

The proof of Theorem 1 is similar to that of case $v=0$, which was studied in [7], with some modifications. For the sake of completeness we give the proof here in details.

Lemma 4.1. (4.1) *has no positive solution when $d\notin(0,d_*)$.*

Proof. We note that the first equation in (4.1) can be rewritten as

$$-DP_{xx}+vP_x+(-g(I))P=-dP. \tag{4.3}$$

If (d,P) is a positive solution of (4.1), from (4.2), (4.3) and the comparison principle of the principal eigenvalue,

$$-d=\lambda_1(-g(I(x)))>\lambda_1(-g(I_0e^{-k_0x}))=-d_*(v,L,D).$$

That is, $d < d_*$. Multiplying the first equation of (4.1) by $e^{-(v/D)x}$, integrating the result in $(0, L)$, and applying the boundary condition in (4.1), we obtain

$$\int_0^L e^{-(v/D)x} P[g(I) - d]\, dx = 0,$$

which implies that $d > 0$. Therefore, (4.1) has no positive solution when $d \notin (0, d_*)$. $\square$

Lemma 4.2. *Given any $\eta > 0$, there exists some positive constant $C(\eta)$ such that every positive solution P of* (4.1) *with $\eta < d < d_*$ satisfies $\|P\|_{L^\infty(0,L)} \le C(\eta)$.*

Proof. We argue by contradiction. If not, suppose that there exists a sequence $d_n \in (\eta, d_*)$, $n = 1, 2, ...,$ and positive solution P_n of (4.1) with $d = d_n$ such that $\|P_n\|_{L^\infty(0,L)} \to \infty$ as $n \to \infty$. Passing to a subsequence if necessary we may assume that $d_n \to d \in [\eta, d_*]$. Set $\tilde{P}_n = P_n / \|P_n\|_{L^\infty(0,L)}$. Then $\tilde{P}_n$ satisfies $\|\tilde{P}_n\|_{L^\infty} = 1$ and

$$\begin{cases} D\tilde{P}_{n,xx} - v\tilde{P}_{n,x} + \tilde{P}_n\,[g(I_n) - d_n] = 0, \quad 0 < x < L, \\ D\tilde{P}_{n,x}(0) - v\tilde{P}_n(0) = 0, \quad D\tilde{P}_{n,x}(L) - v\tilde{P}_n(L) = 0, \end{cases} \tag{4.4}$$

where

$$I_n(x) = I_0 e^{-k_0 x} \exp(-k_1 \int_0^x P_n(s)ds). \tag{4.5}$$

Integrating the first equation of (4.4) from 0 to x we have

$$D\tilde{P}_{n,x}(x) - v\tilde{P}(x) + \int_0^x \tilde{P}_n\,[g(I_n) - d_n] = 0.$$

As $g(I_n)$ and $\tilde{P}_n$ are uniformly bounded, $\tilde{P}_{n,x}$ is uniformly bounded. By (4.4), $\tilde{P}_{n,xx}$ is uniformly bounded. Passing to a sequence if necessary we may assume that $\tilde{P}_n \to \tilde{P}$ in $C^1[0, L]$, $\tilde{P} \ge 0$, $\|\tilde{P}\|_{L^\infty} = 1$. As $0 \le g(I_n) \le g(I_0)$ in $[0, L]$, we may assume that $g(I_n) \to q(x)$ weakly in $L^2(0, L)$ for some function q satisfying $0 \le q \le g(I_0)$. Hence, $\tilde{P}$ is a weak solution of

$$\begin{cases} D\tilde{P}_{xx} - v\tilde{P}_x + \tilde{P}\,[q(x) - d] = 0, \quad 0 < x < L, \\ D\tilde{P}_x(0) - v\tilde{P}(0) = 0, \quad D\tilde{P}_x(L) - v\tilde{P}(L) = 0. \end{cases} \tag{4.6}$$

As $\tilde{P} \ge 0$, $\tilde{P} \not\equiv 0$ and $q \in L^\infty(0, L)$, by the strong maximum principle we have $\tilde{P} > 0$ in $(0, L)$. As $\tilde{P}_n \to \tilde{P} > 0$ in $(0, L)$ and $\|P_n\|_{L^\infty(0,L)} \to \infty$,

$$I_n(x) = I_0 e^{-k_0 x} \exp(-k_1 \|P_n\|_{L^\infty([0,L])} \int_0^x \tilde{P}_n(s)ds) \to 0 \tag{4.7}$$

for every $x \in (0, L)$ as $n \to \infty$. This implies that $q \equiv 0$. Integrating (4.6) in $(0, L)$, we obtain $d = 0$, which is a contradiction. $\square$

Proof of Theorem 1. By a standard bifurcation argument of Crandall and Rabinowitz [3] and Rabinowitz [18], (4.1) has an unbounded connected branch of positive solutions, denote by $\Gamma = \{(d, P) \subset \mathbb{R}^1 \times C^1([0, 1])\}$, which bifurcations from the trivial branch $\{(d, 0)\}$ at $(d_*(v, L, D), 0)$. Since (4.1) has no positive solution when $d \notin (0, d_*)$ (Lemma 4.1) and all positive solutions of (4.1) are uniformly bounded when d is positive and bounded away from zero (Lemma 4.2), we see that Γ can only become unbounded as $d \to 0+$. As Γ is connected, (4.1) has at least one positive solution for every $d \in (0, d_*)$.

It remains to show the uniqueness. Let $U(x) = e^{-(v/D)x} P(x)$. Then (4.1) becomes

$$\begin{cases} DU_{xx} + vU_x + [g(I) - d]\, U = 0, \quad 0 < x < L, \\ U_x(0) = 0,\ U_x(L) = 0, \end{cases} \tag{4.8}$$

where

$$I = I(x) = I_0 e^{-k_0 x} \exp(-k_1 \int_0^x e^{(v/D)s} U(s) ds). \tag{4.9}$$

(4.8) can be rewritten as

$$\begin{cases} D(e^{(v/D)x} U_x)_x + [g(I) - d]\, U e^{(v/D)x} = 0, & 0 < x < L, \\ U_x(0) = 0,\ U_x(L) = 0. \end{cases} \tag{4.10}$$

The proof of the uniqueness of positive solution of (4.1) basically follows from the argument in [7] applying to (4.10). Suppose that (4.8) has two positive solutions $U_1 \not\equiv U_2$. If $U_1 \le U_2$ then we deduce

$$\begin{aligned} -d &= \lambda_1[-g(I_0 e^{-k_0 x} \exp(-k_1 \int_0^x e^{(v/D)s} U_1(s) ds))] \\ &< \lambda_1[-g(I_0 e^{-k_0 x} \exp(-k_1 \int_0^x e^{(v/D)s} U_2(s) ds))] = -d, \end{aligned}$$

a contradiction. Therefore $U_1 - U_2$ changes sign in $(0, L)$. We claim that $U_1(0) \neq U_2(0)$. Otherwise, for $i = 1, 2$, we denote $V_i(x) = \int_0^x U_i(s) e^{(v/D)s} ds$, $W_i(x) = U_i'(x) e^{(v/D)x}$, and find that (U_i, V_i, W_i) are solution of the initial value problem

$$\begin{cases} U' = W e^{-(v/D)x}, \\ V' = e^{(v/D)x} U, \\ DW' = -[g(I_0 e^{-k_0 x} \exp(-k_1 V)) - d] e^{(v/D)x} U, \\ (U(0), V(0), W(0)) = (U(0), 0, 0). \end{cases}$$

By the uniqueness of ODE, we conclude that $(U_1, V_1, W_1) = (U_2, V_2, W_2)$, a contradiction. Therefore $U_1(0) \neq U_2(0)$.

For definiteness we assume $U_1(0) < U_2(0)$. Since $U_1 - U_2$ changes sign in $(0, L)$, there exists $x_0 > 0$ such that $U_2(x) > U_1(x)$ in $[0, x_0)$, $U_1(x_0) = U_2(x_0)$, and $U_1'(x_0) \ge U_2'(x_0)$. From (4.10) we have

$$-D \int_0^{x_0} \left(U_1' e^{(v/D)x}\right)_x U_2 = \int_0^{x_0} \left[g\left(I_0 e^{-k_0 x} \exp(-k_1 \int_0^x e^{(v/D)s} U_1(s) ds) \right) - d \right] U_1 U_2 e^{(v/D)x}.$$

Using integration by parts, we deduce

$$\begin{aligned} & - D U_1'(x_0) e^{(v/D)x_0} U_2(x_0) + D \int_0^{x_0} e^{(v/D)x} U_1' U_2' dx \\ & = \int_0^{x_0} \left[g\left(I_0 e^{-k_0 x} \exp(-k_1 \int_0^x e^{(v/D)s} U_1(s) ds) \right) - d \right] U_1 U_2 e^{(v/D)x} dx. \end{aligned}$$

Similarly,

$$\begin{aligned} & - D U_2'(x_0) e^{(v/D)x_0} U_1(x_0) + D \int_0^{x_0} e^{(v/D)x} U_1' U_2' dx \\ & = \int_0^{x_0} \left[g\left(I_0 e^{-k_0 x} \exp(-k_1 \int_0^x e^{(v/D)s} U_2(s) ds) \right) - d \right] U_1 U_2 e^{(v/D)x} dx. \end{aligned}$$

Therefore

$$\begin{aligned} & D e^{(v/D)x_0} U_1(x_0) \left[U_2'(x_0) - U_1'(x_0) \right] \\ = & \int_0^{x_0} \left[g\left(I_0 e^{-k_0 x} \exp(-k_1 \int_0^x e^{\frac{v}{D}s} U_1(s)) \right) - g\left(I_0 e^{-k_0 x} \exp(-k_1 \int_0^x e^{\frac{v}{D}s} U_2(s)) \right) \right] U_1 U_2 e^{\frac{v}{D}x}. \end{aligned}$$

The right hand side of the above equality is positive while the left hand side is nonpositive, a contradiction. Thus we complete the proof of Theorem 1. □

5. Dependence of $d_*(v,L,D)$ on v: Proofs of Theorems 2 and 3

This section is devoted to proofs of Theorems 2 and 3.

