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Multiple steady-states in phytoplankton population induced by photoinhibition[☆]

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Abstract

We study the effect of photoinhibition in a nonlocal reaction–diffusion–advection equation, which models the dynamics of a single phytoplankton species in a water column where the growth of the species depends solely on light. Our results show that, in contrast to the case of no photoinhibition, where at most one positive steady state can exist, the model with photoinhibition possesses at least two positive steady states in certain parameter ranges. Our approach involves bifurcation theory and perturbation–reduction arguments.

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1. Introduction

Phytoplankton are microscopic plants that float in oceans and lakes and form the base of the aquatic food chain. Since they transport significant amounts of atmospheric carbon dioxide into the deep oceans, they may also play a crucial role in the climate dynamics. Phytoplankton species typically compete for nutrients and light [4,5,16,19,28,29]. But in oligotrophic ecosystems with ample supply of light, they tend to compete only for nutrients [20,22], and in eutrophic environments with ample nutrients supply, they compete only for light [8,15]. In a water column, a phytoplankton population diffuses due to turbulent mixing caused by wind and wave actions. In many cases, phytoplankton also sinks due to its own weight.

In this paper, we consider a single sinking phytoplankton species in an eutrophic water column. Our analysis is based on a nonlocal reaction–diffusion–advection model given by Huisman and colleagues in [8,14], but the growth function $g(I)$ of phytoplankton species in the model is modified to include photoinhibition into consideration.

Photoinhibition is characterized by a decreasing rate of photosynthesis with increasing light, which occurs in many phytoplankton species that are sensitive to strong light. This phenomenon is caused by damage to the photosynthetic machinery of cells and by protective mechanisms to avoid this damage [23,27].

Without photoinhibition, the growth function $g(I)$ is generally assumed to be strictly increasing in I , representing the fact that increase of the light level I leads to better growth of the phytoplankton. In such a case this model was investigated recently through rigorous mathematical analysis in [6,7,13,21] (see also earlier work in [17,18,26] and references therein), which show that the phytoplankton population either stabilizes at a unique positive steady-state or converges to 0 as time goes to infinity, depending on whether the loss rate is below or above a critical level.

With photoinhibition, observations in many laboratory studies [10,11,24] suggest that the function $g(I)$ should be increasing before I reaches a certain critical level $I_* > 0$ where $g(I)$ has a maximum, after which $g(I)$ decreases and converges to 0 as $I \rightarrow \infty$. In a completely mixed water column, the reaction–diffusion–advection model reduces to an ODE model, and the effect of photoinhibition was studied in the recent papers [9,12]. With a growth function $g(I)$ as above, [9] demonstrates that the phytoplankton population may have two stable steady-states (one positive, the other 0), plus another unstable positive steady state, causing a bistable dynamical behavior with the phytoplankton population stabilizing at one or the other stable steady state, depending on its initial value. (The multi-species case was also considered in [9] and [12].)

In this paper, we examine the effect of photoinhibition in an incompletely mixed water column, through a single species reaction–diffusion–advection model, where photoinhibition is incorporated into the growth function $g(I)$ as described above. We show that the phenomenon of multiple positive steady-states observed in completely mixed water column persists, and their stability suggests a bistable dynamical behavior.

Multiplicity results for similar reaction–diffusion equations are usually obtained by making use of the upper and lower solution technique, combined with tools from global analysis (such as the topological degree theory or global bifurcation theory). However, such upper and lower solution techniques are difficult to apply here due to the nonlocal nature of the problem. To overcome this difficulty, apart from employing local and global bifurcation analysis, we also use a perturbation and reduction approach, which is new to this kind of nonlocal reaction–diffusion equations. It is our hope that the mathematical techniques developed here may find more applications in phytoplankton models.

We now describe the model in more detail. Consider a vertical water column with a cross section of one unit area and depth h . Let $p(x, t)$ be the population density of the phytoplankton at depth $x \in [0, h]$ and time t . Then the change of density is governed by the following reaction–diffusion–advection problem

$$\begin{cases} p_t = Dp_{xx} - \sigma p_x + [g(I_0 e^{-k_0 x - k \int_0^x p(s,t) ds}) - d]p, & 0 < x < h, \quad t > 0, \\ Dp_x(x, t) - \sigma p(x, t) = 0, & x = 0 \text{ or } h, \quad t > 0, \\ p(x, 0) = p_0(x) \geq 0, & 0 \leq x \leq h, \end{cases} \quad (1.1)$$

where $d > 0$ is the loss rate of the species, the positive constants D, σ represent the diffusion rate and the sinking rate, respectively.

The term

$$I(x, t) = I_0 e^{-k_0 x - k \int_0^x p(s,t) ds} \quad (1.2)$$

is known as the light intensity, with $k_0 \geq 0$ the background turbidity, $k > 0$ the light attenuation coefficient of the phytoplankton species, and $I_0 > 0$ the incident light intensity.

The function $g(I)$ governs the growth rate according to the change of light level I . We always assume that g is C^1 . Taking into account of photoinhibition we assume, as in [9], that $g(I)$ has the following properties:

$$\begin{cases} \text{(i)} & g(0) = 0, \\ \text{(ii)} & \text{there exists } I_* > 0 \text{ such that } (I_* - I)g'(I) > 0 \text{ for } I \neq I_*, \\ \text{(iii)} & \lim_{I \rightarrow \infty} g(I) = 0. \end{cases} \quad (1.3)$$

The boundary conditions at $x = 0$ and $x = h$ imply that there is no population flux at the surface or bottom of the water column.

We are interested in the multiplicity of positive steady states of (1.1). To simplify notations we assume that $D = h = I_0 = 1$. We stress that this is for simplicity of the notations only; our method can deal with the general case without extra difficulties. Thus we will study the positive solutions of the nonlocal elliptic boundary value problem

$$\begin{cases} p_{xx} - \sigma p_x + p[g(I) - d] = 0, & 0 < x < 1, \\ qp_x(0) - \sigma p(0) = 0, & p_x(1) - \sigma p(1) = 0, \end{cases} \quad (1.4)$$

with

$$I = I(x) = e^{-k_0 x - k \int_0^x p(s) ds}. \quad (1.5)$$

Our first existence and multiplicity result is obtained by a standard argument involving local and global bifurcation theory of Crandall and Rabinowitz [1,2,25]. The multiplicity result is local in nature.

Theorem 1.1. *Suppose that (1.3) holds and $I_* < e^{-k_0}$. Then there exist some positive constants $d_* < d^* < g(I_*)$ such that (1.4) has at least one positive solution for $d \in (0, d_*]$, two positive solutions for $d \in (d_*, d^*)$, and no positive solution for $d > g(I^*)$.*

Here d_* is uniquely determined by an eigenvalue problem, and $d^* > d_*$ is sufficiently close to d_* , whose existence arises from a bifurcation analysis along the line of trivial solutions $\{(d, 0) : d \in \mathbb{R}^1\}$, which shows that a branch of positive solutions $\{(d, p)\}$ bifurcates from the line of trivial solutions at $(d_*, 0)$, and it goes rightward initially but has to become unbounded through d converging to 0. It can be shown that for $d \in (d_*, d^*)$, one of the positive steady state is unstable (see Lemma 2.3), but we have no information on the stability of the other positive steady state, though we believe it is stable.

By making use of a perturbation–reduction approach, we can obtain a multiplicity result which is global in nature, together with information on the asymptotic profile and stability of the solutions, but only for large σ .

Theorem 1.2. Suppose that (1.3) holds and $I_* < e^{-k_0}$.

(i) Define

$$G(\mu) = \frac{1}{\mu} \int_0^\mu g(e^{-k_0-s}) ds.$$

Then there exists a unique $\mu_* > \ln(e^{-k_0}/I_*)$ such that

$$G'(\mu_*) = 0, \quad G'(\mu)(\mu_* - \mu) > 0 \quad \text{for } \mu \in (0, +\infty) \setminus \{\mu_*\}.$$

Moreover, for each $d \in (g(e^{-k_0}), G(\mu_*))$, the equation $d = G(\mu)$ has exactly two positive solutions μ_1, μ_2 , and $0 < \mu_1 < \mu_* < \mu_2$.

(ii) For each $d \in (g(e^{-k_0}), G(\mu_*))$, there exists $\epsilon^* > 0$ such that for every $\sigma > 1/\epsilon^*$, (1.4) has two positive solutions of the form

$$p_1(x) = \frac{\mu_1}{k} \sigma e^{\sigma(x-1)} + z_{1,\sigma}(x), \quad p_2(x) = \frac{\mu_2}{k} \sigma e^{\sigma(x-1)} + z_{2,\sigma}(x),$$

with $z_{i,\sigma}$ satisfying $\lim_{\sigma \rightarrow \infty} \int_0^1 |z_{i,\sigma}(x)| dx = 0$, $i = 1, 2$.

Remark 1.3. If $I_* \geq 1$, we can show that (1.4) has at most one positive solution for any σ . Indeed, we can modify $g(I)$ for $I > I_*$ to obtain a new C^1 function $\tilde{g}(I)$ which is strictly increasing in I for all $I > 0$. When $I_* \geq 1$, it is easily seen that if p is a positive solution of (1.4), then it is also a positive solution of (1.4) with $g(I)$ replaced by $\tilde{g}(I)$. Hence we are back in the no-photoinhibition case and can apply the result in [13,7] to conclude that there is at most one positive solution, and the dynamics of (1.1) is simple. Biologically this fact is rather natural, as 1 is the highest possible level of light intensity felt by the species in the water column, so only the values of $g(I)$ for $I \in (0, 1]$ contribute to the growth of the species.

