MONOTONICITY AND GLOBAL DYNAMICS OF A NONLOCAL TWO-SPECIES PHYTOPLANKTON MODEL*

DANHUA JIANG†, KING-YEUNG LAM‡, YUAN LOU§, AND ZHICHENG WANG¶

Abstract. We investigate a nonlocal reaction-diffusion-advection system modeling the population dynamics of two competing phytoplankton species in a eutrophic environment, where nutrients are in abundance and the species are limited by light only for their metabolism. We first demonstrate that the system does not preserve the competitive order in the pointwise sense. Then we introduce a special cone $\mathcal{K}$ involving the cumulative distributions of the population densities, and a generalized notion of super- and subsolutions of the nonlocal competition system where the differential inequalities hold in the sense of the cone $\mathcal{K}$. A comparison principle is then established for such super- and subsolutions, which implies the monotonicity of the underlying semiflow with respect to the cone $\mathcal{K}$ (Theorem 2.1). As application, we study the global dynamics of the single species system and the competition system. The latter has implications for the evolution of movement for phytoplankton species.

Key words. Phytoplankton; competition for light; nonlocal reaction-diffusion equations; monotone dynamical system.

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1. Introduction.

Phytoplankton are microscopic plant-like photosynthetic organisms that drift in the water columns of lakes and oceans. They grow abundantly around the globe and are the foundation of the marine food chain. Since they transport significant amounts of atmospheric carbon dioxide into the deep oceans, they play a crucial role in climate dynamics. Nutrients and light are the essential resources for the growth of phytoplankton. There are three possible ways for phytoplankton to compete for nutrients and light. At one extreme, in oligotrophic ecosystems with an ample supply of light, species compete for limiting nutrients [22, 27]. At the other extreme, in eutrophic ecosystems with ample nutrient supply, species compete for light [8, 16, 17, 33]. In some ecosystems of intermediate conditions, they compete for both nutrients and light [3, 4, 18, 21, 36]. In the water column, phytoplankton diffuse by water turbulence, and also sink or buoy, depending on whether they are heavier than water or not [8].

In this paper, we study the two-species nonlocal reaction-diffusion-advection system proposed by Huisman et al. [16, 18]. The system models the growth of phytoplankton species in a eutrophic vertical water column, where the species is limited by light only for their metabolism. Consider a water column with unit cross-sectional area and with two phytoplankton species. Let x denote the depth within the water column where x varies from 0 (the top) to L (the bottom), and let $u(x,t), v(x,t)$ stand for the population densities of two phytoplankton species at the location x and time

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†School of Mathematics and Statistics, Lanzhou University, Lanzhou 730000, China and Department of Mathematics, The Ohio State University, Columbus, OH 43210, USA (jiangdh15@lzu.edu.cn).

‡Department of Mathematics, The Ohio State University, Columbus, OH 43210, USA (lam.184@math.ohio-state.edu).

§Institute for Mathematical Sciences, Renmin University of China, Beijing 100872, China and Department of Mathematics, The Ohio State University, Columbus, OH 43210, USA (lou@math.ohio-state.edu).

¶School of Mathematics and Statistics, Lanzhou University, Lanzhou 730000, China (wangzhch@lzu.edu.cn).

t, respectively. The following system of reaction-diffusion-advection equations was proposed in [16] to describe the population dynamics of two phytoplankton species:

$$\left\{\begin{array}{ll} u_t = D_1 u_{xx} - \alpha_1 u_x + [g_1(I(x,t)) - d_1]u, & 0 < x < L,\ t > 0, \\ v_t = D_2 v_{xx} - \alpha_2 v_x + [g_2(I(x,t)) - d_2]v, & 0 < x < L,\ t > 0, \end{array}\right. \tag{1.1}$$

with no-flux boundary conditions

$$\left\{\begin{array}{ll} D_1 u_x(x,t) - \alpha_1 u(x,t) = 0, & x = 0, L,\ t > 0, \\ D_2 v_x(x,t) - \alpha_2 v(x,t) = 0, & x = 0, L,\ t > 0, \end{array}\right. \tag{1.2}$$

and initial conditions

$$u(x,0) = u_0(x) \geq, \not\equiv 0, \quad v(x,0) = v_0(x) \geq, \not\equiv 0, \quad 0 \leq x \leq L, \tag{1.3}$$

where for $i = 1, 2$, $D_i > 0$ is the diffusion coefficient, $\alpha_i \in \mathbb{R}$ is the sinking ($\alpha_i > 0$) or buoyant ($\alpha_i < 0$) velocity, $d_i > 0$ is the death rate, $g_i(I)$ represents the specific growth rate of phytoplankton species as a function of light intensity $I(x,t)$.

Light intensity is decreasing with depth due to light absorption via phytoplankton and water. By the Lambert-Beer law [23], the light intensity $I(x,t)$ is given by

$$I(x,t) = I_0 \exp\Big(- k_0 x - \int_0^x [k_1 u(s,t) + k_2 v(s,t)] ds \Big), \tag{1.4}$$

where $I_0 > 0$ is the incident light intensity, $k_0 > 0$ is the background turbidity that summarizes light absorption by all non-phytoplankton components, and k_i is the absorption coefficient of the corresponding phytoplankton species. In this model ample nutrient supply is assumed so that the phytoplankton growth is only limited by the light availability. We assume that $g_i(I)$ is a smooth function satisfying

$$g_i(0) = 0 \ \text{ and } \ g_i'(I) > 0 \ \text{ for } \ I \geq 0. \tag{1.5}$$

A typical example of $g_i(I)$ takes the Michaelis-Menten form

$$g_i(I) = \frac{m_i I}{a_i + I},$$

where $m_i > 0$ is the maximal growth rate and $a_i > 0$ is the half saturation constant.

Most existing mathematical literatures on phytoplankton are focused on a single species. The single species model was considered in [33] for the self-shading case (i.e. $k_0 = 0$) and infinite long water column ($L = \infty$). The existence, uniqueness and global stability of the steady state are established in [20, 33]. It is shown in [24] that the self-shading model with any finite water column depth has a stable positive steady state, which means that the self-shading model has no critical water column depth beyond which the phytoplankton cannot persist.

For the case $k_0 > 0$, it is illustrated in [8] that the condition for phytoplankton bloom development can be characterized by critical water column depth and some critical values of the vertical turbulent diffusion coefficient. Du and Hsu [5] studied both single and two species competing for light with no advection. For the single species model, the existence, uniqueness, and global attractivity of a positive equilibrium was established. Hsu and Lou [13] analyzed the critical death rate, critical water column depth, critical sinking or buoyant coefficient and critical turbulent diffusion rate. Du and Mei [7] investigated the global dynamics of the single species model for the case $D = D(x)$, $\alpha = \alpha(x)$ and the asymptotic profiles of the positive steady states for small or large diffusion and deep water column when D, α are constants. Peng and Zhao [31,32] considered the effect of time-periodic light intensity I_0 at the surface, due to diurnal light cycle and seasonal changes. Ma and Ou [28] further studied the model in [31,32] and assume that $D(t), \alpha(t)$ are time periodic functions. They obtained the uniqueness and the global attractivity of the positive periodic solution of the single species model, when it exists.