Recall that $d_*(v,L,D)$ satisfies

$$\begin{cases} -D\varphi_{xx}+v\varphi_x-g(I_0e^{-k_0x})\varphi=-d_*(v,L,D)\varphi \quad \text{in } (0,L),\\ D\varphi_x(0)=v\varphi(0), \quad D\varphi_x(L)=v\varphi(L), \quad \varphi>0 \quad \text{in } (0,L). \end{cases} \tag{5.1}$$

Set $\psi=e^{-(v/D)x}\varphi$. Then, ψ satisfies

$$\begin{cases} -D\psi_{xx}-v\psi_x-g(I_0e^{-k_0x})\psi=-d_*(v,L,D)\psi \quad \text{in } (0,L),\\ \psi_x(0)=\psi_x(L)=0, \quad \psi>0 \quad \text{in } (0,L). \end{cases} \tag{5.2}$$

Lemma 5.1. *$\psi_x<0$ in $(0,L)$.*

Proof. Multiplying (5.2) by $e^{(v/D)x}$, we rewrite the resulting equation as

$$\begin{cases} -D(e^{(v/D)x}\psi_x)_x-e^{(v/D)x}g(I_0e^{-k_0x})\psi=-d_*(v,L,D)\psi e^{(v/D)x} \quad \text{in } (0,L),\\ \psi_x(0)=\psi_x(L)=0. \end{cases} \tag{5.3}$$

Integrating (5.3) in $(0,L)$, we have

$$\int_0^L e^{(v/D)x}\psi[g(I_0e^{-k_0x})-d_*]\,dx=0,$$

which implies that $g(I_0e^{-k_0x})-d_*$ changes sign in $(0,L)$. Since $g(I_0e^{-k_0x})$ is strictly decreasing in $(0,L)$, there exists a unique $x_0\in(0,L)$ such that $g(I_0e^{-k_0x})>d_*$ for $0<x<x_0$ and $g(I_0e^{-k_0x})<d_*$ for $x_0<x<L$. Hence, by (5.3) we see that $(e^{(v/D)x}\psi_x)_x<0$ for $0<x<x_0$ and $(e^{(v/D)x}\psi_x)_x>0$ for $x_0<x<L$, i.e., $e^{(v/D)x}\psi_x$ is strictly decreasing in $(0,x_0)$ and strictly increasing in (x_0,L). Since $\psi_x(0)=\psi_x(L)=0$, we have $\psi_x<0$ in $(0,L)$. □

Lemma 5.2. *$d_*(v,L,D)$ is strictly monotone decreasing in v.*

Proof. Recall that $d_*(v,L,D)$ satisfies

$$\begin{cases} D\psi_{xx}+v\psi_x+g(I_0e^{-k_0x})\psi=d_*(v,L,D)\psi \quad \text{in } (0,L),\\ \psi_x(0)=\psi_x(L)=0. \end{cases} \tag{5.4}$$

We normalize ψ such that $\int_0^L\psi^2=1$. It can be shown that d_* and ψ are smooth functions of v (see e.g., [1, 2]). For simplicity of the notation, we denote $\partial\psi/\partial v$ by ψ', etc. Differentiating (5.4) with respect to v, we have

$$\begin{cases} D\psi'_{xx}+v\psi'_x+\psi_x+g(I_0e^{-k_0x})\psi'=d'_*\psi+d_*\psi' \quad \text{in } (0,L),\\ \psi'_x(0)=\psi'_x(L)=0. \end{cases} \tag{5.5}$$

Multiplying (5.5) by $e^{(v/D)x}$, we rewrite the result as

$$D(e^{(v/D)x}\psi'_x)_x+e^{(v/D)x}\psi_x+e^{(v/D)x}g(I_0e^{-k_0x})\psi'=d'_*\psi e^{(v/D)x}+d_*\psi'e^{(v/D)x} \quad \text{in } (0,L). \tag{5.6}$$

Multiplying (5.6) by ψ and integrating the resulting equation in $(0,L)$, we have

$$\begin{aligned} &-D\int_0^L e^{(v/D)x}\psi_x\psi'_x+\int_0^L e^{(v/D)x}\psi\psi_x+\int_0^L e^{(v/D)x}\psi'\psi g(I_0e^{-k_0x})\\ &=d'_*\int_0^L\psi^2e^{(v/D)x}+d_*\int_0^L\psi\psi'e^{(v/D)x}. \end{aligned} \tag{5.7}$$

Multiplying (5.4) by $e^{(v/D)x}$, we write the result as

$$D(e^{(v/D)x}\psi_x)_x + e^{(v/D)x}g(I_0e^{-k_0x})\psi = d_*e^{(v/D)x}\psi. \tag{5.8}$$

Multiplying (5.8) by ψ' and integrating it in $(0, L)$, we have

$$-D\int_0^L e^{(v/D)x}\psi_x\psi'_x + \int_0^L e^{(v/D)x}\psi'\psi g(I_0e^{-k_0x}) = d_*\int_0^L \psi\psi' e^{(v/D)x}. \tag{5.9}$$

It follows from (5.7) and (5.9) that

$$d'_* = \frac{\int_0^L e^{(v/D)x}\psi\psi_x\,dx}{\int_0^L e^{(v/D)x}\psi^2}. \tag{5.10}$$

This together with Lemma 5.1 and the positivity of ψ imply that $d'_* < 0$. □

To study the asymptotic behavior of d_* for sufficiently large v (either positive or negative), we first recall the following result (Theorem 1, [4]):

Lemma 5.3. *Let $\lambda(v)$ denote the principal eigenvalue of*

$$\begin{cases} -\Delta\psi - v\nabla m\cdot\nabla\psi + c(x)\psi = \lambda\psi \quad \text{in } \Omega, \\ \nabla\psi\cdot n|_{\partial\Omega} = 0, \end{cases} \tag{5.11}$$

where Ω is a domain in R^N with smooth boundary $\partial\Omega$ and n is the outward unit normal vector on $\partial\Omega$. Suppose that $m \in C^2(\bar\Omega)$ and $c \in C(\bar\Omega)$, and all critical points of m are non-degenerate. Then

$$\lim_{v\to\infty}\lambda(v) = \min_{\mathcal{M}} c,$$

where $\mathcal{M}$ is the set of local maximum of $m(x)$.

Lemma 5.4. *We have*

$$\lim_{v\to\infty} d_*(v, L, D) = g(I_0e^{-k_0L}), \quad \lim_{v\to-\infty} d_*(v, L, D) = g(I_0).$$

Proof. Applying Lemma 5.3 with $\Omega = (0, L)$ and $m(x) = x$, we see that $\mathcal{M} = \{L\}$ and

$$\lim_{v\to\infty}(-d_*(v, L, D)) = \min_{\mathcal{M}}(-g(I_0e^{-k_0x})) = -g(I_0e^{-k_0L}).$$

Similarly, applying Lemma 5.3 with $\Omega = (0, L)$ and $m(x) = -x$, we see that $\mathcal{M} = \{0\}$ and

$$\lim_{v\to-\infty}(-d_*(v, L, D)) = \min_{\mathcal{M}}(-g(I_0e^{-k_0x})) = -g(I_0),$$

which completes the proof. □

Lemma 5.5. *Suppose that $0 < d < g(I_0e^{-k_0L})$. Then for any $v \in (-\infty, \infty)$,*

$$\int_0^L P(x; v)\,dx > \frac{1}{k_1}\ln\frac{I_0e^{-k_0L}}{g^{-1}(d)} > 0.$$

Proof. Integrate the equation of $P(x; v)$ in $(0, L)$, we have

$$\int_0^L P(x; v)\,[g(I(x)) - d]\,dx = 0.$$

Hence, $g(I(x)) - d$ changes sign in $(0, L)$. Since $I(x)$ is strictly decreasing, $g(I(x)) - d$ must be negative at $x = L$. That is,

$$g(I_0e^{-k_0L}e^{-k_1\int_0^L P(x;v)\,dx}) < d,$$

which is equivalent to

$$\int_0^L P(x; v)\,dx > \frac{1}{k_1}\ln\frac{I_0e^{-k_0L}}{g^{-1}(d)} > 0,$$

where the last inequality follows from $0 < d < g(I_0 e^{-k_0 L})$. □

Proofs of Theorems 2, 3. Theorem 2 follows from Lemmas 5.2 and 5.4. Theorem 3 follows from Theorems 1, 2 and Lemma 5.5. □

6. Dependence of $d_*(v, L, D)$ on L: Proofs of Theorems 4 and 5

In this section we investigate the dependence of d_* on L. First, we establish the monotonicity of d_* in L.

Lemma 6.1. *$d_*(v, L, D)$ is strictly monotone decreasing in L.*

Proof. Given any $0 < L_1 < L_2$, we show that $d_*(v, L_1, D) > d_*(v, L_2, D)$. For simplicity, we write $d_*(v, L_i, D)$ as d_i, and denote corresponding eigenfunctions $\psi(x; v, L_i, D)$ as ψ_i, $i = 1, 2$. Rewrite the equations of ψ_i as

$$\begin{cases} D(e^{(v/D)x}\psi_{i,x})_x + g(I_0 e^{-k_0 x})e^{(v/D)x}\psi_i = d_i \psi_i e^{(v/D)x} & \text{in } (0, L_i), \\ \psi_{i,x}(0) = \psi_{i,x}(L_i) = 0. \end{cases} \tag{6.1}$$

Multiplying the equation of ψ_1 by ψ_2, the equation of ψ_2 by ψ_1, and subtracting, we have

$$(d_1 - d_2)\psi_1\psi_2 e^{(v/D)x} = D\left[(e^{(v/D)x}\psi_{1,x})_x\psi_2 - (e^{(v/D)x}\psi_{2,x})_x\psi_1\right].$$

Integrating the above equation in $(0, L_1)$ and applying boundary conditions of ψ_1, ψ_2 at $x = 0$, we have

$$(d_1 - d_2)\int_0^{L_1} \psi_1\psi_2 e^{(v/D)x}\, dx = -De^{(v/D)L_1}\psi_{2,x}(L_1)\psi_1(L_1).$$

Since $\psi_i > 0$ for $i = 1, 2$ and $\psi_{2,x}(L_1) < 0$ (Lemma 5.1), we see that $d_1 > d_2$. □

The next two results concern the limiting behaviors of d_* for small and large L.

