SINGLE PHYTOPLANKTON SPECIES GROWTH WITH LIGHT AND CROWDING EFFECT IN A WATER COLUMN

Danfeng Pang, Hua Nie* and Jianhua Wu

School of Mathematics and Information Science
Shaanxi Normal University
Xi’an, Shaanxi 710119, China

(Communicated by Cyril Imbert)

Abstract. We investigate a nonlocal reaction-diffusion-advection model which describes the growth of a single phytoplankton species in a water column with crowding effect. The longtime dynamical behavior of this model and the asymptotic profiles of its positive steady states for small crowding effect and large advection rate are established. The results show that there is a critical death rate such that the phytoplankton species survives if and only if its death rate is less than the critical death rate. In contrast to the model without crowding effect, our results show that the density of the phytoplankton species will have a finite limit rather than go to infinity when the death rate disappears. Furthermore, for large sinking rate, the phytoplankton species concentrates at the bottom of the water column with a finite population density. For large buoyant rate, the phytoplankton species concentrates at the surface of the water column with a finite population density.

1. Introduction. Phytoplankton are microscopically small plants that drift in the water column of lakes and oceans, which form the base of the aquatic food chain. Phytoplankton require light for photosynthesis. Hence, phytoplankton populations should stay in the well-illuminated upper regions of the water column, since light availability decreases with depth. However, many phytoplankton species are heavier than water. They have a tendency to sink. Sinking phytoplankton plays an important role in several biogeochemical cycles as they can act as a carbon pump. For instance, sinking phytoplankton have the capability of directly affecting the global carbon cycle by exporting photosynthetic carbon from the atmosphere into the ocean interior[1, 7, 12]. Hence, a better understanding of the population dynamics of sinking phytoplankton species may contribute to a better understanding of the biogeochemical cycling of elements in aquatic ecosystems. On the other hand, some species, like the green algae Botryococcus, have a lower density than water and will float upwards, which is called buoyant. In freshwater lakes and rivers, phytoplankton communities can have a major impact on ecosystem dynamics. The
appearance of algae blooms are often a signal of dangerous eutrophication and may result in serious water-quality problems.

The formation of phytoplankton blooms has attracted considerable attention from mathematical, experimental and numerical viewpoints. In the classic work, Riley et al. [24] proposed a linear partial differential equation with respect to phytoplankton concentration to describe the vertical structure of phytoplankton growth dynamics. Although they focused on the interplay between vertical turbulent diffusion and sinking velocity, their mathematical analysis neglected the light dependence of phytoplankton growth. Shigesada and Okubo [26] investigated the self-shading effect on algal vertical distribution in the water column by developing a nonlocal reaction-diffusion-advection model in which they incorporated light-dependent growth rate but neglected light absorption. In order to study the combined effect of vertical turbulent diffusion, sinking velocity, the light-dependent growth and death processes of phytoplankton, Huisman et al. proposed and analyzed a new reaction-diffusion-advection model of light-limited phytoplankton [11, 15] in an eutrophic water column. It turned out that the conditions for phytoplankton bloom development can be captured by a critical depth and one or two critical threshold values for vertical turbulent diffusion rate. Moreover, their numerical simulations illustrated that phytoplankton as a whole can maintain a position in the well-illuminated zone near the surface of the water column at intermediate levels of turbulent diffusion.

The rigorous mathematical analysis of the critical conditions for phytoplankton bloom has been established by Hsu and Lou in [14]. They showed that a critical water column depth, a critical sinking or buoyant velocity and a critical turbulent diffusion rate can exist for some intermediate range of phytoplankton death rate by means of the strict monotonicity of the critical death rate with respect to the water column depth, the sinking or buoyant velocity and the turbulent diffusion rate. Furthermore, their analysis indicated that the phytoplankton forms a thin layer at the surface of the water column for large buoyant rate, and forms a thin layer at the bottom of the water column for large sinking rate. In [9], Du and Mei extended the results in [8, 14] to the model with variable diffusion and sinking rate. The effects of photo-inhibition on the growth of a single phytoplankton species are investigated in [10]. It turns out that the model with photo-inhibition possesses at least two positive steady states in certain parameter ranges. In [22], Peng and Zhao established a threshold type result on the global dynamics of the model of a single phytoplankton with time-periodic incident light intensity and time-periodic death rate in terms of the basic reproduction number. By analyzing various properties of the basic reproduction number with respect to the vertical turbulent diffusion rate, the sinking or buoyant rate and the water column depth, respectively, they revealed some new interesting effects of the modeling parameters and the time-periodic heterogeneous environment on persistence and extinction of the phytoplankton species.

In the current paper, we study the following reaction-diffusion-advection model, which describes the population dynamics of a single phytoplankton species in a water column with crowding effect

\[
P_t = DP_{xx} - vP_x + P[g(I(x,t)) - \beta P - d], \quad x \in (0, L), \quad t > 0,
\]

with boundary conditions

\[
DP_x(0, t) - vP(0, t) = 0, \quad DP_x(L, t) - vP(L, t) = 0, \quad t > 0,
\]
SINGLE PHYTOPLANKTON SPECIES GROWTH

43

and initial condition

\[ P(x, 0) = P_0(x) \geq 0, \neq 0, \text{ on } 0 \leq x \leq L, \tag{3} \]

where \( P = P(x, t) \) denotes the population density of the phytoplankton species. We assume that \( P_0(x) \in C([0, L]) \) for simplicity. \( D > 0 \) is the vertical turbulent diffusion rate, \( v \) is the sinking velocity (\( v > 0 \)) or the buoyant velocity (\( v < 0 \)), \( L > 0 \) is the depth of the water column, and \( d > 0 \) is the natural death rate. The positive parameter \( \beta \) gives rise to death rate \( \beta P \) which is due to crowding effect.

The assumption that the light gradient follows Lambert-Beer’s law indicates that the light intensity \( I(x, t) \) can be given by

\[ I(x, t) = I_0 \exp \left( -k_0 x - k_1 \int_0^x P(s, t) ds \right), \tag{4} \]

where \( I_0 \) is the incident light intensity, \( k_0 \) is the total background turbidity due to all non-phytoplankton components, and \( k_1 \) is the specific light attenuation coefficient of the phytoplankton. \( g(I) \) is the specific growth rate of phytoplankton as a function of light intensity \( I(x, t) \). Here we assume that the specific growth rate \( g(I) \in C^1([0, \infty)) \) satisfies

\[ g(0) = 0, \quad g'(I) > 0 \text{ for } I \geq 0, \quad \text{and } g(I) \geq aI^\rho \text{ for } I \in [0, I_0], \tag{5} \]

where \( a > 0 \) and \( \rho > 0 \). A typical example of \( g(I) \) takes the Michaelis–Menten form

\[ g(I) = \frac{mI}{b + I}, \]

where \( m \) is the maximal growth rate and \( b \) is the half saturation constant.

Du and Hsu investigated the special case \( \beta = 0, v = 0 \) in [8]. They first established a special comparison lemma and a boundedness lemma (see Lemma 3.1 and Lemma 3.2 in [8]). Then using this two key lemmas, a complete description of the longtime dynamical behavior for the model with \( \beta = 0, v = 0 \) is established.

As mentioned before, Hsu and Lou studied the combined effect of the death rate, sinking or buoyant coefficient, water column depth, and vertical turbulent diffusion rate on the persistence of a single phytoplankton species when \( \beta = 0, v \neq 0 \) in [14]. The asymptotic profiles of steady states for large advection rates are also investigated there. It turns out that the vertical distribution looks like a Dirac function at the bottom of the water column when the sinking velocity is sufficiently large, which indicates that the phytoplankton forms a thin layer at the bottom of the water column for large sinking rate. Similarly, the vertical distribution looks like a Dirac function at the surface of the water column when the buoyant coefficient is sufficiently large, which indicates that the phytoplankton forms a thin layer at the surface of the water column for large buoyant rate.

We focus on the longtime dynamical behavior for the general model (1)-(3) and the asymptotic profiles of steady states for large sinking or buoyant rates. Our results show that there is also a critical death rate such that the phytoplankton species survives if and only if its death rate is less than the critical death rate. In contrast to the model without crowding effect, our results show that the density of the phytoplankton species will have a finite limit rather than go to infinity when the death rate disappears. Furthermore, when the sinking velocity is sufficiently large, the phytoplankton species concentrates at the bottom of the water column with a finite population density. And the phytoplankton species concentrates at the surface of the water column with a finite population density when the buoyant velocity is
large enough. Although the idea is motivated by [8, 14], significant changes are needed in the detailed arguments due to the introduction of crowding effect (see Lemma 3.2 and Lemma 4.6).

The organization of this paper is as follows. In section 2, we establish the existence and uniqueness of positive steady states in terms of the death rate of the phytoplankton species. The longtime behavior of the solution is established by comparison principle and various analytical techniques in section 3. The aim of section 4 is to investigate the asymptotic profiles of positive equilibria for small crowding effect and large advection rate.

We end the introduction by mentioning some related mathematical research on the ecological models with crowding effect. Crowding effect is the phenomenon that population growth rate decreases with the increase of density in the process of population growth. If the environmental condition is infinite, the population may increase exponentially. But in the limited environment it follows the form of logistic growth, which is called environmental resistance or crowding effect. In [19, 20], the well-stirred chemostat model with crowding effect is proposed. The mathematical analysis illustrates that coexistence occurs when crowding effect is large enough. In [18], the authors studied the unstirred chemostat with crowding effect. It turns out that crowding effect is sufficiently effective in the occurrence of coexisting, and overcrowding of a species has an inhibiting effect on itself. More works concerning crowding effect can be seen in [17, 21, 28] and references therein.

2. Existence and uniqueness of positive steady states. The purpose of this section is to study the existence and uniqueness of positive steady states of the single population growth model in a water column

\[
\begin{align*}
DP_{xx} - \upsilon P_x + P[g(I(x)) - \beta P - d] &= 0, \quad 0 < x < L, \\
DP_x(0) - \upsilon P(0) &= 0, \quad DP_x(L) - \upsilon P(L) = 0,
\end{align*}
\]

where \(D > 0, \upsilon \in \mathbb{R}, g(I)\) satisfies (5), and

\[I(x) = I_0 \exp \left(-k_0x - k_1 \int_0^x P(s) ds\right).\]

With this in mind, we consider the linear eigenvalue problem

\[
\begin{align*}
-D\varphi_{xx} + \upsilon \varphi_x + q(x)\varphi &= \lambda \varphi, \quad 0 < x < L, \\
D\varphi_x(0) - \upsilon \varphi(0) &= 0, \quad D\varphi_x(L) - \upsilon \varphi(L) = 0,
\end{align*}
\]

where \(q(x) \in C([0, L])\). Set \(\psi(x) := e^{-(\upsilon/D)x}\varphi(x)\). Then \(\psi\) satisfies

\[
\begin{align*}
-D(e^{(\upsilon/D)x}\psi_x)_x + q(x)e^{(\upsilon/D)x}\psi &= \lambda e^{(\upsilon/D)x}\psi, \quad 0 < x < L, \\
\psi_x(0) &= \psi_x(L) = 0.
\end{align*}
\]

Lemma 2.1. [3, 14] All eigenvalues of (8) are real, and the smallest eigenvalue \(\lambda_1(q)\) can be characterized as

\[
\lambda_1(q) = \inf_{\psi \neq 0, \psi \in H^1(0, L)} \frac{\int_0^L e^{(\upsilon/D)x}(D\psi_x^2 + q\psi^2) dx}{\int_0^L e^{(\upsilon/D)x}\psi^2 dx},
\]

which corresponds to a positive eigenfunction \(\psi_1\), and \(\lambda_1(q)\) is the only eigenvalue whose corresponding eigenfunction does not change sign. Moreover,

(i) \(q_1(x) \geq q_2(x)\) implies \(\lambda_1(q_1(x)) \geq \lambda_1(q_2(x))\), and the equality holds only if \(q_1(x) \equiv q_2(x)\).
(ii) \( q_n(x) \to q(x) \) in \( C([0, L]) \) implies \( \lambda_1(q_n(x)) \to \lambda_1(q(x)) \).

For every \( v \in \mathbb{R}, \ L > 0 \) and \( D > 0 \), we define
\[
d_s(v, L, D) := -\lambda_1(-g(I_0 e^{-k_0 x})).
\]
Obviously, \( d_s(v, L, D) > 0 \). At first, we derive the priori estimates for positive equilibria of (6).

**Lemma 2.2.** Suppose \( P \) is a nonnegative solution of (6) with \( P \neq 0 \). Then \( 0 < P \leq C \) and \( d < d_s \), where \( C = \frac{1}{\beta} e^{(\vert v \vert/D)L}(g(I_0) + d) \).

**Proof.** Let \( Q = e^{-\frac{(v)}{D}x} P \). Then \( Q \) satisfies
\[
\begin{align*}
&D(e^{\frac{(v)}{D}x}Q_x)_x + e^{\frac{(v)}{D}x}Q[\hat{g}(\hat{I}(x)) - \beta e^{\frac{(v)}{D}x}Q - d] = 0, \quad 0 < x < L, \\
&Q_x(0) = Q_x(L) = 0,
\end{align*}
\]
where \( \hat{I}(x) = I_0 \exp \left(-k_0 x - k_1 \int_0^x e^{\frac{(v)}{D}s}Q(s)ds \right) \). We claim that \( Q(x) > 0 \) on \([0, L]\) by the strong maximum principle and the Hopf boundary lemma (see [23]).

In fact, since \( P(x) \geq 0, \neq 0 \) on \([0, L]\), we have \( Q(x) \geq 0, \neq 0 \) on \([0, L]\). Suppose \( Q(x_*) = \min Q(x) = 0 \), where \( x_* \in [0, L] \). It follows from (10) that
\[
-D(e^{\frac{(v)}{D}x}Q_x)_x + [\beta e^{\frac{(v)}{D}x}Q + d]e^{\frac{(v)}{D}x}Q = e^{\frac{(v)}{D}x}Qg(\hat{I}(x)) \geq 0.
\]
If \( x_\ast \in (0, L) \), by the strong maximum principle (see [23, Theorem 3 in Chapter 1]), we have \( Q(x) \equiv 0 \) on \([0, L]\), a contradiction. If \( x_\ast = 0 \), by the Hopf boundary lemma (see [23, Theorem 4 in Chapter 1]), we obtain that \( Q_x(0) > 0 \), which contradicts the boundary condition. Similarly, if \( x_\ast = L \), we also have a contradiction to the boundary condition. Hence, \( P(x) = e^{\frac{(v)}{D}x}Q(x) > 0 \) on \([0, L]\).

Suppose \( Q(x_0) = \max Q(x) \), where \( x_0 \in [0, L] \). We claim that
\[
e^{\frac{(v)}{D}x_0}Q(x_0)[g(\hat{I}(x_0)) - \beta e^{\frac{(v)}{D}x_0}Q(x_0) - d] \geq 0. \tag{11}
\]
At first, if \( x_0 \in (0, L) \), then \( Q_x(x_0) = 0 \) and \( Q_{xx}(x_0) \leq 0 \). By using the equation (10), we get that (11) holds. If \( x_0 = 0 \), we argue by contradiction. Suppose that \( Q(0)[g(I_0) - \beta Q(0) - d] < 0 \). Then by the continuity of \( g \) and \( Q \), there exists a small interval \([0, \delta]\) such that \( e^{\frac{(v)}{D}x}Q(x)[g(\hat{I}(x)) - \beta e^{\frac{(v)}{D}x}Q(x) - d] < 0 \) for \( x \in [0, \delta] \). It follows from (10) that \( e^{\frac{(v)}{D}x}Q_x(x) > 0 \) for \( x \in (0, \delta) \). Since \( x_0 = 0 \) is the maximum point of \( Q \) on \([0, \delta]\), it follows from the Hopf boundary lemma that \( Q_x(0) < 0 \), which contradicts the boundary condition in (10). Hence, (11) holds if \( x_0 = 0 \). Similarly, we can show that (11) holds if \( x_0 = L \). In summary, (11) holds if \( Q(x_0) = \max Q(x) \), which means \( \beta e^{\frac{(v)}{D}x_0}Q(x_0) \leq g(\hat{I}(x_0)) - d \leq g(I_0) + d \) by using the assumption (5). Hence, \( Q(x_0) \leq \frac{1}{\beta} e^{-\frac{(v)}{D}x_0}g(I_0) + d \). If \( v > 0 \), then \( Q(x_0) \leq \frac{1}{\beta} e^{-\frac{(v)}{D}x_0}g(I_0) + d \), and \( P(x) = e^{\frac{(v)}{D}x}Q(x) \leq \frac{1}{\beta} e^{\frac{(v)}{D}L}g(I_0) + d \). If \( v < 0 \), then \( Q(x_0) \leq \frac{1}{\beta} e^{-\frac{(v)}{D}x_0}g(I_0) + d \), and \( P(x) = e^{\frac{(v)}{D}x}Q(x) \leq \frac{1}{\beta} e^{\frac{(v)}{D}L}g(I_0) + d \). Thus we have \( 0 < P(x) \leq \frac{1}{\beta} e^{\frac{(v)}{D}L}g(I_0) + d \).