Du et al. [6] studied the effect of photoinhibition on the single phytoplankton species, and they found that, in contrast to the case of no photoinhibition, where at most one positive steady state can exist, the model with photoinhibition possesses at least two positive steady states in certain parameter ranges. Hsu et al. [14] examined the dynamics of a single species under the assumption that the amount of light absorbed by individuals is proportional to cell size, which varies for populations that reproduced by simple cell division into two equal-sized daughter cells.

Although many mathematical theories have been developed for single species phytoplankton model, there are very few results for two or more phytoplankton species competing for light. The existence of positive steady state and uniform persistence for two-species model were proved in [5], where there is no sinking or buoyancy. In [29], Mei and Zhang studied a nonlocal reaction-diffusion-advection system modeling the growth of multiple competitive phytoplankton species and they found that when the diffusion of the system is large, there are no positive steady states, and when the diffusion is not large, there exists at least one positive steady state under proper conditions.

Unlike two-species Lotka-Volterra competition model with diffusion, one main difficulty for system (1.1)-(1.4) is the lack of comparison principle, i.e.

$$\begin{aligned} &u_1(x,0) \le u_2(x,0),\ v_1(x,0) \ge v_2(x,0) \qquad \forall x \in [0,L] \\ &\not\Longrightarrow\ u_1(x,t) \le u_2(x,t),\ v_1(x,t) \ge v_2(x,t) \quad \forall (x,t) \in [0,L]\times(0,\infty), \end{aligned}$$

due to the nonlocal nature of the nonlinearity. See Remark 3.10.

For order-preserving properties in the single species model, Shigesada and Okubo [33] observed that the cumulative distribution function $U(x,t) := \int_0^x u(s,t)ds$ satisfies a single reaction-diffusion equation without nonlocal terms. Subsequently, Ishii and Takagi [20] showed that the flow retains the natural order in U. For a related model with a water column of infinite depth, they made use of this fact to obtain a complete classification of the long-time behavior of the population. This fact was used again in Du and Hsu [5] to determine the long-time dynamics for a single species model with finite water depth. More recently, Ma and Ou [28] established the comparison principle for U in the single species model.

For the competition model, we will show, by adapting arguments due to Du and Hsu [5] and Ma and Ou [28], that the cumulative distribution functions

$$(U(x,t), V(x,t)) = \left(\int_0^x u(s,t)\,ds, \int_0^x v(s,t)\,ds \right)$$

satisfy a nonlocal, strongly coupled system, with non-standard boundary condition (see (3.3)), and that the resulting system has the strong order-preserving property.

Our main result (Theorem 2.1) says that system (1.1)-(1.4) forms a strongly monotone dynamical system with respect to the order induced by the special cone

$\mathcal{K} = \mathcal{K}_1 \times (-\mathcal{K}_1)$, where

$$\mathcal{K}_1 = \left\{ \phi \in C([0, L], \mathbb{R}) : \int_0^x \phi(s)\, ds \geq 0 \ \text{ for } \ x \in (0, L] \right\}. \tag{1.6}$$

The new features of this paper can be described as follows: First, Theorem 2.1 is the first monotonicity result for the nonlocal competition system involving two phytoplankton species. Second, the definition of the relevant cone $\mathcal{K}$ facilitates the connection with general theory of monotone dynamical systems. Third, generalized notion of super- and subsolutions (see Definition 3.2), which is new even for the case of single species, are given. They can potentially be used to obtain qualitative properties of solutions for the nonlocal system (1.1)-(1.4).

The rest of the paper is organized as follows: In Section 2, we state our main results. In Section 3, we first introduce the notion of super- and subsolutions of (1.1)-(1.4) with respect to the cone $\mathcal{K}$, and establish the comparison principle for the super- and subsolutions. Then we apply the monotonicity result to establish the global dynamics of the single species model in a general setting. Section 4 is devoted to the spectral analysis of semi-trivial steady states, and the global dynamics of system (1.1)-(1.4) are established for three different biological scenarios. In Section 5, we present some numerical results and discussion.

2. Main Results. Let $\mathbf{X}$ be a Banach space over $\mathbb{R}$. We call a subset $K \subset \mathbf{X}$ a *cone* if (i) K is convex, (ii) $\mu K \subset K$ for all $\mu \geq 0$, and (iii) $K \cap (-K) = \{0\}$. A cone K is said to be solid if it has nonempty interior. Furthermore, for $x, y \in \mathbf{X}$, we write $x \leqslant_K y$, $x <_K y$ and $x \ll_K y$ if $y - x \in K$, $y - x \in K \setminus \{0\}$ and $y - x \in \operatorname{Int} K$ respectively.

Let $\mathcal{K}_1$ be given by (1.6). It is straightforward to verify that $\mathcal{K}_1$ is a solid cone in the Banach space $C([0, L]; \mathbb{R})$ with interior

$$\text{Int } \mathcal{K}_1 = \left\{ \phi \in C([0, L]; \mathbb{R}) : \phi(0) > 0, \int_0^x \phi(s)\, ds > 0 \ \text{ for } x \in (0, L] \right\}.$$

Let $\mathcal{K} = \mathcal{K}_1 \times (-\mathcal{K}_1)$. Then $\mathcal{K}$ is likewise a solid cone in the Banach space $C([0, L]; \mathbb{R}^2)$ with interior given by Int $\mathcal{K} =$ Int $\mathcal{K}_1 \times (-$Int $\mathcal{K}_1)$. The cone $\mathcal{K}$ induces the partial order relations $\leqslant_{\mathcal{K}}$, $<_{\mathcal{K}}$ and $\ll_{\mathcal{K}}$ in the usual way.

We shall prove that (1.1)-(1.4) is a strongly monotone dynamical system with respect to the order induced by the cone $\mathcal{K}$.

THEOREM 2.1. *Suppose $\{(u_i, v_i)\}_{i=1,2}$ are non-negative solutions of* (1.1)-(1.4) *such that $u_2(\cdot, 0) \geq, \not\equiv 0$ and $v_1(\cdot, 0) \geq, \not\equiv 0$ and*

$$(u_1(\cdot, 0), v_1(\cdot, 0)) <_{\mathcal{K}} (u_2(\cdot, 0), v_2(\cdot, 0)).$$

Then $(u_1(\cdot, t), v_1(\cdot, t)) \ll_{\mathcal{K}} (u_2(\cdot, t), v_2(\cdot, t))$ for all $t > 0$.

