DYNAMICS OF PHYTOPLANKTON SPECIES COMPETITION
FOR LIGHT AND NUTRIENT WITH RECYCLING
IN A WATER COLUMN

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(This paper is dedicated to the seventieth birthday of Professor Sze-Bi Hsu)

Abstract. This paper analytically investigates a nonlocal system of reaction-
diffusion-advection equations modeling the competition of two phytoplankton
species for a limiting nutrient and light in a water column, where dead phy-
toplankton species can get recycled back into the system as a resource for
growth. The threshold dynamics of the single population model is first es-
tablished. Then the utilization of abstract persistence theory enables us to
show that two species population system admits a coexistence steady state
and the system is uniformly persistent if the trivial steady state and two global
attractors on the boundary are all weak repellers.

1. Introduction. Phytoplankton are the autotrophic plant-like organisms that
drift in oceans, seas and lakes. It was known that phytoplankton form the base
of the marine food chain and they play a central role in the absorption of carbon
dioxide. Thus, phytoplankton have a significant influence on the global carbon
dynamics in the environment. In this paper, we shall investigate a model of com-
petition between two phytoplankton species in a water column, where two species
compete for nutrient and light which are essential resources for population growth
[1, 2, 9, 13, 25] in a vertically heterogeneous environment determined by turbulent
variations.

We shall describe the nonlocal system of reaction-diffusion-advection equations
modeling the competition of two phytoplankton species for a limiting nutrient and
light within a water column proposed in [9, 25]. Assume $x$ indicates the depth in
the water column from the surface $(x = 0)$ to the bottom $(x = L)$. Let $u_i(x,t)$
denote the phytoplankton population density of species $i$, $i = 1, 2$, and let $R(x,t)$
denote the nutrient concentration in the water column. Then the dynamics of the

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phytoplankton population and the nutrient concentration in the water column is governed by the following system \([9, 25]\):

\[
\begin{aligned}
(R)_t &= D_R R_{xx} - q_1 \min\{f_1(R), g_1(I(x, t))\} u_1 - q_2 \min\{f_2(R), g_2(I(x, t))\} u_2 \\
&\quad + q_1 \theta_1 d_1 u_1 + q_2 \theta_2 d_2 u_2, \\
(u_1)_t &= D_1 (u_1)_{xx} - \alpha_1 (u_1)_x + \left[\min\{f_1(R), g_1(I(x, t))\} - d_1\right] u_1, \\
(u_2)_t &= D_2 (u_2)_{xx} - \alpha_2 (u_2)_x + \left[\min\{f_2(R), g_2(I(x, t))\} - d_2\right] u_2,
\end{aligned}
\]

for \((x, t) \in (0, L) \times (0, \infty)\) with boundary conditions

\[
\begin{aligned}
&\begin{cases}
R_x(0,t) = 0, & R_x(L,t) = \gamma (R^0 - R(L,t)), \quad t > 0, \\
D_i(u_i)_x(0,t) - \alpha_i u_i(0,t) = D_i(u_i)_x(L,t) - \alpha_i u_i(L,t) = 0, \quad t > 0, \quad i = 1, 2,
\end{cases}
\end{aligned}
\]

and initial conditions

\[
\begin{aligned}
&\begin{cases}
R(x, 0) = R^0(x) \geq 0, \quad 0 \leq x \leq L, \\
u_i(x, 0) = u_i^0(x) \geq 0, \quad 0 \leq x \leq L, \quad i = 1, 2.
\end{cases}
\end{aligned}
\]

Here \(D_R > 0\) and \(D_i > 0\) are the diffusion coefficients of the nutrient and phytoplankton species \(i\) caused by the water turbulence, respectively; \(\alpha_i\) is the phytoplankton sinking (\(\alpha_i > 0\)) or buoyant (\(\alpha_i < 0\)) velocity of species \(i\); \(d_i > 0\) (resp. \(q_i > 0\)) is the specific loss rate (resp. the nutrient content) of the phytoplankton species \(i\); \(\theta_i\) is the proportion of resource(s) in dead phytoplankton species \(i\) that is recycled and \(0 \leq \theta_i \leq 1\).

Assuming that the specific growth rate of the phytoplankton species \(i\) depends on the limiting nutrient \(R(x, t)\) and available light \(I(x, t)\), and is determined by the resource that is the most limiting according to Liebig’s law of the minimum \([15]\), namely, it takes the following form:

\[
\min\{f_i(R), g_i(I(x, t))\},
\]

where \(f_i(R)\) and \(g_i(I(x, t))\) are the growth rates of species \(i\) when \(R\) and \(I(x, t)\) limit the growth, respectively. Here \(f_i\) satisfies

\[
f_i(0) = 0, \quad f_i'(R) > 0, \quad \forall R > 0, \quad i = 1, 2.
\]

A typical example of \(f_i\) is the Monod function

\[
f_i(R) = \frac{\mu_{\max,i} R}{K_i + R}, \quad i = 1, 2.
\]

The function \(g_i\) in this paper takes the following form:

\[
g_i(I) = \frac{m_i I}{a_i + I}, \quad i = 1, 2,
\]

or

\[
g_i(I) = \beta_i I^{\vartheta_i}, \quad \text{with} \quad \beta_i > 0, \quad 0 < \vartheta_i \leq 1, \quad i = 1, 2.
\]

Following \([8, 12]\), the light distribution function \(I(x, t)\) is described by Lambert-Beer law, namely, \(I(x, t)\) takes the form

\[
I(x, t) = I_0 e^{-k_0 x} \exp \left( - \int_0^x k_1 u_1(s, t) ds - \int_0^x k_2 u_2(s, t) ds \right),
\]

where \(I_0 > 0\) is the incident light intensity, \(k_0 > 0\) is the background turbidity, \(k_i\) is the absorption coefficient of the phytoplankton species \(i\).
The boundary condition (2.1) was taken from [25]. Precisely, the authors in [25] assume that no boundary flux for phytoplankton species \( u_i(x, t) \), and nutrients \( R(x, t) \) enter the water column only from the bottom sediment. In (1.2), \( \gamma \) is a transfer velocity of nutrients relative to \( D_R \) at the sediment interface, and \( R^{(0)} \) is the nutrient concentration at the sediment.

On the end of this section, we briefly mention two extreme cases closely related to the model studied in this paper. In oligotrophic ecosystems with ample supply of light, the specific growth rate of the phytoplankton species depends only on available light and species compete only for nutrients, see, e.g., [14, 16] for biological interpretations, and [3, 4, 7] for theoretical analysis. In this current paper, we shall investigate system (1.1)-(1.3) with two species competing for two essential resources, nutrient and light, in a water column. The rest of the paper is organized as follows. Some basic properties of solutions of system (1.1)-(1.3) are presented in section 2. The threshold dynamics of single population model is studied in section 3. In section 4, we investigate the possibility of coexistence for two phytoplankton species model (1.1)-(1.3).

2. Basic properties of solutions. This section is devoted to the establishment of some basic properties of the solutions of system (1.1)-(1.3). The feasible domain \( \mathcal{X} \) for (1.1)-(1.3) takes the following form:

\[
\mathcal{X} = \{(R, u_1, u_2) \in C([0, L], \mathbb{R}^3) : R(x) \geq 0, \ u_i(x) \geq 0, \ x \in [0, L], \ i = 1, 2\},
\]

where \( C([0, L], \mathbb{R}^3) \) denotes the Banach space of continuous functions from the interval \([0, L]\) to \( \mathbb{R}^3 \) with the supremum norm. In symbol, \( \mathcal{X} = C([0, L], \mathbb{R}^3) \).

Next, we first show that system (1.1)-(1.3) has a unique non-continuable solution and the solutions to (1.1)-(1.3) remain non-negative on their interval of existence if they are non-negative initially. Finally, we will also show that solutions of (1.1)-(1.3) are ultimately bounded.

**Lemma 2.1.** For every initial value function \( \mathbf{v}^0 := (R^0, u_1^0, u_2^0) \in \mathcal{X} \), system (1.1)-(1.3) admits a unique classical solution

\[
\mathbf{v}(x, t, \mathbf{v}^0) := (R(x, t, \mathbf{v}^0), u_1(x, t, \mathbf{v}^0), u_2(x, t, \mathbf{v}^0)) \in \mathcal{X}, \ \forall \ t > 0,
\]

with \( \mathbf{v}(\cdot, 0, \mathbf{v}^0) = \mathbf{v}^0 \). Moreover, system (1.1)-(1.3) generates a semiflow \( \Sigma(t) : \mathcal{X} \to \mathcal{X} \) by

\[
\Sigma(t)(\mathbf{v}^0)(x) = (R(x, t, \mathbf{v}^0), u_1(x, t, \mathbf{v}^0), u_2(x, t, \mathbf{v}^0)), \ \forall \ x \in [0, L], \ t \geq 0,
\]

and \( \Sigma(t) : \mathcal{X} \to \mathcal{X}, t \geq 0 \), admits a global compact attractor.