The results in Theorem 1.2 suggest that for large σ , the two solutions p_1 and p_2 form a “ \supset ”-shaped curve in the (d, p) -space as d is varied in the range $(g(e^{-k_0}), G(\mu_*))$, which resembles the solution curve of the equation $d = G(\mu)$ in the (d, μ) -plane. Fig. 1 shows the graph of the curve $G(\mu)$ and the two solutions μ_1 and μ_2 of $d = G(\mu)$ for the case $I_* < e^{-k_0}$.

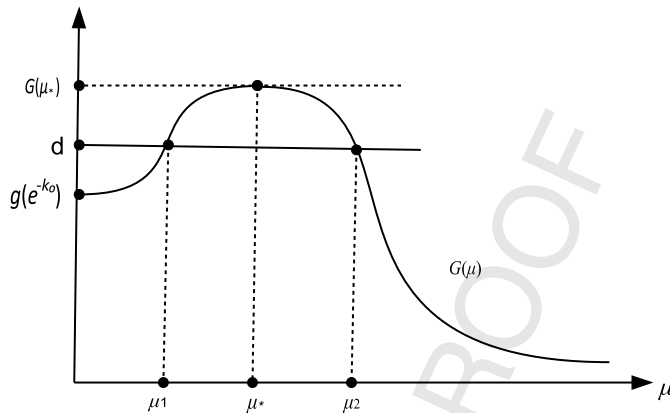


Fig. 1. Illustrative graph of $G(\mu)$ and the solutions of $d = G(\mu)$.

It is interesting to note that, by Theorem 3.2 of [13], as $\sigma \rightarrow +\infty$, the bifurcation value d_* in Theorem 1.1 converges to $g(e^{-k_0})$, suggesting that the global bifurcation curve in Theorem 1.1 for large σ looks like the solution curve of the equation $d = G(\mu)$ in the (d, μ) -plane, and the two positive solutions in Theorem 1.2 are from the “lower” and “upper” branches of the global bifurcation curve.

Let us also note that for large σ , the solutions $p_1(x)$ and $p_2(x)$ are well approximated by $\frac{\mu_1}{k}\sigma e^{\sigma(x-1)}$ and $\frac{\mu_2}{k}\sigma e^{\sigma(x-1)}$, respectively, which have values close to 0 away from $x = 1$, while their values at $x = 1$ go to ∞ as $\sigma \rightarrow \infty$. The fact that the populations concentrate at the bottom of the water column is due to the assumption of large sinking rate σ . The information on the asymptotic profiles of $p_1(x)$ and $p_2(x)$ enables us to investigate their stability, see Theorem 4.1 in Section 4, which suggests that p_1 is unstable, p_2 is stable, as expected for the bistable phenomenon. (Note that 0 is a stable steady state for d in the range of Theorem 1.2.)

The rest of the paper is organized as follows. In Section 2 we use a bifurcation approach to prove Theorem 1.1, with d as the bifurcation parameter. To overcome some of the limitations encountered in Section 2 in the bifurcation approach, in Section 3 we use a perturbation and reduction approach to study the steady-state solutions of (1.1) with large sinking rate and prove Theorem 1.2. In Section 4 we consider the linearized stability of the two positive steady states found in Section 3.

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2. Multiple steady-states through a bifurcation approach

In this section we use a bifurcation approach to prove Theorem 1.1. We focus on the existence of positive solutions by studying the bifurcation of a branch of positive solutions of (1.4) from the trivial solution $p = 0$, with coefficient d as the bifurcation parameter.

We first consider the stability of $p = 0$, which is determined by the sign of the largest eigenvalue, denoted by $\lambda = d_*$, of the linear eigenvalue problem

$$\begin{cases} \varphi_{xx} - \sigma \varphi_x + g(e^{-k_0 x})\varphi = \lambda \varphi, & 0 < x < 1, \\ \varphi_x(0) - \sigma \varphi(0) = 0, & \varphi_x(1) - \sigma \varphi(1) = 0. \end{cases} \quad (2.1)$$

By the well-known Krein–Rutman theorem it is known that d_* exists and is positive. Its corresponding eigenfunction can be chosen to be positive in $[0, 1]$, denoted by φ_* , which is uniquely determined by the normalization $\max_{[0,1]} \varphi_* = 1$. To investigate the structure of the set of solutions of (1.4) near $(d, p) = (d_*, 0)$, we first introduce a few notations. Set $X = \{u \in C^2([0, 1]) : u_x - \sigma u = 0 \text{ at } x = 0, 1\}$, $Y = C([0, 1])$. Define mapping $F(d, p) : (0, \infty) \times X \rightarrow Y$ by

$$F(d, p) = p_{xx} - \sigma p_x + p[g(I) - d].$$

Clearly, $F(d, 0) = 0$ for $d \in (0, \infty)$. Since

$$F_p(d, 0)\varphi = \varphi_{xx} - \sigma \varphi_x + [g(e^{-k_0 x}) - d]\varphi, \quad (2.2)$$

we see that (i) the kernel of $F_p(d_*, 0)$ is spanned by φ_* , and is thus one dimensional; (ii) the range of $F_p(d_*, 0)$, denoted by $R(F_p(d_*, 0))$, is given by

$$\left\{ \zeta \in Y : \int_0^1 e^{-\sigma x} \varphi_* \zeta dx = 0 \right\},$$

and is thus of co-dimension one. Furthermore, $F_{pd}(d_*, 0)\varphi_* = -\varphi_* \notin R(F_p(d_*, 0))$. By Theorem 1.7 of [1], we obtain the result:

Lemma 2.1. *Let Z be any complement of span of $\{\varphi_*\}$ in X . Then there exists some $\delta > 0$ and continuously differentiable functions $d : (-\delta, \delta) \rightarrow \mathbb{R}$ and $\psi : (-\delta, \delta) \rightarrow X$ such that $d(0) = d_*$, $\psi(0) = 0$, and $F(d(s), p(s)) = 0$, where $p(s) = s\varphi_* + s\psi(s)$. Moreover, $F^{-1}(\{0\})$ near $(d_*, 0)$ consists precisely of the curves $p = 0$ and $(d(s), p(s))$, $s \in (-\delta, \delta)$. Furthermore,*

$$d'(0) \int_0^1 e^{-\sigma x} \varphi_*^2 dx = -k \int_0^1 e^{-\sigma x} e^{-k_0 x} g'(e^{-k_0 x}) \varphi_*^2 \left(\int_0^x \varphi_* \right) dx. \quad (2.3)$$

Proof. It suffices to check (2.3). Dividing $F(d(s), p(s)) = 0$ by s and differentiating the result with respect to s at $s = 0$, using $p = s\varphi_* + s\psi(s)$ we have

$$(\psi'(0))_{xx} - \sigma (\psi'(0))_x + \psi'(0)[g(e^{-k_0 x}) - d_*] + \varphi_* \left[-k g'(e^{-k_0 x}) e^{-k_0 x} \int_0^x \varphi_* - d'(0) \right] = 0.$$

Multiplying the above equation by $e^{-\sigma x} \varphi_*$ and integrating by parts we obtain (2.3). \square

In the terminology of [2], 0 is an $F_{pd}(d_*, 0)$ -simple eigenvalue of the operator $F_p(d_*, 0)$. By Corollary 1.13 and Theorem 1.16 of [2] we have

Proposition 2.2. *There exist some positive constants δ_1 and δ_2 and continuously differentiable functions $\gamma : (d_* - \delta_1, d_* + \delta_1) \rightarrow \mathbb{R}$, $\mu : (-\delta_2, \delta_2) \rightarrow \mathbb{R}$, $v : (d_* - \delta_1, d_* + \delta_1) \rightarrow X$, $w : (-\delta_2, \delta_2) \rightarrow X$ such that*

$$\begin{aligned} F_p(d, 0)v(d) &= -\gamma(d)v(d), \\ F_p(d(s), p(s))w(s) &= -\mu(s)w(s), \\ \lim_{s \rightarrow 0, \mu(s) \neq 0} \frac{-sd'(s)\gamma'(d_*)}{\mu(s)} &= 1, \end{aligned} \quad (2.4)$$

where $\gamma(d_*) = \mu(0) = 0$, $v(d_*) = w(0) = \varphi_*$.

The next result suggests that for $s > 0$ small, the nontrivial (positive) solution $p(s) = s\varphi_* + s\psi(s)$ is unstable under suitable conditions.

Lemma 2.3. Suppose that (1.3) holds and $I_* < e^{-k_0}$. Then for any sufficiently small $s > 0$, $\mu(s) < 0$.

Proof. By (2.2) and the definition of d_* , we see that $\gamma(d) = d - d_*$. If (1.3) holds, $g'(e^{-k_0x}) < 0$ for $x \in (0, 1)$, which together with (2.3) implies that $d'(0) > 0$. By (2.4), we see that $\mu(s) < 0$ for $s > 0$ small. \square

Lemma 2.4. Suppose that (1.3) holds. If $d \notin (0, g(I_*))$, then (1.4) has no positive solution.

Proof. Let p denote a positive solution of (1.4). Integrating (1.4) in $(0, h)$ and applying the boundary condition in (1.4), we have

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

Since $g(I) \in (0, g(I_*))$ and $I \neq I_*$, we see that $d \in (0, g(I_*))$. Therefore, (1.4) has no positive solution when $d \notin (0, g(I_*))$. \square

Lemma 2.5. Given any $\eta > 0$, there exists some positive constant $C(\eta)$ such that every positive solution p of (1.4) with $d \geq \eta$ satisfies $\|p\|_{L^\infty(0,1)} \leq C(\eta)$.

The proof of Lemma 2.5 is identical to that of Lemma 4.2 of [13] and is omitted.