By Theorem 2.1, system (1.1)-(1.4) is a strongly monotone dynamical system on $C([0, L]; \mathbb{R}^2_+)$ with respect to the order generated by $\mathcal{K}$, which together with the theory of strongly monotone dynamical systems [2, 12, 15, 25, 34, 37], provides a useful tool to investigate the global dynamics of two-species system (1.1)-(1.4). As a by-product of our monotonicity result, we also generalize the existing results for single species (see Subsection 3.2) and give a simple proof based on monotonicity arguments and the concept of subhomogeneous mappings.

As application, we turn our attention to the effects of diffusion and advection on the global dynamics of (1.1)-(1.4).

THEOREM 2.2. *If $D_1 = D_2$, $\alpha_1 < \alpha_2$, $g_1 = g_2$, $d_1 = d_2$, and that both semi-trivial steady states exist, then the first species u drives the second species v to extinction, regardless of initial condition.*

Theorem 2.2 shows that the competitor with smaller advection rate has competitive advantages, i.e., *smaller advection rate is selected*. By the Lambert-Beer law, the deeper the water column, the weaker the light intensity. Therefore, it is more advantageous for phytoplankton species to move up.

THEOREM 2.3. *If $D_1 < D_2$, $\alpha_1 = \alpha_2 \geq [g(1) - d]L$, $g_1 = g_2$, $d_1 = d_2$, and that both semi-trivial steady states exist, then the faster diffuser v drives the slower diffuser u to extinction, regardless of initial condition.*

Theorem 2.3 implies that if sinking rate is large, competitor with faster diffusion will always displace the slower one, i.e., *faster diffuser wins*. Intuitively, when both species are sinking with equal and large velocity, faster diffusion can counter balance the tendency to sink and provide individuals with better access to light.

THEOREM 2.4. *If $D_1 < D_2$, $\alpha_1 = \alpha_2 \leq 0$, $g_1 = g_2$, $d_1 = d_2$, and that both semi-trivial steady states exist, then the slower diffuser u drives faster diffuser v to extinction, regardless of initial condition.*

Theorem 2.4 suggests that if the phytoplankton species are buoyant, the competitor with slower diffusion rate will always displace the faster one, i.e., *slower diffusion rate will be selected*. This is in sharp contrast to Theorem 2.3. The reason for this result is that when the phytoplankton are buoyant, turbulent diffusion actually displaces individuals from the top of the water column, where the light intensity is the strongest.

3. A General Model with Spatio-Temporally Varying Coefficients. We shall study a generalized version of system (1.1)-(1.4), which allows coefficients to vary explicitly with both space and time. We formulate the nonlocal reaction-diffusion-advection model as follows:

$$
\begin{cases}
u_t = (D_1 u_x - \alpha_1 u)_x + f_1(x,t,\int_0^x u(s,t)\,ds, \int_0^x v(s,t)\,ds)u, & 0 < x < L,\ t > 0,\\
v_t = (D_2 v_x - \alpha_2 v)_x + f_2(x,t,\int_0^x u(s,t)\,ds, \int_0^x v(s,t)\,ds)v, & 0 < x < L,\ t > 0,\\
D_1 u_x - \alpha_1 u = 0, & x = 0, L,\ t > 0,\\
D_2 v_x - \alpha_2 v = 0, & x = 0, L,\ t > 0,\\
u(x,0) = u_0(x) \geq, \not\equiv 0,\ v(x,0) = v_0(x) \geq, \not\equiv 0, & 0 \leq x \leq L,
\end{cases}
\tag{3.1}
$$

where, for $i = 1, 2$, $D_i = D_i(x,t) > 0$, $\alpha_i = \alpha_i(x,t)$, and the functions $f_i(x,t,p,q)$ are smooth and satisfy

(H) $\dfrac{\partial f_i}{\partial p} < 0$, $\dfrac{\partial f_i}{\partial q} < 0$ and $\dfrac{\partial f_i}{\partial x} \leq 0$ for all $x \in [0,L]$ and $t, p, q \geq 0$.

The assumption holds, e.g. when $f_i(x,t,p,q) = g_i(I_0 \exp(-k_0 x - k_1 p - k_2 q)) - d_i(x,t)$ such that g_i is non-decreasing, and d_i is non-decreasing in x. In particular, it includes (1.1)-(1.4), and the previous works [5,29] as particular cases.

3.1. Strong Monotonicity of (3.1). This subsection is devoted to proving the monotonicity of system (3.1) with respect to the order induced by cone $\mathcal{K}$ under the assumption (**H**). First, we state the following standard result (see, e.g. [10, Ch. 3]).

PROPOSITION 3.1. *For continuous, non-negative initial data $(u_0(x), v_0(x))$, system (3.1) has a unique solution*

$$(u,v) \in C([0,\infty); C([0,L];\mathbb{R}_+^2)) \cap C^1((0,\infty); C^\infty([0,L];\mathbb{R}_+^2)),$$

which depends continuously on initial data. Moreover, if $u_0(x) \not\equiv 0$, (*resp.* $v_0(x) \not\equiv 0$), *then* $u(x,t) > 0$ (*resp.* $v(x,t) > 0$) *for* $(x,t) \in [0,L] \times (0,\infty)$.

Next, we define the following super- and subsolution concepts for (3.1). Note that the differential inequalities appearing below are to be understood in the sense of cone $\mathcal{K}$ for each time t. These inequalities hold, in particular, if the differential inequalities hold in the pointwise sense everywhere.

DEFINITION 3.2. *We say that*

$$(\overline{u}, \underline{v}), (\underline{u}, \overline{v}) \in C([0,T]; C([0,L]; \mathbb{R}^2_+)) \cap C^1((0,T]; C^\infty([0,L]; \mathbb{R}^2_+))$$