**Proof.** Since \( R^0(\cdot), u_i^0(\cdot) \in C([0, L], \mathbb{R}) \) and the functions in the reaction terms of system (1.1)-(1.3) are at least Lipschitz continuous, it is standard to establish the local existence and uniqueness of the solution. Thus, for every initial value function \( \mathbf{v}^0 \in \mathcal{X} \), system (1.1)-(1.3) admits a unique non-continuable mild solution

\[
\mathbf{v}(x, t, \mathbf{v}^0) := (R(x, t, \mathbf{v}^0), u_1(x, t, \mathbf{v}^0), u_2(x, t, \mathbf{v}^0)) \text{ on } (0, \tau_{\mathbf{v}^0}) \text{ with } \mathbf{v}(\cdot, 0, \mathbf{v}^0) = \mathbf{v}^0.
\]

Since \( u_i^0(\cdot) \geq 0 \), it follows from the equation for \( u_i \) in system (1.1)-(1.3) and the maximum principle that \( u_i(x, t) \geq 0 \), for all \( (x, t) \in [0, L] \times (0, \tau_{\mathbf{v}^0}) \). Assume that \( f_i(R^0) \equiv 0 \) if \( R \leq 0 \). Then by the fact \( R^0(\cdot) \geq 0 \), the equation for \( R \) and the maximum principle, we can deduce that \( R(x, t) \geq 0 \), for all \( (x, t) \in [0, L] \times (0, \tau_{\mathbf{v}^0}) \).
Therefore, $v(x,t,v^0) \in \mathbb{X}$ on $(0, \tau_{\psi})$. Moreover, $v(x,t,v^0)$ is a classical solution of system (1.1)-(1.3) for $t > 0$.

Let $H_i(x) := g_i(I_0e^{-k_0x})$. Then $H_i(x)$ is bounded and $\min\{f_i(R), g_i(I)\} \leq H_i(x)$. Observing that the $v_i$ equation of system (1.1)-(1.3) satisfies

\[
\begin{cases}
(u_i)_t \leq D_i(u_i)_{xx} - \alpha_i u_i_x + [H_i(x) - d_i] u_i, \quad (x,t) \in [0,L] \times [0,\infty), \\
D_i(u_i)(0,t) = D_i(u_i)(L,t) = 0, \quad t \geq 0.
\end{cases}
\]

Thus, the $u_i$ equation in system (1.1)-(1.3) is dominated by the following linear system

\[
\begin{align*}
&u_t = D_i u_{xx} - \alpha_i u_x + [H_i(x) - d_i] u, \quad (x,t) \in [0,L] \times [0,\infty), \\
&D_i(u)(0,t) = D_i(u)(L,t) = 0, \quad t \geq 0.
\end{align*}
\]

Then the standard parabolic comparison theorem (see, e.g., [22, Theorem 7.3.4]) implies that $u_i(x,t)$ is bounded on $[0,\tau_{\psi})$. Therefore, there exists a positive number $Q_i$ such that the first equation $(R(x,t))$ of system (1.1)-(1.3) is dominated by the equation

\[
\begin{align*}
R_t & = D_i R_{xx} + q_1 \theta_1 d_1 Q_1 + q_2 \theta_2 d_2 Q_2, \quad 0 < x < L, \quad t > 0, \\
R_x(0,t) = R_x(L,t) & = \gamma (R(0) - R(L,t)), \quad t > 0.
\end{align*}
\]

On the other hand, by the similar arguments in [10, Lemma 2.3], we can show that system (2.2) admits a unique positive steady state $R^*(x)$ which is globally attractive in $C([0,L], \mathbb{R})$. Again, the standard parabolic comparison theorem (see, e.g., [22, Theorem 7.3.4]) implies that $R(x,t)$ is bounded on $[0,\tau_{\psi})$. It then follows that $v(x,t,v^0) := (R(x,t), v^0), u_1(x,t,v^0), u_2(x,t,v^0))$ is bounded on $[0,\tau_{\psi})$, and hence, $\tau_{\psi} = \infty$, for each $v^0 := (R^0, u_1^0, u_2^0) \in \mathbb{X}$. Therefore, system (1.1)-(1.3) defines a semiflow $\Sigma(t) : \mathbb{X} \to \mathbb{X}$ by (2.1).

Next, we show that solutions of system (1.1)-(1.3) are ultimately bounded. By the similar arguments in [3, Lemma 3.2], we will first show that $u_i(x,t)$ is ultimately bounded. To this end, we begin by showing that $\int_0^L u_i(x,t)dx$ is ultimately bounded. For the case where $g_i$ takes the form in (1.4), we have $g_i(I) \leq \frac{m_i}{a_i} I$ and

\[
\begin{align*}
\left( \int_0^L u_i(x,t)dx \right)_t & \leq \int_0^L g_i(I_0e^{-k_i} \int_0^L u_i(s,t)dx) u_i(x,t)dx - d_i \int_0^L u_i(x,t)dx \\
& \leq \int_0^L \frac{m_i}{a_i} I_0 e^{-k_i} \int_0^L u_i(s,t)dx u_i(x,t)dx - d_i \int_0^L u_i(x,t)dx \\
& = \frac{m_i I_0}{a_i k_i} \left( 1 - e^{-k_i \int_0^L u_i(x,t)dx} \right) - d_i \int_0^L u_i(x,t)dx \\
& \leq \frac{m_i I_0}{a_i k_i} - d_i \int_0^L u_i(x,t)dx.
\end{align*}
\]

It follows that

\[
\left( e^{d_i t} \int_0^L u_i(x,t)dx \right)_t \leq \frac{m_i I_0}{a_i k_i} e^{d_i t},
\]

and hence,

\[
\int_0^L u_i(x,t)dt \leq \frac{m_i I_0}{a_i d_i k_i} + e^{-d_i t} \int_0^L u_i^0(x)dx.
\]

(2.3)
For the case where $g_i$ takes the form in (1.5), we can also show that
\[
\int_0^L u_i(x, t) dt \leq \frac{\beta_i t^s}{\vartheta_i d_i k_i} + e^{-d_i t} \int_0^L u_i^0(x) dx.
\]
This means the total population is ultimately bounded by a constant irrespective of the initial condition. By the similar arguments in [3, Lemma 3.2], we are ready to show that $u_i(x, t)$ is ultimately bounded. Set $W_i(t') = \sup_{x \in [0, L], t \in [0, t')} u_i(x, t)$.

Suppose on the contrary that $u_i(x, t)$ is not ultimately bounded. Then there exists a sequence $t_n \to \infty$ such that
\[
W_i(t_n) = \sup_{x \in [0, L], t \in [0, t_n]} u_i(x, t) \to \infty \text{ as } n \to \infty.
\]
We may assume that $t_n > 2$ for all $n \geq 1$. Set
\[
v_n(x, t) = \frac{u_i(t + t_n - 2)}{W_i(t_n)}.
\]
Then $v_n$ satisfies
\[
\begin{cases}
(v_n)_t = D_i(v_n)_{xx} - \alpha_i(v_n)_x + c_n v_n, & x \in (0, L), \ t > 0, \\
D_i(v_n)_x - \alpha_i v_n = 0, & x = 0, L, \ t > 0, \\
0 \leq v_n(x, 0) \leq 1, & x \in [0, L],
\end{cases}
\]
where $c_n = \min\{f_i(R(x, t + t_n - 2)), g_i(I(x, t + t_n - 2)) - d_i\}$ and so that $|c_n| \leq C_i := \sup_{t \in [0, t_n]} |g_i(I) - d_i|$. A simple comparison argument then gives that
\[
0 \leq v_n(x, t) \leq e^{C_i t e^{(\alpha_i/D_i)x}} \text{ for } 0 \leq x \leq L, \ t \geq 0.
\]
By the standard parabolic regularity, $\{v_n\}$ is bounded in $C^{1+\vartheta, \vartheta}([0, L] \times [1, 3])$, for any $\vartheta \in (0, 1)$. Therefore by passing to a subsequence if necessary we have $v_n \to v^*$ in $C^{1, \vartheta}([0, L] \times [1, 3])$. Since $|c_n| \leq C_i$, up to a further subsequence, we may assume that $c_n \to c^*$ weakly in $L^2([0, L] \times [1, 3])$. Clearly $|c^*| \leq C_i$. It follows that $v^*$ is a weak solution to
\[
\begin{cases}
v_t = D_i v_{xx} - \alpha_i v_x + c^* v, & x \in (0, L), \ t \in [1, 3], \\
D_i v_x - \alpha_i v = 0, & x = 0, L, \ t \in [1, 3], \\
0 \leq v(x, 0) \leq e^{3C_i e^{(\alpha_i/D_i)x}}, & x \in [0, L],
\end{cases}
\]
Since $\max_{x \in [0, L]} v_n(x, 2) = 1$, we have $\max_{x \in [0, L]} v^*(x, 2) = 1$, and hence, $v^*$ is not identically zero. By the strong maximum principle $v^*(x, 2) \geq \eta_0 > 0$ for all $x \in [0, L]$. Therefore, $v_n(x, 2) \geq \eta_0/2 > 0$ for large $n$ and $x \in [0, L]$. Thus,
\[
u_i(x, t_n) \geq \frac{\eta_0}{2} W_i(t_n), \text{ for all large } n \text{ and } x \in [0, L],
\]
and hence,
\[
\int_0^L u_i(x, t_n) dx \geq \frac{\eta_0 L}{2} W_i(t_n) \to \infty \text{ as } n \to \infty,
\]
which, however, contradicts (2.3). Hence $u_i(x, t)$ is ultimately bounded. Thus, there exists $\tilde{t}_1 = \tilde{t}_1(y^0) > 0$ and $\tilde{Q}_1 > 0$ such that
\[
u_i(x, t) \leq \tilde{Q}_1, \quad \forall \ x \in [0, L], \ t \geq \tilde{t}_1, \ i = 1, 2.
\]
Then the $R(x, t)$ equation of system (1.1)-(1.3) satisfies
\[
\begin{cases}
R_t \leq D_R R_{xx} + q_1 \theta_1 d_1 \tilde{Q}_1 + q_2 \theta_2 d_2 \tilde{Q}_2, & 0 < x < L, \ t \geq \tilde{t}_1, \\
R_x(0, t) = 0, \ R_x(L, t) = \gamma(R^{(0)} - R(L, t)), & t \geq \tilde{t}_1.
\end{cases}
\]
Again, we can use the similar arguments in [10, Lemma 2.3] to show that \( \tilde{R}(x) \) is the unique positive steady state for
\[
\begin{aligned}
R_t &= D_R R_{xx} + q_1 \theta_1 d_1 \tilde{Q}_1 + q_2 \theta_2 d_2 \tilde{Q}_2, \quad 0 < x < L, \quad t > 0, \\
R_x(0, t) &= 0, \quad R_x(L, t) = \gamma (R(0) - R(L, t)), \quad t > 0,
\end{aligned}
\]
and \( \tilde{R}(x) \) is globally attractive in \( C([0, L], \mathbb{R}) \). Therefore, there exists \( \tilde{t}_2 = \tilde{t}_2(v^0) \) with \( \tilde{t}_2 > \tilde{t}_1 \) such that \( R(x, t) \leq 2\tilde{R}(x), \quad x \in [0, L], \quad t > \tilde{t}_2 \). Thus, we have proved that the solution \((R(x, t), v^0), u_1(x, t, v^0), u_2(x, t, v^0)\) is ultimately bounded, that is, the semiflow \( \Sigma(t) : X \to X \) is point dissipative. Obviously, \( \Sigma(t) : X \to X \) is compact, \( \forall t > 0 \). By [6, Theorem 3.4.8], it follows that \( \Sigma(t) : X \to X, \quad t \geq 0, \) has a global compact attractor.