For any positive solution \( P \) of (6), let \( Q = e^{-\frac{(v)}{D}x}P \). Then \( Q \) satisfies (10), which can be rewritten as
\[
\begin{align*}
&\begin{cases}
-D(e^{\frac{(v)}{D}x}Q_x)_x + [\tilde{g}(\hat{I}(x)) + \beta e^{\frac{(v)}{D}x}Q]e^{\frac{(v)}{D}x}Q = -d e^{\frac{(v)}{D}x}Q, \quad 0 < x < L, \\
Q_x(0) = Q_x(L) = 0,
\end{cases}
\end{align*}
\]
It follows from (12) and Lemma 2.1 that
\[ -d = \lambda_1 \left(-g(I(x)) + \beta e^{(v/D)x}Q\right) > \lambda_1 \left(-g(I(x))\right) > \lambda_1 \left(-g(I_0e^{-k_0x})\right) \]
\[ = -d_*(v, L, D). \]
That is, \( d < d_* \).

To investigate the existence of positive steady states of (6), we need first establish the existence and uniqueness of positive solutions to the following auxiliary system
\[
\begin{cases}
DP_{xx} - vP_x + P[g(I(x)) - \beta P] = 0, & 0 < x < L, \\
DP_x(0) - vP(0) = 0, \quad DP_x(L) - vP(L) = 0,
\end{cases}
\tag{13}
\]
where \( I(x) \) takes the form (7). This auxiliary system plays an important role in determining the profiles of positive solutions to (6), and makes the difference between bifurcation diagrams Fig.1(a) and Fig.1(b).

**Lemma 2.3.** There exists a unique positive solution \( P_0(\beta; x) \) of equation (13).

**Proof.** We first show the existence of positive solutions of (13). Let \( U = e^{-(v/D)x}P \). Then \( U \) satisfies
\[
\begin{cases}
D(e^{(v/D)x}U)_x + e^{(v/D)x}[g(I(x)) - \beta e^{(v/D)x}U] = 0, & 0 < x < L, \\
U_x(0) = U_x(L) = 0,
\end{cases}
\tag{14}
\]
where \( I(x) = I_0 \exp \left(-k_0x - k_1 \int_0^x e^{(v/D)s}U(s)ds\right) \). By similar arguments as in Lemma 2.2, we can show that any positive solution \( U \) of (14) satisfying
\[
0 < U \leq \frac{1}{\beta} e^{(v/D)L}g(I_0),
\tag{15}
\]
Introduce the following spaces
\[
E = C^1([0, L]), \\
W = \{U \in E : U(x) \geq 0, \; x \in [0, L]\}, \\
\Omega = \{U \in W : U(x) < \frac{1}{\beta} e^{(v/D)L}g(I_0) + 1, \; x \in [0, L]\}.
\]
Define a differentiable operator \( T_\tau : [0, 1] \times \Omega \rightarrow E \) by
\[
T_\tau(U) := K \left(e^{(v/D)x}U(\tau g(I(x)) - \beta e^{(v/D)x}U) + MU\right),
\]
where \( K \) is the solution operator \( \xi = K(m(x)) \) for the problem
\[
\begin{cases}
-D(e^{(v/D)x}\xi)_x + M\xi = m(x), & 0 < x < L, \\
\xi_x(0) = \xi_x(L) = 0,
\end{cases}
\]
and \( M \) is large enough such that \( e^{(v/D)x}(\tau g(I(x)) - \beta e^{(v/D)x}U) + M > 0 \) for all \( U \in \Omega, \; \tau \in [0, 1] \) and \( x \in [0, L] \). Then \( T_\tau : [0, 1] \times \Omega \rightarrow W \). It follows from the standard elliptic regularity theory that \( T_\tau \) is compact and continuously differentiable. Let \( T = T_1 \). Then (14) has a nonnegative solution if and only if \( T \) has a fixed point in \( \Omega \).

It follows from (15) that for \( \tau \in [0, 1] \), \( T_\tau \) has no fixed point on \( \partial \Omega \). By the homotopic invariance of the degree, we have
\[
\text{index}(T, \Omega, W) = \text{index}(T_\tau, \Omega, W) = \text{index}(T_0, \Omega, W).
\]
We claim that $T_0$ has a unique fixed point 0 in $\Omega$. To this end, let $T_0(U) = U$. Then
\[-D(e^{(\nu/D)x}U_x)_x = -\beta e^{2(\nu/D)x}U^2, \quad 0 < x < L, \quad U_x(0) = U_x(L) = 0.\]
Integrating this equation over $[0, L]$, we obtain that $\beta \int_0^L e^{2(\nu/D)x}U^2 dx = 0$, which implies that $U(x) \equiv 0$. Hence, 0 is the unique fixed point of $T_0$ in $\Omega$, and
\[\text{index}(T_0, \Omega, W) = \text{index}(T_0, 0, W).\]
Next, we show that $\text{index}(T_0, 0, W) = 1$ by using Lemma A.2. Let $T'_0(0)$ be the Fréchet derivative of $T_0$ with respect to $U$ at 0. For $\varphi \in W$, let $T'_0(0)\varphi = \lambda \varphi$ and $\varphi \neq 0$. Then
\[-D(e^{(\nu/D)x}\varphi_x)_x = \left(\frac{1}{\lambda} - 1\right)M\varphi, \quad 0 < x < L, \quad \varphi_x(0) = \varphi_x(L) = 0.\]
Multiplying this equation by $\varphi$ and integrating over $[0, L]$ by parts, we get
\[\frac{1}{\lambda} - 1 = \frac{D \int_0^L e^{(\nu/D)x}\varphi_x^2}{M \int_0^L \varphi^2} > 0.\]
Thus, $\lambda < 1$ and the spectral radius $r(T'_0(0)) < 1$. It follows from Lemma A.2 that $\text{index}(T_0, 0, W) = 1$. Hence, we deduce that
\[\text{index}(T, \Omega, W) = \text{index}(T_0, \Omega, W) = \text{index}(T_0, 0, W) = 1.\]
Next, we show that $\text{index}(T, 0, W) = 0$ by Lemma A.2 again. To this end, let $T'(0)$ be the Fréchet derivative of $T$ with respect to $U$ at 0. For $U \in W$, $T'(0)U = U$ is equivalent to
\[
\begin{align*}
&\left\{-D(e^{(\nu/D)x}U_x)_x + MU = e^{(\nu/D)x}Ug(I_0e^{-k_0x}) + MU, \quad 0 < x < L, \\
&U_x(0) = U_x(L) = 0.\right.
\end{align*}
\]
It is easy to see that $U \equiv 0$, that is, 1 is not an eigenvalue of $T'(0)$ in $W$. Hence, 0 is an isolated fixed point of $T$ in $W$. Let $T'(0)U = \lambda U$ and $U \neq 0$. Then
\[
\begin{align*}
&\left\{-D(e^{(\nu/D)x}U_x)_x + MU = \frac{1}{\lambda}[e^{(\nu/D)x}Ug(I_0e^{-k_0x}) + MU], \quad 0 < x < L, \\
&U_x(0) = U_x(L) = 0.\right.
\end{align*}
\]
Consider the eigenvalue problem
\[
\begin{align*}
&\left\{-D(e^{(\nu/D)x}\psi_x)_x - e^{(\nu/D)x}g(I_0e^{-k_0x})\psi = \mu \psi, \quad 0 < x < L, \\
&\psi_x(0) = \psi_x(L) = 0.\right.
\end{align*}
\]
Let $\mu_1 \left(-e^{(\nu/D)x}g(I_0e^{-k_0x})\right)$ be the smallest eigenvalue of (16), and let $\mu_1(0)$ be the smallest eigenvalue of
\[-D(e^{(\nu/D)x}\psi_x)_x = \mu \psi, \quad 0 < x < L, \quad \psi_x(0) = \psi_x(L) = 0.\]
Clearly, $\mu_1(0) = 0$. In view of $e^{(\nu/D)x}g(I_0e^{-k_0x}) > 0$, it follows from monotonicity of the smallest eigenvalue with respect to the weight function that
\[
\mu_1 \left(-e^{(\nu/D)x}g(I_0e^{-k_0x})\right) < \mu_1(0) = 0.
\]
By Lemma A.1, the eigenvalue problem
\[
\begin{align*}
&\left\{-D(e^{(\nu/D)x}\psi_x)_x + M \psi = \eta[e^{(\nu/D)x}g(I_0e^{-k_0x})\psi + M \psi], \quad 0 < x < L, \\
&\psi_x(0) = \psi_x(L) = 0.\right.
\end{align*}
\]
has an eigenvalue less than 1, denoted by \( \eta_1 \). Hence, it is easy to see that \( \frac{1}{\eta_1} > 1 \) is an eigenvalue of \( T'(0) \). That is, \( T'(0) \) has an eigenvalue greater than 1. It follows from Lemma A.2 that \( \text{index}(T, 0, W) = 0 \).

In view of \( \text{index}(T, \Omega, W) \neq \text{index}(T, 0, W) \), it follows from Leray-Schauder degree theory that \( T \) has at least one nonzero fixed point in \( \Omega \). Namely, \((14)\) (thus \((13)\)) has at least one non-trivial nonnegative solution. By similar arguments as in Lemma 2.2, we can show that the non-trivial nonnegative solution of \((13)\) is a positive solution of \((13)\) by the strong maximum principle and Hopf boundary lemma.

Next, we verify the uniqueness of positive solutions to \((13)\). The idea is motivated by the arguments in [8]. Firstly, it follows from the strong maximum principle that all nontrivial nonnegative solutions of \((14)\) must be strictly positive on \([0, L] \).

Suppose \((14)\) has two positive solutions \( U_1 \neq U_2 \). If \( U_1 \leq U_2 \), then we deduce

\[
0 = \lambda_1 \left[-g \left( I_0 e^{-k_0 x} \exp(-k_1 \int_0^x e^{(\nu/D)s} U_1(s) ds) + \beta e^{(\nu/D)x} U_1 \right) \right]
\]

\[
< \lambda_1 \left[-g \left( I_0 e^{-k_0 x} \exp(-k_1 \int_0^x e^{(\nu/D)s} U_2(s) ds) + \beta e^{(\nu/D)x} U_2 \right) \right] = 0,
\]

a contradiction. Here \( \lambda_1 [-g \left( I_0 e^{-k_0 x} \exp(-k_1 \int_0^x e^{(\nu/D)s} U_i(s) ds) + \beta e^{(\nu/D)x} U_i \right) \) is defined by \((9)\) with \( q(x) = -g(I_0 e^{-k_0 x} \exp(-k_1 \int_0^x e^{(\nu/D)s} U_i(s) ds) + \beta e^{(\nu/D)x} U_i \) \((i = 1 \text{ or } 2)\). Therefore \( U_1 - U_2 \) changes sign in \((0, L)\). We claim that \( U_1(0) \neq U_2(0) \).

Otherwise, let \( V_i(x) = I_0 \int_0^x e^{(\nu/D)s} U_i(s) ds, \ Y_i(x) = U_i'(x) e^{(\nu/D)x} \) with \( i = 1, 2 \). Then \((U_1, V_i, Y_i)\) are solutions of the initial value problem

\[
\begin{cases}
U' = Ye^{-(\nu/D)x}, \\
V' = U e^{(\nu/D)x}, \\
DY' = -U e^{(\nu/D)x}\left[ g(I_0 e^{-k_0 x} \exp(-k_1 V)) - \beta U e^{(\nu/D)x} \right], \\
U(0), V(0), Y(0) = (U(0), 0, 0).
\end{cases}
\]

By the uniqueness of the ODE, we obtain that \((U_1, V_i, Y_i) = (U_2, V_2, Y_2)\), a contradiction. Therefore \( U_1(0) \neq U_2(0) \).

Without loss of generality, we may assume \( U_1(0) < U_2(0) \). Since \( U_1 - U_2 \) changes sign in \((0, L)\), there exists \( x_0 > 0 \) such that \( U_1(x) < U_2(x) \) in \([0, x_0)\), \( U_1(x_0) = U_2(x_0)\), and \( U_1'(x_0) \geq U_2'(x_0) \). Observe that \( U_1(i = 1, 2)\) satisfy

\[
\begin{cases}
D(e^{(\nu/D)x} U_i(x)) + e^{(\nu/D)x} U_i g(\hat{I}_i(x)) - \beta e^{(\nu/D)x} U_i = 0, & 0 < x < L, \\
U_i(x) = 0, & x = 0, L.
\end{cases}
\]

where \( \hat{I}_i(x) = I_0 \exp(-k_0 x - k_1 \int_0^x e^{(\nu/D)s} U_i(s) ds) \). Multiplying \((17)\) with \( i = 1 \) by \( U_2 \) and \((17)\) with \( i = 2 \) by \( U_1 \), integrating over \((0, x_0)\) by parts, and subtracting each other, we obtain that

\[
\begin{aligned}
& D e^{(\nu/D)x} U_1(x_0) \left[ U_2'(x_0) - U_1'(x_0) \right] \\
& = \int_0^{x_0} e^{(\nu/D)x} U_1 U_2 g(I_0 e^{-k_0 x} \exp(-k_1 \int_0^x e^{(\nu/D)s} U_1(s) ds) \\
& - g(I_0 e^{-k_0 x} \exp(-k_1 \int_0^x e^{(\nu/D)s} U_2(s) ds)) - \beta (U_1 - U_2) e^{(\nu/D)x} dx.
\end{aligned}
\]
The right-hand side of (18) is positive, while its left-hand side is non-positive, a contradiction. Therefore the problem (14)(hence (13)) has a unique positive solution \( P_0(\beta; x) \).

The following results show that \( d_* \) is the critical death rate, that is, the phytoplankton species survives if and only if its death rate is less than \( d_* \).

**Theorem 2.4.** (i) If \( d \geq d_*(v, L, D) \), then zero is the only nonnegative steady state of (1)-(2);

(ii) If \( 0 < d < d_*(v, L, D) \), then (1)-(2) has a unique positive steady state, denoted by \( P_d(\beta; x) \), which satisfies \( \lim_{d \to 0} P_d(\beta; x) = P_0(\beta; x) \).

**Proof.** It follows from Lemma 2.2 that part (i) holds. Now, we focus our attention on the proof of (ii).

**Step 1.** Local bifurcation. Let \( Q = e^{-(v/D)x}P \). Then (6) is equivalent to (10). Let \( X = W^{2,p}(0, L) \), where \( p > 1 \). Then \( X \hookrightarrow C^1([0, L]) \). Define \( F : \mathbb{R}_+ \times X \to X \) by

\[
F(d, Q) = \mathcal{K} \left( e^{(v/D)x}Q[g(\tilde{I}(x)) - \beta e^{(v/D)x}Q - d + d_*] \right),
\]

where \( \mathcal{K} \) is the solution operator \( \zeta(x) = \mathcal{K}(r(x)) \) for the problem

\[
\begin{aligned}
-D(e^{(v/D)x}x_\beta)_x + d_* e^{(v/D)x}x_\beta &= r(x), \quad 0 < x < L, \\
\zeta_x(0) &= \zeta_x(L) = 0.
\end{aligned}
\]

Clearly, \( \mathcal{K} \) is a strongly positive compact operator. By standard elliptic regularity theory we know that \( F \) is a compact differential operator on \( X \). Let \( G(d, Q) = Q - F(d, Q) \). Then \( G : \mathbb{R}_+ \times X \to X \) is \( C^1 \) smooth, and the zeros of \( G(d, Q) = 0 \) with \( 0 < Q \leq C \max e^{-\frac{\beta}{Q}} \) correspond to the positive solutions of (10).

Now we begin to construct a positive solution branch \((d, Q) \subset \mathbb{R}_+ \times X \) bifurcating from the trivial solution branch \((d, 0)\) by bifurcation theory (see [2, 25] or Theorems A.4 and A.5 in the appendix). Let \( L(d_*, 0) \) be the Fréchet derivative of \( G(d_*, Q) \) with respect to \( Q \) at 0. Then \( L(d_*, 0) \Phi = 0 \) gives

\[
\begin{aligned}
-D(e^{(v/D)x}x_\Phi)_x + g(I_0 e^{-k_0 x}) e^{(v/D)x}x_\Phi &= -d_* e^{(v/D)x}x_\Phi, \quad 0 < x < L, \\
\Phi_x(0) = \Phi_x(L) = 0.
\end{aligned}
\]

By the definition of \( d_* \), we know that \( \Phi = c\psi_1 \), where \( c \) is a constant, and \( \psi_1 \) is the corresponding eigenfunction of \( \lambda_1(-g(I_0 e^{-k_0 x})) \). Hence, we conclude that the kernel \( N(L(d_*, 0)) = \text{span}\{\psi_1\} \).