Lemma 6.2. $\lim_{L\to 0+} d_*(v, L, D) = g(I_0)$.

Proof. Set $x = Ly$ and $w(y) = \psi(x)$. Then w satisfies

$$\begin{cases} Dw_{yy} + vLw_y + L^2 g(I_0 e^{-k_0 L y})w = d_*(v, L, D)L^2 w & \text{in } (0, 1), \\ w_y(0) = w_y(1) = 0. \end{cases} \tag{6.2}$$

We normalize w such that $\max_{[0,1]} w = 1$. It is easy to show that as $L \to 0+$, passing to a subsequence if necessary, $w \to w_0$ in $C^2[0, 1]$, where w_0 satisfies $w_{0,yy} = 0$ in $(0, 1)$, $w_{0,y}(0) = w_{0,y}(1) = 0$, and $\max_{[0,1]} w_0 = 1$. Hence, $w_0 \equiv 1$; i.e., $w \to 1$ in $C^2[0, 1]$.

Multiplying (6.2) by $e^{(v/D)Ly}$, we can rewrite (6.2) as

$$\begin{cases} D\left(e^{(v/D)Ly}w_y\right)_y + L^2 e^{(v/D)Ly} g(I_0 e^{-k_0 L y})w = d_*(v, L, D)L^2 e^{(v/D)Ly} w & \text{in } (0, 1), \\ w_y(0) = w_y(1) = 0. \end{cases} \tag{6.3}$$

Integrating (6.3) in $(0, 1)$ and dividing the result by L^2, we have

$$\int_0^1 e^{(v/D)Ly} g(I_0 e^{-k_0 L y}) w\, dy = d_* \int_0^1 e^{(v/D)Ly} w\, dy. \tag{6.4}$$

By letting $L \to 0$ in (6.4) and applying $w \to 1$, we see that $d_* \to g(I_0)$ as $L \to 0+$. □

Lemma 6.3. $\lim_{L\to\infty} d_*(v, L, D) = d_\infty$*, where* $d_\infty := d_\infty(v, D) \geq 0$*, and is monotone decreasing function of* $v \in R^1$*. Moreover, there exists some* $v_0 > 0$ *such that* $d_\infty(v, D) > 0$ *for* $v < v_0$*.*

Proof. Since d_* is monotone decreasing in L and $d_* > 0$, we see that $\lim_{L\to\infty} d_*(v, L, D) = d_\infty(v, D)$ for some $d_\infty = d_\infty(v, D) \geq 0$. Since d_* is monotone decreasing in v, we see that d_∞ is also monotone decreasing in v. It remains to show that $d_\infty > 0$ for $v \in (-\infty, v_0)$ for some $v_0 > 0$. Recall that

$$
\begin{aligned}
-d_* &= \inf_{\varphi\in H^1((0,L))} \frac{\int_0^L e^{(v/D)x}\left[D\varphi_x^2 - g(I_0e^{-k_0x})\varphi^2\right]\,dx}{\int_0^L e^{(v/D)x}\varphi^2} \\
&\leq \inf_{\varphi\in H^1((0,L))} \frac{\int_0^L e^{(v/D)x}(D\varphi_x^2 - aI_0^\gamma e^{-k_0\gamma x}\varphi^2)\,dx}{\int_0^L e^{(v/D)x}\varphi^2},
\end{aligned}
$$

where the last inequality follows from assumption $g(I) \geq aI^\gamma$ for $I \in [0, I_0]$. Choose the test function $\varphi(x) = e^{-(v/D)x}$. By direct calculation,

$$
-d_* \leq \frac{v^2}{D} - \frac{aI_0^\gamma(v/D)}{k_0\gamma + v/D}\frac{1 - e^{-(v/D+k_0)L}}{1 - e^{-(v/D)L}}.
$$

By letting $L \to \infty$ in the above inequality, we have

$$
-d_\infty \leq \frac{v^2}{D} - \frac{aI_0^\gamma(v/D)}{k_0\gamma + v/D} < 0,
$$

where the last inequality holds provided that $v(k_0\gamma + v/D) < aI_0^\gamma$. Clearly, if

$$
v_0 := \min\{aI_0^\gamma/(2k_0\gamma), \sqrt{aI_0^\gamma D/2}\},
$$

then $d_\infty(v, D) > 0$ for $v < v_0$. □

Proofs of Theorems 4, and 5. Theorem 4 follows from Lemmas 6.1, 6.2 and 6.3; Theorem 5 follows from Theorems 1 and 4. □

7. Dependence of $d_*(v, L, D)$ on D: Proofs of Theorems 6, 7 and 8

In this section we investigate the dependence of d_* on D. The proof of the following result is similar to that of Lemma 5.2:

Lemma 7.1. *For any $v \leq 0$ and $L > 0$, $d_*(v, L, D)$ is strictly monotone decreasing in D.*

Proof. For simplicity of notation, we denote $\partial\psi/\partial D$ by ψ', etc, where ψ satisfies (5.4). Differentiate (5.4) with respect to D, we have

$$
\begin{cases} D\psi'_{xx} + \psi_{xx} + v\psi'_x + g(I_0e^{-k_0x})\psi' = d'_*\psi + d_*\psi' & \text{in } (0, L), \\ \psi'_x(0) = \psi'_x(L) = 0. \end{cases} \tag{7.1}
$$

Multiplying (7.1) by $e^{(v/D)x}\psi$ and integrating the resulting equation in $(0, L)$, we have

$$
\begin{aligned}
&- D\int_0^L e^{(v/D)x}\psi_x\psi'_x + \int_0^L e^{(v/D)x}\psi\psi_{xx} + \int_0^L e^{(v/D)x}\psi'\psi g(I_0e^{-k_0x}) \\
&= d'_*\int_0^L \psi^2 e^{(v/D)x} + d_*\int_0^L \psi\psi' e^{(v/D)x}.
\end{aligned} \tag{7.2}
$$

Similarly, multiplying (5.4) by $e^{(v/D)x}\psi'$ and integrating it in $(0, L)$, we have

$$
-D\int_0^L e^{(v/D)x}\psi_x\psi'_x + \int_0^L e^{(v/D)x}\psi'\psi g(I_0e^{-k_0x}) = d_*\int_0^L \psi\psi' e^{(v/D)x}. \tag{7.3}
$$

It follows from (7.2) and (7.3) that

$$d_*' = \frac{\int_0^L e^{(v/D)x}\psi\psi_{xx}}{\int_0^L e^{(v/D)x}\psi^2}. \tag{7.4}$$

By Lemma 5.1, $\psi_x < 0$ in $(0, L)$. Hence,

$$\int_0^L e^{(v/D)x}\psi\psi_{xx} = -\int_0^L \psi_x \left(e^{(v/D)x}\psi\right)_x = -\int_0^L e^{(v/D)x}[\psi_x^2 + (v/D)\psi\psi_x] < 0,$$

where the last inequality holds for $v \le 0$. Hence, $d_*' < 0$ for any $v \le 0$ and $D, L > 0$. □

Lemma 7.2. *Given any $v \in (-\infty, \infty)$ and $L > 0$,*

$$\lim_{D\to\infty} d_*(v, L, D) = \frac{1}{L}\int_0^L g(I_0 e^{-k_0 x})\, dx. \tag{7.5}$$

Proof. Recall that ψ satisfies (5.4). We normalize that ψ such that $\max_{[0,L]}\psi = 1$. By standard elliptic regularity and Sobolev embedding theorem, ψ is uniformly bounded in $C^2[0, L]$ for all $D \ge 1$. Therefore, passing to some sequence if necessary, we may assume that $\psi \to \Psi$ in C^1, where Ψ satisfies $\Psi_{xx} = 0$ in $[0, L]$, $\Psi_x(0) = \Psi_x(L) = 0$, and $\max_{[0,L]}\Psi = 1$. Therefore, $\Psi \equiv 1$; i.e., $\psi \to 1$ in $C^1[0, L]$. Integrating (5.4) in $[0, L]$, we have

$$D[\psi_x(L) - \psi_x(0)] + v[\psi(L) - \psi(0)] + \int_0^L g(I_0 e^{-k_0 x})\psi\, dx = d_* \int_0^L \psi.$$

Since $\psi_x(0) = \psi_x(L) = 0$ and $\psi \to 1$ as $D \to \infty$, by letting $D \to \infty$ in the above equation, we obtain (7.5). □

Lemma 7.3. *Suppose that $v \le 0$. Then*

$$\lim_{D\to 0+} d_*(v, L, D) = g(I_0).$$

Proof. Recall that

$$-d_* = \inf_{\psi\in H^1(0,L)} \frac{\int_0^L e^{(v/D)x}\left[D\psi_x^2 - g(I_0 e^{-k_0 x})\psi^2\right] dx}{\int_0^L e^{(v/D)x}\psi^2 dx}. \tag{7.6}$$