By the boundedness of the function \( \min\{f_i(R), g_i(I)\} \), the strong maximum principle and the Hopf boundary lemma (see [19]), we further have the following result.

**Lemma 2.2.** Let \((R(x, t), u_1(x, t), u_2(x, t))\) be the solution of system (1.1)-(1.3) with initial value in \( \mathbb{X} \). If there is a \( t_0 \geq 0 \) such that \( u_i(\cdot, t_0) \neq 0 \), for some \( i \in \{1, 2\} \), then \( u_i(x, t) \neq 0 \), for all \( x \in [0, L] \) and \( t > t_0 \).

We note that Lemma 2.2 will play an important role when we establish the possibility of coexistence for system (1.1)-(1.3).

### 3. Single population model

In this section, we will study the threshold dynamics of the single population model corresponding to system (1.1)-(1.3). Mathematically, it simply means that we set \( u_1 = 0 \) or \( u_2 = 0 \) in system (1.1)-(1.3). In order to simplify notation, all subscripts are dropped in the remaining equations and we consider
\[
\begin{aligned}
R_t &= D_R R_{xx} - q \min\{f(R), g(I(x, t))\} u + q_\theta du, \quad t > 0, \quad 0 < x < L, \\
u_t &= Du_{xx} - \alpha u + \left[ \min\{f(R), g(I(x, t))\} - d \right] u, \quad t > 0, \quad 0 < x < L, \\
R_x(0, t) &= 0, \quad R_x(L, t) = \gamma (R(0) - R(L, t)), \quad t \geq 0, \\
Du_x(0, t) - \alpha u(0, t) &= Du_x(L, t) - \alpha u(L, t) = 0, \quad t \geq 0, \\
R(x, 0) &= R^0(x) \geq 0, \quad 0 \leq x \leq L, \\
u(x, 0) &= u^0(x) \geq 0, \quad 0 \leq x \leq L,
\end{aligned}
\]
where the light distribution function \( I(x, t) \) takes the form
\[
I(x, t) = I_0 e^{-k_0 x} \exp \left( -k \int_0^x u(s, t) ds \right).
\]
From the biological view of point, the feasible domain \( \mathbb{Y} \) for system (3.1) should be
\[
\mathbb{Y} = \{(R, u) \in C([0, L], \mathbb{R}^2) : R(x) \geq 0, \quad u(x) \geq 0, \quad x \in [0, L]\}.
\]
In symbol, \( \mathbb{Y} = C([0, L], \mathbb{R}^2_+) \).

By the same arguments to those in Lemma 2.1, we have the following results:

**Lemma 3.1.** For every initial value function \( u^0 := (R^0, u^0) \in \mathbb{Y} \), system (3.1) has a unique classical solution
\[
\begin{aligned}
u(x, t, u^0) := (R(x, t, u^0), u(x, t, u^0)) \in \mathbb{Y}, \quad \forall t > 0,
\end{aligned}
\]
with \( u(\cdot, 0, u^0) = u^0 \). Moreover, system (3.1) generates a semiflow \( \Psi(t) : \mathbb{Y} \to \mathbb{Y} \) by
\[
\Psi(t)(u^0)(x) = (R(x, t, u^0), u(x, t, u^0)), \quad \forall x \in [0, L], \quad t \geq 0,
\]
and \( \Psi(t) : \mathbb{Y} \to \mathbb{Y}, \quad t \geq 0, \) admits a global compact attractor.
Lemma 3.2. Let \((R(x, t), u(x, t))\) be the solution of system (3.1) with initial value in \(Y\). If there is a \(t_0 \geq 0\) such that \(u(\cdot, t_0) \neq 0\), then \(u(x, t) > 0\), for all \(x \in [0, L]\) and \(t > t_0\).

Let \(\lambda_0 (a(x); \alpha, D, L)\) denote the principal eigenvalue of
\[
\begin{cases}
-D\varphi_{xx} + \alpha \varphi_x + a(x)\varphi = \lambda \varphi, & 0 < x < L, \\
D\varphi_x(0) = \alpha \varphi(0), & D\varphi_x(L) = \alpha \varphi(L).
\end{cases}
\tag{3.3}
\]
It is well known that \(\lambda_0 (a(x); \alpha, D, L)\) is real, and it can be characterized as (see, e.g., [7])
\[
\lambda_0 (a(x); \alpha, D, L) = \inf_{\psi \in H^1 (0, L)} \frac{\int_0^L e^{-(\alpha/D) x} [D(\psi(x))^2 + a(x)(\psi(x))^2] dx}{\int_0^L e^{-(\alpha/D) x} (\psi(x))^2 dx},
\]
where \(H^1 (0, L)\) is the closure of \(C^1 [0, L]\) under the norm
\[
\|u\| = \left( \int_0^L u^2 dx \right)^{1/2} + \left( \int_0^L u_x^2 dx \right)^{1/2}.
\]

In order to study the dynamics of system (3.1), we first consider the following system
\[
\begin{align*}
u_t &= Du_{xx} - \alpha u_x + [\min \{f(R(0)), g(I_0 e^{-k_0 x})\} - d] u, \quad t > 0, \quad 0 < x < L, \\
Du_x(0, t) - \alpha u(0, t) &= Du_x(L, t) - \alpha u(L, t) = 0, \quad t \geq 0, \\
u(x, 0) &= u^0(x) \geq 0, \quad 0 \leq x \leq L.
\end{align*}
\tag{3.4}
\]
Substituting \(u(x, t) = e^{-\mu t} \varphi(x)\) into (3.4), we obtain the following associated eigenvalue problem:
\[
\begin{cases}
-D\varphi_{xx} + \alpha \varphi_x - [\min \{f(R(0)), g(I_0 e^{-k_0 x})\} - d] \varphi = \mu \varphi, & 0 < x < L, \\
D\varphi_x(0) - \alpha \varphi(0) = D\varphi_x(L) - \alpha \varphi(L) = 0.
\end{cases}
\tag{3.5}
\]
We denote the principal eigenvalue of (3.5) by \(\mu^0\). For every \(\alpha \in (-\infty, +\infty), \ D > 0\) and \(L > 0\), we set
\[
d^* = d^*(\alpha, D, L) := -\lambda_0 \left( -\min \{f(R(0)), g(I_0 e^{-k_0 x})\}; \alpha, D, L \right),
\]
where \(\lambda_0 (a(x); \alpha, D, L)\) denotes the principal eigenvalue of (3.3). It is easy to show that \(d^*(\alpha, D, L)\) is positive, and \(\mu^0 = d - d^*(\alpha, D, L)\). Therefore,
\[
d > d^*(\alpha, D, L) \iff \mu^0 > 0, \quad \text{and} \quad d < d^*(\alpha, D, L) \iff \mu^0 < 0.
\]

The following result shows that \(d^*\) can be the critical death rate of the phytoplankton if we ignore the nutrient recycling; i.e., if we put \(\theta = 0\) in system (3.1), then the phytoplankton survives if and only if its death rate is less than \(d^*\). For convenience, we set
\[
\mathcal{Y}_0 := \{(R^0(\cdot), u^0(\cdot)) \in \mathcal{Y} : R^0(\cdot) \neq 0, \ u^0(\cdot) \neq 0\},
\]
and \(\partial \mathcal{Y}_0 := \mathcal{Y} \setminus \mathcal{Y}_0\).

Theorem 3.1. For any \((R^0(\cdot), u^0(\cdot)) \in \mathcal{Y}\), we assume \((R(x, t), u(x, t))\) is the solution of system (3.1) with \((R(\cdot, 0), u(\cdot, 0)) = (R^0(\cdot), u^0(\cdot))\). Then the following statements are valid.
(i) If \( \theta = 0 \) and \( d > d^* \), then \( \lim_{t \to \infty} (R(x,t), u(x,t)) = (R(0), 0) \), uniformly for \( x \in [0, L] \);
(ii) If \( 0 \leq \theta \leq 1 \), and \( 0 < d < d^* \), then system (3.1) is uniformly persistent with respect to \((\mathcal{Y}_0, \partial \mathcal{Y}_0)\) in the sense that there is an \( \eta > 0 \) such that for any \((R^0, u^0) \in \mathcal{Y}_0 \), we have

\[
\liminf_{t \to \infty} u(x,t) \geq \eta, \text{ uniformly for all } x \in [0, L].
\]

Furthermore, system (3.1) admits at least one (componentwise) positive steady state \((\hat{R}(x), \hat{u}(x))\).