Next we determine the range of \( L(d_*, 0) \). Suppose \( \Psi \in R(L(d_*, 0)) \). Then there exists \( Q \in X \) such that \( L(d_*, 0)Q = \Psi \), that is

\[
\begin{aligned}
-D(e^{(v/D)x}Q)_x - [g(I_0 e^{-k_0 x}) - d_*] e^{(v/D)x}Q &= -d_* e^{(v/D)x}x_\Psi, \quad 0 < x < L, \\
Q_x(0) = Q_x(L) = 0.
\end{aligned}
\]

Multiplying the first equation of (19) by \( \psi_1 \), and integrating over \((0, L)\) by parts, we obtain

\[
\int_0^L g(I_0 e^{-k_0 x}) e^{(v/D)x}x_\Psi \psi_1 dx = 0.
\]

Hence, the range of \( L(d_*, 0) \) is

\[
R(L(d_*, 0)) = \{ \Psi \in X : \int_0^L g(I_0 e^{-k_0 x}) e^{(v/D)x}x_\Psi \psi_1 dx = 0 \},
\]

and \( \text{codim} R(L(d_*, 0)) = 1 \). Thus \( L(d_*, 0) \) is a Fredholm operator with index zero (see Definition A.3 in the appendix). Moreover, by the strong maximum principle,
it is easy to see that $D^2_{d,Q}G(d_*,0)\psi_1 = K(e^{(v/D)x}\psi_1) > 0$. Hence, one can conclude that $D^2_{d,Q}G(d_*,0)\psi_1 \neq R(L(d_*,0))$.

Let $Z = R(I_0(d_*,0)) = \{ \Psi \in X : \int_0^L g(I_0 e^{-k_0 x}) e^{(v/D)x}\psi_1 \Psi dx = 0 \}$. It is easy to see that $Z \oplus \text{span}\{\psi_1\} = X$. By the application of the standard bifurcation theorem from a simple eigenvalue (see Theorem A.4), $(d_*,0)$ is a bifurcation point, and there exists $\delta > 0$ and $C^1$ curve $(d(\epsilon),\phi(\epsilon)) : (-\delta,\delta) \to \mathbb{R} \times Z$, such that $d(0) = d_*$, $\phi(0) = 0$, $\phi(\epsilon) \in Z$, and

$$(d(\epsilon),Q(\epsilon)) = (d(\epsilon),e(\psi_1 + \phi(\epsilon))),$$

which satisfies $G(d(\epsilon),Q(\epsilon)) = 0$. Let $P(\epsilon) = e^{(v/D)x}Q(\epsilon)$. Then the bifurcation branch $\Gamma = \{(d(\epsilon),P(\epsilon)) : 0 < \epsilon < \delta \}$ is exactly the positive solution of (6).

**Step 2.** Global bifurcation. We show that the local solution branch $\Gamma$ can be extended to a global one by the application of the global bifurcation results for Fredholm operators (see Theorems A.4 and A.5 in the appendix.) Noting that $F : \mathbb{R}_+ \times X \to X$ is $C^1$ smooth and compact, we can conclude that the Fréchet derivative $D_QG(d,Q)$ is a Fredholm operator with index zero for any $(d,Q) \in \mathbb{R}_+ \times X$. Now we can apply Theorem A.4 to obtain a connected component $C$ of the closure of the set $\{(d,Q) \in \mathbb{R}_+ \times X : G(d,Q) = 0, Q \neq 0 \}$. Moreover, either $C$ is not compact in $\mathbb{R}_+ \times X$ or $C$ contains a point $(\hat{d},0)$ with $\hat{d} \neq d_*$. Set

$$C' = \{(d,P) : P = e^{(v/D)x}Q, (d,Q) \in C\};$$

Then $\Gamma \subset C'$. Let

$$X_0 = \{P \in C^1[0,L] : P > 0, x \in [0,L]\}.$$

Then $C' \cap (\mathbb{R}_+ \times X_0) \neq \emptyset$.

Let $C^* = C' \cap (\mathbb{R}_+ \times X_0)$. Then $C^*$ consists of the local positive solution branch $\Gamma$ near the bifurcation point $(d_*,0)$. That is $C^* \subset \mathbb{R}_+ \times X_0$ in a small neighborhood of $(d_*,0)$.

Let $C^+$ be the connected component of $C' \setminus \{(d(\epsilon),P(\epsilon)) : -\delta < \epsilon < 0\}$. Then $C^* \subset C^+$. It follows from Theorem A.5 that $C^+$ satisfies one of the following alternatives:

(i) it is not compact in $\mathbb{R}_+ \times X$;

(ii) it contains a point $(\hat{d},0)$ with $\hat{d} \neq d_*$;

(iii) it contains a point $(\hat{d},e^{(v/D)x}Q)$, where $Q \neq 0, Q \in Z$.

Suppose (iii) holds. For any $P \in C^*$, we have $Q = e^{-(v/D)x}P > 0$. Thus

$$\int_0^L g(I_0 e^{-k_0 x}) \psi_1 Q dx > 0,$$ which contradicts $Q \in Z$. Hence, (iii) is impossible.

Suppose (ii) holds. Then we can find a sequence of points $\{(d_*,P_n)\} \subset C^+ \cap (\mathbb{R}_+ \times X_0)$ with $P_n > 0$ on $[0,L]$, which converges to $(\hat{d},0)$ as $n \to \infty$. Let $Q_n = e^{-(v/D)x}P_n$, and $\hat{Q}_n = \frac{Q_n}{\|Q_n\|}$. Then $Q_n \to 0$ uniformly on $[0,L]$ as $n \to \infty$, and $\hat{Q}_n \in L^\infty(0,L)$ satisfies

$$\begin{cases}
D(e^{(v/D)x}\hat{Q}_n,x)x + e^{(v/D)x}\hat{Q}_n[g(I_n(x)) - \beta e^{(v/D)x}Q_n-d_n] = 0, & 0 < x < L,
\hat{Q}_n,x(0) = 0, \hat{Q}_n,x(L) = 0,
\end{cases}$$

(20)

where $I_n(x) = I_0 \exp(-k_0 x - k_1 \int_0^x e^{(v/D)s}Q_n(s)ds)$. Integrating the first equation of (20) from 0 to $x$, we have

$$D e^{(v/D)x}\hat{Q}_n,x + \int_0^x e^{(v/D)s}\hat{Q}_n[g(I_n(s)) - \beta e^{(v/D)s}Q_n-d_n]ds = 0.$$


As \( g(\hat{T}_n(x)) \), \( Q_n(x) \) and \( \hat{Q}_n(x) \) are uniformly bounded in \((0, L)\), we conclude that \( \hat{Q}_{n,x} \) is uniformly bounded in \((0, L)\). By \((20)\), \( \hat{Q}_{n,xx} \) is uniformly bounded in \((0, L)\). Hence, for any \( p > 1 \), \( \hat{Q}_n \in W^2_p(0, L) \). By Sobolev embedding theorems, there exists a convergent subsequence of \( \hat{Q}_n \), which we still denote by \( \hat{Q}_n \) for sake of convenience, such that \( \hat{Q}_n \to \hat{Q} \geq 0(\neq 0) \) in \( C^1([0, L]) \) as \( n \to \infty \), and

\[
\begin{cases}
D(e^{(v/D)x}\hat{Q}_x)_x + e^{(v/D)x}\hat{Q}[g(I_0 e^{-k_0 x}) - \hat{d}] = 0, & 0 < x < L, \\
\hat{Q}_x(0) = 0, & \hat{Q}_x(L) = 0.
\end{cases}
\]

It follows from the strong maximum principle that \( \hat{Q} > 0 \) on \([0, L]\), which implies \( \hat{d} = d_* \), a contradiction.

Notice that any positive solution of \((6)\) satisfies \( 0 < P < C, 0 < d < d_* \). Thus (i) implies that \( C^* - \{(d_*, 0)\} \not\subset \mathbb{R}_+ \times X_0 \). Hence there exists \((\hat{d}, \hat{P}) \in (C^* - \{(d_*, 0)\}) \cap \partial(\mathbb{R}_+ \times X_0) \), which is the limit of a sequence \( \{(d_m, P_m)\} \subset C^* \cap (\mathbb{R}_+ \times X_0), P_m > 0 \) on \([0, L]\). Then \((\hat{d}, \hat{P}) \in \partial(\mathbb{R}_+ \times X_0) \) implies that (a) \( \hat{P} \geq 0 \), \( \hat{P}(x_0) = 0 \) for some point \( x_0 \in [0, L] \); or (b) \( \hat{d} = 0 \).

If \( \hat{P} \geq 0 \) and \( \hat{P}(x_0) = 0 \), then it follows from the strong maximum principle that \( \hat{P} \equiv 0 \) (see Lemma 2.2 for details). Thus \((d_m, P_m) \to (d, 0) \) in \( \mathbb{R}_+ \times X \) as \( m \to \infty \), \( P_m \) satisfies

\[
\begin{cases}
DP_{m,x} - vP_{m,x} + P_m g(I_m(x)) - \beta P_m - d_m = 0, & 0 < x < L, \\
DP_{m,x}(0) - vP_{m,x}(0) = 0, & DP_{m,x}(L) - vP_{m}(L) = 0,
\end{cases}
\]

where \( I_m(x) = I_0 e^{(-k_0 x - k_1)\int_0^x P_m(s)ds} \). Let \( Q_m = e^{-(v/D)x}P_m \) and \( \tilde{Q}_m = \frac{Q_m}{\|Q_m\|_\infty} \). Then \( Q_m \to 0 \) in \( X \) and \( \tilde{Q}_m \) satisfies

\[
\begin{cases}
D(e^{(v/D)x}\tilde{Q}_m)_x + e^{(v/D)x}\tilde{Q}_m[g(\tilde{I}_m(x)) - \beta e^{(v/D)x}Q_m - d_m] = 0, & 0 < x < L, \\
\tilde{Q}_m(x) = 0, & \tilde{Q}_m(L) = 0,
\end{cases}
\]

where \( \tilde{I}_m(x) = I_0 e^{(-k_0 x - k_1)\int_0^x e^{(v/D)s}Q_m(s)ds} \). Integrating the first equation of \((22)\) from \( 0 \) to \( x \), we have

\[
De^{(v/D)x}\tilde{Q}_m + \int_0^x e^{(v/D)s}\tilde{Q}_m[g(\tilde{I}_m(s)) - \beta e^{(v/D)s}Q_m - d_m]ds = 0.
\]

As \( g(\tilde{I}_m(x)) \), \( Q_m(x) \) and \( \tilde{Q}_m(x) \) are uniformly bounded in \((0, L)\), we conclude that \( \tilde{Q}_{m,x} \) is uniformly bounded in \((0, L)\). It follows from \((22)\) that \( \tilde{Q}_{m,xx} \) is uniformly bounded in \((0, L)\). Hence, for any \( p > 1 \), \( \tilde{Q}_m \in W^2_p(0, L) \). By Sobolev embedding theorems, there exists a convergent subsequence of \( \tilde{Q}_m \), which we still denote by \( \tilde{Q}_m \) for simplicity, such that \( \tilde{Q}_m \to \tilde{Q} = 0(\neq 0) \) in \( C^1([0, L]) \) as \( n \to \infty \). Taking the limit in \((22)\) as \( m \to \infty \), we get

\[
\begin{cases}
D(e^{(v/D)x}\tilde{Q}_x)_x + e^{(v/D)x}\tilde{Q}[g(I_0 e^{-k_0 x}) - \hat{d}] = 0, & 0 < x < L, \\
\tilde{Q}_x(0) = 0, & \tilde{Q}_x(L) = 0.
\end{cases}
\]

It follows from the strong maximum principle that \( \tilde{Q} > 0 \) on \([0, L]\), which implies that \( \hat{d} = d_* \), a contradiction.

The remaining possibility is that \( \hat{d} = 0, \hat{P} > 0 \), namely, \((d_m, P_m) \to (0, \hat{P}) \). Integrating the first equation of \((21)\) from \( 0 \) to \( x \), we have

\[
DP_{m,x}(x) - vP_{m,x}(x) + \int_0^x P_m[g(I_m) - \beta P_m - d_m]ds = 0.
\]
Since $g(I_m)$ and $P_m$ are uniformly bounded, one concludes that $P_{m,x}$ is uniformly bounded. Thus $P_{m,xx}$ is uniformly bounded by (21) again. Passing to a subsequence if necessary, we may assume that $P_m \to \hat{P}$ in $C^1([0,L])$. Letting $m \to \infty$ in (21), we have
\[
\begin{align*}
DP_{xx} - vP_x + \hat{P}[g(\hat{I}(x)) - \beta\hat{P}] &= 0, \quad 0 < x < L, \\
DP_x(0) - v\hat{P}(0) &= 0, \quad DP_x(L) - v\hat{P}(L) = 0,
\end{align*}
\]
where $\hat{I}(x) = I_0 \exp \left(-k_0 x - k_1 \int_0^x \hat{P}(s)ds\right)$. By virtue of $\hat{P} > 0$, it follows from Lemma 2.3 that $\hat{P} = P_0(\beta;x)$. Thus the global bifurcation branch $C^*$ must meet the branch \{(0, P) : P > 0\} at the point $(0, P_0(\beta;x))$ as $d \to 0$ due to the continuity of $P_d(\beta;x)$. That is, $\lim_{d \to 0} P_d(\beta;x) = P_0(\beta;x)$.

**Step 3. Uniqueness.** The proof of uniqueness is exactly similar to that of uniqueness of (13), see Lemma 2.3. $\square$

3. Longtime behavior. In this section we study the longtime dynamical behavior of the reaction-diffusion-advection model (1)-(3) satisfying (4) and (5), which describes the population dynamics of a single phytoplankton species in a water column with crowding effect. To this end, let $Q = e^{-(\upsilon/D)x}P$. Then $Q$ satisfies
\[
\begin{align*}
Q_t &= DJ_{xx} + vQ_x + Q[g(\hat{I}(x,t)) - \beta e^{(\upsilon/D)x}Q - d], \quad 0 < x < L, \ t > 0, \\
Q_x(0,t) &= Q_x(L,t) = 0, \quad t > 0, \\
Q(x,0) &= Q_0(x), \quad 0 \leq x \leq L,
\end{align*}
\]
where $\hat{I}(x,t) = I_0 \exp \left(-k_0 x - k_1 \int_0^t e^{(\upsilon/D)s}Q(s,t)ds\right)$, and $Q_0(x) = e^{-(\upsilon/D)x}P_0(x)$. Clearly, $Q_0(x) \geq 0$ on $[0,L]$, and $Q_0(x) \in C([0,L])$ by the assumption on $P_0(x)$. Hence, we only need to investigate the longtime dynamical behavior of the solution $Q(x,t)$ to (23).

By standard arguments, it is not hard to prove the uniqueness and global existence of the solution $Q(x,t)$ of (23). Moreover, $Q(x,t) > 0$ for $t > 0$, $x \in [0,L]$ by the strong maximum principle. The main result of this section is as follows, which indicates that $d_*$ is the critical death rate, that is, the phytoplankton species survives if and only if its death rate is less than $d_*$.

**Theorem 3.1.** Suppose that $P(x,t)$ is the solution of (1)-(3). Then
(i) $P(x,t)$ converges to 0 as $t \to \infty$ uniformly on $x \in [0,L]$ provided that $d \geq d_*$; (ii) $P(x,t)$ converges to the unique positive steady state $P_d(\beta;x)$ as $t \to \infty$ uniformly on $x \in [0,L]$ provided that $0 < d < d_*$.