For $\epsilon \in (0, L/4)$, set

$$\psi(x) = \begin{cases} 1, & 0 \le x \le \epsilon, \\ 2 - \dfrac{x}{\epsilon}, & \epsilon \le x \le 2\epsilon, \\ 0, & 2\epsilon \le x \le L. \end{cases}$$

Hence,

$$\begin{aligned} -d_* &\le \frac{D\int_\epsilon^{2\epsilon} e^{(v/D)x}\psi_x^2}{\int_0^{2\epsilon} e^{(v/D)x}\psi^2} - \frac{\int_0^{2\epsilon} e^{(v/D)x} g(I_0 e^{-k_0 x})\psi^2}{\int_0^{2\epsilon} e^{(v/D)x}\psi^2} \\ &\le \frac{D}{\epsilon^2}\frac{e^{2v\epsilon/D} - e^{v\epsilon/D}}{e^{v\epsilon/D} - 1} - g(I_0 e^{-2k_0\epsilon}). \end{aligned}$$

By letting $D \to 0+$, as $v \le 0$, we have $\liminf_{D\to 0+} d_* \ge g(I_0 e^{-2k_0\epsilon})$. By letting $\epsilon \to 0$, we obtain $\liminf_{D\to 0+} d_* \ge g(I_0)$. As $d_* < g(I_0)$, we see that $\lim_{D\to 0+} d_* = g(I_0)$. □

Lemma 7.4. *Suppose that $v > 0$. Then*

$$\lim_{D\to 0+} d_*(v, L, D) = g(I_0 e^{-k_0 L}).$$

Proof. Recall that $d_*(v,L,D)$ satisfies

$$\begin{cases} D\varphi_{xx} - v\varphi_x + g(I_0e^{-k_0x})\varphi = d_*\varphi \quad \text{in } (0,L), \\ D\varphi_x(0) = v\varphi(0), \quad D\varphi_x(L) = v\varphi(L), \quad \varphi > 0 \quad \text{in } (0,L). \end{cases} \tag{7.7}$$

Set $w(x) = e^{-(v/D)\eta x}\varphi$, where η is some constant which will be chosen differently for different purposes. Then, w satisfies

$$\begin{cases} Dw_{xx} + v(2\eta-1)w_x + w\left[\dfrac{v^2}{D}\eta(\eta-1) + g(I_0e^{-k_0x}) - d_*\right] = 0 \quad \text{in } 0 < x < L, \\ Dw_x = v(1-\eta)w \quad \text{at } x = 0, L. \end{cases} \tag{7.8}$$

Set $\eta = 1 - C_1D/v^2$, where C_1 is some positive constant to be chosen later. Then w satisfies

$$\begin{cases} Dw_{xx} + v(1-\dfrac{2C_1D}{v^2})w_x + w[-C_1(1-\dfrac{C_1D}{v^2}) + g(I_0e^{-k_0x}) - d_*] = 0, \quad 0 < x < L, \\ w_x = (C_1/v)w \quad \text{at } x = 0, L. \end{cases} \tag{7.9}$$

Let $x^* \in [0,L]$ such that $w(x^*) = \max_{0\le x\le L} w(x)$. Since $w_x(0) > 0$, $x^* \neq 0$. If $x^* \in (0,L)$, $w_{xx}(x^*) \le 0$ and $w_x(x^*) = 0$. By (7.9) we have

$$-C_1(1 - C_1D/v^2) + g(I_0e^{-k_0x^*}) - d_* \ge 0,$$

which is impossible if we choose $C_1 = 2g(I_0)$ and $D < v^2/(4g(I_0))$. Therefore, $x^* = L$; i.e., $w(x) \le w(L)$ for every $x \in [0,L]$. Hence,

$$\frac{\varphi(x)}{\varphi(L)} \le e^{-\frac{v}{D}(1-\frac{C_1D}{v^2})(L-x)}.$$

Next, we choose $\eta = 1 + C_2D/v^2$, where $C_2 > 0$ is to be chosen later. By (7.8), w satisfies

$$\begin{cases} Dw_{xx} + v(1+\dfrac{2C_2D}{v^2})w_x + w[C_2(1+\dfrac{C_2D}{v^2}) + g(I_0e^{-k_0x}) - d_*] = 0, \quad 0 < x < L, \\ w_x = -(C_2/v)w \quad \text{at } x = 0, L. \end{cases} \tag{7.10}$$

Let $x_* \in [0,L]$ such that $w(x_*) = \min_{0\le x\le L} w(x)$. Since $w_x(0) < 0$, $x_* \neq 0$. If $x_* \in (0,L)$, $w_{xx}(x_*) \ge 0$ and $w_x(x_*) = 0$. By (7.10) we have

$$C_2(1 + C_2D/v^2) + g(I_0e^{-k_0x_*}) - d_* \le 0,$$

which implies that $d_* > C_2$. Choose $C_2 = g(I_0)$. As $d_* < g(I_0)$, we must have $x_* = L$; i.e., $w(x) \ge w(L)$ for every $x \in [0,L]$. Therefore,

$$\frac{\varphi(x)}{\varphi(L)} \ge e^{-\frac{v}{D}(1+\frac{C_2D}{v^2})(L-x)}.$$

Integrating (7.7) in $(0,L)$ and dividing the result by $\varphi(L)$, we have

$$\int_0^L \frac{\varphi(x)}{\varphi(L)}\left[g(I_0e^{-k_0x}) - d_*\right] dx = 0. \tag{7.11}$$

Set $y = (L-x)/D$. Then φ satisfies

$$e^{-v(1+\frac{C_2D}{v^2})y} \le \frac{\varphi(L-Dy)}{\varphi(L)} \le e^{-v(1-\frac{C_1D}{v^2})y}. \tag{7.12}$$

We can rewrite (7.11) as

$$\int_0^{L/D} \frac{\varphi(L-Dy)}{\varphi(L)}\left[g(I_0e^{-k_0(L-Dy)}) - d_*\right] dy = 0. \tag{7.13}$$

By (7.12), we can apply Lebesgue dominant convergent theorem and pass to the limit in (7.13) to obtain

$$\begin{aligned}\lim_{D\to 0+} d_* &= \frac{\lim_{D\to 0+}\int_0^{L/D}\frac{\varphi(L-Dy)}{\varphi(L)}g(I_0e^{-k_0(L-Dy)})\,dy}{\lim_{D\to 0+}\int_0^{L/D}\frac{\varphi(L-Dy)}{\varphi(L)}\,dy}\\ &= \frac{\int_0^\infty e^{-vy}g(I_0e^{-k_0L})\,dy}{\int_0^\infty e^{-vy}\,dy}\\ &= g(I_0e^{-k_0L}).\end{aligned}$$

This completes the proof. □

Lemma 7.5. *For any $L>0$, there exists some $v_1>0$ such that if $v<v_1$, then*

$$d_*(v,L,D) > \frac{1}{L}\int_0^L g(I_0e^{-k_0x})\,dx \tag{7.14}$$

for sufficiently large D.

Proof. Let ψ_1 be the unique solution of

$$\begin{cases}\psi_{1,xx} = \dfrac{1}{L}\displaystyle\int_0^L g(I_0e^{-k_0x})\,dx - g(I_0e^{-k_0x}), & 0<x<L,\\ \psi_{1,x}(0)=\psi_{1,x}(L)=0, & \displaystyle\int_0^L \psi_1(x)\,dx = 0.\end{cases} \tag{7.15}$$

In particular, multiplying the first equation of (7.15) by ψ_1 and integrating the result in $(0,L)$, we have

$$\int_0^L g(I_0e^{-k_0x})\psi_1(x)\,dx = \int_0^L \psi_{1,x}^2\,dx > 0, \tag{7.16}$$

where the last strict inequality follows from the fact that $g(I_0e^{-k_0x})$ is non-constant.

Set $\psi = 1+\psi_1/D$ in (7.6), we have

$$d_* \ge \frac{\int_0^L e^{(v/D)x}\left[-D\psi_x^2 + g(I_0e^{-k_0x})\psi^2\right]dx}{\int_0^L e^{(v/D)x}\psi^2 dx}. \tag{7.17}$$

By direct calculations,

$$\begin{aligned}&\int_0^L e^{(v/D)x}\left[-D\psi_x^2 + g(I_0e^{-k_0x})\psi^2\right]dx\\ &= \int_0^L g + \frac{1}{D}\left[v\int_0^L xg(I_0e^{-k_0x})\,dx - \int_0^1 \psi_{1,x}^2 + 2\int_0^L g(I_0e^{-k_0x})\psi_1\right] + O(1/D^2)\\ &= \int_0^L g + \frac{1}{D}\left[v\int_0^L xg(I_0e^{-k_0x})\,dx + \int_0^1 \psi_{1,x}^2\right] + O(1/D^2),\end{aligned}$$

where the last equality follows from (7.16); Similarly,

$$\int_0^L e^{(v/D)x}\psi^2 dx = L + \frac{v}{2D}L^2 + O(1/D^2).$$

Hence,

$$\begin{aligned}&d_* - \frac{1}{L}\int_0^L g(I_0e^{-k_0x})\\ &\ge \frac{1}{DL}\left[\int_0^L \psi_{1,x}^2 - v\left(\frac{L}{2}\int_0^L g(I_0e^{-k_0x}) - \int_0^L xg(I_0e^{-k_0x})\right)\right] + O(1/D^2).\end{aligned} \tag{7.18}$$

We claim that

$$\Lambda := \frac{L}{2}\int_0^L g(I_0e^{-k_0x}) - \int_0^L xg(I_0e^{-k_0x}) > 0. \tag{7.19}$$

To establish this assertion, note that

$$\begin{aligned}\Lambda &= \int_0^L g(I_0e^{-k_0x})(\frac{L}{2} - x) \\ &= \int_0^L [g(I_0e^{-k_0x}) - g(I_0e^{-k_0L/2})](\frac{L}{2} - x),\end{aligned} \tag{7.20}$$

where the last equality follows from

$$\int_0^L g(I_0e^{-k_0L/2})(\frac{L}{2} - x) = g(I_0e^{-k_0L/2})\int_0^L (\frac{L}{2} - x) = 0.$$

Since functions $g(I_0e^{-k_0x}) - g(I_0e^{-k_0L/2})$ and $L/2 - x$ are strictly monotone decreasing, and both vanish at $x = L/2$, we see that $[g(I_0e^{-k_0x}) - g(I_0e^{-k_0L/2})](\frac{L}{2} - x) > 0$ for any $x \neq L/2$. This together with (7.20) imply that $\Lambda > 0$, i.e., (7.19) holds.