Proof of Theorem 1.1. By Lemma 2.1 and the global bifurcation result of Rabinowitz [25], (1.4) has an unbounded connected branch of positive solutions, denoted by $\Gamma = \{(d, p)\} \subset \mathbb{R} \times C^1([0, 1])$, which bifurcates from the trivial solution branch $\{(d, 0)\}$ at $(d_*, 0)$. Since (1.4) has no positive solutions when $d \notin (0, g(I_*))$ (Lemma 2.4) and all positive solutions of (1.4) are uniformly bounded when d is positive and bounded away from zero (Lemma 2.5), we see that Γ can only become unbounded as $d \rightarrow 0^+$. As Γ is connected, (1.4) has at least one positive solution for every $d \in (0, d_*)$. Denote $\{(d, p) \in \Gamma : 0 < d < d_*\}$ by Γ_1 . By Lemma 2.1, Γ contains a branch of positive solutions, denoted by Γ_2 , which is given by $(d(s), p(s))$ for $s > 0$ small. By (1.3) and $I_* < e^{-k_0}$, we have $d'(0) > 0$. In particular, there exists some $d^* > d_*$ such that the projection of Γ_2 onto the d -axis is given by (d_*, d^*) . Hence Γ_1 and Γ_2 must be disjoint. As Γ is connected and $\Gamma_1, \Gamma_2 \subset \Gamma$, we see that the projection of $\Gamma \setminus \Gamma_2$ onto the d -axis must contain

(0, d^*), i.e. (1.4) has at least two positive solutions for $d \in (d_*, d^*)$. By Lemma 2.4, (1.4) has no positive solution for $d > g(I_*)$. Thus we complete the proof of Theorem 1.1. \square

The proof of Theorem 1.1 indicates that there exists $d^{**} \in [d^*, g(I_*)]$ such that (1.4) has no positive solution lying on Γ for $d > d^{**}$, and it has at least one positive solution for $d \in (0, d^{**}]$. In such a case, it is natural to expect that there exist two positive solutions for $d \in (d_*, d^{**})$, and the global bifurcation curve is “ \cap ”-shaped, with a turning point at $d = d^{**}$. Moreover, one expects the following typical conclusions:

For $d \in (d_, d^{**})$, there are two positive solutions, and the solution on the “upper” branch of the global bifurcation curve is stable, while that located on the “lower” branch is unstable. Note also that the zero solution $p = 0$ is always stable for $d > d_*$.*

Such a global bifurcation picture can be partially proved by techniques of [3] for increasing operators, if the problem at hand has the usual order-preserving property. Unfortunately, due to the nonlocal nature of our problem, this nice property is lost and we cannot use such tools involving the order-preserving property as in [3] or the usual upper and lower solution technique. We remark that even the modified order-preserving property used in [6] is lost here due to the fact that $g(I)$ is no longer increasing in I for all $I > 0$.

To overcome these difficulties, in the next two sections, we employ a perturbation and reduction approach, which strongly suggests the validity of the global bifurcation picture described above, at least for large σ .

3. Multiple steady-states via a perturbation–reduction approach

In this section, we use a perturbation and reduction approach to study the positive solutions of (1.4). Their stability will be considered in Section 4 later. We will examine the problem with a large σ , and write it in the form

$$\sigma = \epsilon^{-1},$$

with $\epsilon > 0$ small.

Let $p(x)$ be a positive solution of (1.4), and define

$$u(x) = p(\epsilon x + 1)e^{-x/2}.$$

A simple calculation shows that

$$\begin{cases} u_{xx} - \frac{1}{4}u + \epsilon^2[g(\tilde{I}) - d]u = 0, & x \in (-\epsilon^{-1}, 0), \\ u_x - \frac{1}{2}u = 0, & x \in \{-\epsilon^{-1}, 0\}, \end{cases} \quad (3.1)$$

where

$$\tilde{I} = \exp\left(-k_0 - \epsilon k_0 x - k\epsilon \int_{-\epsilon^{-1}}^x u(s)e^{s/2} ds\right).$$

We will look for a solution to (3.1) of the form

$$u(x) = \epsilon^{-1} \eta e^{x/2} + z(x)$$

with $\eta > 0$ and

$$z \in H := \left\{ z : \int_{-\epsilon^{-1}}^0 z(x) e^{x/2} dx = 0, \int_{-\epsilon^{-1}}^0 |z(x)| e^{x/2} dx < \infty \right\}.$$

Since the function $e^{x/2}$ satisfies

$$u_{xx} - \frac{1}{4}u = 0 \quad \text{in } (-\epsilon^{-1}, 0), \quad u_x - \frac{1}{2}u = 0 \quad \text{at } x = -\epsilon^{-1}, 0,$$

we necessarily have

$$\begin{cases} -z_{xx} + \frac{1}{4}z = \epsilon^2 [g(\tilde{I}) - d]u, & x \in (-\epsilon^{-1}, 0), \\ z_x - \frac{1}{2}z = 0, & x \in \{-\epsilon^{-1}, 0\}, \end{cases}$$

with \tilde{I} as above, and $u(x) = \epsilon^{-1} \eta e^{x/2} + z(x)$.

We now define

$$f(x) = f(x; \epsilon, \eta, z) := \epsilon^2 \{g(\tilde{I})[\epsilon^{-1} \eta e^{x/2} + z(x)]^+ - d[\epsilon^{-1} \eta e^{x/2} + z(x)]\}$$

(here $u^+ = \max\{u, 0\}$) and consider the auxiliary problem

$$\begin{cases} -z_{xx} + \frac{1}{4}z = f(x) - \lambda e^{x/2}, & x \in (-\epsilon^{-1}, 0), \\ z_x - \frac{1}{2}z = 0, & x \in \{-\epsilon^{-1}, 0\}, \end{cases} \quad (3.2)$$

with λ determined by

$$\lambda \int_{-\epsilon^{-1}}^0 e^x dx = \int_{-\epsilon^{-1}}^0 f(x) e^{x/2} dx. \quad (3.3)$$

Then from (3.2) we find that $z \in H$ has the expression

$$z(x) = \int_x^0 f(y) 2 \sinh\left(\frac{x-y}{2}\right) dy - \lambda \int_x^0 e^{y/2} 2 \sinh\left(\frac{x-y}{2}\right) dy + \alpha e^{x/2},$$

where $\sinh(x) = (e^x - e^{-x})/2$ and $\alpha \in \mathbb{R}^1$ is chosen such that $\int_{-\epsilon^{-1}}^0 z(x) e^{x/2} dx = 0$. A simple calculation gives

$$z(x) = \int_x^0 f(y) 2 \sinh\left(\frac{x-y}{2}\right) dy + \lambda e^{x/2} (x-1 + e^{-x}) + \alpha e^{x/2}.$$

For $z \in H$, we now define the nonlinear operator

$$F_{\epsilon, \eta}(z)(x) := F_{\epsilon, \eta}^1(z)(x) + \alpha(\epsilon, \eta, z) e^{x/2},$$

with

$$F_{\epsilon, \eta}^1(z)(x) := \int_x^0 f(y; \epsilon, \eta, z) 2 \sinh\left(\frac{x-y}{2}\right) dy + \lambda(\epsilon, \eta, z) e^{x/2} (x-1 + e^{-x}),$$

where $\lambda(\epsilon, \eta, z)$ is determined by (3.3) with $f(x) = f(x; \epsilon, \eta, z)$, and $\alpha(\epsilon, \eta, z)$ is determined by

$$\int_{-1/\epsilon}^0 e^{x/2} F_{\epsilon, \eta}^1(z)(x) dx + \alpha \int_{-1/\epsilon}^0 e^x dx = 0,$$

that is,

$$\alpha(\epsilon, \eta, z) := -\left(1 - e^{-1/\epsilon}\right)^{-1} \int_{-1/\epsilon}^0 e^{x/2} F_{\epsilon, \eta}^1(z)(x) dx. \quad (3.4)$$

We will show that for all small $\epsilon > 0$ and all $\eta > 0$ in a certain interval J , the operator $F_{\epsilon, \eta}$ is a contraction mapping in H , and hence it has a unique fixed point $z = z_{\epsilon, \eta}$. We will then choose $\eta = \eta_\epsilon$ so that $\lambda(\epsilon, \eta, z) = 0$ for $z = z_{\epsilon, \eta}$ and $\eta = \eta_\epsilon$. We will show that this gives a positive solution $u = \epsilon^{-1} \eta_\epsilon e^{x/2} + z_{\epsilon, \eta_\epsilon}(x)$ to (3.1) for all small $\epsilon > 0$. A key point in this approach is that with our assumptions on $g(I)$, for each small $\epsilon > 0$, for $d > 0$ in a certain range, we always have two solutions for η_ϵ , and hence this approach yields two positive steady-states for (3.1).

We will show that for $\epsilon > 0$ small, the equation $\lambda(\epsilon, \eta, z_{\epsilon, \eta}) = 0$ is a perturbation of the equation

$$d = \int_0^{k\eta} \frac{1}{k\eta} g(\xi_0 e^{-s}) ds, \quad \xi_0 = e^{-k_0} \in (0, 1].$$

Denote

$$\mu = k\eta, \quad G(\mu) = \frac{1}{\mu} \int_0^\mu g(\xi_0 e^{-s}) ds \quad \text{and} \quad G_0(\mu) = \int_0^\mu g(\xi_0 e^{-s}) ds,$$

then the above equation is equivalent to

$$d = G(\mu). \quad (3.5)$$

In order to determine the range J for η so that $F_{\epsilon, \eta}$ is a contraction mapping, and multiple solutions to (3.1) exist, we need to obtain several simple properties of the functions $G(\mu)$ and $G_0(\mu)$ first.