**Proof.** Part (i). Assume that \( \theta = 0 \) and \( d > d^* \). Since \( d > d^* \), we have \( \mu_0 > 0 \), and hence, there exists an \( \epsilon_1 > 0 \) such that \( \mu_{\epsilon_1} > 0 \), where \( \mu_{\epsilon_1} \) is the principal eigenvalue of

\[
\begin{cases}
-D\varphi_{xx} + \alpha \varphi_x - \left[ \min\{f(R(0)), g(I_0e^{-k_0x})\} + \epsilon_1 - d \right] \varphi = \mu \varphi, & t > 0, \ 0 < x < L, \\
D\varphi_x(0) - \alpha \varphi(0) = D\varphi_x(L) - \alpha \varphi(L) = 0.
\end{cases}
\]

By the continuity of \( f \), it is easy to see that there exists a \( \delta_1 > 0 \) such that

\[
f(R) < f(R(0)) + \epsilon_1, \text{ for any } |R - R(0)| < \delta_1.
\]

In view of the equation of \( R \) in (3.1), it follows that

\[
\begin{cases}
R_t \leq DR_{xx}, & t > 0, \ 0 < x < L, \\
R_x(0,t) = 0, \ R_x(L,t) = \gamma(R(0) - R(L,t)), & t \geq 0, \\
R(x,0) = R^0(x) \geq \delta_1, & 0 \leq x \leq L.
\end{cases}
\]

Then

\[
\limsup_{t \to \infty} R(x,t) \leq R(0), \text{ for all } x \in [0, L].
\]

Thus, there exists a \( T_1 > 0 \) such that \( R(x,t) \leq R(0) + \frac{\delta_1}{2} \), for all \( t \geq T_1 \). The monotonicity of \( f \) ensures that

\[
f(R(x,t)) \leq f(R(0) + \frac{\delta_1}{2}), \ \forall \ t \geq T_1.
\]

(3.7)

From (3.6) and (3.7), it follows that

\[
f(R(x,t)) < f(R(0)) + \epsilon_1, \ \forall \ t \geq T_1.
\]

(3.8)

The monotonicity of \( g \) ensures that

\[
g(I(x,t)) = g \left( I_0e^{-k_0x}e^{-k \int_0^t u(s,t)ds} \right) \leq g(I_0e^{-k_0x}) \leq g(I_0e^{-k_0x}) + \epsilon_1, \ \forall \ t \geq 0.
\]

(3.9)

In view of (3.8) and (3.9), we see that

\[
\min\{f(R), g(I(x,t))\} \leq \min\{f(R(0)) + \epsilon_1, g(I_0e^{-k_0x}) + \epsilon_1\} = \min\{f(R(0)), g(I_0e^{-k_0x})\} + \epsilon_1, \ \forall \ t \geq T_1.
\]

From the second equation of (3.1), it follows that

\[
\begin{cases}
\frac{\partial u}{\partial t} \leq Du_{xx} - \alpha u_x + \left[ \min\{f(R(0)), g(I_0e^{-k_0x})\} + \epsilon_1 - d \right] u, & t \geq T_1, \ 0 < x < L, \\
Du_x(0,t) - \alpha u(0,t) = Du_x(L,t) - \alpha u(L,t) = 0, & t \geq T_1.
\end{cases}
\]
Consider the following auxiliary system

\[
\begin{aligned}
\{ u_t &= Du_{xx} - \alpha u + \min\{ f(R^0), g(I_0e^{-k0x}) \} + \epsilon_1 - d \} \ u, \ t \geq T_1, \ 0 < x < L, \\
Du_x(0, t) - \alpha u(0, t) &= Du_x(L, t) - \alpha u(L, t) = 0, \ t \geq T_1.
\end{aligned}
\]  

(3.10)

Given \( C_1 > 0 \), we set \( \bar{u}(x, t) = C_1e^{-\mu_3^0(t-T_1)}\phi_{\epsilon_1}^0(x) \), where \( \phi_{\epsilon_1}^0(x) \) is the eigenfunction corresponding to \( \mu_3^0 \). It is easy to see that \( \bar{u}(x, t) \) satisfies system (3.10) and \( \bar{u}(x, T_1) = C_1\phi_{\epsilon_1}^0(x) \). Choosing \( C_1 > 0 \) such that \( u(\cdot) \leq \bar{u}(\cdot, T_1) := C_1\phi_{\epsilon_1}^0(x) \). Then the comparison principle implies that

\[
u(x, t) \leq \bar{u}(x, t) := C_1e^{-\mu_3^0(t-T_1)}\phi_{\epsilon_1}^0(x), \ t \geq T_1.
\]

Since \( \mu_3^0 > 0 \), it follows that \( \lim_{t \to \infty} u(x, t) = 0 \), uniformly for \( x \in [0, L] \). Thus, the equation for \( R \) is asymptotic to the following system

\[
\begin{aligned}
R_t &= DR_{xx}, \ t > 0, \ 0 < x < L, \\
R_x(0, t) &= 0, \ R_x(L, t) = \gamma(R(0) - R(L, t)), \ t \geq 0, \\
R(x, 0) &= R^0(x) \geq 0, \ 0 \leq x \leq L.
\end{aligned}
\]  

(3.11)

Then the theory for asymptotically autonomous semiflows (see, e.g., [24, Corollary 4.3]) implies that \( \lim_{t \to \infty} R(x, t) = R^0(x) \) uniformly for \( x \in [0, L] \). We complete the proof of Part (i).

Part (ii). Assume that \( 0 \leq \theta \leq 1 \) and \( d < d^* \). Since \( d < d^* \), we see that \( \mu^0 < 0 \).

From Lemma 3.1, we recall that \( \Psi(t) : Y \to Y \) is the semiflows associated with system (3.1), and \( \Psi(t) : Y \to Y, \ t \geq 0 \), has a global compact attractor. From Lemma 3.2, it follows that \( \Psi(t)Y_0 \subseteq Y_0 \) for all \( t \geq 0 \).

Let

\[
M_\beta := \{ u^0 \in \partial Y_0 : \Psi(t)u^0 \in \partial Y_0, \forall t \geq 0 \},
\]

and \( \omega(u^0) \) be the omega limit set of the orbit \( O^+(u^0) := \{ \Psi(t)u^0 : t \geq 0 \} \). We will show the following claim.

Claim 1. \( \omega(\psi) = \{ (R^0, 0) \}, \ \forall \psi \in M_\beta \).

For any given \( \psi \in M_\beta \), we have \( \Psi(t)\psi \in M_\beta, \ \forall t \geq 0 \), that is, \( u(\cdot, t, \psi) \equiv 0 \), for any given \( t \geq 0 \). Then \( R \) satisfies system (3.11), and hence, \( \lim_{t \to \infty} R(x, t) = R^0(x) \) uniformly for \( x \in [0, L] \). Claim 1 is proved.

Since \( \mu^0 < 0 \), there exists an \( \epsilon_2 > 0 \) such that \( \mu_{\epsilon_2}^0 < 0 \), where \( \mu_{\epsilon_2}^0 \) is the principal eigenvalue of

\[
\begin{aligned}
-D\varphi_{xx} + \alpha\varphi_x - \min\{ f(R^0), g(I_0e^{-k0x}) \} - \epsilon_2 - d \} \varphi = \mu\varphi, \ t > 0, \ 0 < x < L, \\
D\varphi_x(0) - \alpha\varphi(0) &= D\varphi_x(L) - \alpha\varphi(L) = 0.
\end{aligned}
\]

Suppose \( \phi_{\epsilon_2}^0(x) \) is the positive eigenfunction corresponding to \( \mu_{\epsilon_2}^0 \), and \( \phi_{\epsilon_2}^0(x) \) is uniquely determined by the normalization \( \max_{\{0, L\}} \phi_{\epsilon_2}^0(x) = 1 \). By the continuity of \( f \) and \( g \), it is easy to see that there exists a \( \delta_2 > 0 \) such that

\[
f(R^0) - \delta_2 > f(R^0) - \epsilon_2, \text{ and } g(I_0e^{-k0x}e^{-k\delta_2L}) > g(I_0e^{-k0x} - \epsilon_2).
\]

Suppose \( \phi_{\epsilon_2}^0(x) \) is the positive eigenfunction corresponding to \( \mu_{\epsilon_2}^0 \), and \( \phi_{\epsilon_2}^0(x) \) is uniquely determined by the normalization \( \max_{\{0, L\}} \phi_{\epsilon_2}^0(x) = 1 \). By the continuity of \( f \) and \( g \), it is easy to see that there exists a \( \delta_2 > 0 \) such that

\[
f(R^0) - \delta_2 > f(R^0) - \epsilon_2, \text{ and } g(I_0e^{-k0x}e^{-k\delta_2L}) > g(I_0e^{-k0x} - \epsilon_2).
\]

(3.12)

We further have the following claim.