To verify this main outcome, we first establish two key results, namely, a comparison lemma and a boundedness lemma. With this in mind, suppose that $Q(x,t)$ is a classical solution to (23), and set $h(x,t) = \int_0^t e^{(\upsilon/D)s}Q(s,t)ds$. Then $h(0,t) \equiv 0$, $h_x(x,t) = e^{(\upsilon/D)x}Q(x,t)$, and direct computations indicate that $h(x,t)$ satisfies
\[
\begin{align*}
h_t &= Dh_{xx} - vh_x - dh + \int_0^x e^{(\upsilon/D)s}Q(s,t)g(I_0 e^{-k_0 s - k_1 h(s,t)})ds - \int_0^x \beta e^{2\upsilon s/D}Q^2 ds \\
&= Dh_{xx} - vh_x - dh + k_1^{-1} \int_0^x g(I_0 e^{-k_0 s - k_1 h(s,t)})d(k_0s + k_1 h(s,t)) \\
&\quad - k_0 k_1^{-1} \int_0^x g(I_0 e^{-k_0 s - k_1 h(s,t)})ds - \int_0^x \beta e^{2\upsilon s/D}Q^2 ds
\end{align*}
\]
\[ \begin{align*}
\text{where} \quad G(\eta) &= k_1^{-1} \int_0^\eta g(I_0 \xi^-)d\xi.
\end{align*} \]

**Lemma 3.2.** (Comparison Lemma). Suppose \( d \in (-\infty, \infty) \) and \( P, \tilde{P} \in C^{2,1}([0, L] \times (0, \infty)) \) satisfy

\[
\begin{cases}
P_t \leq DP_{xx} - vP_x + P[g(I_0 \xi^{-k_0 x - k_1 h(x,t)}) - \beta P - d], & 0 < x < L, \quad t > 0, \\
DP_x(0,t) - vP(0,t) = 0, & DP_x(L,t) - vP(L,t) = 0, \quad t > 0,
\end{cases}
\]

and

\[
\begin{cases}
\tilde{P}_t \geq D\tilde{P}_{xx} - v\tilde{P}_x + \tilde{P}[g(I_0 \xi^{-k_0 x - k_1 h(x,t)}) - \beta \tilde{P} - d], & 0 < x < L, \quad t > 0, \\
D\tilde{P}_x(0,t) - v\tilde{P}(0,t) = 0, & D\tilde{P}_x(L,t) - v\tilde{P}(L,t) = 0, \quad t > 0.
\end{cases}
\]

If \( P(x,t) < \tilde{P}(x,t) \) for \( x \in [0, L] \) and all small \( t \geq 0 \) (say \( t \in [0, \epsilon] \)), then \( h(x,t) < \tilde{h}(x,t) \) for all \( t > 0 \) and \( x \in [0, L] \), where

\[ h(x,t) := \int_0^x P(s,t)ds, \quad \tilde{h}(x,t) := \int_0^x \tilde{P}(s,t)ds. \]

**Proof.** It is easy to see that \( h(x,t), \tilde{h}(x,t) \in C^{3,1}([0, L] \times (0, \infty)) \) since \( P, \tilde{P} \in C^{2,1}([0, L] \times (0, \infty)) \). Since \( P(x,t) < \tilde{P}(x,t) \) for \( t \geq 0 \) small and \( x \in [0, L] \), we have

\[ h(x,t) < \tilde{h}(x,t) \quad \text{for} \quad t \geq 0 \text{ small and} \quad x \in [0, L]. \] (26)

Suppose the conclusion of Lemma 3.2 is not true. Then there exists a finite maximal time denoted by \( t^* \) such that (26) holds for every \( t \in [0, t^*) \). Obviously, \( h(x,t^*) \leq \tilde{h}(x,t^*) \) for all \( x \in [0, L] \). We claim that

\[ h(x,t^*) = \tilde{h}(x,t^*) \quad \text{for some} \quad x \in [0, L]. \] (27)

Otherwise we have \( h(x,t^*) < \tilde{h}(x,t^*) \) for all \( x \in [0, L] \). Set \( w(x,t) = \tilde{h}(x,t) - h(x,t) \). Then \( w(x,t) > 0 \) for \( 0 \leq t \leq t^*, \ 0 < x \leq L \). Let \( Q = e^{-(v/D)x}P \) and \( \tilde{Q} = e^{-(v/D)x}\tilde{P} \). Then

\[
\int_0^x (e^{(v/D)s} \tilde{Q}(s,t) - e^{(v/D)s}Q(s,t))ds = w(x,t) > 0 \text{ on } (0, L] \times [0, t^*].
\]

In view of \( P, \tilde{P} \in C^{2,1}([0, L] \times (0, \infty)) \), it is easy to see that \( w(x,t) \in C^{3,1}([0, L] \times (0, \infty)) \), and \( \tilde{Q}(x,t), Q(x,t) \) are bounded for \( 0 \leq t \leq t^*, \ 0 \leq x \leq L \). Hence, for \( 0 \leq t \leq t^* \), we have

\[
\lim_{x \to 0+} \int_0^x e^{v/D}Q(s,t) + Q(s,t)(e^{v/D} \tilde{Q}(s,t) - e^{v/D}Q(s,t))ds = \tilde{Q}(0,t) + Q(0,t),
\]

which is bounded for \( 0 \leq t \leq t^* \). Recalling that \( w(0,0) = 0 \) for \( 0 \leq t \leq t^* \), we conclude that for \( 0 \leq t \leq t^*, \ 0 \leq x \leq L \), there exist positive constant \( C \) large
enough such that
\[ \int_0^x e^{us/D} (\tilde{Q}(s,t) + Q(s,t)) (e^{us/D} \tilde{Q}(s,t) - e^{us/D} Q(s,t)) \, ds \leq C w(x,t). \quad (28) \]

Hence, it follows from (24)-(25) and the mean value theorem that
\[ w_t \geq Dw_{xx} - vw_x - dw + C(x,t)w \]
\[ + k_0 k_1^{-1} \int_0^x [g(I_0 e^{-k_0 x - k_1 h(s,t)}) - g(I_0 e^{-k_0 x - k_1 \tilde{h}(s,t)})] \, ds \]
\[ - \int_0^x \beta e^{us/D} (\tilde{Q}(s,t) + Q(s,t)) (e^{us/D} \tilde{Q}(s,t) - e^{us/D} Q(s,t)) \, ds \]
\[ \geq Dw_{xx} - vw_x - dw + C(x,t)w - \beta C w \]
\[ + k_0 k_1^{-1} \int_0^x [g(I_0 e^{-k_0 x - k_1 h(s,t)}) - g(I_0 e^{-k_0 x - k_1 \tilde{h}(s,t)})] \, ds \]
for 0 < x < L, 0 < t \leq t^*, where C(x,t) = \mathcal{G}'(k_0 x + k_1 \theta(x,t)), \theta(x,t) \in [h(x,t), \tilde{h}(x,t)]. Noting that
\[ \int_0^x [g(I_0 e^{-k_0 x - k_1 h(s,t)}) - g(I_0 e^{-k_0 x - k_1 \tilde{h}(s,t)})] \, ds \geq 0, \]
we have
\[ w_t \geq Dw_{xx} - vw_x - dw + C(x,t)w - \beta C w, \]
that is,
\[
\begin{align*}
\left\{ \begin{array}{ll}
w_t & \geq Dw_{xx} - vw_x + [C(x,t) - d - \beta C] w, & 0 < x < L, 0 < t \leq t^*, \\
w(0,t) & = 0, w(L,t) > 0, & 0 < t \leq t^*, \\
w(x,0) & > 0, & 0 < x \leq L.
\end{array} \right.
\] (30)
\]
By the strong maximum principle and the Hopf boundary lemma, we can conclude that w(x,t) > 0 for t \in (0,t^*) and x \in (0,L], and w_x(0,t^*) > 0. Furthermore, by the smoothness of w(x,t), we obtain w_x(x,t) > 0 for all t close to t^* and x close to 0. Thus it follows from w(0,t) \equiv 0 that w(x,t) > 0 for 0 < x < \delta, t^* \leq t \leq t^* + \delta, \delta > 0 small. By w(x,t^*) > 0 for x \in [\delta, L], we can find \delta_0 \in (0, \delta) such that w(x,t) > 0 for x \in [\delta, L] and t \in [t^*, t^* + \delta_0]. Thus w(x,t) > 0 for x \in (0,L] and t \in (0, t^* + \delta_0], a contradiction to the maximality of t^*. Hence (27) holds.

In view of (27), there exists x_0 \in (0,L) such that w(x_0,t^*) = 0. If x_0 = L, namely, w(L,t^*) = 0, then \dot{w}_t(L,t^*) \leq 0. Direct computations yield that w_x(L,t^*) = e^{(v/D)L} [\tilde{Q}(L,t^*) - Q(L,t^*)] \) and \( w_x(L,t^*) = (v/D)e^{(v/D)L} [\tilde{Q}(L,t^*) - Q(L,t^*)]. \) Therefore we can use (29) to get
\[ 0 \geq w_t(L,t^*) \geq k_0 k_1^{-1} \int_0^L [g(I_0 e^{-k_0 s - k_1 h(s,t)}) - g(I_0 e^{-k_0 s - k_1 \tilde{h}(s,t)})] \, ds. \]
Since \( h(x,t^*) \leq \tilde{h}(x,t^*) \) on [0,L], the above inequality holds only if h(x,t^*) \equiv \tilde{h}(x,t^*). Namely, w(x,t^*) \equiv 0.

On the other hand, from the inequality in (30), we see that w(x,t) is an upper solution of the problem
\[
\begin{align*}
\dot{\bar{w}}_t & = Dw_{xx} - v\bar{w}_x - (d + \beta C)\bar{w}, & 0 < x < L, 0 < t \leq t^*, \\
\dot{\bar{w}}(0,t) & = \bar{w}(L,t) = 0, & 0 < t \leq t^*, \\
\dot{\bar{w}}(x,0) & = w(x,0) > 0, & 0 < x \leq L.
\end{align*}
\]
By the strong maximum principle, \( \bar{w}(x,t) > 0 \) for x \in (0,L) and 0 < t \leq t^*. Meanwhile, by the comparison principle, we have w(x,t) \geq \bar{w}(x,t) for x \in (0,L).
and $0 < t \leq t^*$. Hence $w(x, t^*) > 0$ for $x \in (0, L)$. This contradicts our earlier conclusion that $w(x, t^*) \equiv 0$. Therefore we must have $w(L, t^*) > 0$. We may now apply the strong maximum principle to (30) to conclude that $w(x, t^*) > 0$ for $x \in (0, L)$, a contradiction to (27). The proof is finished. 

Remark 1. The estimation (28) is crucial for us to extend the comparison lemma in [8] to the case of $\beta > 0$.

Lemma 3.3. (*Boundedness lemma*). Suppose $d > 0$, and let $P(x, t)$ be the solution of (1)-(3). Then there exists a positive constant $\mathcal{M}$ such that

$$P(x, t) \leq \mathcal{M} \text{ for all } x \in [0, L], \ t > 0.$$  

Proof. The assumption on $g$ implies that

$$g(I) \leq \gamma I \text{ for some } \gamma > 0 \text{ and all } I \in [0, I_0].$$  

In view of $I(x, t) = I_0 \exp \left(-k_0 x - k_1 \int_0^x e^{(v/D)y}Q(y, t)dy\right)$, we have

$$g(I(x, t)) \leq \gamma I(x, t) \leq \gamma I_0 e^{-k_1 \int_0^x e^{(v/D)y}Q(y, t)dy}.$$  

It follows from the equation (23) that

$$Q_t \leq DQ_{xx} + vQ_x + Q[\gamma I_0 e^{-k_1 \int_0^x e^{(v/D)y}Q(y, t)dy} - d].$$  

Namely,

$$e^{(v/D)x}Q_t \leq D(e^{(v/D)x}Q_x)_x + e^{(v/D)x}Q[\gamma I_0 e^{-k_1 \int_0^x e^{(v/D)y}Q(y, t)dy} - d].$$  

Integrating for $x$ from 0 to $L$, we get

$$\left[\int_0^L e^{(v/D)x}Qdx\right]_t \leq \gamma I_0 \int_0^L e^{(v/D)x}Qe^{-k_1 \int_0^x e^{(v/D)y}Q(y, t)dy}dx - d \int_0^L e^{(v/D)x}Qdx.$$  

Denote $f(t) = \int_0^L e^{(v/D)x}Q(x, t)dx$, $h(x, t) = \int_0^x e^{(v/D)y}Q(s, t)ds$. Then

$$\int_0^L e^{(v/D)x}Qe^{-k_1 \int_0^x e^{(v/D)y}Q(y, t)dy}dx$$

$$= \int_0^L e^{-k_1 h}e^{uh}dx = k_1^{-1} \left[ek_1 h(0, t) - e^{-k_1 h(L, t)}\right] = k_1^{-1} \left[1 - e^{-k_1 f(t)}\right].$$

Hence, $f_t \leq \gamma I_0 k_1^{-1} \left[1 - e^{-k_1 f(t)}\right] - df$, which leads to

$$f_t + df \leq \gamma I_0 k_1^{-1} := M_0.$$  

It follows that $(e^{dt}f)_t \leq M_0 e^{dt}$, from which we deduce

$$f(t) \leq f(0) e^{-dt} + M_0 e^{-dt} \int_0^t e^{ds}ds \leq f(0) + M_0/d := M_1. \quad (31)$$

Let $W(t) := \max_{x \in [0, L], t \in [0, t]} Q(x, s)$. Clearly $W(t)$ is nondecreasing. Suppose for contradiction that $W(t) \to \infty$ as $t \to \infty$. Then we can find $t_n \to \infty$ such that $W(t_n) = \max_{x \in [0, L]} Q(x, t_n)$ and $W(t_n) \to \infty$. We may assume that $t_n > 1$ for all $n \geq 1$. Define

$$z_n(x, t) = \frac{Q(x, t + t_n - 1)}{W(t_n)}.$$
Clearly $z_n$ satisfies
\[
\begin{cases}
(z_n)_{tt} = D(z_n)_{xx} + v(z_n)_x \\
+ |(g(I(x, t + t_n - 1)) - \beta e^{(v/D)\tau}Q - d)z_n|, \quad 0 < x < L, t > 0,
\end{cases}
\]
where $z_n(0, t) = (z_n)_x(L, t) = 0, \quad t > 0,$
and $z_n(x, 0) \in [0, 1].$

Let $c_n(x, t) = g(I(x, t + t_n - 1)) - \beta e^{(v/D)\tau}Q - d.$ Then it follows from Lemma 2.2 that $|c_n| \leq M_2 := (g(I_0) + d)(1 + e^{(v/D)L}).$ A simple comparison consideration gives
\[
0 \leq z_n(x, t) \leq e^{M_2t} \text{ for } x \in [0, L] \text{ and } t \geq 0.
\]

Hence we may apply standard parabolic regularity to conclude that $\{z_n\}$ is bounded in $C^{1,\alpha}([0, L] \times [1/2, 2])$ for any $\alpha \in (0, 1).$ Therefore by passing to a subsequence if necessary we have $z_n \rightarrow z^*$ in $C^{1,0}([0, L] \times [1/2, 2]).$ Since $|c_n| \leq M_2,$ by passing to a further subsequence, we may assume that $c_n \rightarrow c^*$ weakly in $L^2([0, L] \times [1/2, 2]).$
Clearly, $|c^*| \leq M_2.$ It follows that $z^*$ is a weak solution to
\[
\begin{cases}
(z^*)_t = D(z^*)_x + vz^*_x + c^*z^*, \quad x \in [0, L], \quad t \in [1/2, 2],
\end{cases}
\]
\[
\begin{cases}
z^*(0, t) = z^*_x(L, t) = 0, \quad t \in [1/2, 2],
\end{cases}
\]
\[
z^* \in [0, e^{2M_2}], \quad x \in [0, L], \quad t \in [1/2, 2].
\]

Since $\max_{x \in [0, L]} z_n(x, 1) = 1,$ we have $\max_{x \in [0, L]} z^*(x, 1) = 1$ and hence $z^*$ is not identically zero. By the strong maximum principle we deduce $z^*(x, 1) \geq \delta_1$ for some small $\delta_1 > 0$ on $[0, L].$ It follows that $z_n(x, 1) \geq \delta_1/2$ for all large $n$ and $x \in [0, L].$ Therefore
\[
Q(x, t_n) \geq (\delta_1/2)W(t_n) \text{ for all large } n \text{ and } x \in [0, L],
\]
from which we deduce
\[
f(t_n) = \int_0^L e^{(v/D)\tau}Q(x, t_n)dx \geq (\delta_1/2)W(t_n) \int_0^L e^{(v/D)\tau}dx \rightarrow \infty
\]
as $n \rightarrow \infty,$ which contradicts (31). Therefore there exists $M_3 > 0$ such that
\[
Q(x, t) \leq M_3 \text{ for all } x \in [0, L] \text{ and } t > 0,
\]
which implies, $P \leq M_3 e^{|v|L/D} := \mathcal{M}.$

Now we are ready to prove the main result of this section.