form a pair of super- and subsolutions of (3.1) *in the interval* $[0,T]$, *if*

$$(3.2)\quad \begin{cases} \overline{u}_t \geqslant_{\mathcal{K}_1} (D_1\overline{u}_x - \alpha_1\overline{u})_x + f_1(x,t,\int_0^x \overline{u}(s,t)\,ds, \int_0^x \underline{v}(s,t)\,ds)\overline{u}, & 0 < t \le T,\\ \underline{v}_t \leqslant_{\mathcal{K}_1} (D_2\underline{v}_x - \alpha_2\underline{v})_x + f_2(x,t,\int_0^x \overline{u}(s,t)\,ds, \int_0^x \underline{v}(s,t)\,ds)\underline{v}, & 0 < t \le T,\\ \underline{u}_t \leqslant_{\mathcal{K}_1} (D_1\underline{u}_x - \alpha_1\underline{u})_x + f_1(x,t,\int_0^x \underline{u}(s,t)\,ds, \int_0^x \overline{v}(s,t)\,ds)\underline{u}, & 0 < t \le T,\\ \overline{v}_t \geqslant_{\mathcal{K}_1} (D_2\overline{v}_x - \alpha_2\overline{v})_x + f_2(x,t,\int_0^x \underline{u}(s,t)\,ds, \int_0^x \overline{v}(s,t)\,ds)\overline{v}, & 0 < t \le T,\\ D_1\overline{u}_x - \alpha_1\overline{u} \le 0 \le D_1\underline{u}_x - \alpha_1\underline{u}, & x = 0,\ 0 < t \le T,\\ D_1\overline{u}_x - \alpha_1\overline{u} \ge 0 \ge D_1\underline{u}_x - \alpha_1\underline{u}, & x = L,\ 0 < t \le T,\\ D_2\overline{v}_x - \alpha_2\overline{v} \le 0 \le D_2\underline{v}_x - \alpha_2\underline{v}, & x = 0,\ 0 < t \le T,\\ D_2\overline{v}_x - \alpha_2\overline{v} \ge 0 \ge D_2\underline{v}_x - \alpha_2\underline{v}, & x = L,\ 0 < t \le T,\\ (\overline{u}(\cdot,0), \underline{v}(\cdot,0)) \geqslant_{\mathcal{K}} (\underline{u}(\cdot,0), \overline{v}(\cdot,0)). \end{cases}$$

The main result of this section is

THEOREM 3.3. *Assume that* f_1, f_2 *satisfy* (**H**). *Let* $(\overline{u}, \underline{v})$ *and* $(\underline{u}, \overline{v})$ *be a pair of super- and subsolutions of* (3.1) *in the interval* $[0,T]$. *If* $\underline{u} > 0$ *and* $\underline{v} > 0$ *in* $[0,L] \times [0,T]$, *then*

$$(\overline{u}(\cdot,t), \underline{v}(\cdot,t)) \geqslant_{\mathcal{K}} (\underline{u}(\cdot,t), \overline{v}(\cdot,t)) \quad \textit{for}\ \ 0 \le t \le T.$$

Moreover, if there exists $t_0 \in (0,T]$ *such that* $\overline{u} > 0$ *and* $\overline{v} > 0$ *in* $[0,L] \times (0,t_0]$, *and*

$$(\overline{u}(\cdot,t_0) - \underline{u}(\cdot,t_0), \underline{v}(\cdot,t_0) - \overline{v}(\cdot,t_0)) \notin \operatorname{Int}\mathcal{K},$$

then $(\overline{u}(x,t), \underline{v}(x,t)) \equiv (\underline{u}(x,t), \overline{v}(x,t))$ *for* $x \in [0,L]$ *and* $0 \le t \le t_0$.

A direct consequence of Theorem 3.3 is the strong monotonicity of the continuous semiflow generated by (3.1). It includes Theorem 2.1 as a particular case.

COROLLARY 3.4. *Assume that* f_1, f_2 *satisfy* (**H**). *Suppose* $\{(u_i, v_i)\}_{i=1,2}$ *are two non-negative solutions of* (3.1), *such that* $u_1(\cdot,0) \ge, \not\equiv 0$, $v_2(\cdot,0) \ge, \not\equiv 0$, *and*

$$(u_1(\cdot,0), v_1(\cdot,0)) >_{\mathcal{K}} (u_2(\cdot,0), v_2(\cdot,0)).$$

Then $(u_1(\cdot,t), v_1(\cdot,t)) \gg_{\mathcal{K}} (u_2(\cdot,t), v_2(\cdot,t))$ *for all* $t > 0$.

The proof is postponed to later in the section.

To show Theorem 3.3, we consider the cumulative distribution functions

$$U(x,t) = \int_0^x u(s,t)\,ds, \quad V(x,t) = \int_0^x v(s,t)\,ds.$$

Then $U(0,t) \equiv 0$, $V(0,t) \equiv 0$ for $t \ge 0$, and $U_x(x,t) = u(x,t), V_x(x,t) = v(x,t)$. In this way, (3.1) is transformed into the following *strongly coupled, non-local* system of

(U,V) (see also [28] for the single species case):

$$
\begin{cases}
U_t = D_1 U_{xx} - \alpha_1 U_x + G_1[U,V,U_x,V_x], & 0<x<L, t>0,\\
V_t = D_2 V_{xx} - \alpha_2 V_x + G_2[U,V,U_x,V_x], & 0<x<L, t>0,\\
U(0,t)=0, \quad D_1 U_{xx}(L,t) - \alpha_1 U_x(L,t) = 0, & t>0,\\
V(0,t)=0, \quad D_2 V_{xx}(L,t) - \alpha_2 V_x(L,t) = 0, & t>0,\\
U(x,0) = \int_0^x u_0(s)\,ds = U_0(x), & 0\le x\le L,\\
V(x,0) = \int_0^x v_0(s)\,ds = V_0(x), & 0\le x\le L,
\end{cases} \tag{3.3}
$$

where, letting $F_1(x,t,U,V) = \int_0^U f_1(x,t,z,V)\,dz$, $F_2(x,t,U,V) = \int_0^V f_2(x,t,U,z)\,dz$,

$$
\begin{aligned}
&G_1[U,V,U_x,V_x](x,t)\\
&= \int_0^x f_1\Big(s,t,\int_0^s u(y,t)\,dy, \int_0^s v(y,t)\,dy\Big) u(s,t)\,ds\\
&= \int_0^x f_1\Big(s,t,U(s,t),V(s,t)\Big) U_x(s,t)\,ds\\
&= \int_0^x \Big\{ \frac{d}{ds}\big[F_1\big(s,t,U(s,t),V(s,t)\big)\big] - \frac{\partial F_1}{\partial x}\Big(s,t,U(s,t),V(s,t)\Big)\\
&\qquad - \frac{\partial F_1}{\partial V}\Big(s,t,U(s,t),V(s,t)\Big) V_x(s,t)\Big\}\,ds\\
&= F_1(x,t,U(x,t),V(x,t)) - \int_0^x \frac{\partial F_1}{\partial x}\Big(s,t,U(s,t),V(s,t)\Big)\,ds\\
&\quad - \int_0^x \frac{\partial F_1}{\partial V}\Big(s,t,U(s,t),V(s,t)\Big) V_x(s,t)\,ds
\end{aligned} \tag{3.4}
$$

and

$$
\begin{aligned}
&G_2[U,V,U_x,V_x](x,t)\\
&= \int_0^x f_2\Big(s,t,\int_0^s u(y,t)dy, \int_0^s v(y,t)dy\Big) v(s,t)ds\\
&= \int_0^x f_2\Big(s,t,U(s,t),V(s,t)\Big) V_x(s,t)\,ds\\
&= F_2\big(x,t,U(x,t),V(x,t)) - \int_0^x \frac{\partial F_2}{\partial x}\Big(s,t,U(s,t),V(s,t)\Big)\,ds\\
&\quad - \int_0^x \frac{\partial F_2}{\partial U}\Big(s,t,U(s,t),V(s,t)\Big) U_x(s,t)\,ds.
\end{aligned} \tag{3.5}
$$