3.1. Properties of $G_0(\mu)$ and $G(\mu)$

Our assumptions on g imply that $g(I) \leq c_0 I$ for some $c_0 > 0$ and all $I > 0$. It follows that

$$G_0(+\infty) = \int_0^{+\infty} g(\xi_0 e^{-s}) ds \in (0, \infty).$$

Clearly

$$G(0) = g(\xi_0) > 0, \quad G(\mu) > 0 \quad \text{for } \mu > 0, \quad G(+\infty) = 0$$

and

$$G'(\mu) = \mu^{-2} [\mu G'_0(\mu) - G_0(\mu)] =: \mu^{-2} \tilde{G}(\mu).$$

If $I_* \geq \xi_0$, then

$$G'_0(\mu) = g(\xi_0 e^{-\mu}) > 0, \quad G''_0(\mu) = -g'(\xi_0 e^{-\mu}) \xi_0 e^{-\mu} < 0 \quad \forall \mu \geq 0.$$

Hence

$$\tilde{G}'(\mu) = \mu G''_0(\mu) < 0 \quad \text{for } \mu > 0.$$

It follows that

$$\tilde{G}(\mu) < \tilde{G}(0) = 0 \quad \text{for } \mu > 0.$$

Thus $G'(\mu) = \mu^{-2} \tilde{G}(\mu) < 0$ for $\mu > 0$. This implies that for each $d \in (0, d_*) := (0, g(\xi_0))$, (3.5) has a unique solution $\mu > 0$, and for each $d \geq d_*$, (3.5) has no solution $\mu > 0$.

If $I_* < \xi_0$, then $G'_0(\mu) > 0$ for $\mu \geq 0$, and

$$G''_0(\mu) > 0 \quad \text{for } \mu \in (0, \ln(\xi_0/I_*)), \quad G''_0(\mu) < 0 \quad \text{for } \mu > \ln(\xi_0/I_*).$$

Thus

$$\tilde{G}'(\mu) > 0 \quad \text{for } \mu \in (0, \ln(\xi_0/I_*)), \quad \tilde{G}'(\mu) < 0 \quad \text{for } \mu > \ln(\xi_0/I_*).$$

Using $G''_0(\mu) < 0$ for all large $\mu > 0$ and $G_0(+\infty) > 0$, it is easily seen that $\tilde{G}(\mu) < 0$ for all large μ . Thus there exists a unique $\mu_* > \ln(\xi_0/I_*)$ such that for $\mu \in (0, \mu_*)$, $\tilde{G}(\mu) > 0$, and for $\mu > \mu_*$, $\tilde{G}(\mu) < 0$. It follows that

$$G'(\mu) > 0 \quad \text{for } \mu \in (0, \mu_*), \quad G'(\mu) < 0 \quad \text{for } \mu > \mu_*.$$

Define $\hat{d}_* := G(\mu_*)$; then for each $d \in (g(\xi_0), \hat{d}_*)$, (3.5) has exactly two solutions $\mu_1 \in (0, \mu_*)$ and $\mu_2 \in (\mu_*, +\infty)$, and (3.5) has a unique solution $\mu > 0$ for $d \in \{\hat{d}_*\} \cup (0, g(\xi_0))$. Moreover,

$$G'(\mu_1) > 0 > G'(\mu_2). \quad (3.6)$$

From now on, we always assume that

$$I_* < \xi_0 \quad \text{and} \quad d \in (g(\xi_0), \hat{d}_*). \quad (3.7)$$

Thus (3.5) has exactly two solutions $0 < \mu_1 < \mu_2$, and apart from (3.6), we have

$$\mu > G(\mu) \quad \text{for } \mu \in (0, \mu_1) \cup (\mu_2, \infty), \quad \mu < G(\mu) \quad \text{for } \mu \in (\mu_1, \mu_2). \quad (3.8)$$

Clearly part (i) of Theorem 1.2 follows from the above discussions. The rest of this section is devoted to the proof of part (ii) of Theorem 1.2. We set

$$J = \left[\frac{\mu_1}{2k}, \frac{2\mu_2}{k} \right].$$

3.2. $F_{\epsilon, \eta}$ maps a subset of H into itself

It is easily seen that $H = H_\epsilon$ endowed with the norm

$$\|z\| = \int_{-\epsilon^{-1}}^0 |z(x)| e^{x/2} dx$$

is a Banach space.

Lemma 3.1. *There exist $\epsilon_0 > 0$ and $M > 0$ such that for each $\epsilon \in (0, \epsilon_0]$ and $\eta \in J$, $F_{\epsilon, \eta}$ maps $\Omega := \{z \in H : \|z\| \leq M\}$ into itself.*

Proof.

$$\begin{aligned} e^{x/2} F_{\epsilon, \eta}^1(z)(x) &= e^{x/2} \int_x^0 f(y; \epsilon, \eta, z) 2 \sinh\left(\frac{x-y}{2}\right) dy + \lambda(\epsilon, \eta, z) [(x-1)e^x + 1] \\ &= S_1(x) + S_2(x). \end{aligned}$$

We have, for $\epsilon > 0$ small,

$$\begin{aligned}
 |\lambda(\epsilon, \eta, z)| &= (1 - e^{-\epsilon^{-1}})^{-1} \left| \int_{-\epsilon^{-1}}^0 \epsilon^2 \{g(\cdot) [\epsilon^{-1} \eta e^{x/2} + z(x)]^+ - d[\epsilon^{-1} \eta e^{x/2} + z(x)]\} e^{x/2} dx \right| \\
 &\leq 2 \int_{-\epsilon^{-1}}^0 \epsilon^2 [c_0 e^{-\epsilon k} \int_{-\epsilon^{-1}}^x (\epsilon^{-1} \eta e^{y/2} - |z(y)|) e^{y/2} dy + d] (\epsilon^{-1} \eta e^x + |z(x)| e^{x/2}) dx \\
 &\leq 2 \int_{-\epsilon^{-1}}^0 [c_0 e^{\epsilon k \|z\|} + d] (\epsilon \eta e^x + \epsilon^2 |z(x)| e^{x/2}) dx \\
 &\leq C(e^{\epsilon k \|z\|} + 1)(\epsilon + \epsilon^2 \|z\|),
 \end{aligned}$$

for some $C > 0$ independent of $\eta \in J$ and small $\epsilon > 0$. In the following, we will use C to denote a generic positive constant that is independent of $\eta \in J$ and small $\epsilon > 0$, whose value may change from line to line.

From the above estimate we obtain

$$\begin{aligned}
 \int_{-\epsilon^{-1}}^0 |S_2(x)| dx &\leq |\lambda(\epsilon, \eta, z)| \int_{-\epsilon^{-1}}^0 |(x-1)e^x + 1| dx \\
 &\leq C(e^{\epsilon k \|z\|} + 1)(1 + \epsilon \|z\|).
 \end{aligned}$$

For the term $S_1(x)$ we have

$$\begin{aligned}
 |S_1(x)| &= \left| e^{x/2} \int_x^0 f(y; \epsilon, \eta, z) 2 \sinh\left(\frac{x-y}{2}\right) dy \right| \\
 &\leq e^{x/2} \int_x^0 \epsilon^2 |g(\cdot) - d| (\epsilon^{-1} \eta e^{y/2} + |z(y)|) 2 \left| \sinh\left(\frac{x-y}{2}\right) \right| dy \\
 &\leq \epsilon^2 \int_x^0 C(e^{\epsilon k \|z\|} + 1) (\epsilon^{-1} e^y + |z(y)| e^{y/2}) |e^{x-y} - 1| dy \\
 &\leq C(e^{\epsilon k \|z\|} + 1)(1 + \epsilon \|z\|) \epsilon.
 \end{aligned}$$

Thus

$$\int_{-\epsilon^{-1}}^0 |S_1(x)| dx \leq C(e^{\epsilon k \|z\|} + 1)(1 + \epsilon \|z\|).$$

We therefore have

$$\|F_{\epsilon,\eta}^1(z)\| \leq C(e^{\epsilon k\|z\|} + 1)(1 + \epsilon\|z\|).$$

By (3.4), we have

$$\|\alpha(\epsilon, \eta, z)e^{x/2}\| \leq \|F_{\epsilon,\eta}^1(z)\| \leq C(e^{\epsilon k\|z\|} + 1)(1 + \epsilon\|z\|).$$

Therefore, taking $M = 3C$ then from the above inequalities we can easily find $\epsilon_0 > 0$ sufficiently small (depending on C) such that for all $\epsilon \in (0, \epsilon_0]$ and $\eta \in J$,

$$\|F_{\epsilon,\eta}(z)\| \leq M \quad \text{if } \|z\| \leq M. \quad \square$$

3.3. $F_{\epsilon,\eta}$ is a contraction mapping

In this subsection we show that there exists $\epsilon^0 \in (0, \epsilon_0]$ such that for each $\epsilon \in (0, \epsilon^0]$ and each $\eta \in J$, $F_{\epsilon,\eta}$ is a contraction mapping on Ω .