Proof of Theorem 3.1. (i) At first, it is easy to see that
\[
Q_t \leq DQ_{xx} + vQ_x - dQ + g(I_0 e^{-k_0 x})Q.
\]
By the comparison principle, we deduce $Q(x, t) \leq C e^{-(d-d_*)t} \psi_1(x) \rightarrow 0$ as $t \rightarrow \infty$ uniformly on $x \in [0, 1],$ where $\psi_1$ is a positive eigenfunction corresponding to $\lambda_1(-g(I_0 e^{-k_0 x}))$ and $C$ is a positive constant such that $Q(x) \leq C \psi_1(x)$ in $[0, L].$ Thus, $P(x, t) \leq e^{(v/D)\tau}C e^{-(d-d_*)t} \psi_1(x) \rightarrow 0$ if $d > d_*.$ Therefore $\lim_{t \rightarrow \infty} P(x, t) = 0$ uniformly for $x \in [0, L]$ if $d > d_*.$

(ii) We may assume that the initial data $P_0(x)$ satisfies $P_0(x) > 0$ on $[0, L],$ otherwise we can replace $P(x, t)$ by $P(x, t+1)$ and $P_0(x)$ by $P(x, 1).$ Thus $Q_0(x) > 0$ on $[0, L].$
Define $\Psi_\delta(x) := -g(I_0e^{-(k_0+\delta)x}) + \beta\delta$. By virtue of $d < d_\ast = -\lambda_1(-g(I_0e^{-k_0x}))$, we can find $\delta > 0$ sufficiently small such that $d < -\lambda_1(\Psi_\delta)$. Fix such a $\delta$ and let $\phi_\delta$ be a positive eigenfunction corresponding to $\lambda_1(\Psi_\delta)$ of the following problem
\[
\begin{cases}
-D((e^{(v/D)x})\phi_\delta(x)) + \Psi_\delta(x)e^{(v/D)x}\phi_\delta = \lambda e^{(v/D)x}\phi_\delta, & 0 < x < L, \\
\phi_\delta(0) = \phi_\delta(L) = 0.
\end{cases}
\]
Then we choose $\varepsilon > 0$ small so that $\varepsilon\phi_\delta < Q_0(x)$ and $\varepsilon\phi_\delta < \delta e^{-(v/D)x}$ on $[0, L]$. Let $Q(x, t)$ be the unique solution of (23) with initial condition $Q(x, 0) = \varepsilon\phi_\delta(x)$. Then we can find $\bar{\sigma} > 0$ small such that
\[
0 < e^{(v/D)x}Q(x, t) < \delta \quad \text{for } t \in (0, \bar{\sigma}) \text{ and } x \in [0, L].
\]
Hence for $t \in (0, \bar{\sigma}]$,
\[
Q_t = DQ_{xx} + vQ_x + Q[g(I_0e^{-k_0x})\int_0^x e^{(v/D)x}Q(s, t)ds] - \beta e^{(v/D)x}Q - d
\]
\[
> DQ_{xx} + vQ_x + Q[-\Psi_\delta(x) - d]
\]
\[
> DQ_{xx} + vQ_x + Q[-\lambda_1(\Psi_\delta)].
\]
It follows that
\[
\begin{cases}
(Q - \varepsilon\phi_\delta)_t > D(Q - \varepsilon\phi_\delta)_{xx} + v(Q - \varepsilon\phi_\delta)_x \\
+ (Q - \varepsilon\phi_\delta)[-\Psi_\delta(x) + \lambda_1(\Psi_\delta)], & x \in [0, L], \ t \in (0, \bar{\sigma}], \\
(Q - \varepsilon\phi_\delta)_x = 0, & x = 0, L, \ t \in (0, \bar{\sigma}], \\
Q - \varepsilon\phi_\delta = 0, & x \in [0, L], \ t = 0.
\end{cases}
\]
By the strong maximum principle we deduce $Q(x, t) - \varepsilon\phi_\delta(x) > 0$ for $t \in (0, \bar{\sigma}]$ and $x \in [0, L]$. Fixing $\tau \in (0, \bar{\sigma}]$, we have
\[
Q(x, \tau) > Q(x, 0) \text{ on } [0, L].
\]
By continuity,
\[
Q(x, \tau + t) > Q(x, t) \text{ on } [0, L] \text{ for all small } t \geq 0.
\]
Thus we can use Lemma 3.2 to conclude that $h(x, t) < h(x, \tau + t)$ for $x \in [0, L], t > 0$, where $h(x, t) = \int_0^t e^{(v/D)\tau}Q(s, t)ds$. It follows that $h(x, t)$ is monotone increasing in $t$.

By Lemma 3.3, $h(x, t)$ is bounded for all $x \in [0, L]$ and $t > 0$. Hence $\lim_{t \to \infty} h(x, t) = h_\ast(x)$ exists. Meanwhile, it follows from Lemma 3.3 again that $\|Q(\cdot, t)\|_\infty$ is also bounded. Hence, we can apply the standard parabolic regularity theory to (23) to conclude that, for any sequence $t_n \to \infty$, there is a subsequence of $\{Q(s, t_n)\}$ which converges in $C^1([0, L])$, say $Q(s, t_n) \to Q_\ast$. Since $h_\ast(\cdot, t_n) \to h_\ast(x)$, we necessarily have $h_\ast(x) = \int_0^\infty e^{(v/D)\tau}Q_\ast(y)d\tau$. Hence $h_\ast'(x) = e^{(v/D)x}Q_\ast$. This implies that $\lim_{t \to \infty} e^{(v/D)x}Q(x, t)$ exists and equals $h_\ast'(x)$. Denote $P(x, t) := e^{(v/D)x}Q(x, t)$, we know that $\lim_{t \to \infty} P(x, t) = h_\ast'(x)$ and thus $h_\ast'(x)$ must be a nonnegative steady state of (1)-(3). Since $h_\ast(0) = 0$ and $h_\ast(x)$ is the limit of an increasing sequence, we have $h_\ast(x) > 0$ for $x \in (0, L]$ and $h_\ast(x) \neq 0$. Therefore $h_\ast'(x)$ is a nontrivial nonnegative steady state of (1)-(3). By the strong maximum principle $h_\ast'(x)$ is positive, and hence we can use Theorem 2.4 to conclude that $h_\ast'(x) \equiv P_d(x)$. 

SINGLE PHYTOPLANKTON SPECIES GROWTH 57
Let $\Psi_A(x) = -g(I_0e^{-(k_0+k_1A)x})$, and $\Phi_A(x)$ be the positive eigenfunction corresponding to $\lambda_1(\Psi_A)$ with $\|\Phi_A\|_\infty = 1$. It is easy to see that $\lambda_1(\Psi_A) \to 0$ and $\Phi_A \to 1$ in $C^1([0,L])$ as $A \to \infty$ by a regularity and compactness argument. Therefore we can find $A_0 > 0$ large so that $d > -\lambda_1(\Psi_A)$ for $A \geq A_0$, $1/2 < \Phi_A(x) \leq 1$. We now choose $B > A_0$ such that $Q_0(x) < 2B\Phi_A(x)$, $A < 2B\Phi_A(x)e^{(v/D)x}$ on $[0,L]$.

Let $\overline{Q}(x,t)$ be the solution of (23) with initial condition $\overline{Q}(x,0) = 2B\Phi_A(x)$. Then we can find $\delta > 0$ small so that $Q_0(x) < \overline{Q}(x,t)$, $A < \overline{Q}(x,t)e^{(v/D)x}$ for $t \in (0,\delta]$ and $x \in [0,L]$. Hence for $t \in (0,\delta]$, we have

$$
\overline{Q}_t = D\overline{Q}_{xx} + v\overline{Q}_x + g(I_0e^{-(k_0+k_1A)x}) - \beta e^{(v/D)x}\overline{Q} - d
$$

Thus for $\omega(x,t) := \overline{Q}(x,t) - 2B\Phi_A(x)$, we have

$$
\omega_t < D\omega_{xx} + v\omega_x + \omega[-\Psi_A(x) + \lambda_1(\Psi_A)], \quad x \in [0,L], \quad t \in (0,\delta],
$$

$$\omega_x = 0, \quad x = 0,\ L, \quad t \in (0,\delta],
$$

$$\omega = 0, \quad x \in [0,L], \quad t = 0.
$$

By the strong maximum principle we deduce $\omega = \overline{Q} - 2B\Phi_A(x) < 0$ for $t \in (0,\delta]$ and $x \in [0,L]$. It follows that $\overline{Q}(x,t) < Q(x,0)$ for $0 < t \leq \delta$. By the same argument as before, we deduce that

$$
\overline{h}(x,t) = \int_0^t e^{(v/D)s}\overline{Q}(s,t)ds
$$

is monotone decreasing in $t$. Moreover, from Lemma 3.2 it follows that $\overline{h}(x,t) > h(x,t) > \overline{h}(x,t)$ for all $t > 0$ and $x \in (0,L]$. Hence $\lim_{t \to \infty} \overline{h}(x,t) = h^*(x)$.

Set $\overline{P}(x,t) := e^{(v/D)t}\overline{Q}(x,t)$, we may use parabolic regularity theory as before to deduce that $\overline{P}(x,t) \to (h^*)'(x)$ in $C^1([0,L])$, and $(h^*)'(x)$ is a positive steady state of (1)-(3). Thus we must have $(h^*)'(x) \equiv P_d(x)$.

Noting that $\overline{h}(x,t) \leq h^*(x)$ and $\lim_{t \to \infty} \overline{h}(x,t) = \lim_{t \to \infty} \overline{h}(x,t) = \int_0^t P_d(s)ds$, we necessarily have $\lim_{t \to \infty} h(x,t) = \int_0^t P_d(s)ds$. Repeating the above arguments, we can conclude that $\lim_{t \to \infty} P(x,t) = P_d(x)$ uniformly for $x \in [0,L]$.

It remains to consider the case $d = d_\ast$. The proof is exactly similar to that of the case $d < d_\ast$ with some simple modification. Let $\overline{Q}(x,t)$ be defined exactly as in the proof above. Then we know that $\overline{h}(x,t) := \int_0^t e^{(v/D)s}\overline{Q}(s,t)ds > 0$ is strictly decreasing in $t$. Hence $\lim_{t \to \infty} \overline{h}(x,t) = h^*(x) \geq 0$ exists. By the same consideration we can show that $\overline{P}(x,t) = e^{(v/D)t}\overline{Q}(x,t) \to (h^*)'(x)$ as $t \to \infty$ in $C^1([0,L])$, which indicates that $(h^*)'(x)$ is a nonnegative steady state of (1)-(3). However, by Theorem 2.4, the only nonnegative steady state of (1)-(3) is the trivial solution 0 when $d = d_\ast$. Hence $\overline{P}(x,t) \to 0$ as $t \to \infty$ uniformly for $x \in [0,L]$, thus $\overline{h}(x,t) \to 0$ as $t \to \infty$.

By Lemma 3.2 we deduce $0 < h(x,t) < \overline{h}(x,t)$, which implies that $h(x,t) \to 0$ as $t \to \infty$. By the application of this fact and parabolic regularity, as before, we deduce $\lim_{t \to \infty} e^{(v/D)t}Q(x,t)$ exists in the $C^1([0,L])$ norm, and the limit is a nonnegative steady state of (1)-(3). By virtue of $d = d_\ast$, this limit must be 0. This complete the proof.
4. Asymptotic profiles of positive steady states.

4.1. Asymptotic profiles for small crowding effect. In this subsection, we focus on the asymptotic profiles of positive steady states when the crowding effect disappears. The motivation comes from the following observation. It follows from Theorem 2.4 and Theorem 3.1 that $d_*$ is the critical death rate, and the phytoplankton species survives if and only if its death rate is less than the critical death rate. Moreover, the results in [14] indicate that the bifurcation diagram of positive steady states for the model without crowding effect with respect to the death rate looks like Fig.1(a). That is, when the death rate goes to zero, the population density of the phytoplankton goes to infinity at the bottom or surface of the water column. In contrast to the model without crowding effect, Theorem 2.4 shows that the density of the phytoplankton species will have a finite limit rather than go to infinity when the death rate disappears (see Fig.1(b)), which is due to the crowding effect.

![Figure 1](image.png)

**Figure 1.** The bifurcation diagrams of positive steady states of (1)-(2) versus the death rate with $\beta = 0$ in (a) and $\beta > 0$ in (b).

**Theorem 4.1.** The unique positive solution $P_0(\beta; x)$ of equation (13) satisfies $\|P_0\|_\infty \to \infty$ as $\beta \to 0$.

**Proof.** Suppose that there exists a sequence $\beta_n$ and positive solutions $P_0^{(n)}$ of (13) with $\beta = \beta_n$ such that $\beta_n \to 0$ and $\|P_0^{(n)}\|_\infty$ is uniformly bounded as $n \to \infty$. Then $P_0^{(n)}$ satisfies

\[
\begin{cases}
DP_{0,x}^{(n)} - vP_{0,x}^{(n)} + P_0^{(n)}[g(I_n) - \beta_n P_0^{(n)}] = 0, & 0 < x < L, \\
DP_{0,x}^{(n)}(0) - vP_{0}^{(n)}(0) = 0, & DP_{0,x}^{(n)}(L) - vP_{0}^{(n)}(L) = 0,
\end{cases}
\]

where $I_n = I_0 \exp(-k_0 x - k_1 \int_0^x P_0^{(n)}(s)ds)$. Integrating the first equation of (32) from 0 to $x$, we have

\[
DP_{0,x}^{(n)}(x) - vP_{0}^{(n)}(x) + \int_0^x P_0^{(n)}[g(I_n) - \beta_n P_0^{(n)}]dx = 0.
\]

As $g(I_n)$ and $P_0^{(n)}$ are uniformly bounded, we deduce that $P_{0,x}^{(n)}$ is uniformly bounded. By (32), $P_{0,x}^{(n)}$ is uniformly bounded. By $L^p$ estimates and Sobolev embedding theorems, passing to a subsequence if necessary, we may assume that $P_0^{(n)} \to \tilde{P}$ in $C^1([0, L])$, $\tilde{P} \geq 0$. As $0 \leq g(I_n) \leq g(I_0)$ in $[0, L]$, we may assume that $g(I_n) \to \tilde{q}(x)$
weakly in \( L^2(0, L) \) for some function \( \tilde{q} \) satisfying \( 0 \leq \tilde{q} \leq g(I_0) \). Hence, \( \hat{P} \) is a weak solution of
\[
\begin{align*}
D\hat{P}_{xx} - v\hat{P}_x + \hat{P}\tilde{q}(x) &= 0, \quad 0 < x < L, \\
D\hat{P}_x(0) - v\hat{P}(0) &= 0, \quad D\hat{P}_x(L) - v\hat{P}(L) = 0.
\end{align*}
\] (33)

On the other hand, it is easy to see that
\[
I_n(x) = I_0 \exp(-k_0x - k_1 \int_0^x \tilde{P}_0(s)ds) \to I_0 \exp(-k_0x - k_1 \int_0^x \tilde{P}(s)ds)
\]
for every \( x \in (0, L) \) as \( n \to \infty \). This implies that \( \tilde{q}(x) = g(I_0 \exp(-k_0x - k_1 \int_0^x \tilde{P}(s)ds)) > 0 \). Integrating (33) in \((0, L)\), we obtain \( \hat{P}(x) \equiv 0 \). That is \( P_0^{(n)} \to 0 \), and \( I_n(x) \to I_0 e^{-k_0x} \) as \( n \to \infty \). Let \( \hat{P}_n = \frac{\tilde{P}_0^{(n)}}{\|\tilde{P}_0^{(n)}\|_\infty} \). Then \( \hat{P}_n \) satisfies \( \|\hat{P}_n\|_\infty = 1 \), and
\[
\begin{align*}
D\hat{P}_{n,xx} - v\hat{P}_{n,x} + \hat{P}_n[g(\hat{I}_n) - \beta_n \hat{P}_n\|P_0^{(n)}\|_\infty] &= 0, \quad 0 < x < L, \\
D\hat{P}_n(0) - v\hat{P}_n(0) &= 0, \quad D\hat{P}_n(L) - v\hat{P}_n(L) = 0,
\end{align*}
\] (34)
where \( \hat{I}_n = I_0 \exp(-k_0x - k_1 \int_0^x \hat{P}_n(s)\|P_0^{(n)}\|_\infty ds) \). Integrating the equation over \((0, x)\), we have
\[
D\hat{P}_{n,x}(x) - v\hat{P}_n(x) + \int_0^x \hat{P}_n[g(\hat{I}_n) - \beta_n \hat{P}_n\|P_0^{(n)}\|_\infty]dx = 0.
\]

Since \( g(\hat{I}_n) \) and \( \hat{P}_n \) are uniformly bounded, we conclude that \( \hat{P}_{n,x} \) is uniformly bounded. It follows from the equation (34) that \( \hat{P}_{n,xx} \) is uniformly bounded. Similarly, by \( L^p \) estimates and Sobolev embedding theorems, we may assume that \( \hat{P}_n \to \hat{P} \) in \( C^1([0, L]) \), \( \hat{P} \geq 0 \), \( \hat{P} \neq 0 \), and \( \hat{P} \) satisfies
\[
\begin{align*}
D\hat{P}_{xx} - v\hat{P}_x + \hat{P}[g(I_0 e^{-k_0x})] &= 0, \quad 0 < x < L, \\
D\hat{P}_x(0) - v\hat{P}(0) &= 0, \quad D\hat{P}_x(L) - v\hat{P}(L) = 0.
\end{align*}
\]

By the strong maximum principle, \( \hat{P} > 0 \) on \([0, L] \). Integrating the above equation in \((0, L)\), we get
\[
\int_0^L \hat{P}[g(I_0 e^{-k_0x})]dx = 0,
\]
which implies that \( \hat{P} \equiv 0 \), a contradiction. Hence, \( \|P_0(\beta; x)\|_\infty \to \infty \) as \( \beta \to 0 \). \( \square \)

**Remark 2.** It follows from Theorem 3.1 and Theorem 4.1 that
\[
\lim_{d \to 0} P_d(\beta; x) = P_0(\beta; x), \quad \text{and} \quad \lim_{\beta \to 0} \|P_0(\beta; x)\|_\infty = \infty.
\]
The limits illustrate that the bifurcation diagram Fig.1(b) of positive steady states for the model (1)-(3) will gradually evolve into Fig.1(a) when the crowding effect disappears.