For (3.3), we define the Banach space

$$X_1 = \{\phi \in C^1([0,L],\mathbb{R}) : \ \phi(0)=0\}$$

with the usual C^1 norm. The usual cone P_1 in X_1 is

$$P_1 = \{\phi \in X_1 : \phi(x) \ge 0 \ \text{ for } \ x\in[0,L]\},$$

with interior

$$\operatorname{Int} P_1 = \{\phi\in X_1 : \phi'(0)>0, \ \phi(x)>0 \ \text{ for } \ x\in(0,L]\}.$$

Let $X = X_1 \times X_1$, and $P = P_1 \times (-P_1)$. Then P is a cone in X with interior given by $\text{Int } P = \text{Int } P_1 \times (-\text{Int } P_1)$. The cone P generates the partial order relations $\leqslant_P, <_P$ and $\ll_P$ on X.

By construction, the solutions (U, V) of (3.3) live in the convex set $E = E_1 \times E_1$, where

$$E_1 = \{\phi \in C^1([0, L]) : \phi(0) = 0, \quad \text{and} \quad \phi'(x) \geq 0 \text{ for } x \in [0, L]\}.$$

From now on we assume the initial data of (3.3) to be in E. Under this assumption, the existence and uniqueness of the solution $(U(x, t), V(x, t))$ can be derived from those of $(u(x, t), v(x, t))$.

Definition 3.5. *We say that*

$$(\overline{U}, \underline{V}), (\underline{U}, \overline{V}) \in C([0, T]; E) \cap C^1((0, T]; C^\infty([0, L]; \mathbb{R}^2_+))$$

form a pair of super- and subsolutions of (3.3) *in the interval* $[0, T]$*, if the derivatives* $(\overline{u}, \underline{v}) = \left(\overline{U}_x, \underline{V}_x\right)$ *and* $(\underline{u}, \overline{v}) = \left(\underline{U}_x, \overline{V}_x\right)$ *form a pair of super- and subsolutions of* (3.1) *in the interval* $[0, T]$*, in the sense of Definition 3.2.*

We now prove a strong maximum principle for the system (3.3), which is the key to proving the strong monotonicity of (3.3).

Lemma 3.6. *Assume that* f_1, f_2 *satisfy* (**H**). *Let* $(\overline{U}, \underline{V})$ *and* $(\underline{U}, \overline{V})$ *be a pair of super- and subsolutions of* (3.3) *in the interval* $[0, t^*]$ *for some* $t^* > 0$*, so that*

$$\overline{U}_x(x, t) > 0 \quad \text{and} \quad \overline{V}_x(x, t) > 0 \quad \text{for } 0 \leq x \leq L, \text{ and } 0 < t \leq t^*, \tag{3.6}$$

and

$$\underline{U}(x, t) \leq \overline{U}(x, t), \quad \overline{V}(x, t) \geq \underline{V}(x, t) \quad \text{for } 0 \leq x \leq L, \text{ and } 0 \leq t \leq t^*.$$

If one of the following holds:
(a) $\underline{U}(x^*, t^*) = \overline{U}(x^*, t^*)$ *or* $\underline{V}(x^*, t^*) = \overline{V}(x^*, t^*)$ *for some* $x^* \in (0, L]$*;*
(b) $(\overline{U} - \underline{U})_x(0, t^*) = 0$ *or* $(\overline{V} - \underline{V})_x(0, t^*) = 0$*,*
then

$$(\underline{U}(x, t), \overline{V}(x, t)) \equiv (\overline{U}(x, t), \underline{V}(x, t)) \quad \text{for } 0 \leq x \leq L,\ 0 \leq t \leq t^*. \tag{3.7}$$

Proof. In the following we improve upon the arguments of [28] to prove the strong maxmimum principle for (3.3). We first consider the case when (a) holds. For definiteness assume that $\underline{U}(x^*, t^*) = \overline{U}(x^*, t^*)$ for some $x^* \in (0, L]$. Denote

$$W(x, t) = \overline{U}(x, t) - \underline{U}(x, t).$$

Then by (3.2),

$$(\overline{u} - \underline{u})_t - [D_1(\overline{u} - \underline{u})_x + \alpha_1(\overline{u} - \underline{u})]_x \geq_{\mathcal{K}_1} f_1(x, t, \overline{U}(x, t), \underline{V}(x, t)) - f_1(x, t, \underline{U}(x, t), \overline{V}(x, t))$$

Fixing t, and integrating the above from 0 to x, we have, in terms of W,

$$\begin{aligned} & W_t - D_1(x, t) W_{xx} + \alpha_1(x, t) W_x \\ & \geq \int_0^x f_1\Big(s, t, \overline{U}(s, t), \underline{V}(s, t)\Big) \overline{U}_x(s, t)\, ds - \int_0^x f_1\Big(s, t, \underline{U}(s, t), \overline{V}(s, t)\Big) \underline{U}_x(s, t)\, ds \\ & \geq \int_0^x f_1\Big(s, t, \overline{U}(s, t), \overline{V}(s, t)\Big) \overline{U}_x(s, t)\, ds - \int_0^x f_1\Big(s, t, \underline{U}(s, t), \overline{V}(s, t)\Big) \underline{U}_x(s, t)\, ds \end{aligned} \tag{3.8}$$

where we used $\overline{V}(x,t) \ge \underline{V}(x,t)$ for $(x,t) \in [0,L] \times [0,t^*]$. Integrating by parts as in (3.4), we have

$$\begin{aligned}
&W_t - D_1(x,t)W_{xx} + \alpha_1(x,t)W_x \\
\ge{}& F_1\Big(x,t,\overline{U}(x,t),\overline{V}(x,t)\Big) - F_1\Big(x,t,\underline{U}(x,t),\overline{V}(x,t)\Big) \\
&+ \int_0^x \left[\frac{\partial F_1}{\partial \overline{V}}\Big(s,t,\underline{U}(s,t),\overline{V}(s,t)\Big) - \frac{\partial F_1}{\partial \overline{V}}\Big(s,t,\overline{U}(s,t),\overline{V}(s,t)\Big)\right] \overline{V}_x(s,t)\,ds \\
&+ \int_0^x \left[\frac{\partial F_1}{\partial x}\Big(s,t,\underline{U}(s,t),\overline{V}(s,t)\Big) - \frac{\partial F_1}{\partial x}\Big(s,t,\overline{U}(s,t),\overline{V}(s,t)\Big)\right] ds \\
\ge{}& h(x,t)W + \int_0^x \left[\frac{\partial F_1}{\partial \overline{V}}\Big(s,t,\underline{U}(s,t),\overline{V}(s,t)\Big) - \frac{\partial F_1}{\partial \overline{V}}\Big(s,t,\overline{U}(s,t),\overline{V}(s,t)\Big)\right]\overline{V}_x(s,t)\,ds,
\end{aligned} \tag{3.9}$$

for $x \in [0,L],\ t \in (0,t^*]$, where

$$h(x,t) = \int_0^1 f_1\Big(x,t,\xi\overline{U}(s,t) + (1-\xi)\underline{U}(s,t),\overline{V}(s,t)\Big)\,d\xi \in L^\infty_{loc}([0,L] \times \mathbb{R}_+).$$