Set

$$v_1 := \frac{\int_0^L \psi_{1,x}^2}{\frac{L}{2}\int_0^L g(I_0e^{-k_0x}) - \int_0^L xg(I_0e^{-k_0x})}.$$

By (7.19), $v_1 > 0$. Hence, by (7.18) and the definition of v_1 we see that, for any $v < v_1$, (7.14) holds for sufficiently large D. □

Proofs of Theorems 6 and 7. Theorem 6 follows from Lemmas 7.1, 7.2, 7.3, 7.4 and 7.5; In particular, (3.5) follows from Lemmas 7.2, 7.4, 7.5 and the fact that $g(I_0e^{-k_0L}) < \frac{1}{L}\int_0^L g(I_0e^{-k_0x})$. Theorem 7 follows from Theorems 1 and 6. □

Proof of Theorem 8. Parts (a) and (c) follow from Theorem 1 and the definitions of $\overline{d}$ and $\underline{d}$. Hence, it suffices to show part (b). Given $L > 0$ and $0 < v < v_1$. Set $f(D) = d - d_*(v, L, D)$. By Lemma 7.4 we have

$$\lim_{D\to 0+} f(D) = d - g(I_0e^{-k_0L}) > 0,$$

where the last inequality follows from assumption on d. Choose $\tilde{D}$ such that $d_*(v, L, \tilde{D}) = \sup_{0<D<\infty} d_*(v, L, D)$. By our assumption $d < \sup_{0<D<\infty} d_*(v, L, D)$, $f(\tilde{D}) < 0$. Let $D_{min} \in (0, \tilde{D})$ be such that $f(D_{min}) = 0$, $f(D) \geq 0$ for $D \in (0, D_{min})$ and there exists some $\delta > 0$ such that $f(D) < 0$ for $D \in (D_{min}, D_{min} + \delta)$. Choose $\underline{D} = D_{min} + \delta$. By the definition of f, we have $d \geq d_*(v, L, D)$ for $0 < D \leq D_{min}$ and $d < d_*$ for $d \in (D_{min}, \underline{D})$. By Theorem 1, (3.1) has no positive steady state for $0 < D \leq D_{min}$ and a unique positive steady state for $d \in (D_{min}, \underline{D})$. Similarly, we can show that there exist D_{max} and $\overline{D}$ such that $\underline{D} \leq \overline{D} < D_{max}$ and (3.1) has no positive steady state for $D \geq D_{min}$ and a unique positive steady state for $d \in (\overline{D}, D_{max})$. □

8. Asymptotic behaviors of steady states $P(x; v)$ for large $|v|$

This section is devoted to proofs of Theorems 9 and 10. Let $P(x; v)$ denote the unique positive steady state of (3.8), i.e.,

$$\begin{cases} P_{xx} - vP_x + (g(I) - d)\,P = 0, \quad 0 < x < 1, \\ P_x(0) - vP(0) = P_x(1) - vP(1) = 0, \end{cases} \tag{8.1}$$

where I is given by (2.4).

Lemma 8.1. *If $v \le 0$, then $P_x < 0$ in $(0,1)$.*

Proof. Integrating the equation of $P(x;v)$ in $(0,1)$, we have

$$\int_0^1 P[g(I(x)) - d]\,dx = 0.$$

Since $I(x)$ is strictly deceasing in $(0,1)$, there exists some $x_0 \in (0,1)$ such that $g(I(x)) > d$ in $(0,x_0)$ and $g(I(x)) < d$ in $(x_0,1)$. By the equation of P, $P_{xx} - vP_x < 0$ in $(0,x_0)$ and $P_{xx} - vP_x > 0$ in $(x_0,1)$. Hence, $P_x - vP$ in strictly monotone decreasing in $(0,x_0)$ and strictly increasing in $(x_0,1)$. As $P_x = vP$ at $x = 0,1$, $P_x - vP < 0$ in $(0,1)$. Since $v \le 0$ and $P > 0$, $P_x < 0$ in $(0,1)$. □

Set

$$w(x) = e^{-v\eta x} P(x;v),$$

where η is some constant which will be chosen differently for different purposes. Clearly,

$$P_x = e^{v\eta x}(v\eta w + w_x)$$

and

$$P_{xx} = e^{v\eta x}(v^2\eta^2 w + 2v\eta w_x + w_{xx}).$$

Then, w satisfies

$$\text{(8.2)} \qquad \begin{cases} w_{xx} + v(2\eta - 1)w_x + w\left[v^2\eta(\eta-1) + g(I(x)) - d\right] = 0 & \text{in } 0 < x < 1, \\ w_x = v(1-\eta)w \quad \text{at } x = 0,1. \end{cases}$$

Lemma 8.2. *If $v > 2\sqrt{g(I_0) - d}$, then $P_x > 0$ for $0 \le x \le 1$.*

Proof. Set $\eta = 1/2$. Then, w satisfies

$$\text{(8.3)} \qquad \begin{cases} w_{xx} + w\left[-\dfrac{v^2}{4} + g(I(x)) - d\right] = 0 & \text{in } 0 < x < 1, \\ w_x = \dfrac{v}{2}w \quad \text{at } x = 0,1. \end{cases}$$

If $v > 2\sqrt{g(I_0) - d}$, then

$$\frac{v^2}{4} - g(I(x)) + d > 0$$

in $(0,1)$, i.e., $w_{xx} > 0$ in $(0,1)$. Since $w_x(0) > 0$, we have $w_x > 0$ in $[0,1]$. This implies that

$$P_x = e^{(v/2)x}\left[(v/2)w + w_x\right] > 0$$

in $[0,1]$. □

Lemma 8.3. *There exist positive constants C_i $(i = 1,2)$, both independent of v, such that*

(a) *if $v \ge C_1$,*

$$e^{-\frac{C_2}{v}(1-x)} \le \frac{P(x;v)}{P(1;v)e^{-v(1-x)}} \le e^{\frac{C_2}{v}(1-x)}$$

for every $x \in [0,1]$;

(b) *if $v \le -C_1$, then*

$$e^{\frac{C_2}{v}x} \le \frac{P(x;v)}{P(0;v)e^{vx}} \le e^{-\frac{C_2}{v}x}$$

for every $x \in [0,1]$.

Proof. We first set $\eta = 1 - C_3/v^2$, where C_3 is some positive constant to be chosen later. Then w satisfies

$$(8.4) \qquad \begin{cases} w_{xx} + v(1-2C_3/v^2)w_x + w[-C_3(1-C_3/v^2) + g(I(x)) - d] = 0 & \text{in } 0 < x < 1, \\ w_x = (C_3/v)w \quad \text{at } x = 0, 1. \end{cases}$$

Let $x^* \in [0,1]$ such that $w(x^*) = \max_{0\le x\le 1} w(x)$. If $x^* \in (0,1)$, $w_{xx}(x^*) \le 0$ and $w_x(x^*) = 0$. By (8.4) we have

$$-C_3(1-C_3/v^2) + g(I(x^*)) - d \ge 0,$$

which is impossible if we choose $C_3 = 2g(I_0)$ and $v > 2\sqrt{g(I_0)}$. Hence, for such choices of C_3 and v, $x^* = 0$ or $x^* = 1$. We consider two cases:

Case 1. $v > 0$. For this case, since $w_x(0) > 0$, $x^* \ne 0$. Therefore, $x^* = 1$; i.e., $w(x) \le w(1)$ for every $x \in [0,1]$. Therefore,

$$P(x;v) \le P(1;v)e^{-v(1-C_3/v^2)(1-x)},$$

which can be written as

$$\frac{P(x;v)}{P(1;v)e^{-v(1-x)}} \le e^{\frac{C_3}{v}(1-x)}.$$

Case 2. $v < 0$. Since $w_x(1) < 0$, $x^* \ne 1$. Therefore, $x^* = 0$; i.e., $w(x) \le w(0)$ for every $x \in [0,1]$, which can be written as

$$\frac{P(x;v)}{P(0;v)e^{vx}} \le e^{-\frac{C_3}{v}x}.$$

For the other side of inequalities, set $\eta = 1 + C_4/v^2$, where $C_4 > 0$ is to be chosen later. By (8.2), w satisfies

$$(8.5) \qquad \begin{cases} w_{xx} + v(1+2C_4/v^2)w_x + w[C_4(1+C_4/v^2) + g(I(x)) - d] = 0 & \text{in } 0 < x < 1, \\ w_x = -(C_4/v)w \quad \text{at } x = 0, 1. \end{cases}$$

Let $x_* \in [0,1]$ such that $w(x_*) = \min_{0\le x\le 1} w(x)$. If $x_* \in (0,1)$, $w_{xx}(x_*) \ge 0$ and $w_x(x_*) = 0$. By (8.5) we have

$$C_4(1+C_4/v^2) + g(I(x_*)) - d \le 0,$$

which implies that $d > C_4$. Hence, if $C_4 = d$, we must have $x_* = 0$ or $x_* = 1$. Next we consider two cases:

Case 1. $v > 0$. Since $w_x(0) < 0$, $x_* \ne 0$. That is, $x_* = 1$; i.e., $w(x) \ge w(1)$ for every $x \in [0,1]$. Therefore,

$$P(x;v) \ge P(1;v)e^{-v(1+C_4/v^2)(1-x)},$$

which can be written as

$$\frac{P(x;v)}{P(1;v)e^{-v(1-x)}} \ge e^{-\frac{C_4}{v}(1-x)}.$$

Case 2. $v < 0$. Since $w_x(1) > 0$, $x_* \ne 1$. That is, $x_* = 0$; i.e., $w(x) \ge w(0)$ for every $x \in [0,1]$, which can be written as

$$\frac{P(x;v)}{P(0;v)e^{vx}} \ge e^{\frac{C_4}{v}x}.$$

This completes the proof. □

Lemma 8.4. *For any $y \ge 0$,*

$$\lim_{v\to\infty} \frac{v}{P(1;v)} \int_0^{1-y/v} P(s;v)\, ds = e^{-y}$$

and

$$\lim_{v\to-\infty}\frac{v}{P(0;v)}\int_0^{-y/v}P(s;v)\,ds=e^{-y}-1.$$

Proof. First of all, we establish the first limit. By part (a) of Lemma 8.3,

$$\frac{P(s;v)}{P(1;v)}\le e^{C_2/v}e^{-v(1-s)}.$$

Hence,

$$\int_0^{1-y/v}\frac{P(s;v)}{P(1;v)}\,ds\le e^{C_2/v}\int_0^{1-y/v}e^{-v(1-s)}\,ds=e^{C_2/v}\frac{e^{-y}-e^{-v}}{v},$$

which can be written as

$$\frac{v}{P(1;v)}\int_0^{1-y/v}P(s;v)\,ds\le e^{C_2/v}[e^{-y}-e^{-v}].$$

Similarly, by part (a) of Lemma 8.3,

$$\frac{P(s;v)}{P(1;v)}\ge e^{-C_2/v}e^{-v(1-s)}.$$

Hence,

$$\frac{v}{P(1;v)}\int_0^{1-y/v}P(s;v)\,ds\ge e^{-C_2/v}[e^{-y}-e^{-v}].$$

This proves the first limit.

For the proof of the second limit, by part (b) of Lemma 8.3, for $v\le -C_1$,

$$e^{C_2/v}e^{vs}\le\frac{P(s;v)}{P(0;v)}\le e^{-C_2/v}e^{vs}.$$

Hence,

$$e^{C_2/v}\frac{e^{-y}-1}{v}\le\int_0^{-y/v}\frac{P(s;v)}{P(0;v)}\,ds\le e^{-C_2/v}\frac{e^{-y}-1}{v},$$

which can be written as

$$e^{C_2/v}[1-e^{-y}]\le\frac{-v}{P(0;v)}\int_0^{-y/v}P(s;v)\,ds\le e^{-C_2/v}[1-e^{-y}].$$

This completes the proof. □

Lemma 8.5. *Suppose that* $d\in(0,g(I_0e^{-k_0}))$. *Then,*

$$\lim_{v\to\infty}\frac{P(1;v)}{v}=\kappa^*,$$

where $\kappa^*>0$ *is uniquely determined by*

$$\int_0^1 g(I_0e^{-k_0-k_1\kappa^*z})\,dz=d.$$

Proof. Dividing (3.1) by $P(1;v)$, integrating in $(0,1)$ and applying the boundary condition in (3.1), we have

$$\int_0^1\frac{P(x;v)}{P(1;v)}\,[g(I(x))-d]\;dx=0.$$

Set $x=1-y/v$. We can rewrite the above equation as

$$\int_0^v\frac{P(1-y/v;v)}{P(1;v)}\left[g(\tilde{I}(y))-d\right]\;dy=0, \tag{8.6}$$

where

$$\tilde{I}(y) = I_0 e^{-k_0(1-y/v) - k_1 \int_0^{1-y/v} P(s;v)ds}.$$

We claim that $P(1;v)/v$ is uniformly bounded for all v. To establish this assertion, we argue by contradiction: If not, passing to a sequence if necessary we may assume that $P(1;v)/v \to \infty$ as $v \to \infty$. Then by Lemma 8.4,

$$\int_0^{1-y/v} P(s;v)ds = \frac{P(1;v)}{v} \cdot \frac{v}{P(1;v)} \int_0^{1-y/v} P(s;v)\,ds \to \infty$$

pointwisely in y as $v \to \infty$. Hence, $\tilde{I}(y) \to 0$ pointwisely as $v \to \infty$. As

$$e^{-C_2/v} e^{-y} \le \frac{P(1-y/v;v)}{P(1;v)} \le e^{C_2/v} e^{-y}$$

for every $y \in (0, v)$, we see that

$$\frac{P(1-y/v;v)}{P(1;v)} \to e^{-y}$$

pointwisely in y as $v \to \infty$. Moreover,

$$\frac{P(1-y/v;v)}{P(1;v)} \left| g(\tilde{I}(y)) - d \right| \le e^{C_2/v} e^{-y} [g(I_0) + d]$$

for every $y \in (0, v)$. Hence, we can apply the Lebesgue Dominant Convergent Theorem and let $v \to \infty$ in (8.6) to conclude that

$$\int_0^\infty e^{-y}(g(0) - d) = 0,$$

which is a contradiction as $g(0) = 0$ and $d > 0$.

Hence, $P(1;v)/v$ is bounded uniformly for large v. Passing to a sequence if necessary, we may assume that $P(1;v)/v \to \kappa$ as $v \to \infty$ for some constant $\kappa \ge 0$. For this case,

$$\int_0^{1-y/v} P(s;v)ds = \frac{P(1;v)}{v} \cdot \frac{v}{P(1;v)} \int_0^{1-y/v} P(s;v)\,ds \to \kappa e^{-y}.$$

Hence,

$$\tilde{I}(y) \to I_0 e^{-k_0 - k_1 \kappa e^{-y}}$$

pointwisely in y as $v \to \infty$. Following the same argument as before, we can apply the Lebesgue Dominant Convergent Theorem and let $v \to \infty$ in (8.6) to conclude that

$$\int_0^\infty e^{-y} [g(I_0 e^{-k_0 - k_1 \kappa e^{-y}}) - d]\,dy = 0. \tag{8.7}$$

We claim that $\kappa > 0$: if $\kappa = 0$, then from (8.7) we obtain $g(I_0 e^{-k_0}) = d$, which contradicts our assumption $d < g(I_0 e^{-k_0})$. By the new variable $z = e^{-y}$, (8.7) can be rewritten as $F(\kappa) = d$, where

$$F(\kappa) :\equiv \int_0^1 g(I_0 e^{-k_0 - k_1 \kappa z})\,dz.$$

Since $F(0) = g(I_0 e^{-k_0}) > d$, $\lim_{\kappa \to \infty} F(\kappa) = 0$, and F is strictly decreasing in $(0, \infty)$ we see that there exists a unique κ^* such that $F(\kappa^*) = d$. Since κ^* is independent of the choice of sequence, we see that $P(1;v)/v \to \kappa^*$ as $v \to \infty$. ☐

Lemma 8.6. *Suppose that $d \in (0, g(I_0))$. Then,*

$$\lim_{v \to -\infty} \frac{P(0; v)}{v} = \kappa_*,$$

where $\kappa_* < 0$ is uniquely determined by

$$\int_0^1 g(I_0 e^{k_1 \kappa_* (1-z)})\, dz = d.$$

Proof. Dividing (3.1) by $P(0; v)$, integrating in $(0, 1)$ and applying the boundary condition in (3.1), we have

$$\int_0^1 \frac{P(x; v)}{P(0; v)} \left[g(I(x)) - d\right]\, dx = 0.$$

Set $x = -y/v$. We can rewrite the above equation as

$$\int_0^{-v} \frac{P(-y/v; v)}{P(0; v)} \left[g(\hat{I}(y)) - d\right]\, dy = 0, \tag{8.8}$$

where

$$\hat{I}(y) = I_0 e^{k_0 y/v - k_1 \int_0^{-y/v} P(s;v) ds}.$$

We claim that $P(0; v)/v$ is uniformly bounded for all large negative v. If not, we may assume that $P(0; v)/v \to \infty$ as $v \to -\infty$. Then by part (b) of Lemma 8.4,

$$\int_0^{-y/v} P(s; v) ds = \frac{P(0; v)}{v} \cdot \frac{v}{P(0; v)} \int_0^{-y/v} P(s; v)\, ds \to \infty$$

pointwisely in y as $v \to -\infty$. Hence, $\tilde{I}(y) \to 0$ pointwisely as $v \to -\infty$. As

$$e^{C_2/v} e^{-y} \le \frac{P(-y/v; v)}{P(0; v)} \le e^{-C_2/v} e^{-y}$$

for every $y \in (0, -v)$, we see that $P(-y/v; v)/P(0; v) \to e^{-y}$ pointwisely in y as $v \to -\infty$. Moreover,

$$\frac{P(-y/v; v)}{P(0; v)} \left| g(\hat{I}(y)) - d \right| \le e^{-C_2/v} e^{-y} [g(I_0) + d]$$

for every $y \in (0, -v)$. By the Lebesgue Dominant Convergent Theorem and let $v \to -\infty$ in (8.8) we have that $\int_0^\infty e^{-y}(g(0) - d) = 0$, which is a contradiction as $g(0) = 0$ and $d > 0$. Hence, $P(0; v)/v$ is bounded uniformly for large negative v. Passing to a sequence if necessary, we may assume that $P(0; v)/v \to \kappa_*$ as $v \to -\infty$ for some constant $\kappa_* \le 0$. For this case,

$$\int_0^{-y/v} P(s; v) ds = \frac{P(0; v)}{v} \cdot \frac{v}{P(0; v)} \int_0^{-y/v} P(s; v)\, ds \to \kappa_* [e^{-y} - 1].$$