### 4.2. Asymptotic profiles for large advection rates.
This subsection is devoted to investigate the asymptotic profiles of the unique positive steady state \( P(x; v) \) of (1)-(3) when the advection coefficient is large enough. For simplicity of notation and clarity of the presentation, we may assume \( D = 1, \beta = 1, L = 1 \) by some scaling. Thus we consider the following steady state system
\[
\begin{align*}
P_{xx} - vP_x + P[g(I(x)) - P - d] &= 0, \quad 0 < x < 1, \\
P_x(0) - vP(0) &= 0, \quad P_x(1) - vP(1) = 0.
\end{align*}
\] (35)
Suppose that Theorem 4.3.

by Lemma 2.1. It follows from Theorem 2.4 that \( P(x; v) \) exists for any \( v \in \mathbb{R} \) if \( 0 < d < g(I_0e^{-k_v}) \). The following results describe the asymptotic profiles of \( P(x; v) \) for large sinking rate \( (v > 0) \) and large buoyant rate \( (v < 0) \).

**Theorem 4.2.** Suppose that \( 0 < d < g(I_0e^{-k_v}) \).

(i) If \( v > 2\sqrt{g(I_0)} - d \), then \( P(x; v) \) is strictly increasing on \([0, 1] \);
(ii) As \( v \to \infty \), \( P(x; v) \to 0 \) uniformly in any compact subset of \([0, 1] \), \( P(1; v) \to \kappa^* \), where \( \kappa^* = 2 (g(I_0e^{-k_v}) - d) \). Moreover,

\[
\lim_{v \to \infty} \| P(x; v) - P(1; v)e^{-v(1-x)} \|_{L^\infty(0,1)} = 0.
\]

**Theorem 4.3.** Suppose that \( 0 < d < g(I_0) \).

(i) If \( v < -2\sqrt{g(I_0)} - d \), then \( P(x; v) \) is strictly decreasing on \([0, 1] \);
(ii) As \( v \to -\infty \), \( P(x; v) \to 0 \) uniformly in any compact subset of \((0, 1] \), \( P(0; v) \to \kappa^* \), where \( \kappa^* = 2 (g(I_0) - d) \). Moreover,

\[
\lim_{v \to -\infty} \| P(x; v) - P(0; v)e^{vx} \|_{L^\infty(0,1)} = 0.
\]

**Remark 3.** Theorem 4.2 indicates that the sinking species is monotone increasingly distributed in the water column, and the phytoplankton species concentrates at the bottom of the water column with a finite population density when the sinking velocity is sufficiently large. It follows from Theorem 4.3 that the buoyant species is monotone decreasingly distributed in the water column and the phytoplankton form a thin layer at the surface of the water column with a finite population density when the buoyant coefficient is sufficiently large.

The proof of Theorems 4.2 and 4.3 is very complicated and lengthy, we divide it into the following nine lemmas.

**Lemma 4.4.** Suppose \( P(x; v) \) is the unique positive solution of (35). Then (i) \( P_x > 0 \) on \([0, 1] \) if \( v > 2\sqrt{g(I_0)} - d \); (ii) \( P_x < 0 \) on \([0, 1] \) if \( v < -2\sqrt{g(I_0)} - d \).

**Proof.** Set \( \omega(x) = e^{-\nu x} P(x; v) \), where \( \nu \) is some constant which will be chosen differently for different purposes. Then \( \omega \) satisfies

\[
\begin{cases}
\omega_{xx} + v(2\eta - 1)\omega_x + \omega[\nu^2\eta(\eta - 1) + g(I(x)) - e^{\nu x}\omega - d] = 0, & 0 < x < 1, \\
\omega_x = \nu(1 - \eta)\omega, & x = 0, 1.
\end{cases}
\]

Let \( \eta = 1/2 \). Then \( \omega \) satisfies

\[
\begin{cases}
\omega_{xx} + \omega[-\frac{\nu^2}{4} + g(I(x)) - e^{\nu x}\omega - d] = 0, & 0 < x < 1, \\
\omega_x = \frac{\nu}{2}\omega, & x = 0, 1.
\end{cases}
\]

(i) If \( v > 2\sqrt{g(I_0)} - d \), then \( \frac{\nu^2}{4} - g(I(x)) + e^{\nu x}\omega + d > 0 \) in \((0, 1) \). Namely, \( \omega_{xx} > 0 \) in \((0, 1) \). Since \( \omega_x(0) > 0 \), we have \( \omega_x > 0 \) on \([0, 1] \). This implies that \( P_x = e^{\nu x}(\eta \nu \omega + \omega_x) > 0 \) on \([0, 1] \).

(ii) If \( v < -2\sqrt{g(I_0)} - d \), then \( \frac{\nu^2}{4} - g(I(x)) + e^{\nu x}\omega + d > 0 \) in \((0, 1) \), i.e., \( \omega_{xx} > 0 \) in \((0, 1) \). Since \( \omega_x(1) < 0 \), we have \( \omega_x < 0 \) on \([0, 1] \). This implies that \( P_x = e^{\nu x}(\eta \nu \omega + \omega_x) < 0 \) on \([0, 1] \). \( \square \)
Lemma 4.5. There exist positive constants $C_1, C_2$, both independent of $v$, such that
\begin{itemize}
  \item[(i)] if $v \geq C_1$, then
  \[ \frac{P(x;v)}{P(1;v)e^{-\nu(1-x)}} \leq e^{\frac{C_2}{2}(1-x)} \text{ on } [0,1]; \]
  \item[(ii)] if $v \leq -C_1$, then
  \[ \frac{P(x;v)}{P(0;v)e^{\nu x}} \leq e^{-\frac{C_2}{2}x} \text{ on } [0,1]. \]
\end{itemize}

Proof. We first set $\eta = 1 - C_2/v^2$ in (36), where $C_2$ is some positive constant to be determined later. Then $\omega$ satisfies
\[
\begin{cases}
\omega_{xx} + v(1 - 2\frac{C_2}{v^2})\omega_x \\
+ \omega[-C_2(1 - \frac{C_2}{v^2}) + g(I(x))] - e^{(\nu - \frac{C_2}{v})x}\omega - d = 0, & 0 < x < 1, \quad (37)
\end{cases}
\]
\[
\omega_x = (C_2/v)\omega, \quad x = 0, 1.
\]
Let $x^* \in [0,1]$ such that $\omega(x^*) = \max_{0 \leq x \leq 1} \omega(x)$. If $x^* \in (0,1)$, then $\omega_{xx}(x^*) \leq 0$ and $\omega_x(x^*) = 0$. By (37) we have
\[
-C_2(1 - C_2/v^2) + g(I(x^*)) - e^{(\nu - C_2/v)x^*}\omega - d \geq 0,
\]
which is impossible if we choose $C_2 = 2g(I_0)$ and $v > 2\sqrt{g(I_0)}$. Hence, for such choices of $C_2$ and $v$, we have $x^* = 0$ or $x^* = 1$.
\begin{itemize}
  \item[(i)] For the case $v > 0$, we have $\omega_x(0) > 0$, which means $x^* \neq 0$. Hence, $x^* = 1$, and $\omega(x) \leq \omega(1)$ for every $x \in [0,1]$. Therefore,
  \[ \frac{P(x;v)}{P(1;v)e^{-\nu(1-x)}} \leq e^{\frac{C_2}{2}(1-x)}. \]
  \item[(ii)] For the case $v < 0$, we have $\omega_x(1) < 0$, which means $x^* \neq 1$. Hence, $x^* = 0$, and $\omega(x) \leq \omega(0)$ for every $x \in [0,1]$. Therefore,
  \[ \frac{P(x;v)}{P(0;v)e^{\nu x}} \leq e^{-\frac{C_2}{2}x}. \]
\end{itemize}

\[ \square \]

Remark 4. The upper bound of positive steady states to (35) has been established in Lemma 4.5 by using the variable transformation $\omega(x) = e^{-v\eta x}P(x;v)$. However, due to the introduction of crowding effect, this method does not work directly when we investigate the lower bound of positive steady states to (35). By means of scaling and Helley’s compactness theorem, we will show the uniform boundedness of positive steady states to (35) for large advection rates by an indirect argument, which is the major distinction in the proof (see Lemma 4.6).

Lemma 4.6. (i) $P(1;v)$ is uniformly bounded as $v \to +\infty$; (ii) $P(0;v)$ is uniformly bounded as $v \to -\infty$.

Proof. (i) Let $y = v(1- x), Q(y;v) = P(1-y/v;v)$. Then $Q$ satisfies
\[
\begin{cases}
Q_{yy} + Q_y + \frac{1}{v^2}Q[g(\bar{I}(y)) - Q - d] = 0, & 0 < y < v, \\
Q_y(0) + Q(0) = 0, \quad Q_y(v) + Q(v) = 0,
\end{cases}
\]
where \( \hat{I}(y) = I_0 \exp \left( -k_0(1 - y/v) - k_1 \int_0^y Q(1 - s; v) ds \right) \). Let \( \bar{Q}(y; v) = \frac{Q(y; v)}{P(y; v)} \). Then \( \bar{Q} \) satisfies

\[
\begin{cases}
\bar{Q}_{yy} + \bar{Q}_y + \frac{1}{v^2} \bar{Q}[g(\hat{I}(y)) - Q(0; v)\bar{Q} - d] = 0, & 0 < y < v, \\
\bar{Q}_y(0) + \bar{Q}(0) = 0, & \bar{Q}_y(v) + \bar{Q}(v) = 0, \\
\bar{Q}(0; v) = 1.
\end{cases}
\]

From Lemma 4.4, we know that \( \bar{Q}(y) \) is decreasing in \( y \) for large \( v \) and \( 0 < \bar{Q} \leq 1 \) on \([0, v]\). Noting that \( Q(0; v) = P(1; v) \), we only need to show \( \bar{Q}(0; v) \) is uniformly bounded as \( v \to +\infty \). To this end, we argue by an indirect argument. By passing to a sequence if necessary, we may assume \( \bar{Q}(0; v) \to +\infty \) as \( v \to +\infty \). Then there exist two cases:

**Case (1).** \( \frac{Q(0; v)}{v^2} \) is uniformly bounded as \( v \to +\infty \);

**Case (2).** \( \frac{Q(0; v)}{v^2} \to +\infty \) as \( v \to +\infty \) by passing to a further subsequence if necessary.

For case (1), since \( \frac{Q(0; v)}{v^2} \) is uniformly bounded as \( v \to +\infty \), by passing to a sequence if necessary, we may assume \( \frac{Q(0; v)}{v^2} \to \kappa \) as \( v \to +\infty \). Since \( 0 < g(I(y)) < g(I_0) \) and \( g(I(y)) \) is strictly increasing with respect to \( y \) in \([0, v]\), it follows from Helley’s compactness theorem that \( g(I(y)) \to h(y) \) locally pointwise in \((0, \infty)\) by passing to a sequence. Integrating (38) in \((0, y)\), we have

\[
\bar{Q}_y(y) + \bar{Q}(y) + \int_0^y \bar{Q} \left( \frac{1}{v^2} g(\hat{I}(\xi)) - \frac{Q(0; v)}{v^2} \bar{Q} - \frac{d}{v^2} \right) d\xi = 0.
\]

Thus

\[
\bar{Q}_y(y) = -\bar{Q}(y) - \int_0^y \bar{Q} \left( \frac{1}{v^2} g(\hat{I}(\xi)) - \frac{Q(0; v)}{v^2} \bar{Q} - \frac{d}{v^2} \right) d\xi
\]

is uniformly bounded as \( v \to +\infty \). By (38), \( \bar{Q}_{yy} \) is uniformly bounded. Passing to a sequence if necessary, we may assume that \( \bar{Q} \to \bar{Q} \) locally in \( C^1((0, +\infty)) \), and \( \bar{Q} \) satisfies

\[
\begin{cases}
\bar{Q}_{yy} + \bar{Q}_y - \bar{Q}^2 \kappa = 0, & 0 < y < v, \\
\bar{Q}_y(0) + \bar{Q}(0) = 0, & \bar{Q}(0; v) = 1.
\end{cases}
\]

By the strong maximum principle, we have \( \bar{Q} > 0 \) on \([0, +\infty)\).

Now, integrating (38) in \((0, v)\), we get

\[
\int_0^v \bar{Q} \left( \frac{1}{v^2} g(\hat{I}(y)) - \frac{Q(0; v)}{v^2} \bar{Q} - \frac{d}{v^2} \right) dy = 0.
\]

Letting \( v \to +\infty \), we obtain that \( \kappa \int_0^{+\infty} \bar{Q}^2 dy = 0 \). This implies \( \kappa = 0 \). Thus \( \bar{Q} \) satisfies

\[
\begin{cases}
\bar{Q}_{yy} + \bar{Q}_y = 0, & 0 < y < v, \\
\bar{Q}_y(0) + \bar{Q}(0) = 0, & \bar{Q}(0; v) = 1.
\end{cases}
\]

Hence, \( \bar{Q} = e^{-y} \).

Multiplying (40) by \( \frac{v^2}{Q(0; v)} \), we have

\[
\int_0^v \bar{Q} \left[ \frac{1}{Q(0; v)} g(\hat{I}(y)) - \bar{Q} - d/Q(0; v) \right] dy = 0.
\]

Letting \( v \to +\infty \), we get \( \int_0^{+\infty} e^{-y} dy = 0 \), which is impossible. Therefore, case (1) cannot occur.
Next, we consider case (2). By (39), we have
\[
\tilde{Q}_y (y) = -\dot{\tilde{Q}}(y) - \frac{1}{\nu^2} \int_0^y \tilde{Q}(\xi)[g(\tilde{I}(\xi)) - d]d\xi + \frac{Q(0; \nu)}{\nu^2} \int_0^y \tilde{Q}^2 d\xi
\]
\[
> -1 - \frac{1}{\nu^2} \int_0^y \tilde{Q}(\xi)[g(\tilde{I}(\xi)) - d]d\xi.
\]
On the other hand,
\[
\frac{1}{\nu^2} \int_0^y \tilde{Q}(\xi)[g(\tilde{I}(\xi)) - d]d\xi \leq \frac{1}{\nu^2} \int_0^y |g(I_0) + d|d\xi = \frac{g(I_0) + d}{\nu^2} y \to 0
\]
as \(v \to +\infty\). Hence, \(\tilde{Q}_y (y) > -\frac{3}{2}\) as long as \(v\) large enough. Noting that
\[
\tilde{Q}_y (0) = -\dot{\tilde{Q}}(0) = -1, \quad \tilde{Q}_y (v; v) = -\frac{Q(v; v)}{Q(0; v)} > -1.
\]
We can conclude that \(\tilde{Q}_y\) is uniformly bounded on \([0, v]\). In view of \(0 < \tilde{Q} \leq 1\), by Arzela-Ascoli Theorem, we may assume \(\tilde{Q} \to Q\) locally uniformly on \([0, +\infty)\). Letting \(v \to +\infty\) in (41), we have \(\int_0^{+\infty} \tilde{Q}^2 dy = 0\). Hence, \(\tilde{Q} = 0\), a contradiction to \(\tilde{Q}(0) = 1\). Therefore, case (2) also cannot occur. So, \(Q(0; v)\) is uniformly bounded as \(v \to +\infty\), that is to say, \(P(1; v)\) is uniformly bounded as \(v \to +\infty\).