Suppose that $z_1, z_2 \in \Omega$, and denote for $i = 1, 2$,

$$I_i(x) = \exp\left(-k_0 - \epsilon k_0 x - k \int_{-\epsilon^{-1}}^x \eta e^y dy\right) e^{-\epsilon k \int_{-\epsilon^{-1}}^x z_i(y) e^{y/2} dy}.$$

Clearly

$$\begin{aligned} |g(I_1) - g(I_2)| &\leq C|I_1 - I_2| \\ &\leq C \left| e^{-\epsilon k \int_{-\epsilon^{-1}}^x z_1(y) e^{y/2} dy} - e^{-\epsilon k \int_{-\epsilon^{-1}}^x z_2(y) e^{y/2} dy} \right| \\ &\leq C e^{\epsilon k(\|z_1\| + \|z_2\|)} \epsilon k \int_{-\epsilon^{-1}}^x |z_1(y) - z_2(y)| e^{y/2} dy \\ &\leq C e^{\epsilon k 2M} \epsilon \|z_1 - z_2\| \\ &\leq \epsilon C \|z_1 - z_2\|. \end{aligned}$$

We write

$$\begin{aligned} &[F_{\epsilon,\eta}^1(z_1)(x) - F_{\epsilon,\eta}^1(z_2)(x)]e^{x/2} \\ &= \epsilon^2 \int_x^0 \{g(I_1)(\epsilon^{-1}\eta e^{y/2} + z_1)^+ - g(I_2)(\epsilon^{-1}\eta e^{y/2} + z_2)^+ - d(z_1 - z_2)\} e^{y/2} (e^{x-y} - 1) dy \\ &\quad + [\lambda(\epsilon, \eta, z_1) - \lambda(\epsilon, \eta, z_2)] e^x (x - 1 + e^{-x}) \\ &= \epsilon^2 \int_x^0 [g(I_1) - g(I_2)] (\epsilon^{-1}\eta e^{y/2} + z_1)^+ e^{y/2} (e^{x-y} - 1) dy \end{aligned}$$

$$\begin{aligned}
 & + \epsilon^2 \int_x^0 \{g(I_2)[(\epsilon^{-1}\eta e^{y/2} + z_1)^+ - (\epsilon^{-1}\eta e^{y/2} + z_2)^+] - d(z_1 - z_2)\} e^{y/2} (e^{x-y} - 1) dy \\
 & + [\lambda(\epsilon, \eta, z_1) - \lambda(\epsilon, \eta, z_2)] e^x (x - 1 + e^{-x}) \\
 & = T_1(x) + T_2(x) + T_3(x).
 \end{aligned}$$

Then

$$\begin{aligned}
 |T_1(x)| & \leq \epsilon^2 C \epsilon \|z_1 - z_2\| \int_x^0 (\epsilon^{-1}\eta e^{y/2} + |z_1| e^{y/2}) dy \\
 & \leq C \epsilon^2 \|z_1 - z_2\|.
 \end{aligned}$$

Since

$$|g(I_2)| + d \leq C I_2 + d \leq C e^{\epsilon k \|z_2\|} + d \leq C,$$

we have

$$\begin{aligned}
 |T_2(x)| & \leq C \epsilon^2 \int_x^0 \{ |(\epsilon^{-1}\eta e^{y/2} + z_1)^+ - (\epsilon^{-1}\eta e^{y/2} + z_2)^+| + |z_1 - z_2| \} e^{y/2} |e^{x-y} - 1| dy \\
 & \leq C \epsilon^2 \int_x^0 |z_1(y) - z_2(y)| e^{y/2} dy \\
 & \leq C \epsilon^2 \|z_1 - z_2\|.
 \end{aligned}$$

To estimate $T_3(x)$, we notice that

$$\begin{aligned}
 & [\lambda(\epsilon, \eta, z_1) - \lambda(\epsilon, \eta, z_2)] \int_{-\epsilon^{-1}}^0 e^x dx \\
 & = \epsilon^2 \int_{-\epsilon^{-1}}^0 \{g(I_1)(\epsilon^{-1}\eta e^{y/2} + z_1)^+ - g(I_2)(\epsilon^{-1}\eta e^{y/2} + z_2)^+ - d(z_1 - z_2)\} e^{y/2} dy \\
 & = \epsilon^2 \int_{-\epsilon^{-1}}^0 [g(I_1) - g(I_2)] (\epsilon^{-1}\eta e^{y/2} + z_1)^+ e^{y/2} dy \\
 & \quad + \epsilon^2 \int_{-\epsilon^{-1}}^0 \{g(I_2)[(\epsilon^{-1}\eta e^{y/2} + z_1)^+ - (\epsilon^{-1}\eta e^{y/2} + z_2)^+] - d(z_1 - z_2)\} e^{y/2} dy.
 \end{aligned}$$

Therefore similar to the estimates for $T_1(x)$ and $T_2(x)$ above, we obtain

$$|\lambda(\epsilon, \eta, z_1) - \lambda(\epsilon, \eta, z_2)| \leq C\epsilon^2 \|z_1 - z_2\|.$$

Since $e^x|x - 1 + e^{-x}| \leq C$ on $[-\epsilon^{-1}, 0]$, we obtain

$$|T_3(x)| \leq C\epsilon^2 \|z_1 - z_2\|.$$

It follows that

$$\begin{aligned} \|F_{\epsilon, \eta}^1(z_1) - F_{\epsilon, \eta}^1(z_2)\| &\leq \int_{-\epsilon^{-1}}^0 (|T_1(x)| + |T_2(x)| + |T_3(x)|) dx \\ &\leq C\epsilon \|z_1 - z_2\|. \end{aligned}$$

By (3.4), we have

$$\|\alpha(\epsilon, \eta, z_1)e^{x/2} - \alpha(\epsilon, \eta, z_2)e^{x/2}\| = \|F_{\epsilon, \eta}^1(z_1) - F_{\epsilon, \eta}^1(z_2)\| \leq C\epsilon \|z_1 - z_2\|.$$

Thus $F_{\epsilon, \eta}$ is a contraction mapping on Ω provided that $\epsilon \in (0, \epsilon^0]$ and $\eta \in J$ with $\epsilon^0 = \min\{\epsilon_0, (3C)^{-1}\}$.

Summarizing, we have proved the following result.

Lemma 3.2. *There exists $\epsilon^0 \in (0, \epsilon_0]$ such that $F_{\epsilon, \eta}$ is a contraction mapping on Ω for every $\epsilon \in (0, \epsilon^0]$ and $\eta \in J$.*

Applying Banach's fixed point theorem, we obtain

Proposition 3.3. *For each $\epsilon \in (0, \epsilon^0]$ and $\eta \in J$, $F_{\epsilon, \eta}$ has a unique fixed point $z_{\epsilon, \eta} \in \Omega$.*

Remark 3.4. Since $F_{\epsilon, \eta}$ depends continuously on (ϵ, η) , the uniqueness of the fixed point implies that $z_{\epsilon, \eta}$ also depends continuously on (ϵ, η) .

3.4. The reduced equation

Proposition 3.5. *Suppose $\epsilon \in (0, \epsilon^0]$. If $\eta \in J$ satisfies*

$$\lambda(\epsilon, \eta, z_{\epsilon, \eta}) = 0, \tag{3.9}$$

then

$$u_{\epsilon, \eta} = \epsilon^{-1}\eta e^{x/2} + z_{\epsilon, \eta}(x)$$

is a positive solution to (3.1).

Proof. Since $F_{\epsilon,\eta} z_{\epsilon,\eta} = z_{\epsilon,\eta}$ and $\lambda(\epsilon, \eta, z_{\epsilon,\eta}) = 0$, from the definition of $F_{\epsilon,\eta}$ we find that $u = u_{\epsilon,\eta}$ satisfies, for $x \in (-\epsilon^{-1}, 0)$,

$$-u_{xx} + \frac{1}{4}u = -(z_{\epsilon,\eta})_{xx} + \frac{1}{4}z_{\epsilon,\eta} = f(x; \epsilon, \eta, z_{\epsilon,\eta}).$$

Using the definition of f we have

$$-u_{xx} + \left(\frac{1}{4} + \epsilon^2 d\right)u = \epsilon^2 g(\tilde{I})u^+ \geq 0 \quad \text{in } (-\epsilon^{-1}, 0), \quad (3.10)$$

with

$$\tilde{I} = \exp\left(-k_0 - \epsilon k_0 x - \epsilon k \int_{-\epsilon^{-1}}^x u(y) e^{y/2} dy\right).$$

Clearly u also satisfies the boundary condition of (3.1). Hence, due to $\epsilon^2 d > 0$, we can apply the maximum principle to (3.10) to conclude that $u \geq 0$. Thus $u^+ = u$ and u solves (3.1).

To show u is a positive solution, by the strong maximum principle, it suffices to show that $u \not\equiv 0$. But this follows trivially from

$$\int_{-\epsilon^{-1}}^0 u(x) e^{x/2} dx = \int_{-\epsilon^{-1}}^0 \epsilon^{-1} \eta e^x dx > 0. \quad \square$$

We next examine closely the reduced equation $\lambda(\epsilon, \eta, z_{\epsilon,\eta}) = 0$, that is

$$\int_{\epsilon^{-1}}^0 e^{x/2} \{g(I_{\epsilon,\eta})[\epsilon^{-1} \eta e^{x/2} + z_{\epsilon,\eta}(x)]^+ - d[\epsilon^{-1} \eta e^{x/2} + z_{\epsilon,\eta}(x)]\} dx = 0, \quad (3.11)$$

with

$$I_{\epsilon,\eta}(x) = \exp\left(-k_0 - \epsilon k_0 x - \epsilon k \int_{-\epsilon^{-1}}^x [\epsilon^{-1} \eta e^{y/2} + z_{\epsilon,\eta}(y)] e^{y/2} dy\right).$$

Multiplying (3.11) by $\epsilon \eta^{-1}$ we obtain

$$\begin{aligned} 0 &= \int_{\epsilon^{-1}}^0 e^{x/2} \{g(I_{\epsilon,\eta})[e^{x/2} + \epsilon \eta^{-1} z_{\epsilon,\eta}(x)]^+ - d[e^{x/2} + \epsilon \eta^{-1} z_{\epsilon,\eta}(x)]\} dx \\ &= \int_{\epsilon^{-1}}^0 e^x [g(I_{\epsilon,\eta}) - d] dx + \delta_1, \end{aligned}$$

with

$$\begin{aligned} |\delta_1| &= \left| \int_{\epsilon^{-1}}^0 e^{x/2} g(I_{\epsilon,\eta}) \{ [e^{x/2} + \epsilon \eta^{-1} z_{\epsilon,\eta}(x)]^+ - e^{x/2} \} dx \right| \\ &\leq C \epsilon \int_{-\epsilon^{-1}}^0 |z_{\epsilon,\eta}(x)| e^{x/2} dx \\ &\leq C \epsilon. \end{aligned}$$