Note that we have used $\frac{\partial}{\partial U}\left(\frac{\partial F_1}{\partial x}\right) = \frac{\partial f_1}{\partial x} \le 0$, i.e. $\frac{\partial F_1}{\partial x}$ is non-increasing in U in the last inequality of (3.9). Summarizing, we have

$$\begin{aligned}
&W_t - D_1(x,t)W_{xx} + \alpha_1(x,t)W_x - h(x,t)W \\
\ge{}& \int_0^x \left[\frac{\partial F_1}{\partial \overline{V}}\Big(s,t,\underline{U}(s,t),\overline{V}(s,t)\Big) - \frac{\partial F_1}{\partial \overline{V}}\Big(s,t,\overline{U}(s,t),\overline{V}(s,t)\Big)\right]\overline{V}_x(s,t)\,ds.
\end{aligned} \tag{3.10}$$

Since $\frac{\partial}{\partial U}\left(\frac{\partial F_1}{\partial \overline{V}}\right) = \frac{\partial f_1}{\partial \overline{V}} < 0$, i.e. $\frac{\partial F_1}{\partial \overline{V}}$ is non-increasing in U, $\overline{U} \ge \underline{U}$, and $\overline{V}_x > 0$, the last integral is non-negative. Thus $W = \overline{U} - \underline{U}$ satisfies the following linear differential inequality:

$$W_t - D_1(x,t)W_{xx} + \alpha_1(x,t)W_x - h(x,t)W \ge 0, \qquad \text{for } x \in (0,L],\ t \in (0,t^*]. \tag{3.11}$$

We claim that $W \equiv 0$ in $[0,L]\times[0,t^*]$. If not, then the parabolic strong maximum principle applied to (3.11) implies that $W(x,t^*) > 0$ for $x \in (0,L)$. Therefore, if there exists some $x^* \in (0,L]$ such that $W(x^*,t^*) = 0$, then $x^* = L$, i.e., $W(L,t^*) = 0$, and hence $W_t(L,t^*) \le 0$. By the boundary conditions at $(x,t) = (L,t^*)$,

$$D_1\overline{U}_{xx} - \alpha_1\overline{U}_x \ge 0 \ge D_1\underline{U}_{xx} - \alpha_1\underline{U}_x,$$

we have $D_1(L,t^*)W_{xx}(L,t^*) - \alpha_1(L,t^*)W_x(L,t^*) \ge 0$. Then by (3.10) we have

$$\begin{aligned}
0 &\ge W_t(L,t^*) \\
&\ge \int_0^L \left[\frac{\partial F_1}{\partial \overline{V}}\Big(s,t^*,\underline{U}(s,t^*),\overline{V}(s,t^*)\Big) - \frac{\partial F_1}{\partial \overline{V}}\Big(s,t^*,\overline{U}(s,t^*),\overline{V}(s,t^*)\Big)\right]\overline{V}_x(s,t^*)\,ds.
\end{aligned}$$

Since $\underline{U}(x,t^*) \le \overline{U}(x,t^*)$ in $[0,L]$, and $\overline{V}_x > 0$, we deduce that the above inequality holds only if $\underline{U}(x,t^*) \equiv \overline{U}(x,t^*)$ for all $x \in [0,L]$, i.e., $W(x,t^*) \equiv 0$ for all $x \in [0,L]$. This is a contradiction and thus $W = \overline{U} - \underline{U} \equiv 0$ in $[0,L] \times [0,t^*]$. It follows that equality holds everywhere in (3.8) and (3.9), in particular,

$$\int_0^x f_1\Big(s,t,\overline{U}(s,t),\underline{V}(s,t)\Big)\overline{U}_x(s,t)\,ds \equiv \int_0^x f_1\Big(s,t,\overline{U}(s,t),\overline{V}(s,t)\Big)\overline{U}_x(s,t)\,ds,$$

for all $x \in [0, L]$ and $0 < t \le t^*$. Since $\overline{U}_x > 0$ and $\frac{\partial f_1}{\partial V} < 0$, we deduce that $\overline{V}(x,t) \equiv \underline{V}(x,t)$ in $[0,L] \times (0,t^*]$ and, by continuity, in $[0,L]\times[0,t^*]$.

The remaining case $\overline{V}(x^*,t^*) = \underline{V}(x^*,t^*)$ for some $x^* \in (0, L]$ can be handled similarly. This completes the proof in case (a) holds.

Next, assume (b) holds. We claim that necessarily there is a sequence of $t_j \nearrow t^*$ such that alternative (a) holds, so that we can deduce similarly that $(\overline{U}, \underline{V}) \equiv (\underline{U}, \overline{V})$ in $[0,L]\times[0,t_j]$ for all j, whence (3.7) holds as well upon letting $t_j \nearrow t^*$. To see the claim, assume for contradiction that $\overline{U} > \underline{U}$ and $\overline{V} > \underline{V}$ for $(x,t) \in (0,L]\times[t^*-\delta', t^*]$ for some δ'. Then, observe that the boundary condition ensures $W(0,t^*) = \overline{U}(0,t^*) - \underline{U}(0,t^*) = 0$. Since W satisfies the differential inequality (3.11), we may apply Hopf's Lemma [26, Lemma 2.8] to deduce that $(\overline{U} - \underline{U})_x(0,t^*) > 0$. Similarly, we can deduce that $(\overline{V} - \underline{V})_x(0,t^*) > 0$ as well, i.e. alternative (b) does not hold in this case. This establishes the claim and finishes the proof. ∎

Theorem 3.3 is a consequence of Lemma 3.6 and the following result:

LEMMA 3.7. *Assume that f_1, f_2 satisfy* (**H**). *Let $(\overline{U}, \underline{V})$ and $(\underline{U}, \overline{V})$ be a pair of super- and subsolutions of* (3.3) *in the time interval* $[0,T]$. *If*

$$\underline{U}_x(x,t) > 0, \quad \textit{and} \quad \underline{V}_x(x,t) > 0 \qquad \textit{for } (x,t) \in [0,L]\times[0,T], \tag{3.12}$$

then

$$\overline{U}(x,t) \ge \underline{U}(x,t) \qquad \textit{and} \qquad \underline{V}(x,t) \le \overline{V}(x,t) \qquad \textit{for } 0 \le x \le L,\ 0 \le t \le T. \tag{3.13}$$

Proof. It is enough to prove the result for arbitrary but finite $T > 0$. Given a pair of super- and subsolutions $(\overline{U}, \underline{V})$ and $(\underline{U}, \overline{V})$ in a bounded interval $[0,T]$, we show (3.13) in two steps.

