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On a nonlocal reaction–diffusion–advection system modelling the growth of phytoplankton with cell quota structure

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Abstract

Phytoplankton species in a water column compete for mineral nutrients and light, and the existing models usually neglect differences in the nutrient content and the amount of light absorbed of individuals. In this current paper, we examine a size-structured and nonlocal reaction–diffusion–advection system which describes the dynamics of a single phytoplankton species in a water column where the species depends simply on light for its growth. Our model is under the assumption that the amount of light absorbed by individuals is proportional to cell size, which varies for populations that reproduce by simple division into two equally-sized daughters. We first establish the existence of a critical death rate and our analysis indicates that the phytoplankton survives if and only if its death rate is less than the critical death rate. The critical death rate depends on a general reproductive rate, the characteristics of the water column (e.g., turbulent diffusion rate, sinking, depth), cell growth, cell division, and cell size.

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1. Introduction

Classical phytoplankton competition studies often assume a simple, well-mixed laboratory system, such as the chemostat culture system, in which a nutrient medium is pumped, balanced by an outflow that removes nutrients and organisms [30]. The chemostat is a basic piece of ideal apparatus and it has been thought of as a lake or pond in a laboratory. However, in many aquatic environments, the habitat may be poorly mixed, and have spatial gradients of resource availability. For example, the vertical transport (motion) of phytoplankton species in the water column is determined by vertical turbulent diffusion and advection (sinking or buoyant).

Another factor that may affect the competition between species for resources is size structure of algal communities. The simplest competition models neglect differences between individuals, assuming a constant quota of resource per individual [12,17]. In fact, quotas may vary. The variable-internal-stores models [11,18,29] assume that all individuals have the same quota at any instant and the dynamics of quota for a species is governed by an ordinary differential equation. Alternatively, Diekmann et al. [3,7,16] proposed a structured population model in which quotas may differ among individuals at any instant.

Investigation of the mechanisms contributing to the emergence of size structures in spatially varying environments is a challenging issue in mathematical ecology. Resource storage within individuals leads to population structure and it must be combined with the spatial variation of the environment. There are at least three possible ways to this issue. One is the Lagrangian modelling approach [13] which assumes that each competitor population is divided into many subpopulations that move through two model habitats with gradient in nutrient availability. This model can not be analyzed mathematically and require extensive computation to achieve results. A second approach is an approximation that averages over differences among individuals at a given location, in their amounts of stored nutrient. Equivalently, one assumes that at any location, all individuals have the same quota, as if there were instantaneous redistribution of resources among individuals at the same place. This assumption yields a set of analytically and computationally tractable partial differential equations [14,20,23,24]. The third one combines the structured population model proposed in [3,7,16] with the physical transport equations governing spatial distributions of populations and nutrients. In [15], the authors assume nutrient content of individuals is proportional to cell size and the habitat is taken to be an unstirred chemostat where organisms and nutrients move by simple diffusion.

The growth of population depends critically on the supply of two fundamental types of resources: light and mineral nutrients. In phytoplankton communities, species typically compete for nutrient and light which are complementary resources for their growth [4,5,21,25]. There are also two possibly extreme cases. In oligotrophic ecosystems with ample supply of light, they tend to compete only for nutrients [26,28], and in eutrophic environments with ample nutrients supply, they compete only for light [6,8,9,19,22].

In this current paper, we focus on the study of the dynamics of a single species in a water column in eutrophic ecosystem, that is, the species depends only on light for its growth. As in [15], we shall assume the amount of light absorbed by individuals is proportional to cell size, which varies for populations that reproduce by simple division into two equally-sized daughters, and species move by vertical turbulent diffusion and advection (sinking or buoyant). Most of phytoplankton species have tendency to sink as they are heavier than water while some species will float as they have a lower density than water and it is called buoyant [9]. In this paper, due to mathematical restrictions, we only consider the sinking case, that is, we shall assume that the advection coefficient is nonnegative.

The rest of the paper is organized as follows. The mathematical model is described in the next section. In Section 3, we study a population operator with vertical turbulent diffusion and advection. In Section 4, we are able to reduce our structured population model into the classical P.D.E. system by using the results in Section 3. We note that our reduced system is similar to those in [6,8,19], but the boundary condition at the bottom of the water column is different. We may not directly apply the previous work [6,8,19] to our system, and hence, the detailed analyses of the reduced system are given in Section 5. Brief discussions are presented in Section 6.

2. Description of the model

In this section, we first review the following single population model with size structure [3,7,16]:

$$\frac{\partial n(t,q)}{\partial t} + \frac{\partial (g(q)n(t,q))}{\partial q} = -b(q)n(t,q) + 4b(2q)n(t,2q). \tag{2.1}$$

Here t denotes time, q stands for the size of an individual cell. n is the population density function, that is, $\int_{q_1}^{q_2} n(t,q)dq$ represents the number of cells with size between q_1 and q_2 at time t. The functions $b(q)$ and $g(q)$ are the rates at which cells of size q divide and grow, respectively. The second term at the left hand side denotes changes due to the growth. The last two terms describe the reproduction process. Note that we ignore the death or dilution of cells in (2.1). The factor 4 in the birth term may be strange to the readers and we refer the Appendix in [3] for a derivation of equation (2.1).

We assume that an individual cannot divide before reaching a minimal size $q_{\min} > 0$. Consequently, cells with size less than $\frac{1}{2}q_{\min}$ can not exist, which is expressed by the boundary condition

$$n(t, \frac{1}{2}q_{\min}) = 0. \tag{2.2}$$

Furthermore, we assume that cells have to divide before reaching a maximal size which is denoted by $q_{\max}$. Thus we have to impose the following condition on b:

$$\int_{q_{\min}}^{q_{\max}} b(q)dq = \infty.$$

Throughout this paper, we impose the following assumptions on g and b:

$$(\mathrm{H_g}) \qquad g \text{ is a continuous, strictly positive function on } [\frac{1}{2}q_{\min}, q_{\max}].$$

$$(\mathrm{H_b}) \qquad b(q) = 0 \text{ on } [\frac{1}{2}q_{\min}, q_{\min}] \text{ and } b(q) > 0 \text{ on } (q_{\min}, q_{\max}),$$

$$b \text{ is integrable on } [q_{\min}, q_{\max} - \epsilon] \text{ for all } \epsilon > 0 \text{ and}$$

$$\lim_{\epsilon \downarrow 0} \int_{q_{\min}}^{q_{\max}-\epsilon} b(q)dq = \infty.$$

We shall assume that the initial condition n^0 is

$$n(0,q) = n^0(q). \tag{2.3}$$

Next, we shall incorporate size structure (2.1) into a water column with a cross section of one unit area. Let x denote the depth within the water column, where x runs from 0 (top) to L (bottom). Let $n(t,q,x)$ represent the density of species having quota q at time t and depth x. We assume that phytoplankton transport is governed by turbulent diffusion D and sinking term ν ($\nu > 0$). The specific growth rate can be determined by a production term $\beta(I(x,t))$ and cell size, which varies for populations that reproduce by division; $dn(t,q,x)$ represents a loss term of species. We assume that the specific production rate of a species, $\beta(I(x,t))$, is an increasing and possibly saturating function of light intensity $I(x,t)$. There is no production without light, that is, $\beta(0) = 0$. Typically, the Monod function is $\beta(I) := \frac{\mu_{\max} I}{a+I}$.

Following [22,27], the light intensity at each depth is described by Lambert–Beer law. This law states that the amount of light absorbed at depth x is proportional to the light intensity at depth x:

$$\frac{\partial I(x,t)}{\partial x} = -K(x,t)I(x,t). \tag{2.4}$$

We assume that the constant of proportionality, $K(x,t)$, consists of all components that absorb light, including the water itself and the number of cells with size between $\frac{q_{\min}}{2}$ and $q_{\max}$ at time t and depth x:

$$K(x,t) = k_0 + k_1 \int_{\frac{q_{\min}}{2}}^{q_{\max}} n(t,q,x)dq, \tag{2.5}$$

where k_0 is the background turbidity that summarizes light absorption by all nonphytoplankton components, and k_1 is the specific light attenuation coefficient of phytoplankton species. From (2.4) and (2.5), it follows that the light intensity $I(x,t)$ is given by

$$I = I(x,t) = I_0 \exp(-k_0 x - k_1 \int_0^x \int_{\frac{q_{\min}}{2}}^{q_{\max}} n(t,q,s)dqds), \tag{2.6}$$

where I_0 is the incident light intensity.

The zero-flux boundary conditions apply to $n(t, q, x)$ at the top of the habitat ($x = 0$), and absorbing conditions apply at the bottom ($x = L$). This kind of boundary conditions were used in the recent work [14]. These assumptions lead to the following system:

$$\begin{cases} \frac{\partial n(t,q,x)}{\partial t} = D\frac{\partial^2 n}{\partial x^2} - \nu\frac{\partial n}{\partial x} + \beta(I(x,t))\{-\frac{\partial[g(q)n(t,q,x)]}{\partial q} - b(q)n(t,q,x) \\ \qquad\qquad + 4b(2q)n(t,2q,x)\} - dn(t,q,x),\ t>0,\ \frac{q_{\min}}{2} < q < q_{\max},\ 0<x<L, \\ \nu n(t,q,0) - D\frac{\partial n}{\partial x}(t,q,0) = n(t,q,L) = 0,\ t>0,\ \frac{q_{\min}}{2} < q < q_{\max}, \\ n(t,\frac{q_{\min}}{2},x) = 0,\ t>0,\ 0<x<L, \\ n(0,q,x) = n^0(q,x),\ \frac{q_{\min}}{2} < q < q_{\max},\ 0<x<L. \end{cases} \tag{2.7}$$

3. Preliminaries

In this section, we shall study a population operator with vertical turbulent diffusion and advection. Let $E(q) = \exp(-\int_{q_{\min}/2}^{q} \frac{b(\eta)}{g(\eta)} d\eta)$. Then the transformation

$$m(t,q) = \frac{g(q)}{E(q)} n(t,q) \tag{3.1}$$

leads the system (2.1), (2.2) and (2.3) into the following evolution equation (see, e.g., [3] and [7, p. 48]):

$$\begin{cases} \frac{\partial m(t,q)}{\partial t} = -g(q)\frac{\partial m(t,q)}{\partial q} + k(q)m(t,2q), \\ m(t,\frac{1}{2}q_{\min}) = 0, \\ m(0,q) = m^0(q), \end{cases} \tag{3.2}$$

where

$$k(q) = \begin{cases} 4\frac{g(q)}{E(q)}\frac{E(2q)}{g(2q)} b(2q),\ \text{for } \frac{1}{2}q_{\min} \le q \le \frac{1}{2}q_{\max}, \\ 0,\ \text{for } q > \frac{1}{2}q_{\max}, \end{cases} \tag{3.3}$$

and $m^0(q) = \frac{g(q)}{E(q)} n^0(q)$. It is clear that $E(q_{\max}) = 0$. From (3.1), it follows that $n(t, q)$ has to go to zero as $q \uparrow q_{\max}$ (see, e.g., [7, p. 49]). That is, $n(t, q_{\max}) = 0$ holds automatically.