Hence, $\hat{I}(y) \to I_0 e^{k_1 \kappa_* [1 - e^{-y}]}$ pointwisely in y as $v \to -\infty$. Following the same argument as before, we can let $v \to -\infty$ in (8.8) to conclude that

$$\int_0^\infty e^{-y} [g(I_0 e^{k_1 \kappa_* [1 - e^{-y}]}) - d]\, dy = 0. \tag{8.9}$$

We claim that $\kappa_* < 0$: if $\kappa_* = 0$, from (8.9) we obtain $g(I_0) = d$, which contradicts our assumption $d < g(I_0)$. By the new variable $z = e^{-y}$, (8.9) can be rewritten as $G(\kappa_*) = d$, where

$$G(\kappa) :\equiv \int_0^1 g(I_0 e^{k_1 \kappa (1-z)})\, dz.$$

Since $G(0) = g(I_0) > d$, $\lim_{\kappa\to-\infty} G(\kappa) = 0$, and G is strictly increasing in $(-\infty, 0)$ we see that there exists a unique $\kappa_* < 0$ such that $G(\kappa_*) = d$. Since κ_* is independent of the choice of sequence, we see that $P(0; v)/v \to \kappa_*$ as $v \to -\infty$. $\square$

Lemma 8.7. *There exist positive constants C_5, C_6, both independent of v, such that*

(a) *if $v \geq C_5$,*

$$\left|\frac{P(x;v)}{P(1;v)} - e^{-v(1-x)}\right| \leq \frac{C_6}{v^2}$$

for every $x \in [0,1]$.

(b) *if $v \leq -C_5$,*

$$\left|\frac{P(x;v)}{P(0;v)} - e^{vx}\right| \leq \frac{C_6}{v^2}$$

for every $x \in [0,1]$.

Proof. We first establish part (a). By part (a) of Lemma 8.3 we have

$$g_1(x;v) \leq \frac{P(x;v)}{P(1;v)} - e^{-v(1-x)} \leq g_2(x;v),$$

where $g_i(x;v)$ $(i = 1, 2)$ are given by

$$g_1(x;v) = (e^{-C_2(1-x)/v} - 1)e^{-v(1-x)}$$

and

$$g_2(x;v) = (e^{C_2(1-x)/v} - 1)e^{-v(1-x)}.$$

It is easy to check that

$$\frac{\partial g_1(x;v)}{\partial x} = ve^{-v(1-x)}[e^{-C_2(1-x)/v}(1 + C_2/v^2) - 1].$$

For large v, the only critical point (denoted by x_1) of g_1 in $[0,1]$ is determined by

$$e^{C_2(1-x_1)/v} = 1 + C_2/v^2,$$

which implies that $x_1 = 1 - (1/v)(1 + o(1))$ for large v. Hence,

$$g_1(x_1;v) \geq -\frac{C_2}{v^2}e^{-v(1-x_1)} \geq -\frac{C_7}{v^2}$$

for some positive constant C_7 independent of v. As g_1 attains the global minimum at $x = x_1$ in $[0,1]$, we see that

$$\frac{P(x;v)}{P(1;v)} - e^{-v(1-x)} \geq -\frac{C_7}{v^2}.$$

For g_2 we have

$$\frac{\partial g_2(x;v)}{\partial x} = (v - C_2/v)e^{-v(1-x)}\left[e^{C_2(1-x)/v} - \frac{1}{1 - C_2/v^2}\right].$$

For large v, the only critical point (denoted by x_2) of g_2 in $[0,1]$ is determined by

$$e^{C_2(1-x_2)/v} = \frac{1}{1 - C_2/v^2},$$

which implies that $x_2 = 1 - (1/v)(1 + o(1))$ for large v. Hence,

$$g_2(x_2;v) = \frac{C_2/v^2}{1 - C_2/v^2}e^{-v(1-x_2)} \leq \frac{C_8}{v^2},$$

where C_8 is some positive constant independent of v. As g_2 attains the global maximum at $x = x_2$ in $[0, 1]$, we see that

$$\frac{P(x;v)}{P(1;v)} - e^{-v(1-x)} \leq \frac{C_8}{v^2}$$

for every $x \in [0, 1]$. This establishes (a).

For the proof of part (b), by part (b) of Lemma 8.3 we have

$$h_1(x;v) \leq \frac{P(x;v)}{P(0;v)} - e^{vx} \leq h_2(x;v),$$

where $h_i(x;v)$ $(i = 1, 2)$ are given by

$$h_1(x;v) = (e^{C_2x/v} - 1)e^{vx}$$

and

$$h_2(x;v) = (e^{-C_2x/v} - 1)e^{vx}.$$

It is easy to check that

$$\frac{\partial h_1(x;v)}{\partial x} = ve^{vx}[e^{C_2x/v}(1 + C_2/v^2) - 1].$$

For large negative v, the only critical point (denoted by x_3) of h_1 in $[0, 1]$ is determined by

$$e^{C_2x_3/v} = 1/(1 + C_2/v^2),$$

which implies that $x_3 = -(1/v)(1 + o(1))$ for large negative v. Hence,

$$h_1(x_3;v) = (-C_2/v^2)/(1 + C_2/v^2)e^{vx_3} \geq -\frac{C_9}{v^2}$$

for some positive constant C_9 independent of v. As h_1 attains the global minimum at $x = x_3$ in $[0, 1]$, we see that

$$\frac{P(x;v)}{P(0;v)} - e^{vx} \geq -\frac{C_9}{v^2}.$$

For h_2 we have

$$\frac{\partial h_2(x;v)}{\partial x} = (v - C_2/v)e^{vx}\left[e^{-C_2x/v} - \frac{1}{1 - C_2/v^2}\right].$$

For large negative v, the only critical point (denoted by x_4) of h_2 in $[0, 1]$ is determined by

$$e^{-C_2x_4/v} = \frac{1}{1 - C_2/v^2},$$

which implies that $x_4 = -(1/v)(1 + o(1))$ for large negative v. Hence,

$$h_2(x_2;v) = \frac{C_2/v^2}{1 - C_2/v^2}e^{vx_4} \leq \frac{C_{10}}{v^2},$$

where C_{10} is some positive constant independent of v. As h_2 attains the global maximum at $x = x_4$ in $[0, 1]$, we see that

$$\frac{P(x;v)}{P(1;v)} - e^{vx} \leq \frac{C_{10}}{v^2}$$

for every $x \in [0, 1]$. This completes the proof. □

Corollary 8.8. *There exists some positive constants C_{11} and C_{12}, both independent of v such that*

(a) *if* $v \geq C_{11}$,

$$\left|P(x;v) - P(1;v)e^{-v(1-x)}\right| \leq \frac{C_{12}}{v}$$

for every $x \in [0,1]$*;*

(b) *if* $v \leq -C_{11}$,

$$|P(x;v) - P(0;v)e^{vx}| \leq \frac{C_{12}}{v}$$

for every $x \in [0,1]$*.*

Proof. For part (a), as $P(1;v)/v \to \kappa^* > 0$ as $v \to \infty$, by (a) of Lemma 8.7 we have

$$\left|P(x;v) - P(1;v)e^{-v(1-x)}\right| = P(1;v)\left|\frac{P(x;v)}{P(1;v)} - e^{-v(1-x)}\right| \leq \frac{C_{12}}{v}.$$

The proof of (b) is similar to that of part (a) and is thus omitted. □

Proofs of Theorems 9 and 10. For the proof of Theorem 9, part (a) follows from Lemma 8.2. For the proof of part (b), it follows from Lemma 8.5 that $P(1;v)/v \to \kappa^*$ as $v \to \infty$ and the existence and uniqueness of κ^* is also established in Lemma 8.5. The limit (3.10) is established in Corollary 8.8, from which it follows that $P(x;v) \to 0$ uniformly in any compact subset of $[0,1)$. It also follows from Lemma 8.5 and Corollary 8.8 that $P(\cdot;v) \to \kappa^*\delta(1)$ as $v \to \infty$. Finally, it follows from Lemma 8.3 that

$$\frac{P(x;v)}{P(1;v)e^{-v(1-x)}} \to 1$$

in $L^\infty(0,1)$ as $v \to \infty$. This together with Lemma 8.5 implies that (3.11) holds. This completes the proof of Theorem 9.

For the proof of Theorem 10, part (a) follows from Lemma 8.1. The proof of part (b) is similar to that of part (b) of Theorem 9 and is thus omitted. □

9. **Discussion**

In this paper we study a mathematical model on the growth of a single phytoplankton species in a water column where the species depends solely on light for its metabolism. The model is described by a nonlocal reaction-diffusion-advection equation, proposed by Huisman et al. [8, 9]. We focused on the combined effect of death rate, advection (sinking or buoyant) coefficient, water column depth and turbulent diffusion rate on the persistence of the single species. Under a general reproductive rate which is an increasing function of light intensity, we established the existence of critical death rate; i.e., the phytoplankton species survives if and only if its death rate is less than the critical death rate. We show that the critical death rate is a strictly monotone decreasing function of advection coefficient and water column depth and is also a strictly monotone decreasing function of vertical turbulent diffusion rate for buoyant species. We also determine the asymptotic behaviors of the critical death rate for sufficiently large sinking or buoyant rate, for shallow or deep water column and for poorly mixing water column (small turbulent diffusion rate) and well-mixing water columns (large turbulent diffusion rate). These results enabled us to investigate critical advection rate, critical water column depth and critical turbulent diffusion rate, which may or may not exist. For example, if the death rate is suitably small (with fixed water column depth), the phytoplankton can persist for any sinking/buoyant velocity, i.e., there is no critical sinking/buoyant velocity under such situation. Similarly, if the death rate is suitably small (with fixed sinking or buoyant rate), the phytoplankton can persist for any water column depth, i.e., there is no critical water column depth. Our analysis shows that these critical values for water column depth, sinking/buoyant velocity and diffusion rate exist for some intermediate range of phytoplankton death rates. In short summary, we have shown that

- Critical death rate always exists and it is unique;
- Critical sinking or buoyant rate and critical water column depth only exist for intermediate values of death rates. They are unique whenever they exist;
- Critical turbulent diffusion rate only exist for intermediate values of death rates. Whenever it exists, it is unique for buoyant species. However, there may exist two critical turbulent diffusion rates for sinking species.