Step 1. For each small $\delta > 0$, define

$$(\overline{U}^\delta, \underline{V}^\delta) = (\overline{U} + \delta\rho_1, \underline{V} - \delta\rho_2), \qquad \text{and} \qquad (\underline{U}^\delta, \overline{V}^\delta) = (\underline{U} - \delta\rho_1, \overline{V} + \delta\rho_2),$$

where $\rho_i(x,t) := \int_0^x \exp\left(Mt + \int_0^y \frac{\alpha_i(s,t)}{D_i(s,t)}\, ds\right) dy$ for $i = 1, 2$. By (3.12), there exists $\delta_0 > 0$ such that for each $\delta \in (0, \delta_0]$,

$$\begin{cases} (\overline{U}^\delta, \underline{V}^\delta), (\underline{U}^\delta, \overline{V}^\delta) \in E & \text{for } t \in [0,T], \\ \overline{U}^\delta_x > 0, \underline{V}^\delta_x > 0, \underline{U}^\delta_x > 0, \overline{V}^\delta_x > 0 & \text{for } (x,t) \in [0,L]\times[0,T], \\ (\overline{U}^\delta(\cdot,0), \underline{V}^\delta(\cdot,0)) \gg_P (\underline{U}^\delta(\cdot,0), \overline{V}^\delta(\cdot,0)). \end{cases} \tag{3.14}$$

It is also clear that there is $C_0 > 0$ (independent of δ) such that

$$\max_{i=1,2} \|\rho_i\|_{C([0,L]\times[0,T])} \le C_0 \min_{i=1,2} \inf_{[0,L]\times[0,T]} (\rho_i)_x(x,t). \tag{3.15}$$

We claim that $(\overline{U}^\delta, \underline{V}^\delta)$ and $(\underline{U}^\delta, \overline{V}^\delta)$ forms a pair of super- and subsolutions for (3.3) in the interval $[0,T]$, in the sense of Definition 3.5. It remains to show the differential inequalities (3.2) for δ small, as the initial and boundary conditions are clearly satisfied. A sufficient condition for the first one to hold is

$$\delta(\rho_1)_{x,t} \geqslant_{\mathcal{K}_1} [f_1(x,t,\overline{U}+\delta\rho_1, \underline{V}-\delta\rho_2) - f_1(x,t,\overline{U},\underline{V})]\overline{U}_x + \delta\rho_{1,x} f_1(x,t,\overline{U}+\delta\rho_1, \underline{V}-\delta\rho_2). \tag{3.16}$$

The inequality (3.16) holds since the following holds pointwisely in $[0, L] \times [0, T]$:

$$\delta(\rho_1)_{x,t} - [f_1(x,t,\overline{U}+\delta\rho_1,\underline{V}-\delta\rho_2) - f_1(x,t,\overline{U},\underline{V})]\overline{U}_x - \delta\rho_{1,x} f_1(x,t,\overline{U}+\delta\rho_1,\underline{V}-\delta\rho_2)$$
$$\geq \delta\left(\rho_{1,x}\left[M + \int_0^x \left(\frac{\alpha_1(s,t)}{D_1(s,t)}\right)_t ds - \|f_1\|_\infty\right] - \|Df_1\|_\infty(\rho_1+\rho_2)\|\overline{U}_x\|_\infty\right),$$

(note that $\overline{U}_x, \overline{V}_x \in C([0,L]\times[0,T])$ by definition of super- and subsolutions) and, by (3.15), the term in the square bracket is non-negative provided the positive parameter $M = M(C_0, \|f\|_{C^1})$ is chosen large enough (but uniformly for $\delta \in (0, \delta_0]$). In the same way, one can show the rest of the differential inequalities. In summary, there is $M > 0$ so that for all $\delta \in (0, \delta_0]$, $(\overline{U}^\delta, \underline{V}^\delta)$ and $(\underline{U}^\delta, \overline{V}^\delta)$ form a pair of super- and subsolutions for (3.3) in the interval $[0, T]$. This proves our first claim.

Step 2. Next, we claim that for all $\delta > 0$,

$$\overline{U}^\delta(x,t) > \underline{U}^\delta(x,t) \quad \text{and} \quad \underline{V}^\delta(x,t) < \overline{V}^\delta(x,t) \quad \text{for } (x,t) \in (0,L]\times[0,T]. \tag{3.17}$$

Suppose not, then it follows from (3.14) that there exists a positive maximal time denoted by $t^* \in (0, T]$ such that $\underline{U}^\delta(x,t) < \overline{U}^\delta(x,t)$, $\overline{V}^\delta(x,t) > \underline{V}^\delta(x,t)$ hold for $0 < x \leq L$ and $0 \leq t < t^*$, and $\underline{U}^\delta(x^*,t^*) = \overline{U}^\delta(x^*,t^*)$ or $\overline{V}^\delta(x^*,t^*) = \underline{V}^\delta(x^*,t^*)$ for some $x^* \in (0, L]$. It follows from Lemma 3.6 that $\underline{U}^\delta(x,t) \equiv \overline{U}^\delta(x,t)$ and $\overline{V}^\delta(x,t) \equiv \underline{V}^\delta(x,t)$ for all $0 \leq x \leq L$ and $0 \leq t \leq t^*$, which is a contradiction to (3.14). This shows (3.17). Letting $\delta \to 0$ in (3.17), we deduce that (3.13) holds for $(x,t) \in [0,L]\times[0,T]$. ∎

Now we prove Corollary 3.4, which includes Theorem 2.1 as a special case.

Proof of Corollary 3.4. For $i = 1, 2$, let

$$(U_i(x,t), V_i(x,t)) = \left(\int_0^x u_i(s,t)\,ds, \int_0^x v_i(s,t)\,ds\right). \tag{3.18}$$

If we assume in addition that

$$u_2(x,0) = U_{2,x}(x,0) > 0 \quad \text{and} \quad v_1(x,0) = V_{1,x}(x,0) > 0 \quad \text{in } [0,L], \tag{3.19}$$

then by applying the strong maximum principle to the first and second equations of (3.1) separately, we deduce that

$$u_2 = U_{2,x} > 0 \quad \text{and} \quad v_1 = V_{1,x} > 0 \quad \text{in } [0,L]\times[0,T].$$

Therefore, applying Lemma 3.7, we see that if $(U_1(\cdot,0), V_1(\cdot,0)) \geqslant_P (U_2(\cdot,0), V_2(\cdot,0))$ and (3.19) holds, then

$$(U_1(\cdot,t), V_1(\cdot,t)) \geqslant_P (U_2(\cdot,t), V_2(\cdot,t)) \quad \text{for all } t > 0. \tag{3.20}$$

By the fact that initial data satisfying (3.19) is dense in E, we can show that for general initial data in E, if $(U_1(\cdot,0), V_1(\cdot,0)) >_P (U_2(\cdot,0), V_2(\cdot,0))$, then (3.20) holds.