Throughout the rest of this paper, we make the following assumption:

$$q_{\min} > \frac{1}{2} q_{\max}, \tag{3.4}$$

which means that the smallest mother is still larger than the biggest daughter or, in other words, a cell which is just created cannot divide.

In [15, Section 3.1], the authors considered the system (3.2) in the Hilbert space $L^2(\frac{q_{\min}}{2}, q_{\max})$, that is,

$$\begin{cases} \frac{\partial m(t,q)}{\partial t} = \mathbf{A}m(t,q), \\ m(t,\frac{1}{2}q_{\min}) = 0, \\ m(0,q) = m^0(q), \end{cases}$$

where $\mathbf{A}$ is the following population operator defined in the $L^2(\frac{q_{\min}}{2}, q_{\max})$ space:

$$\mathbf{A}\phi(q) = \begin{cases} -g(q)\frac{d\phi(q)}{dq} + k(q)\phi(2q), \text{ for } \frac{q_{\min}}{2} \le q \le \frac{q_{\max}}{2}, \\ -g(q)\frac{d\phi(q)}{dq}, \text{ for } \frac{q_{\max}}{2} < q \le q_{\max}, \end{cases} \tag{3.5}$$

with a domain $D(\mathbf{A}) = \{\phi(q) \mid \phi, \ \mathbf{A}\phi \in L^2(\frac{q_{\min}}{2}, q_{\max}), \ \phi(\frac{q_{\min}}{2}) = 0\}$.

For $\lambda \in C$, we assumes that $\mathrm{R}(\lambda, \mathbf{A}) := (\lambda I - \mathbf{A})^{-1}$ denotes the resolvent of $\mathbf{A}$. Let

$$G(q) = \int_{\frac{q_{\min}}{2}}^{q} \frac{d\xi}{g(\xi)}, \tag{3.6}$$

$$\pi(\lambda) = \int_{\frac{q_{\min}}{2}}^{\frac{q_{\max}}{2}} e^{\lambda(G(\xi)-G(2\xi))} \frac{k(\xi)}{g(\xi)} d\xi, \tag{3.7}$$

$$\zeta(\lambda, f) = \int_{\frac{q_{\min}}{2}}^{\frac{q_{\max}}{2}} e^{\lambda(G(\xi)-G(q_{\max}/2))} \left[f(\xi) + k(\xi) \int_{\frac{q_{\max}}{2}}^{2\xi} e^{\lambda(G(\eta)-G(2\xi))} \frac{f(\eta)}{g(\eta)} d\eta \right] \frac{d\xi}{g(\xi)}. \tag{3.8}$$

Then

Lemma 3.1. *(See [15, Lemma 3.1].) Suppose that the assumption (3.4) holds. Let $\rho(\mathbf{A})$ and $\sigma_p(\mathbf{A})$ represent the resolvent set and point spectral set of $\mathbf{A}$, respectively.*

(i) *If $\pi(\lambda) \ne 1$, then $\lambda \in \rho(\mathbf{A})$ and the corresponding resolvent $\mathrm{R}(\lambda, \mathbf{A})$ can be expressed as*

$$(\mathrm{R}(\lambda, \mathbf{A})f)(q) = (1 - \pi(\lambda))^{-1}\zeta(\lambda, f)\Psi(\lambda, q) + Q(\lambda, f, q), \tag{3.9}$$

where

$$\Psi(\lambda, q) = \begin{cases} e^{\lambda(G(q_{\max}/2)-G(q))} & \text{for } \frac{q_{\max}}{2} \le q \le q_{\max}, \\ \int_{\frac{q_{\min}}{2}}^{q} e^{\lambda(G(\xi)-G(2\xi)-G(q)+G(q_{\max}/2))} \frac{k(\xi)}{g(\xi)} d\xi & \text{for } \frac{q_{\min}}{2} \le q \le \frac{q_{\max}}{2}, \end{cases} \tag{3.10}$$

and

$$Q(\lambda, f, q) = \begin{cases} \int_{\frac{q_{\max}}{2}}^{q} e^{\lambda(G(\xi)-G(q))} \frac{f(\xi)}{g(\xi)} d\xi, \ \text{for } \frac{q_{\max}}{2} \le q \le q_{\max}, \\ \int_{\frac{q_{\min}}{2}}^{q} e^{\lambda(G(\xi)-G(q))} [f(\xi) + k(\xi) \int_{\frac{q_{\max}}{2}}^{2\xi} e^{\lambda(G(\eta)-G(2\xi))} \frac{f(\eta)}{g(\eta)} d\eta] \frac{d\xi}{g(\xi)}, \\ \qquad \text{for } \frac{q_{\min}}{2} \le q \le \frac{q_{\max}}{2}. \end{cases}$$

Furthermore, $\mathrm{R}(\lambda, \mathbf{A})$ is a compact operator.

(ii) *$\pi(\lambda) = 1$ implies $\lambda \in \sigma_p(\mathbf{A})$. For any $\lambda \in \sigma_p(\mathbf{A})$, its geometrical multiplicity is 1 and $\Psi(\lambda, q)$ is its corresponding eigenfunction.*

Suppose that $\hat{\lambda}_0$ is the unique real number satisfying

$$\pi(\hat{\lambda}_0) = 1. \tag{3.11}$$

Use the similar arguments to those in [7, Chapter II, Theorem 5.1, Theorem 5.10], we have the following results:

Lemma 3.2. *(See [15, Lemma 3.2].) The operator* $\mathbf{A}$ *has precisely one real eigenvalue* $\hat{\lambda}_0$ *which is simple. Furthermore, if* $g(2q) \neq 2g(q)$ *for some* $q \in [\frac{1}{2}q_{\min}, \frac{1}{2}q_{\max}]$ *then* $\hat{\lambda}_0$ *is strictly dominant (i.e.* $\hat{\lambda}_0$ *is greater than the real part of the other eigenvalues of* $\mathbf{A}$*) and it corresponds to a positive eigenvector* $\Psi(\hat{\lambda}_0, q)$*, where* $\Psi(\lambda, q)$ *is defined in (3.10).*

For technical reasons, we impose the following additional condition on the function k, which is defined in (3.3):

(H$_\text{k}$) $$k(\frac{q_{\max}}{2}) \text{ is finite.}$$

Lemma 3.3. *(See [15, Theorem 3.1].) The operator* $\mathbf{A}$ *generates a* C_0 *semi-group* $\mathbf{T}(t)$ *on* $L^2(\frac{q_{\min}}{2}, q_{\max})$ *under the additional condition (H$_k$).*

Throughout the rest of this paper, we impose the following additional condition on the function g:

(H$_\text{gg}$) $$g(2q) < 2g(q) \text{ for all } q \in [\frac{1}{2}q_{\min}, \frac{1}{2}q_{\max}].$$

Lemma 3.4. *(See [7, p. 67, Corollary 9.7].) Suppose (H$_k$) and (H$_{gg}$) hold. Then* $\mathbf{T}(t) := e^{\mathbf{A}t}$ *is compact for* $t \geq G(q_{\max})$*, where* G *is defined in (3.6).*

Next, we consider the population operator with diffusion and advection in L^2 space:

$$\begin{cases} \frac{\partial m(t,q,x)}{\partial t} = D\frac{\partial^2 m}{\partial x^2} - \nu\frac{\partial m}{\partial x} + \{-g(q)\frac{\partial m(t,q,x)}{\partial q} + k(q)m(t,2q,x)\}, \\ \qquad\qquad t > 0,\ \frac{q_{\min}}{2} < q < q_{\max},\ 0 < x < L, \\ \nu m(t,q,0) - D\frac{\partial m}{\partial x}(t,q,0) = m(t,q,L) = 0,\ t > 0,\ \frac{q_{\min}}{2} < q < q_{\max}, \\ m(t, \frac{q_{\min}}{2}, x) = 0,\ t > 0,\ 0 < x < L, \\ m(0,q,x) = m^0(q,x),\ \frac{q_{\min}}{2} < q < q_{\max},\ 0 < x < L, \end{cases} \tag{3.12}$$

We introduce the state $\mathbb{X} = L^2((\frac{q_{\min}}{2}, q_{\max}) \times (0, L))$ with the usual norm and the operator $\mathbb{A} : \mathbb{X} \to \mathbb{X}$ is defined by

$$\begin{cases} \mathbb{A}\phi(q,x) = D\frac{\partial^2\phi(q,x)}{\partial x^2} - \nu\frac{\partial\phi(q,x)}{\partial x} + \{-g(q)\frac{\partial\phi(q,x)}{\partial q} + k(q)\phi(2q,x)\},\ \forall\phi \in D(\mathbb{A}), \\ D(\mathbb{A}) = \{\phi(q,x) \mid \phi,\ \mathbb{A}\phi \in \mathbb{X},\ \phi(\frac{q_{\min}}{2}, x) = 0,\ \phi \text{ satisfies (BC)}\}, \end{cases}$$

where

$$\text{(BC)} \qquad \nu\phi(q,0) - D\frac{\partial \phi}{\partial x}(q,0) = \phi(q,L) = 0, \ \frac{q_{\min}}{2} < q < q_{\max}.$$