We may write

$$I_{\epsilon,\eta}(x) = \xi_0 \exp(-\epsilon k_0 x - k \eta e^x) m_{\epsilon,\eta}(x),$$

with

$$m_{\epsilon,\eta}(x) = \xi_0^{-1} e^{-k_0} \exp\left(-k \epsilon \int_{-\epsilon^{-1}}^x z_{\epsilon,\eta}(y) e^{y/2} dy\right) \exp(k \eta e^{-\epsilon^{-1}}) \rightarrow 1$$

uniformly for $x \in [-\epsilon^{-1}, 0]$ and $\eta \in J$ as $\epsilon \rightarrow 0$. Therefore

$$g(I_{\epsilon,\eta}(x)) = g(\xi_0 e^{-\epsilon k_0 x - k \eta e^x}) + \tilde{\delta}_2(x)$$

with

$$\tilde{\delta}_2(x) \rightarrow 0 \text{ uniformly as } \epsilon \rightarrow 0.$$

It follows that

$$0 = \int_{-\epsilon^{-1}}^0 [g(\xi_0 e^{-\epsilon k_0 x - k \eta e^x}) - d] e^x dx + \delta_1 + \delta_2,$$

where

$$\delta_2 = \int_{-\epsilon^{-1}}^0 \tilde{\delta}_2(x) e^x dx = o(1) \quad \text{as } \epsilon \rightarrow 0.$$

We thus have

$$d[1 - \exp(-\epsilon^{-1})] = \int_{-\epsilon^{-1}}^0 g(\xi_0 e^{-\epsilon k_0 x - k \eta e^x}) e^x dx + \delta_1 + \delta_2,$$

and

$$d = \int_{-\epsilon^{-1}}^0 g(\xi_0 e^{-\epsilon k_0 x - k\eta e^x}) e^x dx + \delta_1 + \delta_2 + \delta_3$$

with

$$\delta_3 = d \exp(-\epsilon^{-1}) = o(1).$$

Finally we have

$$\begin{aligned} \int_{-\epsilon^{-1}}^0 g(\xi_0 e^{-\epsilon k_0 x - k\eta e^x}) e^x dx &= \int_{-\epsilon^{-1}}^0 g(\xi_0 e^{-\epsilon k_0 x - k\eta e^x}) (\epsilon k_0 x + k\eta e^x)' \frac{1}{k\eta} dx \\ &\quad - \frac{\epsilon k_0}{k\eta} \int_{-\epsilon^{-1}}^0 g(\xi_0 e^{-\epsilon k_0 x - k\eta e^x}) dx \\ &= \frac{1}{k\eta} \int_{-k_0 + k\eta \exp(-\epsilon^{-1})}^{k\eta} g(\xi_0 e^{-\mu}) d\mu \\ &\quad - \frac{1}{k\eta} \int_{-k_0}^0 g(\xi_0 e^{-\mu - k\eta \exp(\frac{\mu}{\epsilon k_0})}) d\mu \\ &= \frac{1}{k\eta} \int_{-k_0}^{k\eta} g(\xi_0 e^{-\mu}) d\mu + o(1) \\ &\quad - \frac{1}{k\eta} \int_{-k_0}^0 g(\xi_0 e^{-\mu}) d\mu + o(1) \\ &= \frac{1}{k\eta} \int_0^{k\eta} g(\xi_0 e^{-\mu}) d\mu + o(1). \end{aligned}$$

Therefore the reduced equation can be written as

$$d = \frac{1}{k\eta} \int_0^{k\eta} g(\xi_0 e^{-s}) ds + o(1),$$

where $o(1) \rightarrow 0$ uniformly in $\eta \in J$ as $\epsilon \rightarrow 0$. Recalling the definition of $G(\mu)$ we find that the reduced equation can be written as

$$d = G(k\eta) + o(1). \quad (3.12)$$

Fix η_1, η_2 and η_3 in J such that

$$\eta_1 \in \left(\frac{\mu_1}{2k}, \frac{\mu_1}{k}\right), \quad \eta_2 \in \left(\frac{\mu_1}{k}, \frac{\mu_2}{k}\right), \quad \eta_3 \in \left(\frac{\mu_2}{k}, \frac{2\mu_2}{k}\right).$$

Then from (3.8) we find that

$$d > G(k\eta_1), \quad d < G(k\eta_2), \quad d > G(k\eta_3).$$

Since $\lambda(\epsilon, \eta, z_{\epsilon, \eta})$ is a continuous function in (ϵ, η) , the term $o(1)$ in (3.12) can be written as $o(\epsilon, \eta)$ which is continuous and satisfies $o(\epsilon, \eta) \rightarrow 0$ uniformly in $\eta \in J$ as $\epsilon \rightarrow 0$. Therefore, for all small $\epsilon > 0$, say $\epsilon \in (0, \epsilon^*]$, with some $\epsilon^* \in (0, \epsilon^0)$, the equation

$$d = G(k\eta) + o(\epsilon, \eta)$$

has at least two solutions in J : $\eta_1^\epsilon \in (\eta_1, \eta_2)$ and $\eta_2^\epsilon \in (\eta_2, \eta_3)$. Moreover,

$$\lim_{\epsilon \rightarrow 0} \eta_1^\epsilon = \frac{\mu_1}{k}, \quad \lim_{\epsilon \rightarrow 0} \eta_2^\epsilon = \frac{\mu_2}{k} \quad \text{and} \quad G'(k\eta_1^\epsilon) > 0 > G'(k\eta_2^\epsilon).$$

We have thus proved the following result.

Theorem 3.6. Suppose that (3.7) holds. Then there exists $\epsilon^* > 0$ such that for each $\epsilon \in (0, \epsilon^*]$, (3.1) has two positive solutions of the form

$$u_1 = \epsilon^{-1}(\eta_1^\epsilon e^{x/2} + z_1^\epsilon), \quad u_2 = \epsilon^{-1}(\eta_2^\epsilon e^{x/2} + z_2^\epsilon)$$

with $z_1^\epsilon, z_2^\epsilon \in H$ satisfying $\|z_i^\epsilon\| \leq C\epsilon$, and

$$\lim_{\epsilon \rightarrow 0} \eta_1^\epsilon = \frac{\mu_1}{k}, \quad \lim_{\epsilon \rightarrow 0} \eta_2^\epsilon = \frac{\mu_2}{k}, \quad G'(\mu_1) > 0 > G'(\mu_2).$$

Since, for $i = 1, 2$,

$$u_i = \epsilon^{-1}(\eta_i^\epsilon e^{x/2} + z_i^\epsilon) = \epsilon^{-1} \left(\frac{\mu_i}{k} e^{x/2} + \tilde{z}_i^\epsilon \right)$$

with $\tilde{z}_i^\epsilon := z_i^\epsilon + o(1)e^{x/2}$, we find that $\|\tilde{z}_i^\epsilon\| = o(1)$, and part (ii) of Theorem 1.2 now follows directly from Theorem 3.6.

4. Stability analysis

In this section, we consider the linearized stability of the two solutions u_1 and u_2 in [Theorem 3.6](#). Let $u^* = u_\epsilon^*$ denote either u_1 or u_2 . The linearized eigenvalue problem of (3.1) at $u = u^*$ is given by

$$\begin{cases} \phi_{xx} - \frac{1}{4}\phi + \epsilon^2[g(I_\epsilon) - d]\phi \\ - \epsilon^2 u^* g'(I_\epsilon) I_\epsilon \epsilon k \int_{-1/\epsilon}^x \phi(s) e^{s/2} ds + \lambda \phi = 0, & x \in (-1/\epsilon, 0), \\ \phi_x - \frac{1}{2}\phi = 0, & x \in \{-1/\epsilon, 0\}, \end{cases} \quad (4.1)$$

where

$$I_\epsilon(x) = e^{-k_0 - \epsilon k_0 x - k \epsilon \int_{-1/\epsilon}^x u^*(s) e^{s/2} ds}.$$

We will show that, for every small $\epsilon > 0$, this problem has an eigenpair (λ, ϕ) of the form

$$\lambda = \epsilon^2 \mu_\epsilon, \quad \phi(x) = e^{x/2} + \epsilon w_\epsilon(x), \quad w_\epsilon \in H,$$

with $\mu_\epsilon \rightarrow \mu_0 \neq 0$ as $\epsilon \rightarrow 0$ and $\|w_\epsilon\| \leq C$ for all $\epsilon > 0$ small. Here H is the Banach space defined in the previous section. Moreover, we will show that $\mu_0 < 0$ when $u^* = u_1$, and $\mu_0 > 0$ when $u^* = u_2$. This implies that u_1 is linearly unstable. Although this does not prove that u_2 is linearly stable, but as explained below, it strongly suggests the validity of such a conclusion.

The difficulty in proving the linearized stability of u_2 is due to the fact that (4.1) is a nonlocal eigenvalue problem, and the corresponding linear operator to this problem is not self-adjoint, nor order-preserving. Therefore it is difficult to use variational characterization or the well-known Krein–Rutman theorem to know the relationship of the eigenvalue obtained above to the rest of the spectrum. However, since $\phi = e^{x/2} + \epsilon w_\epsilon$ is a small perturbation of a positive function, it is reasonable to believe that $\lambda = \epsilon \mu_\epsilon$ behaves like a principle eigenvalue, with all other eigenvalues having real parts strictly greater than λ , which would imply the linearized stability of u_2 .