Claim 2. \( (R^0, 0) \) is a uniform weak repellor for the system (3.1) in the sense that

\[
\lim_{t \to \infty} \sup_{\Psi(t)Y_0}(R^0, u^0) - (R^0, 0) \geq \delta_2, \ \forall (R, u^0) \in Y_0.
\]
Thus, there exists a $T_2 > 0$ such that
\[ R(x,t) > R(0) - \delta_2, \quad u(x,t) < \delta_2, \quad \forall \ t \geq T_2, \quad x \in [0,L]. \]
This together with the monotonicity of $f$ and $g$ imply that
\[ f(R(x,t)) > f(R(0) - \delta_2), \quad \forall \ t \geq T_2, \quad x \in [0,L]. \tag{3.13} \]
and
\[ g(I(x,t)) = g \left( I_0 e^{-k_0 x} e^{-k \int_0^x u(s,t) ds} \right) \geq g \left( I_0 e^{-k_0 x} e^{-k \int_0^x \delta_2 ds} \right) \]
\[ = g(I_0 e^{-k_0 x} e^{-kL\delta_2}), \quad \forall \ t \geq T_2, \quad x \in [0,L]. \tag{3.14} \]
In view of (3.12), (3.13) and (3.14), we see that
\[ f(R(x,t)) > f(R(0)) - \epsilon_2, \quad \text{and} \quad g(I(x,t)) > g(I_0 e^{-k_0 x}) - \epsilon_2, \quad \forall \ t \geq T_2, \quad x \in [0,L], \]
and hence,
\[ \min \{ f(R), g(I(x,t)) \} > \min \{ f(R(0)) - \epsilon_2, g(I_0 e^{-k_0 x}) - \epsilon_2 \} \]
\[ = \min \{ f(R(0)), g(I_0 e^{-k_0 x}) \} - \epsilon_2, \quad \forall \ t \geq T_2, \quad x \in [0,L]. \tag{3.15} \]
From (3.15) and the second equation of (3.1), it follows that
\[ \begin{cases} u_t \geq D_{uu} - \alpha u_x + \left[ \min \{ f(R(0)), g(I_0 e^{-k_0 x}) \} - \epsilon_2 - d \right] u, \quad \forall \ t \geq T_2, \quad 0 < x < L, \\ D_{u_0}(0,t) - \alpha u(0,t) = D_{u_0}(L,t) - \alpha u(L,t) = 0, \quad \forall \ t \geq T_2. \end{cases} \]
Consider the following auxiliary system
\[ \begin{cases} u_t = D_{uu} - \alpha u_x + \left[ \min \{ f(R(0)), g(I_0 e^{-k_0 x}) \} - \epsilon_2 - d \right] u, \quad \forall \ t \geq T_2, \quad 0 < x < L, \\ D_{u_0}(0,t) - \alpha u(0,t) = D_{u_0}(L,t) - \alpha u(L,t) = 0, \quad \forall \ t \geq T_2. \tag{3.16} \end{cases} \]
Given $C_2 > 0$, we set $\hat{u}(x,t) = C_2 e^{\mu_2^0 (t-T_2)} \phi_{e_2}^0(x)$. It is easy to see that $\hat{u}(x,t)$ satisfies system (3.16) and $\hat{u}(x,T_2) = C_2 \phi_{e_2}^0(x)$. Since $u^0 := (R(0), u^0) \in \mathbb{Y}_0$, it follows from Lemma 3.2 that $u(x,t,u^0) > 0, \quad \forall \ x \in [0,L], \quad t > 0$. Thus, we may choose $C_2 > 0$ such that
\[ u(x,T_2,u^0) \geq \hat{u}(x,T_2) := C_2 \phi_{e_2}^0(x). \]
Then the Comparison Principle implies that
\[ u(x,t,u^0) \geq \hat{u}(x,t) := C_2 e^{\mu_2^0 (t-T_2)} \phi_{e_2}^0(x), \quad t \geq T_2. \]
Since $\mu_2^0 < 0$, it follows that $\lim_{t \to \infty} u(x,t,u^0) = \infty$. This contradiction proves Claim 2.

Next, we define a continuous function $p : \mathbb{Y} \to [0,\infty)$ by
\[ p(u^0) := \min_{x \in [0,L]} u(x), \quad \forall \ u^0 := (R(0), u^0) \in \mathbb{Y}_0. \]
By the strong maximum principle and the Hopf boundary lemma (see Lemma 3.2 and [19]), it follows that $p^{-1}(0,\infty) \subset \mathbb{Y}_0$ and $p$ has the property that if $p(u^0) > 0$ or $u^0 \in \mathbb{Y}_0$ with $p(u^0) = 0$, then $p(\Psi(t)u^0) > 0, \quad \forall \ t > 0$. Thus, $p$ is a generalized distance function for the semiflow $\Psi(t) : \mathbb{Y} \to \mathbb{Y}$ (see, e.g., [23]).

For convenience, we set $E_0 := (R(0), 0)$. By Claim 1 and Claim 2, it follows that any forward orbit of $\Psi(t)$ in $M_0$ converges to $E_0$, $E_0$ is an isolated invariant set.
in \( Y \), and \( W^s(E_0) \cap p^{-1}(0, \infty) = \emptyset \), where \( W^s(E_0) \) is the stable set of \( E_0 \). It is obvious that there is no cycle from \( E_0 \) to \( E_0 \) in \( \partial Y_0 \). By [23, Theorem 3], there exists an \( \eta > 0 \) such that any compact internal chain transitive set \( I \) with \( \mathcal{I} \neq \{ E_0 \} \) satisfies \( \min_{\psi \in \mathcal{I}} p(u^0) > \eta \). For any \( u^0 \in Y_0 \), we see from Claim 2 that \( \omega(u^0) \neq \{ E_0 \} \). Letting \( \mathcal{I} = \omega(u^0) \), we then obtain \( \min_{\psi \in \mathcal{I}} p(\psi) > \eta \) for all \( u^0 \in Y_0 \). This implies that \( \lim \inf_{t \to \infty} u(x, t) \geq \eta \), uniformly for all \( x \in [0, L] \). Then, the uniform persistence stated in statement (ii) are true.

By [17, Theorem 3.7 and Remark 3.10], it follows that \( \Psi(t) : Y_0 \to Y_0 \) has a global attractor \( A_0 \). It then follows from [17, Theorem 4.7] that \( \Psi(t) \) has a steady-state solution \( (\tilde{R}, \tilde{u}) \in Y_0 \), which together with the strong maximum principle and the Hopf boundary lemma (see [19]) imply that \( \hat{u}(x) > 0 \), for any \( x \in [0, L] \). It remains to prove that

\[
\tilde{R}(x) > 0, \quad \forall x \in [0, L].
\]

(3.17)

Indeed, \( \hat{R}(x) \) satisfies

\[
\begin{aligned}
D_R \hat{R}'' - q \min\{f(\hat{R}), g(I_0e^{-k_0x}e^{-k_0}\hat{u}(s)ds)\} \hat{u} + q\hat{u}d\hat{u} = 0, & \quad 0 < x < L, \\
\hat{R}'(0) = 0, & \quad \hat{R}'(L) = \gamma(\hat{R}(L) - \hat{R}(L)), 
\end{aligned}
\]

and hence,

\[
\begin{aligned}
D_R \hat{R}'' - qf(\hat{R}) \hat{u} \leq D_R \hat{R}'' - q \min\{f(\hat{R}), g(I_0e^{-k_0x}e^{-k_0}\hat{u}(s)ds)\} \hat{u} + q\hat{u}d\hat{u} = 0, & \quad 0 < x < L, \\
\hat{R}'(0) = 0, & \quad \hat{R}'(L) = \gamma(\hat{R}(L) - \hat{R}(L)),
\end{aligned}
\]

which implies

\[
\begin{aligned}
D_R \hat{R}'' - \left[q\hat{u}\int_0^1 f'(\theta \hat{R})d\theta\right]\hat{R} \leq 0, & \quad 0 < x < L, \\
\hat{R}'(0) = 0, & \quad \hat{R}'(L) = \gamma(\hat{R}(L) - \hat{R}(L)).
\end{aligned}
\]

(3.18)

From (3.18), the strong maximum principle and the Hopf boundary lemma (see [19]), we conclude that (3.17) is valid. We complete the proof of Part (ii).

\[\square\]

4. Coexistence for system (1.1)-(1.3). This section is devoted to the study of the possibility of coexistence for system (1.1)-(1.3). For \( i = 1, 2 \), we set

\[d_i^* = d_i^*(\alpha, D, L) := -\lambda_0 \left( -\min\{f_i(R_i^{(0)}), g_i(I_0e^{-k_0x})\}; \alpha_i, D_i, L \right),\]

where \( \lambda_0(a(x); \alpha, D, L) \) denotes the principal eigenvalue of (3.3). Assume that \( 0 \leq \theta_i \leq 1 \) and \( 0 < d_i < d_i^* \). By Theorem 3.1, we may assume that \( (\tilde{R}_i, \tilde{u}_i) \) is a positive steady-state solution of system (3.1) with \( (f, g, q, \alpha, D, k) = (f_i, g_i, q_i, \alpha_i, D_i, k_i) \).