Note that $\mathbb{A} = \mathcal{L} + \mathbf{A}$, where

$$\mathcal{L} := D\frac{\partial^2}{\partial x^2} - \nu\frac{\partial}{\partial x} \tag{3.13}$$

subject to the boundary condition (BC). Then the system (3.12) can be rewritten as follows:

$$\begin{cases} \frac{dm(t,q,x)}{dt} = \mathbb{A}m(t,q,x), \ t > 0, \ \frac{q_{\min}}{2} < q < q_{\max}, \ 0 < x < L, \\ m(0,q,x) = m^0(q,x), \ \frac{q_{\min}}{2} < q < q_{\max}, \ 0 < x < L. \end{cases} \tag{3.14}$$

We denote by $(\bar{\lambda}_i, \phi_i)_{i\ge 0}$ the eigenvalue–eigenfunction pair of the following problem

$$\begin{cases} -D\phi''(x) + \nu\phi'(x) = \bar{\lambda}\phi(x), \ x \in (0,L), \\ \nu\phi(0) - D\phi'(0) = \phi(L) = 0. \end{cases} \tag{3.15}$$

Suppose $\bar{\lambda}_0$ is the principal eigenvalue corresponding to the positive eigenfunction $\phi_0(x)$ which is uniquely determined by the normalization $\max_{[0,1]}\phi_0(x) = 1$. We may assume that $0 < \bar{\lambda}_0 < \bar{\lambda}_1 \le \bar{\lambda}_2 \le \ldots \le \bar{\lambda}_n \to \infty$. See a detailed explanation for the sign of $\bar{\lambda}_0$ in Section 5.1.

Recall that $\mathbf{A}$ is defined in (3.5), the usual population operator without diffusion and advection in $L^2(\frac{q_{\min}}{2}, q_{\max})$ space. We denote $\{\hat{\lambda}_j\}_{j\ge 0}$ to be the eigenvalues of $\mathbf{A}$, that is, $\{\hat{\lambda}_j\}_{j\ge 0}$ satisfy $\pi(\hat{\lambda}_j) = 1, \ j \ge 0$, where π is defined in (3.7). Following [7, Eq. (5.1) on page 58], it is easy to see that $\hat{\lambda}_j$ satisfies

$$1 = 2\int_{q_{\min}}^{q_{\max}} \frac{b(\xi)}{g(\xi)} \exp[-\int_{\xi/2}^{\xi} \frac{\hat{\lambda}_j + b(\eta)}{g(\eta)} d\eta] d\xi.$$

From Lemma 3.2, it follows that we may assume $\hat{\lambda}_0$ is the unique real eigenvalue of $\mathbf{A}$. Further, $\hat{\lambda}_0$ is greater than the real part of the other eigenvalues of $\mathbf{A}$ and it corresponds to a positive eigenvector $\psi^0 := \Psi(\hat{\lambda}_0, q)$. Thus, we may assume that

$$\hat{\lambda}_0 > \operatorname{Re}\hat{\lambda}_1 \ge \operatorname{Re}\hat{\lambda}_2 \ge \ldots.$$

Theorem 3.1. *Suppose* ($\mathrm{H_k}$) *and* ($\mathrm{H_{gg}}$) *hold. Then the following statements hold.*

(i) *The operator $\mathbb{A}$ generates a C_0 semi-group $\mathbb{T}(t)$ on $\mathbb{X}$.*
(ii) $\mathrm{R}(\lambda, \mathbb{A})$ *is a compact operator* $\forall \lambda \in \rho(\mathbb{A})$, *where* $\mathrm{R}(\lambda,\mathbb{A}) := (\lambda - \mathbb{A})^{-1}$ *is the resolvent of* $\mathbb{A}$.
(iii) $\sigma(\mathbb{A}) = \sigma_p(\mathbb{A}) = \{\hat{\lambda}_i - \bar{\lambda}_j\}_{i,j=0}^{\infty}$, *where* $\sigma(\mathbb{A})$ *and* $\sigma_p(\mathbb{A})$ *are the spectrum and the point spectrum of* $\mathbb{A}$, *respectively.*

(iv) *The operator* $\mathbb{A}$ *has a real dominant eigenvalue* λ_0*, that is,* λ_0 *is greater than the real part of any other eigenvalue of* $\mathbb{A}$*. Furthermore,* λ_0 *is simple.*

(v) $\mathbb{T}(t)$ *is compact for* $t \geq G(q_{\max})$*, where* $G(q)$ *is defined in* (3.6).

Proof. Our proof is motivated by [1,2] and [15, Theorem 3.2]. In fact, if one can establish the following claim then the rest of the proofs are same to [15, Theorem 3.2] after we replace the operator $d\Delta$ there by $\mathcal{L}$. Note that the operator $\mathcal{L}$ is defined in (3.13).

Claim. Given $\phi(q,x) \in D(\mathbb{A})$, define $< \mathbb{A}\phi, \phi >_{\mathbb{X}} := \int_0^L \int_{q_{\min}/2}^{q_{\max}} \mathbb{A}\phi(q,x)\phi(q,x)dqdx$. Then $< \mathbb{A}\phi, \phi >_{\mathbb{X}} \leq M \parallel \phi \parallel_{\mathbb{X}}^2$, $\forall \phi(q,x) \in D(\mathbb{A})$.

Obviously, $< \mathbb{A}\phi, \phi >_{\mathbb{X}}$ equals

$$\int_{q_{\min}/2}^{q_{\max}} \int_0^L [D\frac{\partial^2 \phi(q,x)}{\partial x^2} - \nu \frac{\partial \phi(q,x)}{\partial x}]\phi(q,x)dxdq + \int_0^L \int_{q_{\min}/2}^{q_{\max}} [-g(q)\frac{\partial \phi(q,x)}{\partial q}\phi(q,x)]dqdx$$
$$+ \int_0^L \int_{q_{\min}/2}^{q_{\max}} [k(q)\phi(2q,x)]\phi(q,x)dqdx. \tag{3.16}$$

The first term of (3.16) equals

$$\begin{aligned}
&\int_{q_{\min}/2}^{q_{\max}} \{\phi(q,x)[D\frac{\partial \phi(q,x)}{\partial x} - \nu\phi(q,x)]\,|_{x=0}^{x=L}\}dxdq \\
&\quad - \int_{q_{\min}/2}^{q_{\max}} \int_0^L \frac{\partial \phi(q,x)}{\partial x}[D\frac{\partial \phi(q,x)}{\partial x} - \nu\phi(q,x)]dxdq \\
&= - \int_{q_{\min}/2}^{q_{\max}} \int_0^L \frac{\partial \phi(q,x)}{\partial x}[D\frac{\partial \phi(q,x)}{\partial x} - \nu\phi(q,x)]dxdq \\
&= -D \int_{q_{\min}/2}^{q_{\max}} \int_0^L (\frac{\partial \phi(q,x)}{\partial x})^2 dxdq + \nu \int_{q_{\min}/2}^{q_{\max}} \int_0^L \frac{\partial \phi(q,x)}{\partial x}\phi(q,x)dxdq \\
&= -D \int_{q_{\min}/2}^{q_{\max}} \int_0^L (\frac{\partial \phi(q,x)}{\partial x})^2 dxdq + \frac{\nu}{2} \int_{q_{\min}/2}^{q_{\max}} \int_0^L \frac{\partial}{\partial x}[(\phi(q,x))^2]dxdq \\
&= -D \int_{q_{\min}/2}^{q_{\max}} \int_0^L (\frac{\partial \phi(q,x)}{\partial x})^2 dxdq + \frac{\nu}{2} \int_{q_{\min}/2}^{q_{\max}} [(\phi(q,L))^2 - (\phi(q,0))^2]dq
\end{aligned}$$

$$= -D \int_{q_{\min}/2}^{q_{\max}} \int_0^L (\frac{\partial \phi(q,x)}{\partial x})^2 dx dq + \frac{\nu}{2} \int_{q_{\min}/2}^{q_{\max}} [0 - (\phi(q,0))^2] dq \leq 0.$$

By the similar arguments to those in the proof of [15, Theorem 3.2], the second term of (3.16) equals

$$\int_0^L \int_{q_{\min}/2}^{q_{\max}} [-g(q) \frac{\partial \phi(q,x)}{\partial q} \phi(q,x)] dq dx$$
$$\leq \frac{1}{2} M_1 \int_0^L \int_{q_{\min}/2}^{q_{\max}} (\phi(q,x))^2 dq dx = \frac{1}{2} M_1 \parallel \phi \parallel_{\mathbb{X}}^2,$$

where $M_1 = \max_{[q_{\min}/2, q_{\max}]} |g'(q)| < \infty$.

Using the fact that $\phi(2q, \cdot) \equiv 0 \; \forall \; q > q_{\max}/2$, it follows that the third term of (3.16) equals

$$\int_0^L \int_{q_{\min}/2}^{q_{\max}/2} k(q)\phi(2q,x)\phi(q,x) dq \leq M_2 \int_0^L \int_{q_{\min}/2}^{q_{\max}/2} \phi(2q,x)\phi(q,x) dq dx dx$$
$$\leq \frac{1}{2} M_2 \{ \int_0^L \int_{q_{\min}/2}^{q_{\max}/2} (\phi(2q,x))^2 dq dx + \int_0^L \int_{q_{\min}/2}^{q_{\max}/2} (\phi(q,x))^2 dq dx \} \leq M_2 \parallel \phi \parallel_{\mathbb{X}}^2,$$

where $M_2 := \max_{[q_{\min}/2, q_{\max}/2]} k(q) < \infty$ by ($\mathrm{H_k}$).

From the discussions above, it follows that

$$< \mathbb{A}\phi, \phi >_{\mathbb{X}} \leq (\frac{1}{2} M_1 + M_2) \parallel \phi \parallel_{\mathbb{X}}^2, \forall \phi \in D(\mathbb{A}),$$

i.e. ($\mathbb{A}$, $D(\mathbb{A})$) is bounded above on the Hilbert space $\mathbb{X}$. Thus, (i)–(iv) are valid by [10, Proposition, p. 91]. □

By the similar arguments to the proofs in [15, Theorem 3.3], we obtain the results concerned with the asymptotic behavior of the solution for (3.14).