9.1. **Critical water column depth.** In 1953 Sverdrup is the first one to introduce the concept of critical depth of the mixed layer beyond which the phytoplankton growth would be impossible [9]. In [8] the authors introduced an interesting way to define the critical water column depth. They considered the positive steady state problem of the same model (2.1)-(2.4) satisfying (2.5). When the positive steady state exists, they prove the following nontrivial properties of steady states:

- Let p_0 be the plankton population density at the surface of the water column. If we treat the depth L as a function of p_0, then
$$L = L(p_0) = \frac{M}{p_0} + O(\frac{1}{p_0^2})$$
as $p_0 \to \infty$, where $M > 0$ is some positive constant.
- $L(p_0)$ is a monotonically decreasing function of p_0: $L(p_{0,1}) > L(p_{0,2})$ if $p_{0,1} < p_{0,2}$.

As a consequence, the critical water column depth is defined in [8] as

$$L^* = \lim_{p_0 \to 0+} L(p_0). \tag{9.1}$$

In this paper, we define the critical water column depth L_* by the equation $d = d_*(v, L_*, D)$, where d_* is the critical death rate. We conjecture that $L_* = L^*$ whenever they are finite; i.e., our definition of the critical depth is equivalent to that given by (9.1).

We establish here some lower bound of L_* in terms of d. For fixed death rate satisfying $d < g(I_0)$, we define the depth L_b as

$$L_b := \frac{1}{k_0} \ln \frac{I_0}{g^{-1}(d)}$$

or equivalently

$$d = g(I_0 e^{-k_0 L_b}).$$

It follows that

$$0 < d < g(I_0 e^{-k_0 L}) \Leftrightarrow 0 < L < L_b.$$

Thus if the water column depth is less than L_b, it follows from part (a) of Theorem 3 that plankton bloom for any sinking/byoent rate and any turbulent diffusion rate. In particular, this implies that

$$L_* \geq L_b := \frac{1}{k_0} \ln \frac{I_0}{g^{-1}(d)}.$$

Interestingly, this implies that $L_* \to \infty$ as $k_0 \to 0+$; i.e., if k_0 is very small (close to the self-shading situation), the critical depth will become sufficiently large. This is consistent with the result from [16] that the self-shading model has positive steady state for any finite water column depth.

9.2. **Monotonicity of critical rates.** By Theorem 2, the critical death rate $d_*(v, L, D)$ is strictly monotone decreasing for v and L, which is biologically intuitive: the larger v and L are, the species has more tendency to sink and the deeper the water column is, which leaves the species less susceptible to the light and makes it harder for the phytoplankton to persist. It is natural to inquire how other critical rates L_*, α_* and D_* depend on their parameters.

- $L_* = L_*(d, v, D)$ is monotone decreasing in d and v and monotone decreasing in D when $v \leq 0$. To see this, differentiating $d = d_*(v, L_*, D)$ with respect to d,
$$\frac{\partial d_*}{\partial L} \cdot \frac{\partial L_*}{\partial d} = 1.$$
As $\partial d_*/\partial L \leq 0$, $\partial L_*/\partial d < 0$ (and also $\partial d_*/\partial L < 0$); Differentiating $d = d_*(v, L_*, D)$ with respect to v, we have
$$\frac{\partial d_*}{\partial L} \cdot \frac{\partial L_*}{\partial v} + \frac{\partial d_*}{\partial v} = 0.$$
As $\partial d_*/\partial L < 0$ and $\partial d_*/\partial v < 0$, $\partial L_*/\partial v < 0$. Similarly, we can show that $\partial L_*/\partial D < 0$ provided that $v \leq 0$.
- By similar argument as before, we can show that the critical rate $v_* = v_*(d, L, D)$ is also monotone decreasing in d and L, and monotone decreasing in D when $v \leq 0$. Similarly, $D_* = D_*(d, v, L)$ is also monotone decreasing in d, v and L when $v \leq 0$; i.e, the buoyant situation.

It will be of interest to understand the asymptotic behaviors of the critical rates L_*, α_* and D_* for large sinking/buoyant rates and poorly and well mixed water columns.

9.3. **Future directions.** In the case of no sinking/buoyant, it is illustrated numerically in [11] that if the turbulent diffusion rate is less than a critical value, the phytoplankton can persist irrespective the water column depth. The role of vertical turbulent diffusion coefficient becomes more complicated if we include the advection of the phytoplankton species in the water column. The analysis in [8] suggests that there might exist two critical vertical turbulent diffusion coefficients for sinking phytoplankton (Figure 5, [8]). When the sinking velocity is suitably small, the existence of two critical turbulent diffusion rates is confirmed by part (b) of Theorem 8, in strong contrast with the buoyant case for which there is at most one critical turbulent diffusion rate, as shown by Theorem 7. It will be of interest to further investigate how the critical death rate depends upon vertical turbulent diffusion, especially when the sinking velocity is suitably large.

Regarding phytoplankton density distributions in the water column, we show that the species forms a thin layer at the surface of the water column for sufficiently large buoyant rate, and it forms a thin layer at the bottom of the water column for sufficiently large sinking rate. It will be of interest to understand the asymptotic behaviors of positive steady states for poorly mixed water columns and for shallow and deep water columns.

Regarding multiple consumer and/or multiple resource problems, we plan to build upon the current work and further study two species competing for light and/or nutrient in a water column with advections. We will also investigate the competition of two species for two complementary nutrients in the oligotrophic ecosystem where the light is amply supplied.

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References

[1] F. Belgacem, Elliptic Boundary Value Problems with Indefinite Weights: Variational Formulations of the Principal Eigenvalue and Applications, Pitman Res. Notes Math. Ser. **368**, Longman Sci., 1997.

[2] R.S. Cantrell and C. Cosner, Spatial Ecology via Reaction-Diffusion Equations, Series in Mathematical and Computational Biology, John Wiley and Sons, Chichester, UK, 2003.

[3] M.G. Crandall and P.H. Rabinowitz, Bifurcation from simple eigenvalues, *J. Funct. Anal.* **8** (1971) 321-340.

[4] X.F. Chen and Y. Lou, Principal eigenvalue and eigenfunction of elliptic operator with large convection and its application to a competition model, *Indiana Univ. Math. J.* **57** (2008) 627-658.

[5] Y. Du and S.B. Hsu, Concentration phenomena in a nonlocal quasilinear problem modelling phytoplankton I: Existence, *SIAM J. Math. Anal.* **40** (2008) 1419-1440.

[6] Y. Du and S.B. Hsu, Concentration phenomena in a nonlocal quasilinear problem modelling phytoplankton II: Limiting profile, *SIAM J. Math. Anal.* **40** (2008) 1441-1470.

[7] Y. Du and S.B. Hsu, On a nonlocal reaction-diffusion problem arising from the modelling of phytoplankton growth, *Preprint*.

[8] U. Ebert, M. Arrayas, N. Temme, B. Sommeojer, J. Huisman, Critical condition for phytoplankton blooms, *Bull. Math. Biol.* **63** (2001) 1095-1124.

[9] J. Huisman, M. Arrayas, U. Ebert, and B. Sommeijer, How do sinking phytoplankton species manage to persist? *American Naturalist* **159** (2002) 245-254.

[10] J. Huisman, P. van Oostveen, and F.J. Weissing, Species dynamics in phytoplankton blooms: incomplete mixing and competition for light, *American Naturalist* **154** (1999) 46-67.

[11] J. Huisman, P. van Oostveen, and F.J. Weissing, Critical depth and critical turbulance: Two different mechanisms for the development of phytoplankton blooms, *Limnol. Oceanogr.* **44** (1999) 1781-1787.

[12] J. Huisman, N.N. Pham Thi, D.K. Karl, B. Sommeijer, Reduced mixing generates oscillations and chaos in oceanic deep chlorophyll, *Nature* **439** (2006) 322-325.

[13] H. Ishii and I. Takagi, Global stability of stationary solutions to a nonlinear diffusion equation in phytoplankton dynamics, *J Math Biol.* **16** (1982) 1-24.

[14] C.A. Klausmeier and E. Litchman, Algal games: The vertical distribution of phytoplankton in poorly mixed water columns, *Limnol. Oceanogr.* **46** (2001) 1998-2007.

[15] C.A. Klausmeier, E. Litchman, and S.A. Levin, Phytoplankton growth and stoichimetry under multiple nutrient limitation, *Limnol Oceangr.* **49** (2004) 1463-1470.

[16] T. Kolokolnikov, C.H. Ou, and Y. Yuan, Phytoplankton depth profiles and their transitions near the critical sinking velocity, *J. Math Biol.* **59** (2009) 105-122.

[17] E. Litchman, C.A. Klausmeier, J.R. Miller, O.M. Schofield, and P.G. Falkowski, Multi-nutrient, multi-group model of present and furture oceanic phytoplankton communities, *Biogeoscience* **3** (2006) 585-606.

[18] P.H. Rabinowitz, Some global results for nonlinear eigenvalue problems, *J. Funct. Anal.* **7** (1971) 487-513.

[19] N. Shigesada and A. Okubo, Analysis of the self-shading effect on algal vertical distribution in natural waters, *J Math Biol.* **12** (1981) 311-326.

[20] K. Yoshiyama, J.P. Mellard, E. Litchman and C.A. Klausmeier, Phytoplankton competition for nutrients and light in a stratified water column, *American Naturalist* **174(2)** (2009) 190-203.

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