Further, \( (\tilde{R}_i, \tilde{u}_i) \) is not necessarily unique. Then system (1.1)-(1.3) has the following possible steady-steady solutions:

(i) Trivial solution: \( \mathcal{E}_0 = (R_i^{(0)}, 0, 0) \) always exists;
(ii) Semi-trivial solution: \( \mathcal{E}_1 = (\tilde{R}_1, \tilde{u}_1, 0) \) exists, provided that \( 0 < d_1 < d_1^* \). We note that \( \mathcal{E}_1 \) may be multiple;
(iii) Semi-trivial solution: \( \mathcal{E}_2 = (\tilde{R}_2, 0, \tilde{u}_1) \) exists, provided that \( 0 < d_2 < d_2^* \). We note that \( \mathcal{E}_2 \) may be multiple;
(iv) There may be positive (coexistence) steady-state solutions, that is, \( \mathcal{E}_c = (\tilde{R}_1, \tilde{u}_1, \tilde{u}_2) \) may exist.
Recall that \( \mathbb{X} = C([0, L], \mathbb{R}_+^3) \) is the positive cone of the Banach space \( C([0, L], \mathbb{R}^3) \) with the usual supremum norm. We also recall that \( \Sigma(t) : \mathbb{X} \rightarrow \mathbb{X} \) is the semiflow generated by system (1.1)-(1.3). Let

\[
\mathcal{X}_0 = \{(R^0, u_1^0, u_2^0) \in \mathbb{X} : u_1^0(\cdot) \neq 0, u_2^0(\cdot) \neq 0\},
\]

and

\[
\partial \mathcal{X}_0 = \mathbb{X} \setminus \mathcal{X}_0.
\]

Assume that \( M_0 = \{\mathcal{X}_0\}, M_1 = A_1 \times \{0\}, \) and

\[
M_2 = \{(R, u_1, u_2) \in \mathbb{X} : u_1 \equiv 0, (R, u_2) \in A_2\},
\]

where \( A_i \subset \text{Int}(C([0, L], \mathbb{R}_+^2)) \) is a global attractor of the semiflows generated by system (3.1) with \( (f, g, q, \theta, \alpha, D, d, k) = (f_i, g_i, q_i, \alpha_i, D_i, d_i, k_i)\).

Motivated by [11], we define two projections \( \mathcal{P}_i^R \) and \( \mathcal{P}_i^u \) on \( C([0, L], \mathbb{R}_+^2) \) by

\[
\mathcal{P}_i^R(R, u_1) = R, \quad \mathcal{P}_i^u(R, u_1) = u_1, \quad \forall (R, u_1) \in C([0, L], \mathbb{R}_+^2).
\]

Let

\[
B_i^R = \mathcal{P}_i^R(A_1) \quad \text{and} \quad m_i^R(x) = \inf_{\phi_i \in B_i^R} f_2(\phi_i(x)), \quad \forall x \in [0, L],
\]

and

\[
B_i^u = \mathcal{P}_i^u(A_1) \quad \text{and} \quad m_i^u(x) = \inf_{\phi_i \in B_i^u} G_2(\phi_i(x)), \quad \forall x \in [0, L],
\]

where \( G_2(\phi_i(x)) = g_2 \left( I_0 e^{-k_0 x} e^{-k_i \int_0^t \phi_i(s) ds} \right) \). Then \( m_i^R(x) \) and \( m_i^u(x) \) are continuous on \([0, L]\) (see [11, Lemma 4.1]). Consider the following system

\[
\begin{cases}
  u_t = D_2 u_{xx} - \alpha_2 u_x + \left[ \min\{m_i^R(x), m_i^u(x)\} - d_2 \right] u, & t > 0, \quad 0 < x < L, \\
  D_2 u_x(0, t) - \alpha_2 u(0, t) = D_2 u_x(L, t) - \alpha_2 u(L, t) = 0, & t \geq 0, \\
  u(x, 0) = u_0(x) \geq 0, & 0 \leq x \leq L.
\end{cases}
\]

Substituting \( u(x, t) = e^{-\Lambda_2 t} \varphi(x) \) into (4.1), we obtained the following associated eigenvalue problem:

\[
\begin{cases}
  -D_2 \varphi_{xx} + \alpha_2 \varphi_x - \left[ \min\{m_i^R(x), m_i^u(x)\} - d_2 \right] \varphi = \Lambda_2 \varphi, & t > 0, \quad 0 < x < L, \\
  D_2 \varphi_x(0) - \alpha_2 \varphi(0) = D_2 \varphi_x(L) - \alpha_2 \varphi(L) = 0.
\end{cases}
\]

We denote the principal eigenvalue of (4.2) by \( \Lambda_2^0 \).

By the similar arguments in [11, Lemma 4.2], we will establish the following results:

**Lemma 4.1.** Assume \( 0 \leq \theta_i \leq 1 \). Let \( 0 < d_1 < d_1^* \) and \( \Lambda_2^0 < 0 \). Then \( M_1 \) is a uniform weak repeller in the sense that there exists a \( \sigma_1 > 0 \) such that

\[
\limsup_{t \to -\infty} \text{dist}(\Sigma(t)(R^0, u_1^0, u_2^0), M_1) \geq \sigma_1, \quad \text{for all} \quad (R^0, u_1^0, u_2^0) \in \mathcal{X}_0.
\]

**Proof.** Since \( \Lambda_2^0 < 0 \), we can choose a sufficiently small \( \varepsilon_2 > 0 \) such that \( \Lambda_2^0 + \varepsilon_2 < 0 \), where \( \Lambda_2^0 + \varepsilon_2 \) is the principal eigenvalue of the eigenvalue problem

\[
\begin{cases}
  -D_2 \varphi_{xx} + \alpha_2 \varphi_x - \left[ \min\{m_2^R(x), m_2^u(x)\} - \varepsilon_2 - d_2 \right] \varphi = \Lambda_2 \varphi, & t > 0, \quad 0 < x < L, \\
  D_2 \varphi_x(0) - \alpha_2 \varphi(0) = D_2 \varphi_x(L) - \alpha_2 \varphi(L) = 0.
\end{cases}
\]

Define \( \tilde{f}_2 : B_i^R \rightarrow C([0, L], \mathbb{R}) \) by

\[
\tilde{f}_2(\phi_i^R(x)) = f_2(\phi_i^R(x)), \quad \forall x \in [0, L], \quad \phi_i^R \in B_i^R,
\]
and \( \hat{G}_2 : B^u_1 \to C([0, L], \mathbb{R}) \) by
\[
\hat{G}_2(\phi_1)(x) = G_2(\phi_1(x)), \quad \forall x \in [0, L], \quad \phi_1 \in B^u_1.
\]

Then there exists a \( \sigma_1 > 0 \) such that
\[
g_2 \left( \int_0^{\infty} e^{k|x-x_k|} f_k u_1(s,t)ds \right) > g_2 \left( \int_0^{\infty} e^{k|x-x_k|} f_k u_1(s,t)ds \right) - \frac{\varepsilon_2}{2},
\]
and
(i) \( \text{dist}(\tilde{f}_2(\phi^R_1), \tilde{f}_2(B^R_1)) < \varepsilon_2 \), whenever \( \phi^R_1 \in C([0, L], \mathbb{R}) \) with \( \text{dist}(\phi^R_1, B^R_1) < \sigma_1 \);
(ii) \( \text{dist}(\tilde{G}_2(\phi_1), \tilde{G}_2(B^u_1)) < \frac{\varepsilon_2}{2} \), whenever \( \phi_1 \in C([0, L], \mathbb{R}) \) with \( \text{dist}(\phi_1, B^u_1) < \sigma_1 \).

For case (i), since \( B^R \) is compact, it follows that for any \( \phi^R_1 \in C([0, L], \mathbb{R}) \) with \( \text{dist}(\phi^R_1, B^R_1) < \sigma_1 \), there exists \( \phi^* \in B^R_1 \) with \( \phi^R_1 \) depending on \( \phi_1 \) such that
\[
\text{dist}(\tilde{f}_2(\phi^R_1), \tilde{f}_2(\phi^R_1^*)) = \text{dist}(\tilde{f}_2(\phi^R_1), \tilde{f}_2(B^R_1)) < \frac{\varepsilon_2}{2}.
\]

Thus, we have
\[
|f_2(\phi^R_1(x)) - f_2(\phi^*_{1,x}(x))| = |\tilde{f}_2(\phi^R_1(x)) - \tilde{f}_2(\phi^*_{1,x}(x))| < \varepsilon_2, \quad \forall x \in [0, L],
\]
whenever \( \phi^R_1 \in C([0, L], \mathbb{R}) \) with \( \text{dist}(\phi^R_1, B^R_1) < \sigma_1 \). For case (ii), since \( B^u_1 \) is compact, it follows that for any \( \phi_1 \in C([0, L], \mathbb{R}) \) with \( \text{dist}(\phi_1, B^u_1) < \sigma_1 \), there exists \( \phi_{1,x} \in B^u_1 \) with \( \phi_{1,x} \) depending on \( \phi_1 \) such that
\[
\text{dist}(\tilde{G}_2(\phi_1), \tilde{G}_2(\phi_{1,x})) = \text{dist}(\tilde{G}_2(\phi_1), \tilde{G}_2(B^u_1)) < \frac{\varepsilon_2}{2}.
\]

Thus, we have
\[
|G_2(\phi_1(x)) - G_2(\phi_{1,x}(x))| = |\tilde{G}_2(\phi_1(x)) - \tilde{G}_2(\phi_{1,x}(x))| < \frac{\varepsilon_2}{2}, \quad \forall x \in [0, L],
\]
whenever \( \phi_1 \in C([0, L], \mathbb{R}) \) with \( \text{dist}(\phi_1, B^u_1) < \sigma_1 \).