Theorem 3.2. *Suppose the notations π, ζ and Ψ are defined in (3.7), (3.8) and (3.10), respectively. Let $\mathbb{T}(t) := e^{\mathcal{L}t} e^{\mathbf{A}t}$ be the C_0 semi-group generated by $\mathbb{A} := \mathcal{L} + \mathbf{A}$ on $\mathbb{X}$, where $e^{\mathcal{L}t}$ and $e^{\mathbf{A}t}$ are the semi-groups generated by $\mathcal{L} := D\frac{\partial^2}{\partial x^2} - \nu \frac{\partial}{\partial x}$ and $\mathbf{A}$ respectively. Then the following statements hold.*

(i) *For $m^0(q,x) \in \mathbb{X}$, there exists a unique solution $m(t,q,x)$ to equation (3.14), which is given by*

$$m(t,q,x) = \mathbb{T}(t) m^0(q,x) \in C((0,\infty), \mathbb{X});$$

(ii) *If* $m^0(q,x) \in D(\mathbb{A})$, *then* $m(t,q,x) = \mathbb{T}(t)m^0(q,x) \in C^1((0,\infty),\mathbb{X})$;
(iii) $m(t,q,x) := e^{\mathcal{L}t}e^{\mathbf{A}t}m^0(q,x)$ *has the following asymptotic expression*

$$e^{\mathcal{L}t}e^{\mathbf{A}t}m^0(q,x) = e^{-\bar{\lambda}_0 t}e^{\hat{\lambda}_0 t}[C\Psi(\hat{\lambda}_0,q)\phi_0(x) + O(e^{-\epsilon t})], \text{ as } t \to \infty,$$

where $C = \frac{\zeta(\hat{\lambda}_0,\mathbf{m}^0)}{-\pi'(\hat{\lambda}_0)}$, $\mathbf{m}^0(q) =< m^0(q,x), \phi_0(x) >$, *and* ϵ *is a small positive number.*

4. The reduction of system (2.7)

In the previous section, we have shown that the structure of the semigroup for the population with turbulent diffusion and sinking term is essentially determined by those of the semigroup for the population without spatial variation. We shall use the property of the asymptotic behavior of this semigroup and then reduces the model (2.7) into a nonlocal reaction–diffusion–advection equation similar to those in [6,19].

Lemma 4.1. *Let* $N(t,x) = \int_{\frac{q_{\min}}{2}}^{q_{\max}} qn(t,q,x)dq$, *where* $n(t,q,x)$ *satisfies the system* (2.7). *Then*

$$\limsup_{t\to\infty} \int_0^L e^{\frac{\nu x}{D}}\phi_0(x)N(x,t)\,dx < \infty, \tag{4.1}$$

where $\phi_0(x)$ *is the positive and normalized eigenfunction of* (5.4).

Proof. By direct computation, $N(t,x)$ satisfies the following equations:

$$\begin{cases} \frac{\partial N(t,x)}{\partial t} = D\frac{\partial^2 N}{\partial x^2} - \nu\frac{\partial N}{\partial x} - dN(t,x) \\ \qquad\qquad + \beta(I(x,t))\int_{\frac{q_{\min}}{2}}^{q_{\max}} g(q)n(t,q,x)dq, \ t>0, \ 0<x<L, \\ \nu N(t,0) - D\frac{\partial N}{\partial x}(t,0) = N(t,L) = 0, \ t>0, \\ N(0,x) = N^0(x), \ 0<x<L, \end{cases} \tag{4.2}$$

Since

$$N(t,x) = \int_{\frac{q_{\min}}{2}}^{q_{\max}} qn(t,q,x)dq \le q_{\max}\int_{\frac{q_{\min}}{2}}^{q_{\max}} n(t,q,x)dq,$$

it follows from (2.6) that

$$I(x,t) \le I_0\exp(-k_0 x - \frac{k_1}{q_{\max}}\int_0^x N(t,s)ds). \tag{4.3}$$

It is easy to see that there exists a positive number $C > 0$ such that

$$g(q) \le Cq, \ \forall\, q \in [\frac{q_{\min}}{2}, q_{\max}]. \tag{4.4}$$

From (4.1), (4.3) and (4.4), it follows that

$$\begin{cases} \frac{\partial N(t,x)}{\partial t} \le D\frac{\partial^2 N}{\partial x^2} - \nu\frac{\partial N}{\partial x} - dN(t,x) \\ \qquad\qquad + C\beta(I_0 \exp(-k_0 x - \frac{k_1}{q_{\max}}\int_0^x N(t,s)ds))N(t,x),\ t>0,\ 0<x<L, \\ \nu N(t,0) - D\frac{\partial N}{\partial x}(t,0) = N(t,L) = 0,\ t>0, \\ N(0,x) = N^0(x),\ 0<x<L, \end{cases} \tag{4.5}$$

By (4.5) and the same arguments to those in Lemma 5.1, we conclude that (4.1) is true. □

Let

$$E(q) = \exp(-\int_{\frac{q_{\min}}{2}}^{q} \frac{b(\xi)}{g(\xi)}d\xi) \text{ and } m(t,q,x) = \frac{g(q)n(t,q,x)}{E(q)}.$$

Then (2.7) becomes

$$\begin{cases} \frac{\partial m(t,q,x)}{\partial t} = D\frac{\partial^2 m}{\partial x^2} - \nu\frac{\partial m}{\partial x} + \beta(I(x,t))\{-g(q)\frac{\partial m(t,q,x)}{\partial q} + k(q)m(t,2q,x)\} \\ \qquad\qquad -dm(t,q,x),\ t>0,\ \frac{q_{\min}}{2} < q < q_{\max},\ 0<x<L, \\ \nu m(t,q,0) - D\frac{\partial m}{\partial x}(t,q,0) = m(t,q,L) = 0,\ t>0,\ \frac{q_{\min}}{2} < q < q_{\max}, \\ m(t,\frac{q_{\min}}{2},x) = 0,\ t>0,\ 0<x<L, \\ m(0,q,x) = m^0(q,x),\ \frac{q_{\min}}{2} < q < q_{\max},\ 0<x<L, \end{cases} \tag{4.6}$$

where $k(q)$ is defined in (3.3) and $m^0(q,x) = g(q)n^0(q,x)/E(q)$. Abstractly, we rewrite the equation of m in (4.6) as follows:

$$\begin{cases} \frac{dm(t,q,x)}{dt} = D\frac{\partial^2 m}{\partial x^2} - \nu\frac{\partial m}{\partial x} - dm + \beta(I)\mathbf{A}m,\ t>0,\ \frac{q_{\min}}{2} < q < q_{\max},\ 0<x<L, \\ m(0,q,x) = m^0(q,x),\ \frac{q_{\min}}{2} < q < q_{\max},\ 0<x<L, \end{cases}$$

where $\mathbf{A}$ satisfies (3.5).

Treating the substrate concentration I as a known function of time we can solve the equation for m by

$$m(t,q,x) = e^{-dt}e^{\mathcal{L}t}e^{\mathbf{A}\int_0^t \beta(I(\tau,x))d\tau}m^0(q,x), \tag{4.7}$$

where $e^{\mathcal{L}t}$ and $e^{\mathbf{A}t}$ are the semi-group generated by $\mathcal{L} := D\frac{\partial^2}{\partial x^2} - \nu\frac{\partial}{\partial x}$ and $\mathbf{A}$ respectively.

Lemma 4.2.

$$\lim_{t\to\infty}\int_0^t \beta(I(\tau,x))d\tau = \infty,\ \forall\, x \in (0,L). \tag{4.8}$$

Proof. Since $\beta(I(\tau,x)) \geq 0 \ \forall\ x \in (0,L)$, the integral $\int_0^t \beta(I(\tau,x))d\tau$ approaches a limit as $t \to \infty$, $\forall\ x \in (0,L)$. We suppose that $\lim_{t\to\infty}\int_0^t \beta(I(\tau,x_0))d\tau < \infty$, for some $x_0 \in (0,L)$. Then

$$I(t,x_0) \to 0 \text{ as } t \to \infty. \tag{4.9}$$

It is easy to see that

$$I(t,x) \geq I_0 \exp(-k_0 x - \frac{2k_1}{q_{\min}}\int_0^x N(t,s)ds),\ \forall\ x \in (0,L). \tag{4.10}$$

From (4.1), (4.9) and (4.10), we get a contradiction. Thus, (4.8) is true and we complete the proof. □

By (4.7) and Theorem 3.2, it follows that

$$m(t,q,x) = e^{-dt}e^{-\bar{\lambda}_0 t}e^{\hat{\lambda}_0\int_0^t \beta(I(\tau,x))d\tau}[C\Psi(\hat{\lambda}_0,q)\phi_0(x) + O(e^{-\epsilon t})] \text{ as } t \to \infty.$$

That is,

$$m(t,q,x) = u(t,x)[\Psi(\hat{\lambda}_0,q) + o(1)] \text{ as } t \to \infty, \tag{4.11}$$

where $u(t,x)$ is a real valued function depending on t and x.