We now look for an eigenpair of (4.1) of the form

$$\lambda = \epsilon^2 \mu, \quad \phi = e^{x/2} + \epsilon w, \quad w \in H.$$

Substituting these into (4.1) we obtain

$$\begin{cases} w_{xx} - \frac{1}{4}w + \epsilon[g(I_\epsilon) - d](e^{x/2} + \epsilon w) \\ - \epsilon u^* g'(I_\epsilon) I_\epsilon \epsilon k \int_{-1/\epsilon}^x [e^s + \epsilon w e^{s/2}] ds + \epsilon \mu (e^{x/2} + \epsilon w) = 0, & x \in (-1/\epsilon, 0), \\ w_x - \frac{1}{2}w = 0, & x \in \{-1/\epsilon, 0\}. \end{cases} \quad (4.2)$$

Multiplying the first equation in (4.2) by $\epsilon^{-1}e^{x/2}$, and integrating over $(-1/\epsilon, 0)$, we obtain

$$\begin{aligned} & \int_{-1/\epsilon}^0 [g(I_\epsilon) - d](e^x + \epsilon w e^{x/2}) dx - \int_{-1/\epsilon}^0 e^{x/2} u^* g'(I_\epsilon) I_\epsilon \epsilon k \int_{-1/\epsilon}^x [e^s + \epsilon w e^{s/2}] ds dx \\ &= -\mu \int_{-1/\epsilon}^0 e^x dx = -\mu(1 - e^{-1/\epsilon}). \end{aligned} \quad (4.3)$$

This defines μ as a functional of w and we may write

$$\mu = \mu(w, \epsilon).$$

Much as in the previous section, from (4.2) we obtain

$$\begin{aligned} w(x) &= \epsilon \int_x^0 [g(I_\epsilon) - d](e^{y/2} + \epsilon w) 2 \sinh\left(\frac{x-y}{2}\right) dy \\ &\quad - \epsilon \int_x^0 u^* g'(I_\epsilon) I_\epsilon \epsilon k \left(\int_{-1/\epsilon}^y [e^s + \epsilon w e^{s/2}] ds \right) 2 \sinh\left(\frac{x-y}{2}\right) dy \\ &\quad + \epsilon \mu \int_x^0 (e^{y/2} + \epsilon w) 2 \sinh\left(\frac{x-y}{2}\right) dy + \gamma e^{x/2}, \end{aligned}$$

with $\gamma \in \mathbb{R}^1$ chosen such that $\int_{-1/\epsilon}^0 e^{x/2} w(x) dx = 0$.

For $w \in H$, we now define the operator

$$L_\epsilon(w)(x) := L_\epsilon^1(w)(x) + L_\epsilon^2(w)(x) + L_\epsilon^3(w)(x) + \gamma(w, \epsilon) e^{x/2},$$

with

$$\begin{aligned} L_\epsilon^1(w)(x) &:= \epsilon \int_x^0 [g(I_\epsilon) - d](e^{y/2} + \epsilon w) 2 \sinh\left(\frac{x-y}{2}\right) dy, \\ L_\epsilon^2(w)(x) &:= -\epsilon \int_x^0 u^* g'(I_\epsilon) I_\epsilon \epsilon k \left(\int_{-1/\epsilon}^y [e^s + \epsilon w e^{s/2}] ds \right) 2 \sinh\left(\frac{x-y}{2}\right) dy, \\ L_\epsilon^3(w)(x) &:= \epsilon \mu(w, \epsilon) \int_x^0 (e^{y/2} + \epsilon w) 2 \sinh\left(\frac{x-y}{2}\right) dy, \end{aligned}$$

where $\mu(w, \epsilon)$ is determined by (4.3), and

$$\gamma(w, \epsilon) = - \left[\int_{-1/\epsilon}^0 e^x dx \right]^{-1} \int_{-1/\epsilon}^0 e^{x/2} [L_\epsilon^1(w)(x) + L_\epsilon^2(w)(x) + L_\epsilon^3(w)(x)] dx.$$

We are going to show that there exists $C > 0$ such that for every small $\epsilon > 0$, L_ϵ maps $B := \{w \in H : \|w\| \leq 2C\}$ into itself, and is a contraction mapping. Therefore L_ϵ has a unique fixed point w_ϵ in B : $L_\epsilon(w_\epsilon) = w_\epsilon$. Clearly this gives an eigenpair to (4.1):

$$(\lambda, \phi) = (\epsilon^2 \mu(w_\epsilon, \epsilon), e^{x/2} + \epsilon w_\epsilon).$$

From (4.3), we easily obtain

$$|\mu(w, \epsilon)| \leq C(1 + \epsilon \|w\|) \quad \text{for all small } \epsilon > 0 \text{ and some } C > 0.$$

Clearly

$$e^{x/2} \left| \int_x^0 (e^{y/2} + \epsilon w) 2 \sinh\left(\frac{x-y}{2}\right) dy \right| \leq \int_x^0 [e^y + \epsilon |w| e^{y/2}] |e^{x-y} - 1| dy \leq C(1 + \epsilon \|w\|).$$

It follows that

$$\|L_\epsilon^3(w)\| = \int_{-1/\epsilon}^0 e^{x/2} |L_\epsilon^3(w)(x)| dx \leq C(1 + \epsilon \|w\|)^2.$$

Using

$$\begin{aligned} e^{x/2} |L_\epsilon^1(w)(x)| &= \epsilon e^{x/2} \left| \int_x^0 [g(I_\epsilon) - d] (e^{y/2} + \epsilon w) (e^{\frac{x-y}{2}} - e^{\frac{y-x}{2}}) dy \right| \\ &\leq \epsilon \int_x^0 [g(I_\epsilon) + d] (e^y + \epsilon |w| e^{y/2}) |e^{x-y} - 1| dy \\ &\leq \epsilon C \int_{-1/\epsilon}^0 (e^y + \epsilon |w| e^{y/2}) dy \leq \epsilon C(1 + \epsilon \|w\|), \end{aligned}$$

we deduce

$$\|L_\epsilon^1(w)\| \leq C(1 + \epsilon \|w\|).$$

To estimate $L_\epsilon^2(w)$ we notice that

$$\left| \int_{-1/\epsilon}^y [e^s + \epsilon w e^{s/2}] ds \right| \leq C(1 + \epsilon \|w\|) \quad \text{for all } y \in (-1/\epsilon, 0),$$

$$|u^* g'(I_\epsilon) I_\epsilon \epsilon k| \leq C(e^{y/2} + \epsilon |z_i^\epsilon(y)|),$$

and hence

$$e^{x/2} |L_\epsilon^2(w)(x)| \leq C(1 + \epsilon \|w\|) \int_x^0 (e^y + \epsilon |z_i^\epsilon(y)| e^{y/2}) |e^{x-y} - 1| dy \leq C(1 + \epsilon \|w\|).$$

It follows that

$$\|L_\epsilon^2(w)\| \leq C(1 + \epsilon \|w\|).$$

From the definition of $\gamma(w, \epsilon)$ we obtain

$$\|\gamma(w, \epsilon) e^{x/2}\| \leq \|L_\epsilon^1(w) + L_\epsilon^2(w) + L_\epsilon^3(w)\| \leq C(1 + \epsilon \|w\|)^2.$$

Therefore

$$\|L_\epsilon(w)\| \leq C(1 + \epsilon \|w\|)^2.$$

If $\|w\| \leq 2C$, we obtain

$$\|L_\epsilon(w)\| \leq C(1 + 2\epsilon C)^2 \leq 2C$$

provided that $\epsilon \in (0, \epsilon_0]$, with ϵ_0 determined by $(1 + 2\epsilon_0 C)^2 = 2$.

Next we show that L_ϵ is a contraction mapping on $B \subset H$ for all small $\epsilon > 0$. Let $w_1, w_2 \in B$. Then

$$L_\epsilon^1(w_1) - L_\epsilon^1(w_2) = \epsilon \int_x^0 [g(I_\epsilon) - d] \epsilon (w_1 - w_2) 2 \sinh\left(\frac{x-y}{2}\right) dy.$$

It follows easily that

$$\|L_\epsilon^1(w_1) - L_\epsilon^1(w_2)\| \leq \epsilon C \|w_1 - w_2\|.$$

Similarly

$$L_\epsilon^2(w_1) - L_\epsilon^2(w_2) = -\epsilon \int_x^0 u^* g'(I_\epsilon) I_\epsilon \epsilon k \left(\int_{-1/\epsilon}^y \epsilon (w_1 - w_2) e^{s/2} ds \right) 2 \sinh\left(\frac{x-y}{2}\right) dy,$$

which gives

$$\|L_\epsilon^2(w_1) - L_\epsilon^2(w_2)\| \leq \epsilon C \|w_1 - w_2\|.$$

Finally

$$\begin{aligned} L_\epsilon^3(w_1) - L_\epsilon^3(w_2) &= \epsilon \mu(w_1, \epsilon) \int_x^0 \epsilon (w_1 - w_2) 2 \sinh\left(\frac{x-y}{2}\right) dy \\ &\quad + \epsilon [\mu(w_1, \epsilon) - \mu(w_2, \epsilon)] \int_x^0 (e^{y/2} + \epsilon w_2) 2 \sinh\left(\frac{x-y}{2}\right) dy. \end{aligned}$$

By (4.3) we easily see that

$$|\mu(w_2, \epsilon) - \mu(w_1, \epsilon)| \leq \epsilon C \|w_1 - w_2\|.$$

It then follows easily that

$$\|L_\epsilon^3(w_1) - L_\epsilon^3(w_2)\| \leq \epsilon C \|w_1 - w_2\|.$$

We now obtain

$$\begin{aligned} &\|\gamma(w_1, \epsilon)e^{x/2} - \gamma(w_2, \epsilon)e^{x/2}\| \\ &\leq \|L_\epsilon^1(w_1) - L_\epsilon^1(w_2)\| + \|L_\epsilon^1(w_1) - L_\epsilon^1(w_2)\| + \|L_\epsilon^3(w_1) - L_\epsilon^3(w_2)\| \\ &\leq \epsilon C \|w_1 - w_2\|. \end{aligned}$$

Thus we have

$$\|L_\epsilon(w_1) - L_\epsilon(w_2)\| \leq \epsilon C \|w_1 - w_2\| \leq \frac{1}{2} \|w_1 - w_2\| \quad \text{for all } w_1, w_2 \in B$$

provided that $\epsilon > 0$ is small enough, say $0 < \epsilon \leq \epsilon_1 \leq \epsilon_0$.