Next, we prove (4.3) by contradiction. Suppose that (4.3) is not true. Then there exists \( (R^0, u^0_1, u^0_2) \in X_0 \) such that
\[
\limsup_{t \to \infty} \text{dist}(\Sigma(t)(R^0, u^0_1, u^0_2), M_1) < \sigma_1.
\]

This implies that
\[
\limsup_{t \to \infty} \text{dist}(R(\cdot, t), B^R_1) < \sigma_1, \quad \limsup_{t \to \infty} \text{dist}(u_1(\cdot, t), B^u_1) < \sigma_1,
\]
and
\[
\limsup_{t \to \infty} \|u_2(\cdot, t)\| < \sigma_1.
\]

From (4.7), we can choose \( t_1 > 0 \) such that
\[
\text{dist}(R(\cdot, t), B^R_1) < \sigma_1, \quad \text{dist}(u_1(\cdot, t), B^u_1) < \sigma_1, \quad u_2(\cdot, t) < \sigma_1, \quad \forall t \geq t_1.
\]

By (4.5) and the first inequality of (4.9), it follows that there exists \( \phi^R_{1,x,t} \in B^R_1 \) such that
\[
|f_2(R(x,t)) - f_2(\phi^R_{1,x,t}(x))| < \varepsilon_2, \quad \forall x \in [0, L], \quad t \geq t_1,
\]
and hence,
\[
f_2(R(x,t)) > f_2(\phi^R_{1,x,t}(x)) - \varepsilon_2 \geq m^R_2(x) - \varepsilon_2, \quad \forall x \in [0, L], \quad t \geq t_1.
\]

In view of (4.6) and the second inequality of (4.9), it follows that there exists \( \phi_{1,x,t} \in B^u_1 \) such that
\[
|G_2(u_1(x,t)) - G_2(\phi_{1,x,t}(x))| < \frac{\varepsilon_2}{2}, \quad \forall x \in [0, L], \quad t \geq t_1,
\]
and hence,
\[ G_2(u_1(x,t)) > G_2(\phi_{1*,t}(x)) - \frac{\varepsilon_2}{2} \geq m_2^u(x) - \frac{\varepsilon_2}{2}, \quad \forall \ x \in [0, L], \ t \geq t_1, \]
which implies that
\[ g_2 \left( I_0 e^{-k_0 x} e^{-k_1 \int_0^s u_1(s,t) ds} \right) > m_2^u(x) - \frac{\varepsilon_2}{2}, \quad \forall \ x \in [0, L], \ t \geq t_1, \quad (4.11) \]
where we have used \( G_2(\phi_1(x)) = g_2 \left( I_0 e^{-k_0 x} e^{-k_1 \int_0^s \phi_1(s) ds} \right) \). By \((4.4)\) and \((4.11)\), it follows that
\[ g_2 \left( I_0 e^{-k_0 x} e^{-k_1 \int_0^s u_1(s,t) ds} e^{-k_2 \sigma_1 L} \right) > m_2^u(x) - \varepsilon_2, \quad \forall \ x \in [0, L], \ t \geq t_1, \quad (4.12) \]
Using the third inequality of \((4.9)\), we see that
\[ e^{-k_2 \int_0^s u_2(s,t) ds} > e^{-k_2 \sigma_1 L}, \quad \forall \ x \in [0, L], \ t \geq t_1. \quad (4.13) \]
By \((4.12)\) and \((4.13)\), it follows that
\[ g_2 \left( I_0 e^{-k_0 x} e^{-k_1 \int_0^s u_1(s,t) ds} e^{-k_2 \int_0^s u_2(s,t) ds} \right) > m_2^u(x) - \varepsilon_2, \quad \forall \ x \in [0, L], \ t \geq t_1. \quad (4.14) \]
In view of \((4.10), (4.14)\), and the third equation of \((1.1)\), we have
\[
\begin{aligned}
(u_2)_t &\geq D_2(u_2)_{xx} - \alpha_2 (u_2)_x \\
&\quad + \left[ \min \{ m_2^R(x), m_2^u(x) \} - \varepsilon_2 - d_2 \right] u_2, \quad 0 < x < L, \ t \geq t_1, \\
P_2(u_2)(0, t) - \alpha_2 u_2(0, t) &= D_2(u_2)(L, t) - \alpha_2 u_2(L, t) = 0, \quad t \geq t_1.
\end{aligned}
\]
Since \( u_2(\cdot, 0) \neq 0 \), we can further show that \( u_2(\cdot, t_1) \to 0 \), and hence, there exists a sufficiently small number \( b_2 > 0 \) such that \( u_2(x, t_1) \geq b_2 \psi_{\varepsilon_2}(x), \ \forall \ x \in [0, L] \), where \( \psi_{\varepsilon_2}(x) \) is the eigenfunction corresponding to \( \Lambda^2_2 \). Then the Comparison Principle ensures that
\[ u_2(x, t) \geq b_2 e^{-\Lambda^2_2(t-t_1)} \psi_{\varepsilon_2}(x), \quad \forall \ x \in [0, L], \ t \geq t_1. \]
Since \( \Lambda^2_2 < 0 \), we deduce that \( \lim_{t \to \infty} u_2(\cdot, t) = \infty \), which contradicts \((4.8)\). This contradiction proves \((4.3)\).

\[ \square \]

We next define another two projections \( P_{2}^R \) and \( P_{2}^u \) on \( C([0, L], \mathbb{R}^2_+) \) by
\[ P_{2}^R(R, u_2) = R, \quad P_{2}^u(R, u_2) = u_2, \ \forall \ (R, u_2) \in C([0, L], \mathbb{R}^2_+). \]
Let
\[ B_{2}^R = P_{2}^R(A_2) \] and \( m_{2}^R(x) = \inf_{\phi_2 \in B_{2}^R} f_1(\phi_2^R(x)), \ \forall \ x \in [0, L], \]
and
\[ B_{2}^u = P_{2}^u(A_2) \] and \( m_{2}^u(x) = \inf_{\phi_2 \in B_{2}^u} G_1(\phi_2(x)), \ \forall \ x \in [0, L], \]
where \( G_1(\phi_2(x)) = g_1 \left( I_0 e^{-k_0 x} e^{-k_1 \int_0^s \phi_2(s) ds} \right) \). Then \( m_{2}^R(x) \) and \( m_{2}^u(x) \) are continuous on \([0, L]\) (see [11, Lemma 4.1]). Consider the following system
\[
\begin{aligned}
u_1 &= D_1 u_{xx} - \alpha_1 u_x + \left[ \min \{ m_{2}^R(x), m_{2}^u(x) \} - d_1 \right] u, \ t > 0, \ 0 < x < L, \\
D_1 u(0,t) - \alpha_1 u(0,t) &= D_1 u(L,t) - \alpha_1 u(L,t) = 0, \ t \geq 0, \\
u(x,0) &= u_0(x) \geq 0, \ 0 \leq x \leq L.
\end{aligned}
\]
\[ (4.15) \]
Substituting $u(x,t) = e^{-\Lambda_1 t} \varphi(x)$ into (4.15), we obtain the following associated eigenvalue problem:

\[
\begin{cases}
-D_1 \varphi_{xx} + \alpha_1 \varphi_x - \left[ \min\{m^R(x), m^n(x)\} \right] \varphi = \Lambda_1 \varphi, & t > 0, \quad 0 < x < L, \\
D_1 \varphi_x(0) - \alpha_1 \varphi(0) = D_1 \varphi_x(L) - \alpha_1 \varphi(L) = 0.
\end{cases}
\]  

(4.16)

We denote the principal eigenvalue of (4.16) by $\Lambda^0_1$. By the similar arguments in [11, Lemma 4.2] and Lemma 4.1, we have following results:

**Lemma 4.2.** Assume $0 \leq \theta_i \leq 1$. Let $0 < d_2 < d^*_2$ and $\Lambda^0_1 < 0$. Then $M_2$ is a uniform weak repeller in the sense that there exists $\sigma_2 > 0$ such that

\[
\limsup_{t \to \infty} \text{dist}(\Sigma(t)(R^0, u^0_1, u^0_2), M_2) \geq \sigma_2, \quad \text{for all } (R^0, u^0_1, u^0_2) \in \mathcal{X}_0.
\]

The following theorem is concerned with the main result in this paper, namely, the possibility of coexistence of two species in the system (1.1)-(1.3).

**Theorem 4.1.** Assume $0 \leq \theta_i \leq 1$. Let $0 < d_2 < d^*_2$ and $\Lambda^0_1 < 0$, for $i = 1, 2$. Then system (1.1)-(1.3) is uniformly persistent with respect to $(\mathcal{X}_0, \partial \mathcal{X}_0)$ in the sense that there is a $\zeta > 0$ such that for any solution $(R(x,t), u_1(x,t), u_2(x,t))$ of system (1.1)-(1.3) with $(R(\cdot,0), u_1(\cdot,0), u_2(\cdot,0)) = (R^0(\cdot), u^0_1(\cdot,0), u^0_2(\cdot)) \in \mathcal{X}_0$, we have

\[
\liminf_{t \to \infty} u_i(x,t) \geq \zeta, \quad i = 1, 2, \quad \text{uniformly for all } x \in [0,L].
\]  

(4.17)

Furthermore, system (1.1)-(1.3) admits at least one (componentwise) positive steady state $(\bar{R}(x), \bar{u}_1(x), \bar{u}_2(x))$.

**Proof.** By Lemma 2.2, it follows that for any $\psi^0 := (R^0, u^0_1, u^0_2) \in \mathcal{X}_0$, we have

\[
u_1(x,t, \psi^0) > 0, \quad \nu_2(x,t, \psi^0) > 0, \quad \forall \ x \in [0,L], \quad t > 0.
\]

This implies that $\Sigma(t) \mathcal{X}_0 \subseteq \mathcal{X}_0$ for all $t \geq 0$. Let

\[M_0 := \{ \psi^0 \in \partial \mathcal{X}_0 : \Sigma(t) \psi^0 \in \partial \mathcal{X}_0, \forall \ t \geq 0\}, \]

and $\varpi(\psi^0)$ be the omega limit set of the orbit $\Omega^+(\psi^0) := \{ \Sigma(t) \psi^0 : t \geq 0 \}$. We further prove the following claims.