Substituting (4.11) into the equation (4.6), it follows that

$$\begin{cases} \frac{\partial u(t,x)}{\partial t} = D\frac{\partial^2 u}{\partial x^2} - \nu\frac{\partial u}{\partial x} + \hat{\lambda}_0\beta(I(x,t))u - du, \\ \nu u(t,0) - D\frac{\partial u}{\partial x}(t,0) = u(t,L) = 0,\ t > 0, \\ u(0,x) = u^0(x), \end{cases} \tag{4.12}$$

where

$$\begin{aligned} I = I(x,t) &= I_0 \exp(-k_0 x - k_1[\int_{\frac{q_{\min}}{2}}^{q_{\max}} \frac{E(q)}{g(q)}\Psi(\hat{\lambda}_0,q)dq][\int_0^x u(t,s)ds]) \\ &= I_0 \exp(-k_0 x - \hat{k}_1\int_0^x u(t,s)ds), \end{aligned} \tag{4.13}$$

and

$$\hat{k}_1 = k_1[\int_{\frac{q_{\min}}{2}}^{q_{\max}} \frac{E(q)}{g(q)}\Psi(\hat{\lambda}_0,q)dq]. \tag{4.14}$$

5. The analysis of the reduced system (4.12)

In this section, we shall concentrate on the study of system (4.12). For convenience, let

$$F(I(x,t)) = \hat{\lambda}_0 \beta(I(x,t)), \tag{5.1}$$

where $I(x,t) = I_0 \exp(-k_0 x - \hat{k}_1 \int_0^x u(s,t)ds)$ and $\hat{k}_1 > 0$ is defined by (4.14). That is, we shall consider the following system:

$$\begin{cases} u_t = Du_{xx} - \nu u_x + F(I(x,t))u - du, & 0 < x < L,\ t > 0, \\ Du_x(0,t) - \nu u(0,t) = u(L,t) = 0, & t > 0, \\ u(x,0) = u^0(x) \geq 0, & 0 \leq x \leq L. \end{cases} \tag{5.2}$$

5.1. *The steady-state solutions*

The steady state of (5.3) is described by the system

$$\begin{cases} -Du_{xx} + \nu u_x = F(I(x))u - du, & 0 < x < L, \\ Du_x(0) - \nu u(0) = u(L) = 0, \end{cases} \tag{5.3}$$

where

$$I(x) = I_0 e^{-k_0 x - \hat{k}_1 \int_0^x u(\eta)\,d\eta}.$$

For a continuous function $\Phi(x)$, consider the eigenvalue problem

$$\begin{cases} -D\phi_{xx} + \nu\phi_x + \Phi(x)\phi = \mu\phi, & 0 < x < L, \\ D\phi_x(0) - \nu\phi(0) = \phi(L) = 0. \end{cases} \tag{5.4}$$

Let $\phi(x) = \psi(x)e^{\frac{\nu}{2D}x}$. Then (5.4) is equivalent to

$$\begin{cases} -D\psi_{xx} + \left(\dfrac{\nu^2}{4D} + \Phi(x)\right)\psi = \mu\psi, & 0 < x < L, \\ \psi_x(0) - \dfrac{\nu}{2D}\psi(0) = \psi(L) = 0. \end{cases} \tag{5.5}$$

Hence $\mu_1(\Phi(x))$ is a real number if $\Phi(x)$ is a real function. Since $\nu \geq 0$, the Krein–Rutman theorem guarantees $\mu_1(\Phi(x))$ has a corresponding eigenfunction which is positive in $(0, L)$. Clearly $\mu_1(\Phi(x))$ is increasing with respect to Φ. Let $\Phi(x) \equiv 0$ and $\phi_0(x)$ be the corresponding normalized positive principal eigenfunction of (5.4). Then we have

$$\mu_1(0)\int_0^L \phi_0(\eta)\,d\eta = -D(\phi_0)_x(L) > 0,$$

which implies $\mu_1(0) > 0$. Note that $\mu_1(0) = \bar{\lambda}_0$, where $\bar{\lambda}_0$ is the principal eigenvalue of (3.15).

Define

$$d_* := -\mu_1\left(-F(I_0e^{-k_0x})\right). \tag{5.6}$$

Then $d_* \le 0$ if $F(I_0e^{-k_0x})$ is small enough, $d_* > 0$ if $F(I_0e^{-k_0x})$ is large enough. If $d_* \le 0$, (5.3) has no positive solution. We assume $d_* > 0$.

Theorem 5.1. *The system (5.3) has no positive solution for $d \ge d_*$, and it has a unique positive solution for each $d \in [0, d_*)$.*

Proof. Clearly, for any $d \in R^1$, $(d, 0)$ is a solution pair to (5.3). By the Crandall–Rabinowitz global bifurcation theory, there is a positive solution continuum Γ emanating from $(d_*, 0)$ and either become unbounded, or meets $\{0\} \times C([0, L])$.

Suppose u is a positive solution of (5.3). Then

$$d = -\mu_1\left(-F(I_0e^{-k_0x-\hat{k}_1\int_0^x u(\eta)\,d\eta})\right) \in (-\mu_1(0), d_*),$$

which implies (5.3) has no positive solution when $d \ge d_*$. Now it is easy to prove that Γ become unbounded only when $d \downarrow -\mu_1(0)$. Since $-\mu_1(0) < 0$, we conclude that for all $d \in [0, d_*)$, (5.3) has at least one positive solution.

Suppose u_1 and u_2 are two positive solutions of (5.3) corresponding to the same $d \in [0, d_*)$. We want to show that $u_1 \equiv u_2$. Assume by contradiction that $u_1 \not\equiv u_2$. We first claim that $u_1(0) \ne u_2(0)$. Otherwise $u_1(0) = u_2(0)$. By the boundary conditions of u_1 and u_2 at $x = 0$, we have $u_1'(0) = u_2'(0)$. Let $\xi_i(x) = u_i'(x)$ and $\eta_i(x) = \int_0^x u_i(s)\,ds$, $i = 1, 2$. Then (u_1, ξ_1, η_1) and (u_2, ξ_2, η_2) are solutions of the ODE system

$$\begin{cases} u' = \xi, & 0 < x < L, \\ \xi' = D^{-1}\left[\nu\xi - F(I_0e^{-k_0x-\hat{k}_1\eta})u + du\right], & 0 < x < L, \\ \eta' = u, & 0 < x < L, \end{cases}$$

with the same initial conditions. Therefore $(u_1, \xi_1, \eta_1) \equiv (u_2, \xi_2, \eta_2)$, a contraction. Hence $u_1(0) \ne u_2(0)$. Without loss of generality, we assume $u_1(0) > u_2(0)$. Assume $u_1(x) > u_2(x)$ for all $x \in [0, L)$. Multiplying the equation for u_1 by $u_2e^{\frac{\nu}{D}x}$ and the equation for u_2 by $u_1e^{\frac{\nu}{D}x}$, then integrating over $[0, L]$ and subtracting, we obtain

$$\int_0^L \left[F\left(I_0e^{-k_0x-\hat{k}_1\int_0^x u_1(\eta)\,d\eta}\right) - F\left(I_0e^{-k_0x-\hat{k}_1\int_0^x u_2(\eta)\,d\eta}\right)\right]u_1(x)u_2(x)e^{\frac{\nu x}{D}}\,dx = 0.$$

This is impossible, since the left hand side is clearly negative according to our assumption. Therefore $u_1 - u_2$ must change sign in $(0, L)$. Let $x_* \in (0, L)$ be the smallest zero of $u_1 - u_2$. Then multiplying the equation for u_1 by $u_2e^{\frac{\nu x}{D}}$ and multiplying the equation for u_2 by $u_1e^{\frac{\nu x}{D}}$, integrating over $[0, x_*]$ and subtracting, we obtain

$$\int_0^L \left[F\left(I_0 e^{-k_0 x - \hat{k}_1 \int_0^x u_1(\eta)\,d\eta}\right) - F\left(I_0 e^{-k_0 x - \hat{k}_1 \int_0^x u_2(\eta)\,d\eta}\right)\right] u_1(x) u_2(x) e^{\frac{\nu x}{D}}\,dx$$
$$= D[u_1(x_*)u_2'(x_*) - u_2(x_*)u_1'(x_*)].$$

The left hand side is negative and the right hand side is nonnegative, which is impossible. In summary, we always have $u_1 \equiv u_2$. This proves the uniqueness. □

5.2. The global asymptotic stability

Let $(\mu_1(0), \phi_0)$ be the positive eigenvalue–eigenfunction pair of (5.4). Then $\mu_1(0) > 0$. We may assume ϕ_0 is positive and $\|\phi_0\|_\infty = 1$.

Lemma 5.1. *Assume that $u(x,t) \ge 0$ satisfies*

$$\begin{cases} u_t \le D u_{xx} - \nu u_x + F(I(x,t))u - du, & 0 < x < L,\ t > 0, \\ D u_x(0,t) - \nu u(0,t) = u(L,t) = 0, & t > 0, \\ u(x,0) = u^0(x) \ge 0, & 0 \le x \le L. \end{cases} \tag{5.7}$$

Then

$$\limsup_{t\to\infty} \int_0^L e^{\frac{\nu x}{D}} \phi_0(x) u(x,t)\,dx < \infty. \tag{5.8}$$

Proof. Let

$$W(t) := \int_0^L e^{\frac{\nu x}{D}} \phi_0(x) u(x,t)\,dx.$$

Let $c > 0$ be a constant such that $F(s) \le cs$ for $s \ge 0$. Then

$$\begin{aligned} W'(t) &= \int_0^L e^{\frac{\nu x}{D}} \phi_0(x) u_t(x,t)\,dx \\ &\le \int_0^L e^{\frac{\nu x}{D}} \phi_0(x) \left[D u_{xx} - \nu u_x + F\left(I_0 e^{-k_0 x - \hat{k}_1 \int_0^x u(\eta,t)\,d\eta}\right) u - du\right] dx \\ &= \int_0^L [D(\phi_0)_{xx} - \nu(\phi_0)_x] e^{\frac{\nu x}{D}} u\,dx + c e^{\frac{\nu L}{D}} \int_0^L e^{-\hat{k}_1 \int_0^x u(\eta,t)d\eta} u(x,t)dx - dW(t) \\ &\le -\mu_1(0) W(t) + c e^{\frac{\nu L}{D}} \hat{k}_1^{-1} \left(1 - e^{-\hat{k}_1 \int_0^L u(x,t)dx}\right) - dW(t) \\ &\le c e^{\frac{\nu L}{D}} \hat{k}_1^{-1} - [\mu_1(0) + d] W(t). \end{aligned}$$