(ii) Let \(y = -vx\), \(Q(y; v) = P(-y/v; v)\). We can use the same arguments as in the proof of (i) to deduce that \(P(0; v)\) is uniformly bounded as \(v \to -\infty\). \(\square\)

**Remark 5.** It follows from Lemmas 4.4 and 4.6 that for large sinking velocity, the population density of the phytoplankton species is strictly increasing and it reaches its maximum at the bottom of the water column. Moreover, there exists a positive constant \(M_4\) such that for large sinking velocity \(\nu\),
\[
P(x; \nu) \leq P(1; \nu) \leq M_4 \text{ on } [0, 1].
\]
Similarly, for large buoyant velocity, the population density of the phytoplankton species is strictly decreasing and it reaches its maximum at the surface of the water column. Moreover, there exists a positive constant \(M_5\) such that for large buoyant velocity \(\nu\),
\[
P(x; \nu) \leq P(0; \nu) \leq M_5 \text{ on } [0, 1].
\]

**Lemma 4.7.** There exist positive constants \(C_3, C_4\), both independent of \(\nu\), such that

(i) if \(\nu \geq C_3\), then
\[
\frac{P(x; \nu)}{P(1; \nu)e^{-\nu(1-x)}} \geq e^{-\frac{C_4}{\nu}(1-x)} \text{ on } [0, 1];
\]

(ii) if \(\nu \leq -C_3\), then
\[
\frac{P(x; \nu)}{P(0; \nu)e^\nu x} \geq e^{\frac{C_4}{\nu} x} \text{ on } [0, 1].
\]

**Proof.** Set \(\eta = 1 + C_4/\nu^2\) in (36), where \(C_4\) is some positive constant to be chosen later. Then \(\omega\) satisfies
\[
\begin{cases}
\omega_{xx} + \nu(1 + 2\frac{C_4}{\nu^2})\omega_x + \omega[C_4(1 + \frac{C_4}{\nu^2}) + g(I(x))] - e^{(\nu + C_4/\nu)x}\omega - d = 0, 0 < x < 1, \\
\omega_x = -(C_4/\nu)\omega, \quad x = 0, 1.
\end{cases}
\]
Let $x^* \in [0,1]$ such that $\omega(x^*) = \min_{0 \leq x \leq 1} \omega(x)$. If $x^* \in (0,1)$, then $\omega_{xx}(x^*) \geq 0$ and $\omega_x(x^*) = 0$. By (42) we have
\[ C_4(1 + C_4/v^2) + g(I(x^*)) - e^{(v+C_4/v)x^*} \omega(x^*) - d \leq 0, \]
which is impossible if we choose $C_4 = d + M_6$, where $M_6 = \max\{M_4, M_5\}$. Hence, for such choice of $C_4$, we have $x^* = 0$ or $x^* = 1$.

(i) In view of $v > 0$, we have $\omega_x(0) < 0$, which implies that $x^* \neq 0$. Therefore, $x^* = 1$, i.e., $\omega(x) \geq \omega(1)$ for every $x \in [0,1]$. Therefore,
\[ \frac{P(x; v)}{P(1; v)e^{-v(1-x)}} \geq e^{-C_4(1-x)}. \]

(ii) In view of $v > 0$, we get $\omega_x(1) > 0$, which implies that $x^* \neq 1$. Therefore, $x^* = 0$, i.e., $\omega(x) \geq \omega(0)$ for every $x \in [0,1]$. Therefore,
\[ \frac{P(x; v)}{P(0; v)e^{vx}} \geq e^{C_4x}. \]

\[ \square \]

**Lemma 4.8.** For any $y \geq 0$,
\[ \lim_{v \to \infty} \frac{v}{P(1; v)} \int_0^{1-v/y} P(s; v)ds = e^{-y} \text{ and } \lim_{v \to \infty} \frac{v}{P(0; v)} \int_0^{-v/y} P(s; v)ds = e^{-y} - 1. \]

**Proof.** By Lemma 4.5(i), we deduce
\[ \frac{P(s; v)}{P(1; v)} \leq e^{C_2/v} e^{-v(1-s)}. \]

Hence,
\[ \int_0^{1-v/y} \frac{P(s; v)}{P(1; v)} ds \leq e^{C_2/v} \int_0^{1-y/v} e^{-v(1-s)} ds = e^{C_2/v} \frac{e^{-y} - e^{-v}}{v}, \]
which can be written as
\[ \frac{v}{P(1; v)} \int_0^{1-v/y} P(s; v)ds \leq e^{C_2/v} [e^{-y} - e^{-v}]. \]

Similarly, it follows from Lemma 4.7(i) that
\[ \frac{P(s; v)}{P(1; v)} \geq e^{-C_4/v} e^{-v(1-s)}. \]

Hence,
\[ \frac{v}{P(1; v)} \int_0^{1-y/v} P(s; v)ds \geq e^{-C_4/v} [e^{-y} - e^{-v}]. \]

This proves the first limit.

For the second limit, it follows from Lemma 4.5(ii) and Lemma 4.7(ii) that, for $v \leq \min\{-C_1, -C_3\},$
\[ e^{C_4/v} e^{vs} \leq \frac{P(s; v)}{P(0; v)} \leq e^{-C_2/v} e^{vs}. \]

Hence,
\[ e^{C_4/v} e^{-y} - 1 \leq \int_0^{-v/y} \frac{P(s; v)}{P(0; v)} ds \leq e^{-C_2/v} e^{-y} - 1. \]
which can be written as
\[ e^{C_2/v}[1 - e^{-y}] \leq \frac{-\nu}{P(0; v)} \int_0^{-y/v} P(s; v)ds \leq e^{-C_2/v}[1 - e^{-y}] . \]
This implies the second limit holds. \qed

**Lemma 4.9.** Suppose \( d \in (0, g(I_0e^{-k_0})) \). Then \( \lim_{\nu \to \infty} P(1; \nu) = \kappa^* \), where \( \kappa^* = 2(g(I_0e^{-k_0}) - d) \).

**Proof.** It follows from Lemma 4.6(i) that \( P(1; \nu) \) is uniformly bounded for large positive \( \nu \). Passing to a sequence if necessary, we may assume that \( P(1; \nu) \to \kappa^* \) as \( \nu \to \infty \) for some constant \( \kappa^* > 0 \). Dividing (35) by \( P(1; \nu) \), integrating in \((0, 1)\), and applying the boundary conditions in (35), we have
\[ \int_0^1 \frac{P(x; \nu)}{P(1; \nu)} [g(I(x)) - P(x; \nu) - d] dx = 0. \]
Set \( x = 1 - y/\nu \). We can rewrite the above equation as
\[ \int_0^{\nu} \frac{P(1 - y/\nu; \nu)}{P(1; \nu)} [g(\tilde{I}(y)) - P(1 - y/\nu; \nu) - d] dy = 0, \] (43)
where
\[ \tilde{I}(y) = I_0e^{-k_0(1-y/\nu) - k_1} \int_0^{1-y/\nu} P(s; \nu)ds. \]

By Lemma 4.8,
\[ \int_0^{1-y/\nu} P(s; \nu)ds = \frac{P(1; \nu)}{\nu} \int_0^{1-y/\nu} P(s; \nu)ds \to 0 \]
pointwisely in \( y \) as \( \nu \to \infty \). Hence, \( \tilde{I}(y) \to I_0e^{-k_0} \) pointwisely in \( y \) as \( \nu \to \infty \).

From Lemmas 4.5 and 4.7, we know that
\[ e^{-C_4/v} e^{-y} \leq \frac{P(1 - y/\nu; \nu)}{P(1; \nu)} \leq e^{C_2/v} e^{-y} \]
for every \( y \in (0, \nu) \), we see that
\[ \frac{P(1 - y/\nu; \nu)}{P(1; \nu)} \to e^{-y} \]
pointwisely in \( y \) as \( \nu \to \infty \). Hence, \( P(1 - y/\nu; \nu) \to \kappa^* e^{-y} \) pointwisely in \( y \) as \( \nu \to \infty \). Moreover,
\[ \frac{P(1 - y/\nu; \nu)}{P(1; \nu)} [g(\tilde{I}(y)) - P(1 - y/\nu; \nu) - d] \leq e^{C_2/v} e^{-y} [g(I_0) + M_4 + d] \]
for every \( y \in (0, \nu) \). Hence, we can apply the Lebesgue dominant convergent theorem and let \( \nu \to \infty \) in (43) to get
\[ \int_0^\infty e^{-y} [g(I_0e^{-k_0}) - \kappa^* e^{-y} - d] dy = 0. \]
After simple calculations, we obtain that \( \kappa^* = 2(g(I_0e^{-k_0}) - d) \). \qed

**Lemma 4.10.** Suppose that \( d \in (0, g(I_0)) \). Then \( \lim_{\nu \to -\infty} P(0; \nu) = \kappa_* \), where \( \kappa_* = 2(g(I_0) - d) \).
Proof. It follows from Lemma 4.6(ii) that $P(0; v)$ is uniformly bounded for sufficiently negative $v$. Passing to a sequence if necessary, we may assume that $P(0; v) \to \kappa_*$ as $v \to -\infty$ for some constant $\kappa_* > 0$. Dividing (35) by $P(0; v)$, integrating in $(0,1)$, and applying the boundary conditions in (35), we have

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

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

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

(44)

where $\hat{I}(y) = I_0 e^{k_0 y/v - k_0 \int_0^{-y/v} P(s; v) ds}$. By Lemma 4.8,

$$
\int_0^{-y/v} P(s; v) ds = \frac{P(0; v)}{v} \left. \frac{v}{P(0; v)} \int_0^{-y/v} P(s; v) ds \right. \to 0
$$

pointwisely in $y$ as $v \to -\infty$. Hence, $\hat{I}(y) \to I_0$ pointwisely in $y$ as $v \to \infty$.

From Lemmas 4.5 and 4.7, we know that

$$
e^{C_4/v} e^{-y} \leq \frac{P(-y/v; v)}{P(0; v)} \leq e^{-C_2/v} e^{-y}
$$

for every $y \in (0, -v)$, which means that

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

pointwisely in $y$ as $v \to -\infty$. Therefore, $P(-y/v; v) \to \kappa_* e^{-y}$ pointwisely in $y$ as $v \to -\infty$. Moreover,

$$
\frac{P(-y/v; v)}{P(0; v)} |g(\hat{I}(y)) - P(-y/v; v) - d| \leq e^{-C_2/v} e^{-y} |g(I_0) + M_5 + d|
$$

for every $y \in (0, -v)$. Hence, we can apply the Lebesgue dominant convergent theorem and let $v \to -\infty$ in (44) to get

$$
\int_0^\infty e^{-y} |g(I_0) - \kappa_* e^{-y} - d| dy = 0.
$$

After calculations, we obtain that $\kappa_* = 2 (g(I_0) - d)$.

\begin{lemma}
There exist positive constants $C_5, C_6$, both independent of $v$, such that
\begin{enumerate}
\item[(i)] if $v \geq C_5$, then

$$
\left| \frac{P(x; v)}{P(1; v)} - e^{-v(1-x)} \right| \leq \frac{C_6}{v^2} \text{ on } [0, 1];
$$

\item[(ii)] if $v \leq -C_5$, then

$$
\left| \frac{P(x; v)}{P(0; v)} - e^{vx} \right| \leq \frac{C_6}{v^2} \text{ on } [0, 1].
$$

\end{enumerate}
\end{lemma}

\begin{proof}
Here we only prove (i), (ii) can be shown similarly and we omit it. It follows from Lemma 4.5(i) and Lemma 4.7(i) that

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

where

$$
g_1(x; v) = v(1-x)^2 \int_0^1 \frac{P(x; v)}{P(1; v)} [g(I(x)) - P(x; v) - d] dx
$$

and

$$
g_2(x; v) = v(1-x)^2 \int_0^1 \frac{P(x; v)}{P(0; v)} [g(I(x)) - P(x; v) - d] dx.
$$

By Lemma 4.8,

$$
\int_0^{-y/v} P(s; v) ds = \frac{P(0; v)}{v} \left. \frac{v}{P(0; v)} \int_0^{-y/v} P(s; v) ds \right. \to 0
$$

pointwisely in $y$ as $v \to -\infty$. Hence, $\hat{I}(y) \to I_0$ pointwisely in $y$ as $v \to \infty$.

From Lemmas 4.5 and 4.7, we know that

$$
e^{C_4/v} e^{-y} \leq \frac{P(-y/v; v)}{P(0; v)} \leq e^{-C_2/v} e^{-y}
$$

for every $y \in (0, -v)$, which means that

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

pointwisely in $y$ as $v \to -\infty$. Therefore, $P(-y/v; v) \to \kappa_* e^{-y}$ pointwisely in $y$ as $v \to -\infty$. Moreover,

$$
\frac{P(-y/v; v)}{P(0; v)} |g(\hat{I}(y)) - P(-y/v; v) - d| \leq e^{-C_2/v} e^{-y} |g(I_0) + M_5 + d|
$$

for every $y \in (0, -v)$. Hence, we can apply the Lebesgue dominant convergent theorem and let $v \to -\infty$ in (44) to get

$$
\int_0^\infty e^{-y} |g(I_0) - \kappa_* e^{-y} - d| dy = 0.
$$

After calculations, we obtain that $\kappa_* = 2 (g(I_0) - d)$.

\end{proof}
where \( g_i(x; v) (i = 1, 2) \) are given by
\[
g_1(x; v) = (e^{-C_4(1-x)/v} - 1)e^{-v(1-x)} \quad \text{and} \quad g_2(x; v) = (e^{C_2(1-x)/v} - 1)e^{-v(1-x)}.
\]

It is easy to check that
\[
\frac{\partial g_1(x; v)}{\partial x} = ve^{-v(1-x)}[e^{-C_4(1-x)/v}(1 + C_4/v^2) - 1].
\]

For large \( v \), the only critical point (denoted by \( x_1 \)) of \( g_1 \) on \([0,1]\) is determined by
\[
e^{C_4(1-x_1)/v} = 1 + C_4/v^2,
\]
which implies that \( x_1 = 1 - (1/v)(1 + o(1)) \) for large \( v \). Hence,
\[
g_1(x_1; v) > -\frac{C_4}{v^2}e^{-v(1-x_1)} \geq -\frac{C_7}{v^2}
\]
for some positive constant \( C_7 \) independent of \( v \). As \( g_1 \) attains the global minimum at \( x = x_1 \) on \([0,1]\), we see that
\[
\frac{P(x; v)}{P(1; v)} - e^{-v(1-x)} \geq -\frac{C_7}{v^2}.
\]

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

For large \( v \), the only critical point (denoted by \( x_2 \)) of \( g_2 \) on \([0,1]\) is determined by
\[
e^{C_2(1-x_2)/v} = \frac{1}{1 - C_2/v^2},
\]
which implies that \( x_2 = 1 - (1/v)(1 + o(1)) \) for large \( v \). Hence,
\[
g_2(x_2; v) = \frac{C_2/v^2}{1 - C_2/v^2}e^{-v(1-x_2)} \leq \frac{C_8}{v^2},
\]
where \( C_8 \) is some positive constant independent of \( v \). As \( g_2 \) attains the global maximum at \( x = x_2 \) on \([0,1]\), we see that
\[
\frac{P(x; v)}{P(1; v)} - e^{-v(1-x)} \leq \frac{C_8}{v^2}
\]
for every \( x \in [0,1] \). Let \( C_0 = \max\{C_7, C_8\} \). Then (i) holds.

\[ \square \]

**Lemma 4.12.** There exist some positive constants \( C_9, C_{10} \), both independent of \( v \), such that

(i) if \( v \geq C_9 \), then
\[
\left| P(x; v) - P(1; v)e^{-v(1-x)} \right| \leq \frac{C_{10}}{v^2} \text{ on } [0,1];
\]

(ii) if \( v \leq -C_9 \), then
\[
\left| P(x; v) - P(0; v)e^{ux} \right| \leq \frac{C_{10}}{v^2} \text{ on } [0,1].
\]

**Proof.** (i) Noting that \( P(1; v) \to \kappa^* > 0 \) as \( v \to \infty \), it follows from Lemma 4.11(i) that
\[
\left| P(x; v) - P(1; v)e^{-v(1-x)} \right| = P(1; v) \left| \frac{P(x; v)}{P(1; v)} - e^{-v(1-x)} \right| \leq \frac{C_{10}}{v^2}.
\]

The proof of part (ii) is similar to that of part (i), and we omit it here.

\[ \square \]
Proof of Theorem 4.2. (i) is a direct result of Lemma 4.4(i). For (ii), it follows from Lemma 4.9 that \( \lim_{v \to \infty} P(1; v) = \kappa^* \), where \( \kappa^* = 2(g(I_0 e^{-k_0}) - d) \). By Lemma 4.12(i), we know that there exist some positive constants \( C_9, C_{10} \), both independent of \( v \), such that for \( v \geq C_9 \),
\[
\left| P(x; v) - P(1; v)e^{-v(1-x)} \right| \leq \frac{C_{10}}{v^2} \text{ on } [0, 1].
\]
Letting \( v \to \infty \), we immediately get that
\[
\lim_{v \to \infty} \left\| P(x; v) - P(1; v)e^{-v(1-x)} \right\|_{L^\infty(0,1)} = 0,
\]
which implies that \( P(x; v) \to 0 \) uniformly in any compact subset of \([0,1]\) as \( v \to \infty \). The proof is finished.

Proof of Theorem 4.3. (i) is a direct result of Lemma 4.4(ii). For (ii), it follows from Lemma 4.10 that \( \lim_{v \to -\infty} P(0; v) = \kappa_* \), where \( \kappa_* = 2(g(I_0) - d) \). By Lemma 4.12(ii), we know that there exist some positive constants \( C_9, C_{10} \), both independent of \( v \), such that for \( v \leq -C_9 \),
\[
\left| P(x; v) - P(0; v)e^{\nu x} \right| \leq \frac{C_{10}}{v^2} \text{ on } [0, 1].
\]
Letting \( v \to -\infty \), we immediately get that
\[
\lim_{v \to -\infty} \left\| P(x; v) - P(0; v)e^{\nu x} \right\|_{L^\infty(0,1)} = 0,
\]
which implies that \( P(x; v) \to 0 \) uniformly in any compact subset of \((0,1]\) as \( v \to -\infty \). The proof is finished.