**Claim 1.** $\varpi(\psi) \subset M_0 \cup M_1 \cup M_2, \forall \ \psi \in M_0$.

For any given $\psi := (R^0, u^0_1, u^0_2) \in M_0$, we have $\Sigma(t) \psi \in \partial \mathcal{X}_0, \forall \ t \geq 0$. Thus, for any given $t \geq 0$, we have $u_1(\cdot,t, \psi) \equiv 0$ or $u_2(\cdot,t, \psi) \equiv 0$. In case where $u_1(\cdot,t, \psi) \equiv 0$, for any $t \geq 0$. Then $(R(x,t), u_2(x,t)), t \geq 0$, satisfies system (3.1) with $f \equiv f_2, g \equiv g_2, q \equiv q_2, D \equiv D_2, \theta \equiv \theta_2, d \equiv d_2$, and $\alpha \equiv \alpha_2$, in which $I(x,t)$ satisfies (3.2) with $k \equiv k_2$ and $u(s,t) \equiv u_2(s,t)$. Since $0 < d_2 < d^*_2$, it follows from Theorem 3.1 that either

\[
\lim_{t \to \infty} (R(x,t), u_2(x,t)) = (R^0(\cdot),0), \quad \text{uniformly for } x \in [0,L],
\]

or $(R(\cdot,t, \psi), u_2(\cdot,t, \psi))$ will eventually enter the global attractor $A_2 \subset \text{Int}(C([0,L], \mathbb{R}^+_2))$. Thus, either

\[
\lim_{t \to \infty} (R(x,t), u_1(x,t), u_2(x,t)) = \mathcal{E}_0 := (R^0(\cdot),0,0), \quad \text{uniformly for } x \in [0,L],
\]

or $\Sigma(t) \psi$ will eventually enter $M_2$. In case where $u_1(\cdot,t_1, \psi) \not\equiv 0$, for some $t_1 \geq 0$. Then Lemma 2.2 implies that $u_1(x,t, \psi) > 0, \forall \ x \in [0,L], \forall \ t > t_1$. Thus, we must have $u_2(x,t, \psi) \equiv 0, \forall \ x \in [0,L], \forall \ t > t_1$. Then $(R(x,t), u_1(x,t)), t > t_1$, satisfies system (3.1) with $f \equiv f_1, g \equiv g_1, q \equiv q_1, D \equiv D_1, \theta \equiv \theta_1, d \equiv d_1$, and $\alpha \equiv \alpha_1$, in which $I(x,t)$ satisfies (3.2) with $k \equiv k_1$ and $u(s,t) \equiv u_1(s,t)$. Since
0 < d_1 < d_1^\ast, we can use Theorem 3.1 and the previous arguments to show that either \lim_{t \to \infty} \Sigma(t) \psi = \mathcal{E}_0 or \Sigma(t) \psi will eventually enter M_1. The proof of Claim 1 is finished.

**Claim 2.** For i = 0, 1, 2, M_i is a uniform weak repeller for \mathcal{X}_0 in the sense that there exists a \sigma_i > 0 such that \limsup_{t \to \infty} ||\Sigma(t) \nu^0 - M_i|| \geq \sigma_i, \forall \nu^0 \in \mathcal{X}_0.

We note that Claim 2 holds when i = 1, 2, due to Lemma 4.1 and Lemma 4.2. By similar arguments to Claim 2 in the proof of Theorem 3.1(ii), we can further show that our Claim 2 holds when i = 0.

Next, we define a continuous function \( p : \mathcal{X} \to [0, \infty) \) by

\[
 p(\nu^0) := \min \{ \min_{x \in [0, L]} u_1^0(x), \min_{x \in [0, L]} u_2^0(x) \}, \forall \nu^0 := (R^0, u_1^0, u_2^0) \in \mathcal{X}.
\]

By Lemma 2.2, it follows that \( p^{-1}(0, \infty) \subseteq \mathcal{X}_0 \) and \( p \) has the property that if \( p(\nu^0) > 0 \) or \( \nu^0 \in \mathcal{X}_0 \), with \( p(\Sigma(t) \nu^0) > 0 \), then \( p(\Sigma(t) \nu^0) > 0 \), \( \forall t > 0 \). That is, \( p \) is a generalized distance function for the semiflow \( \Sigma(t) : \mathcal{X} \to \mathcal{X} \) (see, e.g., [23]).

By the above claims, it follows that any forward orbit of \( \Sigma(t) \) in \( \mathcal{M}_0 \) converges to either \( \mathcal{M}_0 \) or \( \mathcal{M}_1 \) or \( \mathcal{M}_2 \). Further, \( \mathcal{M}_0, \mathcal{M}_1, \) and \( \mathcal{M}_2 \) are isolated in \( \mathcal{X} \) and \( \mathcal{W}^s(\mathcal{M}_i) \cap p^{-1}(0, \infty) = \emptyset \), where \( \mathcal{W}^s(\mathcal{M}_i) \) is the stable set of \( \mathcal{M}_i \), \( \forall i = 0, 1, 2 \) (see [23]). It is easy that no subsets of \( \mathcal{M}_0, \mathcal{M}_1, \mathcal{M}_2 \) forms a cycle in \( \partial \mathcal{X}_0 \). By Lemma 2.1, we see that \( \Sigma(t) : \mathcal{X} \to \mathcal{X} \) has a global compact attractor in \( \mathcal{X}, \forall t \geq 0 \). It follows from [23, Theorem 3] that there exists a \( \zeta > 0 \) such that

\[
 \min_{\psi \in \nu^0} p(\psi) > \zeta, \forall \nu^0 \in \mathcal{X}_0.
\]

This implies that (4.17) holds. Hence, the uniform persistence stated in our theorem is valid. By [17, Theorem 3.7 and Remark 3.10], it then follows that \( \Sigma(t) : \mathcal{X}_0 \to \mathcal{X}_0 \) has a global attractor. It then follows from [17, Theorem 4.7] that \( \Sigma(t) \) has a steady-state solution \( (\hat{R}(\cdot), \hat{u}_1(\cdot), \hat{u}_2(\cdot)) \in \mathcal{X}_0 \). Note that \( \hat{R}(x) \) satisfies the following system:

\[
 \left\{ \begin{array}{l}
 D_R \hat{R}_{xx} - q_1 \min\{f_1(\hat{R}), g_1(\hat{I}(x))\}\hat{u}_1 - q_2 \min\{f_2(\hat{R}), g_2(\hat{I}(x))\}\hat{u}_2 \\
 + q_1 t_1 \hat{u}_1 + q_2 t_2 \hat{u}_2, \quad 0 < x < L, \\
 \hat{R}_x(0) = 0, \quad \hat{R}_x(L) = \gamma(R^0 - \hat{R}(L)),
 \end{array} \right.
\]

where

\[
 \hat{I}(x) = I_0 e^{-k_0 x} \exp \left( - \int_0^x k_1 \hat{u}_1(s) ds - \int_0^x k_2 \hat{u}_2(s) ds \right).
\]

By the boundedness of the function \( \min\{f_1(\hat{R}), g_1(\hat{I})\} \), the strong maximum principle and the Hopf boundary lemma for Elliptic equations (see [19]), we conclude that \( \hat{R}(x) > 0 \), for all \( x \in [0, L] \). Then we complete the proof of this theorem. \( \square \)

Before ending this section, we briefly give interpretations and comments on the analytical results obtained in Theorem 4.1. System (1.1)-(1.3) was proposed to model the competition between two phytoplankton species for light and a (limiting) nutrient in a partially mixed water column, where the distributions of light and a nutrient have opposing gradients. Biologically, we expect that coexistence of two phytoplankton species along vertical resources can occur in system (1.1)-(1.3) if each of the two species can invade the habitat dominated by the other. This prediction was confirmed by numerical simulations in [20, 21, 25], and the simulations in [25] also indicate that the conditions for coexistence depend on physical and chemical parameters, e.g., the nutrient concentration at the sediment \( (R^{00}) \), the incident light intensity \( (I_0) \), the background turbidity \( (k_0) \), and so on. The condition \( 0 < d_i < d_i^\ast \)
in Theorem 4.1 guarantees that species \( i, i = 1, 2 \), can persist as a single species (see also Theorem 3.1 (ii)). Ecologically, Lemma 4.1 and Lemma 4.2 mean that the semi-trivial steady state(s), \( \mathcal{E}_i \), is invasible by the missing competitor \( 3 - i \) if \( \Lambda_{3-i}^0 < 0 \), for \( i = 1, 2 \). Therefore, our analytical result in Theorem 4.1 shows that if both of the semi-trivial steady state(s), \( \mathcal{E}_1 \) and \( \mathcal{E}_2 \), are invasible by the missing competitor, then there is at least one steady state representing coexistence of the two species. Basically, our theoretical results in Theorem 4.1 coincide with the numerical simulations in [20, 21, 25]. However, we should point out that it remains a challenging task to compute the principal eigenvalue \( \Lambda_i^0 \) since the semi-trivial steady state(s), \( \mathcal{E}_i \), is not necessarily unique and the associated eigenvalue problems (4.2) and (4.16) are complicated. We leave this challenging problem for future investigation.

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