By Gronwall's inequality,

$$W(t) \le W(0)e^{-[\mu_1(0)+d]t} + ce^{\frac{\nu L}{D}}\hat{k}_1^{-1}(\mu_1(0)+d)\left(1 - e^{-[\mu_1(0)+d]t}\right),$$

which implies (5.8). □

Lemma 5.2. *If $u(x,t)$ is a nonnegative solution of (5.2), then*

$$\limsup_{t\to\infty} \|u(x,t)\|_\infty < \infty.$$

Proof. Set

$$J(t) = \max_{x\in[0,L],s\in[0,t]} u(x,t).$$

Then $J(t)$ is nondecreasing. Suppose for contradiction that $J(t) \to \infty$ as $t \to \infty$. We can find $t_n \to \infty$ such that $J(t_n) = \max_{x\in[0,L]} u(x,t_n) = u(x_n,t_n) \to \infty$. Define

$$v_n(x,t) = \frac{u(x,t+t_n-1)}{J(t_n)}.$$

Then v_n satisfies

$$\begin{cases} (v_n)_t = D(v_n)_{xx} - \nu(v_n)_x + [F_n(x,t)-d]v_n, \\ D(v_n)_x(0,t) - \nu v_n(0,t) = v_n(L,t) = 0, \\ v_n(x,0) \in [0,1], \end{cases}$$

where $F_n(x,t) = F(I_0e^{-k_0x-\hat{k}_1\int_0^x u(y,t+t_n-1)dy})$. Clearly $|F_n(x,t)-d| \le M_0$ for some $M_0 > 0$. A simple comparison argument gives $0 \le v_n(x,t) \le e^{M_0t}$ for all $x \in [0,L]$ and $t \ge 0$. By the standard parabolic regularity $\{v_n\}$ is bounded in $C^{1+\alpha,\alpha}([0,L]\times[1/2,2])$. Hence by passing to a subsequence we may assume $v_n \to v^*$ in $C^{1,0}([0,L]\times[1/2,2])$. Since $|F_n| \le M_0+d$, we may assume, subject to a further subsequence, $F_n \to \rho_*$ weakly in $\mathbb{L}^2([0,L]\times[1/2,2])$. Clearly $|\rho_*| \le M_0+d$. And v^* is a weak solution of

$$\begin{cases} v_t = Dv_{xx} - \nu v_x + [\rho_*(x,t)-d]v, \\ Dv_x(0,t) - \nu v(0,t) = v(L,t) = 0, \\ v(x,0) \in [0,1]. \end{cases}$$

Since $\max_{x\in[0,L],t\in[0,1]} v_n(x,t) = v_n(x_n,1) = 1$, we have $v^*(x_0,1) = \max_{x\in[0,L]} v^*(x,1) = 1$. By the strong maximum principle, $v^*(x,1) > 0$ for all $x \in [0,L)$. Let $\kappa_0 = \min_{x\in[0,L/2]} v^*(x,1)$. Then $\kappa_0 > 0$, and hence

$$u(x,t_n) \ge (\kappa_0/2)J(t_n) \to \infty \;\text{ uniformly for } x \in [0,L/2],$$

which implies

$$\lim_{t_n\to\infty}\int_0^L e^{\frac{\nu x}{D}}\phi_0(x)u(x,t_n)dx=\infty.$$

This is in contradiction to Lemma 5.1. The proof is complete. □

Suppose $u(x,t)$ and $\tilde{u}(x,t)$ are two nonnegative functions. Set

$$v(x,t)=\int_0^x u(\eta,t)d\eta,\quad \tilde{v}(x,t)=\int_0^x \tilde{u}(\eta,t)d\eta.$$

Then we have the following comparison lemma

Lemma 5.3. *Suppose two nonnegative functions $u(x,t),\tilde{u}(x,t)\in C^{2,1}([0,L]\times(0,\infty))$ satisfy*

$$u_t\le Du_{xx}-\nu u_x+F\left(I_0e^{-k_0x-\hat{k}_1\int_0^x u(\eta)d\eta}\right)u-du,\quad Du_x(0,t)-\nu u(0,t)=u(L,t)=0,$$

and

$$\tilde{u}_t\ge D\tilde{u}_{xx}-\nu\tilde{u}_x+F\left(I_0e^{-k_0x-\hat{k}_1\int_0^x \tilde{u}(\eta)d\eta}\right)\tilde{u}-d\tilde{u},\quad D\tilde{u}_x(0,t)-\nu\tilde{u}(0,t)=\tilde{u}(L,t)=0.$$

If $u(x,t)<\tilde{u}(x,t)$ for all $x\in[0,L)$ and small $t\ge 0$, then $v(x,t)<\tilde{v}(x,t)$ for all $t>0$ and $x\in(0,L]$.

Proof. It is clear that $v(x,t)<\tilde{v}(x,t)$ for $t>0$ small and $x\in(0,L]$. Suppose there is a finite maximal time t_* such that the lemma is true for $t<t_*$. Clearly $v(x,t_*)\le\tilde{v}(x,t_*)$ for all $x\in[0,L]$. We claim that

$$v(x,t_*)=\tilde{v}(x,t_*)\quad\text{for some } x\in(0,L]. \tag{5.9}$$

If this is not the case, we set $w(x,t)=\tilde{v}(x,t)-v(x,t)$. Then

$$\begin{aligned}
w_t &\ge Dw_{xx}-\nu w_x+\hat{k}_1^{-1}\left[\int_{k_0x+\hat{k}_1v(x,t)}^{k_0x+\hat{k}_1\tilde{v}(x,t)}F(e^{-s})ds\right]-dw\\
&\quad+k_0\hat{k}_1^{-1}\int_0^x[F(I_0e^{-k_0y-\hat{k}_1v(y,t)})-F(I_0e^{-k_0y-\hat{k}_1\tilde{v}(y,t)})]dy\\
&\ge Dw_{xx}-\nu w_x+[C(x,t)-d]w\ \text{ for } 0<x<L,\ 0<t\le t_*,\\
&w(0,t)=0,\ w(L,t)>0,\ \text{for } 0<t\le t_*,\\
&w(x,0)>0,\ \text{for } 0<x\le L.
\end{aligned}\tag{5.10}$$

The strong maximum principle then implies $w(x,t) > 0$ for all $0 < t \le t_*$ and $x \in (0, L]$. Moreover by the boundary point lemma we have $w_x(0, t_*) > 0$. Since w_x is smooth we can find $\delta_1 > 0$ such that $w_x(0,t) > 0$ for $t \in [t_*, t_* + \delta_1]$. By the smoothness of w we then can find $\delta_2 \in (0, \delta_1)$ such that $w(x,t) > 0$ for all $x \in (0, L]$ and $t \in (0, t_* + \delta_2]$, which contracts the maximality of t_*. Therefore there exists a point $x \in (0, L]$ such that $w(x, t_*) = 0$.

Now if $w(x,t_*) = 0$ for some $x \in (0, L)$. Then the maximum principle implies $w(x,t_*) = 0$ for all $x \in [0, L]$. If $w(x,t_*) > 0$ for all $x \in (0, L)$ while $w(L, t_*) = 0$, then at (L, t_*), $w_t \le 0$, $w_x = \tilde{u} - u = 0$. By (5.10) we deduce $w_{xx} < 0$ at (L, t_*). By continuity, we may assume $w_{xx}(x, t_*) < 0$ for $x \in (L - \delta, L)$, where $\delta > 0$ is suitably small. By Hopf's boundary lemma for elliptic equations we conclude that $w_x(L, t_*) < 0$, which contradicts the boundary condition that $\tilde{u}(L, t_*) = u(L, t_*) = 0$. This finish the proof of the lemma. □

We use $u_d(x)$ to denote the unique positive solution of (5.3) for $d \in [0, d_*)$.

Theorem 5.2. *Let $u(x,t)$ be the unique solution of (5.2) with initial data $u^0(x) \ge\not\equiv 0$. Then*

$$\lim_{t\to\infty} u(x,t) = \begin{cases} u_d(x), & \text{if } 0 \le d < d_*, \\ 0, & \text{if } d \ge d_*. \end{cases} \tag{5.11}$$

Proof. By the maximum principle and the boundary point lemma, $u(x,t) > 0$ for all $t > 0$ and $x \in [0, L)$, $u_x(L,t) < 0$ for all $t > 0$. So we may assume $u^0(x) > 0$ for $x \in [0, L)$ and $u^0_x(x) < 0$, for otherwise we can replace $u(x,t)$ by $u(x, t+1)$ and $u^0(x)$ by $u(x, 1)$. Let $d \in [0, d_*)$. Since $d < d_* = -\mu_1(-F(I_0 e^{-k_0 x}))$ and

$$F(I_0 e^{-(k_0 + \hat{k}_1 \delta)x}) \to F(I_0 e^{-k_0 x})$$

uniformly in $[0, L]$ as $\delta \to 0$, we may find $\delta > 0$ small enough such that $d < -\mu_1(-F(I_0 e^{-(k_0+\hat{k}_1\delta)x}))$. Fix such a δ and let ϕ be a positive eigenfunction corresponding to $\mu_1(-F(I_0 e^{-(k_0+\hat{k}_1\delta)x}))$. Choose $\epsilon > 0$ small so that $\epsilon\phi < u_0$ in $[0, L)$ and $\epsilon\phi < \delta$ in $[0, L]$. Let $\underline{u}(x,t)$ be the unique solution of (5.2) with initial condition $\underline{u}(x, 0) = \epsilon\phi(x)$. Then we can find $\sigma > 0$ small such that

$$0 < \underline{u}(x,t) < \delta \text{ for } t \in (0, \sigma] \text{ and } x \in [0, L].$$

Hence for $t \in (0, \sigma]$,

$$\begin{aligned} \underline{u}(x,t) &= D\underline{u}_{xx} - \nu \underline{u}_x + \left[F(I_0 e^{-k_0 x - \hat{k}_1 \int_0^x \underline{u}(\eta,t)d\eta}) - d\right]\underline{u} \\ &\ge D\underline{u}_{xx} - \nu \underline{u}_x + \left[F(I_0 e^{-(k_0+\hat{k}_1\delta)x}) - d\right]\underline{u} \\ &> D\underline{u}_{xx} - \nu \underline{u}_x + \left[F(I_0 e^{-(k_0+\hat{k}_1\delta)x}) + \mu_1(-F(I_0 e^{-(k_0+\hat{k}_1\delta)x}))\right]\underline{u}. \end{aligned}$$