5. Discussion. Phytoplankton are microscopically small plants that drift in oceans and lakes, which form the base of the aquatic food chain. Since they transport significant amounts of atmospheric carbon dioxide into the deep oceans, they may play a crucial role in the climate dynamics. In freshwater lakes and rivers, phytoplankton communities can have a major impact on ecosystem dynamics. The appearance of algae blooms are often a signal of dangerous eutrophication and may result in serious water-quality problems. Hence, the formation of phytoplankton blooms has recently attracted considerable attention from mathematical, experimental and numerical viewpoints.

Under the assumption that phytoplankton transport is governed by turbulent diffusion, Du and Hsu [8] studied the global dynamics of a nonlocal reaction-diffusion model proposed by Huisman [16] (i.e. (1)-(3) with \( \beta = 0, \nu = 0 \)), which describes the evolution of a single phytoplankton species in an eutrophic vertical water column where the species relies solely on light for its metabolism. It turns out that there exists a critical death rate \( d_* > 0 \) such that if \( d \in (0, d_*) \), the model admits a unique positive steady state which is a global attractor of it, whereas it has no positive steady state and zero is a global attractor if \( d \in [d_*, \infty) \). Considering the effect of sinking or buoyant motion, Hsu and Lou [14] studied a nonlocal reaction-diffusion-advection model of light-limited phytoplankton [11, 15] in an eutrophic water column. The model is a special case of (1)-(3) with \( \beta = 0, \nu \neq 0 \). Their results show that there also exists a critical death rate \( d_* > 0 \) so that for \( d \in (0, d_*) \), the model has a unique positive steady state and for \( d \in [d_*, \infty) \) it has no positive steady state. Moreover, the bifurcation diagram of positive steady states with respect to the death rate looks like Fig.1(a). That is, when the death rate goes to zero, the
population density of the phytoplankton goes to infinity at the bottom or surface of the water column. By means of the strict monotonicity of the critical death rate with respect to the water column depth, the sinking or buoyant velocity and the turbulent diffusion rate, they showed that a critical water column depth, a critical sinking or buoyant velocity and a critical turbulent diffusion rate can exist for some intermediate range of phytoplankton death rate. Furthermore, their analysis on the asymptotic profiles of steady states for large advection rates indicates that the vertical distribution looks like a Dirac function at the bottom of the water column when the sinking velocity is sufficiently large, which indicates that the phytoplankton forms a thin layer at the bottom of the water column for large sinking rate. Similarly, the vertical distribution looks like a Dirac function at the surface of the water column when the buoyant coefficient is sufficiently large, which indicates that the phytoplankton forms a thin layer at the surface of the water column for large buoyant rate.

The purpose of this paper is to incorporate the crowding effect into the population dynamics of a single phytoplankton species in a water column, and to study the longtime dynamical behavior of the nonlocal reaction-diffusion-advection model (1)-(3) and the asymptotic profiles of its positive steady states for large sinking or buoyant rates. Our results show that there is also a critical death rate $d^*$ such that the phytoplankton species survives if and only if its death rate is less than the critical death rate $d^*$. In contrast to the model without crowding effect, Theorem 2.4 shows that the density of the phytoplankton species will have a finite limit rather than go to infinity when the death rate disappears (see Fig.1(b)), which is due to the crowding effect. Furthermore, the limits

$$\lim_{d \to 0} P_d(\beta; x) = P_0(\beta; x), \quad \text{and} \quad \lim_{\beta \to 0} \|P_0(\beta; x)\|_{\infty} = \infty$$

illustrate that the bifurcation diagram Fig.1(b) of positive steady states for the model (1)-(3) will gradually evolve into Fig.1(a) when the crowding effect disappears. Furthermore, Theorems 4.2 and 4.3 indicate that the sinking phytoplankton species concentrates at the bottom of the water column with a finite population density, and the buoyant phytoplankton species concentrates at the surface of the water column with a finite population density when phytoplankton transport is governed by the advection motion (see Fig.2).

Acknowledgments. The authors are very grateful to the anonymous referees for their kind and valuable suggestions leading to a substantial improvement of the manuscript. The authors would like to give their sincere thanks to Professor Yuan Lou for some discussions on the asymptotic profiles of positive equilibria. Also the authors would like to give their sincere thanks to Professor Linfeng Mei for some discussions on the estimates of positive equilibria for large advection rates.

Appendix. We state the following well-known lemmas and theorems as appendix without proof.

**Lemma A.1.** [27] Let $q(x) \in C(\Omega)$ and $q(x) + p > 0$ on $\bar{\Omega}$ with $p > 0$, and let $\eta_1$ be the first eigenvalue of the eigenvalue problem

$$-\Delta \varphi - q(x) \varphi = \eta \varphi, \ x \in \Omega, \quad \frac{\partial \varphi}{\partial n} + \gamma(x) \varphi = 0, \ x \in \partial \Omega,$$
Figure 2. Vertical distributions of phytoplankton for large advection rates with crowding effect. Here we take a typical Michaelis-Menten form \( g(I) = \frac{mI}{b+I} \) as the specific growth rate of phytoplankton, and choose the basic parameters of the species to be \( D = 0.1, d = 0.2, I_0 = 1, k_0 = 1, k_1 = 0.1, m = 1, b = 1. \) We further fix the parameter \( \beta = 0.01 \) in (a) and (b); \( \beta = 0.05 \) in (c) and (d); \( \beta = 0.15 \) in (e) and (f). The advection rates \( \nu = 0.2, 0.5, 1, 5 \) in (a), (c) and (e) for the red, blue, green and black line respectively; the advection rates \( \nu = -0.1, -0.5, -1, -3 \) in (b), (d) and (f) for the red, blue, green and black line respectively. We observe that phytoplankton concentrates at the bottom or surface of water column with a finite population density for large advection rates.

where \( \gamma(x) \in C(\partial\Omega) \) and \( \gamma(x) \geq 0. \) If \( \eta_1 > 0 (\text{or } \eta_1 < 0) \), then the eigenvalue problem

\[-\Delta \varphi + p \varphi = t(q(x) + p)\varphi, \ x \in \Omega, \ \frac{\partial \varphi}{\partial n} + \gamma(x)\varphi = 0, \ x \in \partial\Omega\]
has no eigenvalue less than or equal to 1 (or has eigenvalue less than 1).

**Lemma A.2.** [4, Theorem 1], [5, Proposition 2] and [6, Theorem 2.1] Let $F : W \to W$ be a compact, continuously differentiable operator, $W$ be a cone in the Banach space $E$ with zero $\Theta$. Suppose that $W - W$ is dense in $E$ and the $\Theta \in W$ is a fixed point of $F$ and $A_0 = F'(\Theta)$. Then the following results hold:

(i) $\text{index}_W(F, \Theta) = 1$ if the spectral radius $r(A_0) < 1$;
(ii) $\text{index}_W(F, \Theta) = 0$ if $A_0$ has an eigenvalue greater than 1 and $\Theta$ is an isolated solution of $x = F(x)$, that is $h \neq A_0 h$ if $h \in W - \Theta$.

**Definition A.3.** [13, Chapter 11.1] Let $X, Y$ be Banach spaces. Then a bounded linear operator $T : X \to Y$ is called a Fredholm operator if

(i) its range $R(T)$ is closed;
(ii) the numbers $\dim \ker T$ and $\text{codim} R(T) := \ker(Y/R(T))$ are finite. Furthermore, $\text{ind} T := \dim \ker T - \text{codim} R(T)$ is said to be the index of the Fredholm operator $T$.

**Theorem A.4.** [25, Theorem 4.3] Let $X$ and $Y$ be real Banach spaces, $V$ be an open connected subset of $\mathbb{R} \times X$ and $(\lambda_0, u_0) \in V$, and let $F$ be a continuously differentiable mapping from $V$ into $Y$. Suppose that

(i) $F(\lambda, u_0) = 0$ for $(\lambda, u_0) \in V$;
(ii) the partial derivative $D_{\lambda u} F(\lambda, u)$ exists and is continuous in $(\lambda, u)$ near $(\lambda_0, u_0)$;
(iii) $D_{\lambda} F(\lambda_0, u_0)$ is a Fredholm operator with index 0, and $\dim \ker(D_{\lambda} F(\lambda_0, u_0)) = 1$;
(iv) $D_{\lambda u} F(\lambda_0, u_0)[w_0] \notin R(D_{\lambda} F(\lambda_0, u_0))$, where $w_0 \in X$ spans $\ker(D_{\lambda} F(\lambda_0, u_0))$.

Here $\ker(D_{\lambda} F(\lambda_0, u_0))$ and $R(D_{\lambda} F(\lambda_0, u_0))$ are the kernel and the range of the operator $D_{\lambda} F(\lambda_0, u_0)$ respectively. Let $Z$ be any complement of $\text{span}\{w_0\}$ in $X$. Then there exist an open interval $I_1 = (-\epsilon, \epsilon)$ and continuous functions $\lambda : I_1 \to \mathbb{R}$, $\psi : I_1 \to Z$, such that $\lambda(0) = 0$, $\psi(0) = 0$, and if $u(s) = u_0 + s w_0 + s \psi(s)$ for $s \in I_1$, then $F(\lambda(s), u(s)) = 0$. Moreover, $F^{-1} \{0\}$ near $(\lambda_0, u_0)$ consists precisely of the curves $u = u_0$ and $\Gamma = \{(\lambda(s), u(s)) : s \in I_1\}$. If in addition, $D_{\lambda u} F(\lambda, u)$ is a Fredholm operator for all $(\lambda, u) \in V$, then the curve $\Gamma$ is contained in $C$, which is a connected component of $S$ where $S = \{(\lambda, u) \in V : F(\lambda, u) = 0, u \neq u_0\}$; and either $C$ is not compact in $V$, or $C$ contains a point $(\lambda_*, u_0)$ with $\lambda_* \neq \lambda_0$.

**Theorem A.5.** [25, Theorem 4.4] Suppose that all conditions in Theorem A.4 are satisfied. Let $C$ be defined as in Theorem A.4. We define $\Gamma_+ = \{(\lambda(s), u(s)) : s \in (0, \epsilon)\}$ and $\Gamma_- = \{(\lambda(s), u(s)) : s \in (-\epsilon, 0)\}$. In addition we assume that

(a) $F_u(\lambda, u_0)$ is continuously differentiable in $\lambda$ for $(\lambda, u_0) \in V$;
(b) the norm function $u \mapsto \|u\|$ in $X$ is continuously differentiable for any $u \neq 0$;
(c) for $k \in (0, 1)$, if $(\lambda, u_0)$ and $(\lambda, u)$ are both in $V$, then $(1 - k)F_u(\lambda, u_0) + kF_u(\lambda, u)$ is a Fredholm operator.

Let $C^+$ (resp. $C^-$) be the connected component of $C \setminus \Gamma_-$ which contains $\Gamma_+$ (resp. the connected component of $C \setminus \Gamma_+$ which contains $\Gamma_-$). Then each of the sets $C^+$ and $C^-$ satisfies one of the following:

(i) it is not compact in $V$;
(ii) it contains a point $(\lambda_*, u_0)$ with $\lambda_* \neq \lambda_0$;
(iii) it contains a point $(\lambda, u_0 + z)$, where $z \neq 0$ and $z \in Z$.  

REFERENCES

[1] K. R. Arrigo, D. H. Robinson and D. L. Worthen, et al, Phytoplankton community structure and the drawdown of nutrients and CO$_2$ in the Southern Ocean, Science, 283 (1999), 365–367. http://science.sciencemag.org/content/283/5400/365.

[2] M. G. Crandall and P. H. Rabinowitz, Bifurcation from simple eigenvalues, J. Functional Analysis, 8 (1971), 321–340.

[3] R. Courant and D. Hilbert, Methods of Mathematical Physics, Vol. I, Interscience Publishers, New York, 1953.

[4] E. N. Dancer, On the indices of fixed points of mappings in cones and applications, J. Math. Anal. Appl., 91 (1983), 131–151.

[5] E. N. Dancer, On positive solutions of some pairs of differential equations, Trans. Amer. Math. Soc., 284 (1984), 729–743.

[6] E. N. Dancer and Y. Du, Positive solutions for a three-competition system with diffusion-I. General existence results, Nonlinear Anal., 24 (1995), 337–357.

[7] G. R. DiTullio, J. M. Grebmeier, K. R. Arrigo, et al, Rapid and early export of Phaeocystis antarctica blooms in the Ross Sea, Antarctica, Nature, 404 (2000), 595–598. https://www.nature.com/articles/35007061.

[8] Y. Du and S. B. Hsu, On a nonlocal reaction-diffusion problem arising from the modeling of phytoplankton growth, SIAM J. Math. Anal., 42 (2010), 1305–1333.

[9] Y. Du and L. Mei, On a nonlocal reaction-diffusion-advection equation modelling phytoplankton dynamics, Nonlinearity, 24 (2011), 319–349.

[10] Y. Du, S. B. Hsu and Y. Lou, Multiple steady-states in phytoplankton population induced by photoinhibition, J. Differential Equations, 258 (2015), 2408–2434.

[11] U. Ebert, M. Arrayas, N. Temme, B. Sommeojer and J. Huisman, Critical condition for phytoplankton blooms, Bull. Math. Biol., 63 (2001), 1095–1124. https://www.journals.uchicago.edu/doi/abs/10.1086/338511.

[12] P. G. Falkowski, R. T. Barber and V. Smetacek, Biogeochemical controls and feedbacks on ocean primary production, Science, 281 (1998), 200–206. http://science.sciencemag.org/content/281/5374/200.

[13] I. Ghoberg, S. Goldberg and M. A. Kaashoek, Classes of Linear Operators, Vol. I, Birkhäuser-Basel, Basel, 1990. http://b-ok.xyz/book/461145/3b6523.

[14] S. B. Hsu and Y. Lou, Single phytoplankton species growth with light and advection in a water column, SIAM J. Math. Anal., 70 (2010), 2942–2974.

[15] J. Huisman, M. Arrayas, U. Ebert, et al, How do sinking phytoplankton species manage to persist?, Amer. Nat., 159 (2002), 245–254. https://www.journals.uchicago.edu/doi/abs/10.1086/338511.

[16] J. Huisman, P. van Oostveen and F. J. Weissing, Species dynamics in phytoplankton blooms: incomplete mixing and competition for light, Amer. Nat., 154 (1999), 46–68. https://www.journals.uchicago.edu/doi/abs/10.1086/303220.

[17] T. W. Hwang and F. B. Wang, Dynamics of a dengue fever transmission model with crowding effect in human population and spatial variation, Discrete Contin. Dyn. Syst. Ser. B, 18 (2013), 147–161.

[18] D. H. Jiang, H. Nie and J. H. Wu, Crowding effects on coexistence solutions in the unstirred chemostat, Appl. Anal., 96 (2017), 1016–1046.

[19] P. De Leenheer, D. Angeli and E. D. Sontag, A feedback perspective for chemostat models with crowding effects, Positive Systems, 167–174, Lect. Notes Control Inf. Sci., 294, Springer, Berlin, 2003.

[20] P. De Leenheer, D. Angeli and E. D. Sontag, Crowding effects promote coexistence in the chemostat, J. Math. Anal. Appl., 319 (2006), 48–60.

[21] H. Lin and F. B. Wang, On a reaction-diffusion system modeling the dengue transmission with nonlocal infections and crowding effects, Appl. Math. Comput., 248 (2014), 184–194.

[22] R. Peng and X. Q. Zhao, A nonlocal and periodic reaction-diffusion-advection model of a single phytoplankton species, J. Math. Biol., 72 (2016), 755–791.

[23] M. H. Protter and H. F. Weinberger, Maximum Principles in Differential Equations, 2nd edition, Springer-Verlag, New York, 1984.

[24] G. A. Riley, H. M. Stommel and D. F. Bumpus, Quantitative ecology of the plankton of the western North Atlantic, Bull. Bingham Oceanogr. Coll., 12 (1949), 1–169.
[25] J. P. Shi and X. F. Wang, On global bifurcation for quasilinear elliptic systems on bounded domains, *J. Differential Equations*, 246 (2009), 2788–2812.

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

[27] M. X. Wang, *Nonlinear Elliptic Equations*, Science Press, Beijing, 2010.

[28] X. Zeng, J. Zhang and Y. Gu, Uniqueness and stability of positive steady state solutions for a ratio-dependent predator-prey system with a crowding term in the prey equation, *Nonlinear Anal. Real World Appl.*, 24 (2015), 163–174.

Received August 2017; revised May 2018.

E-mail address: 674165711@qq.com
E-mail address: Corresponding author(H.Nie): niehua@snnu.edu.cn
E-mail address: jianhuaw@snnu.edu.cn