We may now use the contraction mapping theorem to conclude that for every small $\epsilon > 0$, say $\epsilon \in (0, \epsilon_1]$, L_ϵ has a unique fixed point w_ϵ in B : $L_\epsilon(w_\epsilon) = w_\epsilon$. It follows that, for such ϵ , (4.1) has an eigenpair of the form $(\lambda, \phi) = (\epsilon^2 \mu(w_\epsilon, \epsilon), e^{x/2} + \epsilon w_\epsilon)$.

Let us now determine the sign of $\mu(w_\epsilon, \epsilon)$ for $u^* = u_1$ and $u^* = u_2$, respectively. We will denote $\mu(w_\epsilon, \epsilon)$ by μ_ϵ^i for $u^* = u_i$, $i = 1, 2$. We define $I_\epsilon^i(x)$ from $I_\epsilon(x)$ analogously. From its definition, we easily see that

$$\lim_{\epsilon \rightarrow 0} I_\epsilon^i(x) = e^{-k_0 - \int_{-\infty}^x k \eta_i e^s ds} = \xi_0 e^{-\mu_i e^x} \quad \text{uniformly in compact subsets of } (-\infty, 0].$$

Thus we can use (4.3) to obtain

$$\begin{aligned} -\lim_{\epsilon \rightarrow 0} \mu_{\epsilon}^i &= \int_{-\infty}^0 [g(\xi_0 e^{-\mu_i e^x}) - d] e^x dx - \int_{-\infty}^0 \eta_i k e^x g'(\xi_0 e^{-\mu_i e^x}) \xi_0 e^{-\mu_i e^x} e^x dx \\ &= \int_0^1 g(\xi_0 e^{-\mu_i s}) ds - d - \int_0^1 \xi_0 \mu_i s e^{-\mu_i s} g'(\xi_0 e^{-\mu_i s}) ds \\ &= G(\mu_i) - d + \mu_i G'(\mu_i) = \mu_i G'(\mu_i). \end{aligned}$$

Therefore

$$\mu_{\epsilon}^1 = -\mu_1 G'(\mu_1) + o_{\epsilon}(1) < 0, \quad \mu_{\epsilon}^2 = -\mu_2 G'(\mu_2) + o_{\epsilon}(1) > 0.$$

Summarizing, we have proved the following result:

Theorem 4.1. *Let u_1 and u_2 be given by Theorem 3.6. Then for each small $\epsilon > 0$, the linearized eigenvalue problem (4.1) with $u^* = u_i$ has an eigenpair of the form*

$$(\lambda, \phi) = (\epsilon^2 \mu_{\epsilon}^i, e^{x/2} + \epsilon w_{\epsilon}^i), \quad i = 1, 2,$$

with $w_{\epsilon}^i \in H$ having a uniform bound independent of ϵ , and

$$\mu_{\epsilon}^1 = -\mu_1 G'(\mu_1) + o_{\epsilon}(1) < 0, \quad \mu_{\epsilon}^2 = -\mu_2 G'(\mu_2) + o_{\epsilon}(1) > 0.$$

References

- [1] M.G. Crandall, P.H. Rabinowitz, Bifurcation from simple eigenvalues, *J. Funct. Anal.* 8 (1971) 321–340.
- [2] M.G. Crandall, P.H. Rabinowitz, Bifurcation, perturbation of simple eigenvalues, and linearized stability, *Arch. Ration. Mech. Anal.* 52 (1973) 161–180.
- [3] Y. Du, The structure of the solution set of a class of nonlinear eigenvalue problems, *J. Math. Anal. Appl.* 170 (1992) 567–580.
- [4] Y. Du, S.-B. Hsu, Concentration phenomena in a nonlocal quasi-linear problem modeling phytoplankton I: existence, *SIAM J. Math. Anal.* 40 (2008) 1419–1440.
- [5] Y. Du, S.-B. Hsu, Concentration phenomena in a nonlocal quasi-linear problem modeling phytoplankton II: limiting profile, *SIAM J. Math. Anal.* 40 (2008) 1441–1470.
- [6] Y. Du, S.-B. Hsu, On a nonlocal reaction–diffusion problem arising from the modeling of phytoplankton growth, *SIAM J. Math. Anal.* 42 (2010) 1305–1333.
- [7] Y. Du, L. Mei, On a nonlocal reaction–diffusion–advection equation modelling phytoplankton dynamics, *Nonlinearity* 24 (2011) 319–349.
- [8] U. Ebert, M. Arayas, N. Temme, B. Sommeijer, J. Huisman, Critical condition for phytoplankton blooms, *Bull. Math. Biol.* 63 (2001) 1095–1124.
- [9] D.J. Gerla, W.M. Wolf, J. Huisman, Photoinhibition and the assembly of light-limited phytoplankton communities, *Oikos* 120 (2011) 359–368.
- [10] E.W. Helbling, et al., UVR-induced photosynthetic inhibition dominates over DNA damage in marine dinoflagellates exposed to fluctuating solar radiation regimes, *J. Exp. Mar. Biol. Ecol.* 365 (2008) 96–102.
- [11] W.J. Henley, Measurement and interpretation of photosynthetic light-response curves in algae in the context of photoinhibition and diel changes, *J. Phycol.* 29 (1993) 729–739.

- [12] S.-B. Hsu, C.-J. Lin, C.-H. Hsieh, K. Yoshiyama, Dynamics of phytoplankton communities under photoinhibition, *Bull. Math. Biol.* 75 (2013) 1207–1232.
- [13] S.-B. Hsu, Y. Lou, Single phytoplankton species growth with light and advection in a water column, *SIAM J. Appl. Math.* 70 (2010) 2942–2974.
- [14] J. Huisman, M. Arrayas, U. Ebert, B. Sommeijer, How do sinking phytoplankton species manage to persist?, *Amer. Nat.* 159 (2002) 245–254.
- [15] J. Huisman, P. van Oostveen, F.J. Weissing, Species dynamics in phytoplankton blooms: incomplete mixing and competition for light, *Amer. Nat.* 154 (1999) 46–67.
- [16] J. Huisman, N.N. Pham Thi, D.M. Karl, B. Sommeijer, Reduced mixing generates oscillations and chaos in oceanic deep chlorophyll maxima, *Nature* 439 (2006) 322–325.
- [17] H. Ishii, I. Takagi, Global stability of stationary solutions to a nonlinear diffusion equation in phytoplankton dynamics, *J. Math. Biol.* 16 (1982) 1–24.
- [18] H. Ishii, I. Takagi, A nonlinear diffusion equation in phytoplankton dynamics with self-shading effect, in: *Mathematics in Biology and Medicine*, Bari, 1983, in: *Lecture Notes in Biomath.*, vol. 57, Springer, Berlin, 1985, pp. 66–71.
- [19] C.A. Klausmeier, E. Litchman, Algal games: the vertical distribution of phytoplankton in poorly mixed water columns, *Limnol. Oceanogr.* 46 (2001) 1998–2007.
- [20] C.A. Klausmeier, E. Litchman, S.A. Levin, Phytoplankton growth and stoichiometry under multiple nutrient limitation, *Limnol. Oceanogr.* 49 (2004) 1463–1470.
- [21] T. Kolokolnikov, C.H. Ou, Y. Yuan, Phytoplankton depth profiles and their transitions near the critical sinking velocity, *J. Math. Biol.* 59 (2009) 105–122.
- [22] E. Litchman, C.A. Klausmeier, J.R. Miller, O.M. Schofield, P.G. Falkowski, Multinutrient, multi-group model of present and future oceanic phytoplankton communities, *Biogeosciences* 3 (2006) 585–606.
- [23] S.P. Long, et al., Photoinhibition of **photosynthesis** in nature, *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 45 (1994) 633–663.
- [24] M. Moser, et al., Photosynthetic and growth response of freshwater picocyanobacteria are strain-specific and sensitive to photoacclimation, *J. Plankton Res.* 31 (2009) 349–357.
- [25] P. Rabinowitz, Some global results for nonlinear eigenvalue problems, *J. Funct. Anal.* 7 (1971) 487–513.
- [26] N. Shigesada, A. Okubo, Analysis of the self-shading effect on algal vertical distribution in natural waters, *J. Math. Biol.* 12 (1981) 311–326.
- [27] S. Takahashi, N. Murata, How do environmental stresses accelerate photoinhibition?, *Trends Plant Sci.* 13 (2008) 178–182.
- [28] K. Yoshiyama, J.P. Mellard, E. Litchman, C.A. Klausmeier, Phytoplankton competition for nutrients and light in a stratified water column, *Amer. Nat.* 174 (2) (2009) 190–203.
- [29] A. Zagaris, A. Doelman, N.N. Pham Thi, B.P. Sommeijer, Blooming in a nonlocal, coupled phytoplankton-nutrient model, *SIAM J. Appl. Math.* 69 (2009) 1174–1204.

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