It follows that

$$\begin{cases} (\underline{u}-\epsilon\phi)_t > D(\underline{u}-\epsilon\phi)_{xx} - \nu(\underline{u}-\epsilon\phi)_x \\ \qquad + \left[F(I_0e^{-(k_0+\hat{k}_1\delta)x}) + \mu_1(-F(I_0e^{-(k_0+\hat{k}_1\delta)x}))\right](\underline{u}-\epsilon\phi), & x\in(0,L), t\in(0,\sigma], \\ D(\underline{u}-\epsilon\phi)_x(0,t) - \nu(\underline{u}-\epsilon\phi)(0,t) = (\underline{u}-\epsilon\phi)(L,t) = 0, & t\in(0,\sigma] \\ (\underline{u}-\epsilon\phi)(x,0) = 0, & x\in[0,L]. \end{cases}$$

By the strong maximum principle we obtain $\underline{u}(x,t)-\epsilon\phi(x) > 0$ for $t\in(0,\sigma]$ and $x\in[0,L)$; moreover $\underline{u}(L,t)-\epsilon\phi(L)=0$ and $\underline{u}_x(L,t)-\epsilon\phi_x(L)<0$. Fixing $s\in(0,\sigma]$ we have

$$\underline{u}(x,s) > \underline{u}(x,0) \text{ in } [0,L), \;\; \underline{u}(L,s) = \underline{u}(L,0), \;\; \underline{u}_x(L,s) - \underline{u}_x(L,0) < 0.$$

By continuity,

$$\underline{u}(x,s+t) > \underline{u}(x,t) \text{ in } [0,L) \text{ for all small } t \ge 0.$$

Thus we can use Lemma 5.3 to conclude that $\underline{v}(x,t) < \underline{v}(x,t+s)$ for $x\in(0,L]$ and $t>0$, where $\underline{v}(x,t) = \int_0^x \underline{u}(\eta,t)d\eta$. Thus $\underline{v}(x,t)$ is monotone increasing in t.

By Lemma 5.2, there exists a positive constant C such that $\underline{v}(x,t) < C$ for all $x\in[0,L]$ and $t>0$. Hence $\lim_{t\to\infty}\underline{v}(x,t) = v_*(x)$ exists. On the other hand, since by Lemma 5.2 $\|\underline{u}(\cdot,t)\|_\infty$ is bounded, we can apply the standard parabolic regularity theory to (5.2) to conclude that, for any sequence $t_n\to\infty$, $\{\underline{u}(\cdot,t_n)\}$ has a subsequence which converges in $C^1([0,L])$ to some function u_*. Since $\underline{v}(\cdot,t_n)\to v_*(\cdot)$, we must have $v_*(x) = \int_0^x u_*(\eta)d\eta$. Hence $u_* = v_*'$. This implies that $\lim_{t\to\infty}\underline{u}(x,t) = u_*(x)$. Since $v_*(0)=0$ and $v(x)$ is the limit of an increasing sequence, we have $v_*(x)>0$ for $x\in(0,L]$. Hence $u_* = v_*' \not\equiv 0$ is a nontrivial nonnegative steady state of (5.2). By the strong maximum principle and Theorem 5.1, u_* is positive and is the unique positive solution of (5.3).

Next we consider $d_M = -\mu_1(-F(I_0e^{-(k_0+\hat{k}_1M)x}))$ with $M>0$ large. Let ϕ_M be the positive eigenfunction corresponding to $\mu_1(-F(I_0e^{-(k_0+\hat{k}_1M)x}))$ with $\|\phi_M\|_\infty = 1$. It is easy to see that as $M\to\infty$, $\mu_1(-F(I_0e^{-(k_0+\hat{k}_1M)x}))\to\mu_1(0)$ and $\phi_M\to\phi_0$ in $C^1([0,L])$, where $(\mu_1(0),\phi_0)$ is the principal eigenpair of (5.4) when $\Phi\equiv 0$. Since $\mu_1(0)>0$, we can find $M_0>0$ large enough such that

$$d > -\mu_1(-F(I_0e^{-(k_0+M\hat{k}_1)x})),$$

and

$$u_0(x) < 3M\phi_M(x) \text{ for } x\in[0,L], \;\; M < \frac{3M\phi_M(x)}{\min_{x\in[0,L/2]}\phi_M(x)} \text{ for } x\in[0,L/2].$$

Let $\bar{u}(x,t)$ be the solution of (5.2) with initial data $\bar{u}(x,0) = \frac{3M\phi_M(x)}{\min_{x\in[0,L/2]}\phi_M(x)}$. Then we can find $\sigma>0$ small such that for $t\in(0,\sigma]$,

$$
\begin{aligned}
\bar{u}_t &= D\bar{u}_{xx} - \nu\bar{u}_x + \left[F(I_0 e^{-k_0 x - \hat{k}_1 \int_0^x \bar{u}(\eta,t)d\eta}) - d\right]\bar{u} \\
&\le D\bar{u}_{xx} - \nu\bar{u}_x + \left[F(I_0 e^{-k_0 x - M\hat{k}_1 x}) - d\right]\bar{u} \\
&< D\bar{u}_{xx} - \nu\bar{u}_x + \left[F(I_0 e^{-k_0 x - M\hat{k}_1 x}) + \mu_1(-F(I_0 e^{-k_0 x - M\hat{k}_1 x}))\right]\bar{u}.
\end{aligned}
$$

Thus for $w(x,t) = \bar{u} - \frac{3M\phi_M(x)}{\min_{x\in[0,L/2]}\phi_M(x)}$, we have

$$
\begin{cases}
w_t < Dw_{xx} - \nu w_x \\
\qquad + \left[F(I_0 e^{-k_0 x - M\hat{k}_1 x}) + \mu_1(-F(I_0 e^{-k_0 x - M\hat{k}_1 x}))\right] w, & x \in (0,L), t \in (0,\sigma], \\
Dw_x(0,t) - \nu w(0,t) = w(L,t) = 0, & t \in (0,\sigma], \\
w = 0, & x \in [0,L], t = 0.
\end{cases}
$$

By the strong maximum principle we obtain $w(x,t) < 0$ for $t \in (0,\sigma]$ and $x \in [0,L)$. It follows that $\bar{u}(x,s) < \bar{u}(x,0)$ for $s \in (0,\sigma]$. As before we can deduce that $\bar{v}(x,t) = \int_0^x \bar{u}(\eta,t)d\eta$ is monotone decreasing in t. From Lemma 5.3, we also have $\bar{v}(x,t) \ge \underline{v}(x,t)$ for all $x \in [0,L]$ and $t > 0$. Therefore $\lim_{t\to\infty} \bar{v}(x,t) = v^*(x) \ge \int_0^x u_d(\eta,t)d\eta$. We then use the parabolic regularity much as before to show that $\bar{u}(x,t) \to (v^*)'(x)$ in $C^1([0,L])$, and $(v^*)'$ is a positive steady state of (5.2). Thus we must have $(v^*)(x) = u_d(x)$.

Since by Lemma 5.3 we have $\bar{v} \ge v \ge \underline{v}$. Hence

$$
\lim_{t\to\infty} v(x,t) = \int_0^x u_d(\eta,t)d\eta.
$$

Much as before we conclude that $u(x,t) \to u_d(x)$ as $t \to \infty$ uniformly for $x \in [0,L]$.

Now suppose $d \ge d_*$. We notice that the second part of the proof in the $d \in [0,d_*)$ case still works. In this case the above defined $\bar{u}(x,t) \to (v^*)'(x)$ and (v^*) is a nonnegative steady state of (5.2). Since by Theorem 5.1, when $d \ge d_*$ the only nonnegative steady state of (5.2) is the trivial solution 0, we have $\bar{u}(x,t) \to 0$ as $t \to \infty$ uniformly for $x \in [0,L]$. Hence $\bar{v}(x,t) \to 0$ uniformly for $x \in [0,L]$ as $t \to \infty$.

Using Lemma 5.3 we deduce $0 < v(x,t) < \bar{v}(x,t)$. This implies $v(x,t) \to 0$ uniformly for $x \in [0,L]$ as $t \to \infty$. Then using the parabolic regularity as before we deduce $u(\cdot,t)$ converges in $C^1([0,L])$ to some nonnegative steady state of (5.2). Since $d \ge d_*$, this nonnegative steady state must be 0. This completes the proof. □

5.3. The critical death rate d_*

The critical death rate, as defined in (5.6), is clearly depended on the diffusion coefficient $D > 0$ and the sinking velocity $\nu \ge 0$. In this section we give a brief discussion on how d_* changes as D and ν change.

We for consider d_* as a function of D: $d_* = d_*(D)$.

Let H be the closure of $\{\theta \in C^1([0, L]) : \theta(L) = 0\}$ under the norm

$$\|\theta\| = \left(\int_0^L \theta^2 dx + \int_0^L \theta_x^2 dx \right)^{1/2}.$$

Then $d_*(D)$ can be characterized as

$$d_*(D) = \sup_{\varphi \neq 0, \varphi \in H} \frac{\int_0^L e^{(\nu/D)x}[F(I_0 e^{-k_0 x})\varphi^2 - D\varphi_x^2]dx}{\int_0^L e^{(\nu/D)x}\varphi^2 dx}. \tag{5.12}$$

Theorem 5.3. *For any $\nu \geq 0$ and $L > 0$,*

$$\lim_{D\to\infty} d_*(D) = -\infty; \quad \lim_{D\to 0+} d_*(D) = \begin{cases} F(I_0) & \text{if } \nu = 0, \\ -\infty & \text{if } \nu > 0. \end{cases}$$

Proof. It is obvious that $d_*(D) \leq F(I_0)$. Assume by contradiction that there is a sequence $D_n \to \infty$ such that $\lim_{n\to\infty} d_*(D_n) > -\infty$. By the definition there are positive functions $\phi_n(x)$ satisfying $\|\phi_n\|_\infty = 1$ and

$$\begin{cases} -D_n\phi_{n,xx} + \nu\phi_{n,x} - F(I_0 e^{-k_0 x})\phi_n = -d_*(D_n)\phi_n \text{ in } (0, L), \\ D_n\phi_{n,x}(0) - \nu\phi_n(0) = \phi_n(L) = 0. \end{cases}$$

Set $\phi_n = \psi_n e^{(\nu/2D_n)x}$. Then $\psi_n(x)$ satisfies

$$\begin{cases} \psi_{n,xx} = \dfrac{1}{D_n}\left(\dfrac{\nu^2}{4D_n} - F(I_0 e^{-k_0 x}) + d_*(D_n)\right)\psi_n \text{ in } (0, L) \\ \psi_{n,x}(0) - \dfrac{\nu}{2D_n}\psi_n(0) = \psi_n(L) = 0. \end{cases}$$

As $D_n \to \infty$, $\|\psi_n\|_\infty$ and $d_*(D_n)$ are both bounded, we can use the L^p regularity to conclude that by passing to a subsequence $\psi_n(x) \to \psi_\infty(x)$ in $C^1([0, L])$, and $\psi_\infty(x)$ is a weak solution of the problem

$$\psi_{\infty,xx} = 0 \text{ in } (0, L), \;\; \psi_{\infty,x}(0) = \psi_\infty(L) = 0.$$

Clearly $\psi_\infty \equiv 0$. On the other hand, it is not difficult to see that $\|\psi_\infty\|_\infty = 1$. This contradiction proves $\lim_{D\to\infty} d_*(D, \nu, L) = -\infty$.

Let $\nu = 0$. Then

$$d_*(D) = \sup_{\varphi \neq 0, \varphi \in H} \frac{\int_0^L [F(I_0 e^{-k_0 x})\varphi^2 - D\varphi_x^2]dx}{\int_0^L \varphi^2 dx}.$$

Set for $\epsilon \in (0, L/4)$,

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

Then we have $\phi_\epsilon \in H$ and

$$d_*(D) \ge \frac{\int_0^L [F(I_0 e^{-k_0 x})\phi_\epsilon^2 - D\phi_{\epsilon,x}^2]dx}{\int_0^L \phi_\epsilon^2 dx} \ge F(I_0 e^{-2k_0\epsilon}) - \frac{D}{\epsilon^2}.$$

Letting $D \to 0+$, we obtain $\limsup_{D\to 0+} d_*(D) \ge F(I_0 e^{-2k_0\epsilon})$. Since ϵ can be arbitrarily small, we get

$$\limsup_{D\to 0+} d_*(D) \ge F(I_0).$$

On the other hand, it is easy to see that $d_*(D) \le F(I_0)$. Hence we have

$$\limsup_{D\to 0+} d_*(D) = F(I_0).$$

Now let $\nu > 0$ be fixed. Recall that there is for each $D > 0$ a function $\phi(x) > 0$ (in $[0, L)$) such that

$$\begin{cases} D\phi_{xx} - \nu\phi_x + F(I_0 e^{-k_0 x})\phi = d_*(D)\phi, & 0 < x < L, \\ D\phi_x(0) - \nu\phi(0) = \phi(L) = 0. \end{cases} \tag{5.13}$$

Let $\psi(x) = e^{-(\nu/D)\eta x}\phi(x)$, where $\eta > 0$ is some constant to be chosen later. Then ψ satisfies

$$\begin{cases} D\psi_{xx} + \nu(2\eta - 1)\psi_x + [\nu^2\eta(\eta - 1)/D + F(I_0 e^{-k_0 x}) - d_*(D)]\psi = 0, \\ D\psi_x(0) - \nu(1 - \eta)\psi(0) = \psi(L) = 0. \end{cases} \tag{5.14}$$

Set $\eta = 1/2$. Then (5.14) becomes

$$\begin{cases} D\psi_{xx} + [-\nu^2/4D + F(I_0 e^{-k_0 x}) - d_*(D)]\psi = 0, \\ D\psi_x(0) - (\nu/2)\psi(0) = \psi(L) = 0. \end{cases} \tag{5.15}$$

Let $x_D \in [0, L]$ such that $\psi(x_D) = \max_{0\le x\le L} \psi(x)$. Since $\psi_x(0) > 0$ and $\psi(L) = 0$, $x_D \in (0, L)$. Hence $\psi_x(x_D) = 0$ and $\psi_{xx}(x_D) \le 0$. From (5.15) one has

$$d_*(D) \le F(I_0 e^{-k_0 x_D}) - \nu^2/(2D),$$

and hence

$$\lim_{D\to 0+} d_*(D) = -\infty.$$

The proof of the theorem is complete. □

To emphasized the dependence of d_* on the sinking velocity ν, we write $d_* = d_*(\nu)$. Then we have

Theorem 5.4. *d_* is a decreasing function of ν, and*

$$\lim_{\nu\to\infty} d_*(\nu) = -\infty. \tag{5.16}$$

Proof. For any fixed $\nu > 0$, let $\phi(x) = \phi_\nu(x)$ with $\|\phi\|_\infty = 1$ be the unique positive eigenfunction such that

$$\begin{cases} -D\phi_{xx} + \nu\phi_x - F(I_0e^{-k_0x})\phi = -d_*(\nu)\phi \text{ in } (0, L), \\ D\phi_x(0) - \nu\phi(0) = \phi(L) = 0. \end{cases}$$

First we observe that by the Hopf boundary lemma, $\phi_x(L) < 0$. Integrating the equation for ϕ over $[0, L]$, one has

$$\int_0^L [F(I_0e^{-k_0x}) - d]\phi(x)\,dx = -D\phi_x(L) > 0.$$

Note that $F(I_0e^{-k_0x}) - d_*$ is a decreasing function, while $\phi(x)$ is positive on $(0, L)$, one has

$$-D\phi_x(x) + \nu\phi(x) = \int_0^x [F(I_0e^{-k_0y}) - d]\phi(y)\,dy > 0 \text{ for any } x \in (0, L).$$

Set $\xi(x) = \phi(x)e^{-\frac{\nu x}{D}}$. Then

$$\xi_x(x) = \phi_x(x) - (\nu/D)\phi(x) < 0 \text{ for any } x \in (0, L).$$

One can also check that ξ satisfies

$$\begin{cases} -D\xi_{xx} - \nu\xi_x = [F(I_0e^{-k_0x}) - d_*(\nu)]\xi \ \text{ in } (0, L), \\ \xi_x(0) = \xi(L) = 0. \end{cases} \tag{5.17}$$

Differentiating (5.17) with respect to ν (denoted by $'$) one has

$$\begin{cases} -D\xi'_{xx} - \nu\xi'_x - \xi_x = [F(I_0e^{-k_0x}) - d_*(\nu)]\xi' - d'_*(\nu)\xi \text{ in } (0, L), \\ \xi'_x(0) = \xi'(L) = 0. \end{cases} \tag{5.18}$$

Multiplying the equation for ξ' with ξ and the equation for ξ with ξ', integrating over $[0, L]$ and subtracting, one obtain

$$-d'_*(\nu)\int_0^L \xi^2 = -\int_0^L \xi\xi_x > 0.$$

Hence

$$d'_*(\nu) < 0,$$

which implies $d_*(\nu)$ is a decreasing function.

Now set $\psi(x) = \phi(x)e^{-\frac{\nu x}{2D}}$. Then $\psi(x)$ satisfies

$$\begin{cases} -D\psi_{xx} + \dfrac{\nu^2}{4D}\psi = [F(I_0 e^{-k_0 x}) - d_*(\nu)]\psi \ \text{ in } (0, L), \\ D\psi_x(0) - (\nu/2)\psi(0) = \psi(L) = 0. \end{cases}$$

Let x_ν be the points such that $\psi(x_\nu) = \max_{0\le x\le L} \psi(x)$. Then from the boundary conditions of ψ we conclude $x_\nu \in (0, L)$ and hence $\psi_{xx}(x_\nu) \le 0$. Therefore

$$F(I_0 e^{-k_0 x_\nu}) - d_*(\nu) - \frac{\nu^2}{4D} \ge 0.$$

Since $F(I_0 e^{-k_0 x_\nu})$ is bounded, (5.16) follows immediately. □

6. Discussion

In this paper, we incorporate size-structured populations into a water column where the species depends only on light for its growth and we assume that the amount of light absorbed by individuals is proportional to cell size. For the restrictions of mathematics, the advection term is assumed to be nonnegative (zero or sinking case) and the boundary conditions at the bottom are the Dirichlet type. This kind of boundary conditions have been used in the recent work [14]. Those two assumptions make Theorem 3.1 valid and we are able to reduce the system (2.7) into (5.2) (or (4.12)) (see Section 4). It is worth pointing out that the analyses of the system (5.2) also rely on the sign of the advection term.

With a general reproductive rate which is an increasing function of light intensity, we first define a critical death rate. Then we show that the phytoplankton survives if and only if its death rate is less than the critical death rate (Theorem 5.2). From (5.1), (5.6) and (5.12), it follows that the critical death rate is also affected by the size structure. With size structure, the prediction of the global dynamics requires the principal eigenvalue $\hat{\lambda}_0$ that depends on the functions governing cell division in relation to size, $b(q)$, and cell growth in relation to size, $g(q)$ (see (3.11)). In other words, the critical death rate depends on the reproductive rate, the characteristics of the water column (e.g., turbulent diffusion rate, sinking, depth), cell growth, cell division, and cell size.

In the previous work [8,19], the zero-flux boundary conditions apply to species at the top and bottom of the habitat. Due to the difference in the boundary conditions at the bottom, the dependence of d_* on the diffusion coefficient $D > 0$ and the sinking velocity $\nu \ge 0$ are very different from those in [19] (see subsection 5.3). Besides, the dependence of d_* on the depth L is difficult and unclear. Finally, we point out that if the boundary conditions at the bottom in (2.7) are changed into the zero-flux type, then the arguments in the proof of Theorem 3.1 don't work. It remains a challenging and interesting problem, and we leave it for future investigation.

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