It remains to show that if $(U_1(\cdot,0), V_1(\cdot,0)) >_P (U_2(\cdot,0), V_2(\cdot,0))$ and that both $U_{1,x}, V_{2,x}$ are non-negative and non-trivial, then

$$(U_1(\cdot,t), V_1(\cdot,t)) \gg_P (U_2(\cdot,t), V_2(\cdot,t)) \quad \text{for all } t > 0.$$

This follows from Lemma 3.6, provided it can be verified that

$$u_1(x,t) = (U_1)_x(x,t) > 0, \quad v_2(x,t) = (V_2)_x(x,t) > 0 \quad \text{for } 0 \leq x \leq L,\ 0 < t \leq T.$$

But this is an immediate consequence of the strong maximum principle applied to the equations of u_1 and v_2 separately. ∎

3.2. Global Dynamics of the Single Species Model. In this section, we generalize some known results about the following single species model, which is obtained by setting $v = 0$ in (3.1):

$$\text{(3.21)}\qquad \begin{cases} \theta_t = (D_1\theta_x - \alpha_1\theta)_x + f_1(x,t,\int_0^x \theta(s,t)\,ds, 0)\theta, & 0 < x < L,\ t > 0,\\ D_1\theta_x - \alpha_1\theta = 0, & x = 0, L,\ t > 0,\\ \theta(x,0) = \theta_0(x) \geq, \not\equiv 0, & 0 \leq x \leq L,\end{cases}$$

where $D_1 = D_1(x,t) > 0$, $\alpha_1 = \alpha_1(x,t)$, and f_1 are smooth and (**H**) holds.

The equation (3.21) generates a continuous semiflow in $C([0,L];\mathbb{R}_+)$ (see, e.g. [10]). Furthermore, by regarding the nonlocal term $f_1(x,t,\int_0^x \theta(s,t)\,ds, 0)$ as a given coefficient, we can view (3.21) as a linear non-autonomous parabolic equation. It follows from the classical maximum principle that $\theta(x,t) > 0$ for $x \in [0,L]$ and $t > 0$.

Define $\overline{\theta} \in C([0,\infty); C([0,L];\mathbb{R}_+)) \cap C^1((0,\infty); C^\infty([0,L];\mathbb{R}_+))$ to be a supersolution of (3.21) if

$$\text{(3.22)}\qquad \begin{cases} \overline{\theta}_t \geqslant_{\mathcal{K}_1} (D_1\overline{\theta}_x - \alpha_1\overline{\theta})_x + f_1\left(x,t,\int_0^x \overline{\theta}(s,t)\,ds, 0\right)\overline{\theta}, & t > 0,\\ D_1\overline{\theta}_x - \alpha_1\overline{\theta} = 0, & x = 0, L,\ t > 0.\end{cases}$$

And define $\underline{\theta}$ to be a subsolution of (3.21) if it satisfies the reverse inequality. As a by-product of the proofs of Lemmas 3.6 and 3.7, we can similarly show that the single species model is strongly monotone with respect to the order generated by cone $\mathcal{K}_1$.

COROLLARY 3.8. *Assume that f_1 satisfies* (**H**). *Let $\overline{\theta}$ and $\underline{\theta}$ be super- and subsolution of* (3.21) *such that*

$$\overline{\theta}(x,t) > 0, \quad \underline{\theta}(x,t) > 0, \quad \textit{in } [0,L]\times[0,T], \quad \textit{and} \quad \overline{\theta}(\cdot,0) \geqslant_{\mathcal{K}_1} \underline{\theta}(\cdot,0).$$

Then $\overline{\theta}(\cdot,t) \geqslant_{\mathcal{K}_1} \underline{\theta}(\cdot,t)$ for all $t > 0$. Furthermore, if for some $t_0 > 0$ we have $\overline{\theta}(\cdot,t_0) - \underline{\theta}(\cdot,t_0) \notin \operatorname{Int}\mathcal{K}_1$, then $\overline{\theta}(\cdot,t) \equiv \underline{\theta}(\cdot,t)$ for $t \in [0,t_0]$.

In particular, the continuous semiflow generated by (3.21) is strongly monotone with respect to the order induced by the cone $\mathcal{K}_1$.

In contrast to Corollary 3.8, we show here that the pointwise competitive order is not preserved by (3.21).

PROPOSITION 3.9. *For $i = 1,2$, let θ_i be a solution of* (3.21)*, with initial conditions $\theta_{i,0} \in \{\psi \in C^2([0,L]) : D_1\psi_x = \alpha_1\psi \text{ for } x = 0, L\}$. If*

$$\theta_{1,0} \leq, \not\equiv \theta_{2,0} \quad \textit{in } [0,L], \quad \textit{and} \quad \theta_{1,0} \equiv \theta_{2,0} \quad \textit{in } [L-\delta, L] \textit{ for some } \delta > 0,$$

then $\theta_1(L,t) > \theta_2(L,t)$ for all $0 < t \ll 1$.

Proof. Since the initial conditions are C^2 and consistent with the boundary condition, the solutions θ_i are of class $C^{2,1}_{x,t}$ in $[0,L]\times[0,\infty)$. Hence, it is enough to show that $(\theta_1)_t(L,0) > (\theta_2)_t(L,0)$. Precisely, at $(x,t) = (L,0)$,

$$\begin{aligned} (\theta_1)_t &= [D_1(\theta_1)_x - \alpha_1\theta_1]_x + f_1(L,0,\int_0^L \theta_1(s,0)\,ds, 0)\theta_1\\ &> [D_1(\theta_1)_x - \alpha_1\theta_1]_x + f_1(L,0,\int_0^L \theta_2(s,0)\,ds, 0)\theta_1\\ &= [D_1(\theta_2)_x - \alpha_1\theta_2]_x + f_1(L,0,\int_0^L \theta_2(s,0)\,ds, 0)\theta_2 = (\theta_2)_t. \end{aligned}$$

∎

To illustrate Proposition 3.9, we choose initial conditions $\{\theta_{i,0}\}_{i=1,2}$ so that

$$\theta_{1,0} \leqslant_{P_1} \theta_{2,0} \quad \text{and} \quad \theta_{1,0} \leqslant_{\mathcal{K}_1} \theta_{2,0},$$

but only the order with respect to $\mathcal{K}_1$ is preserved by the semiflow; see Figure 1.

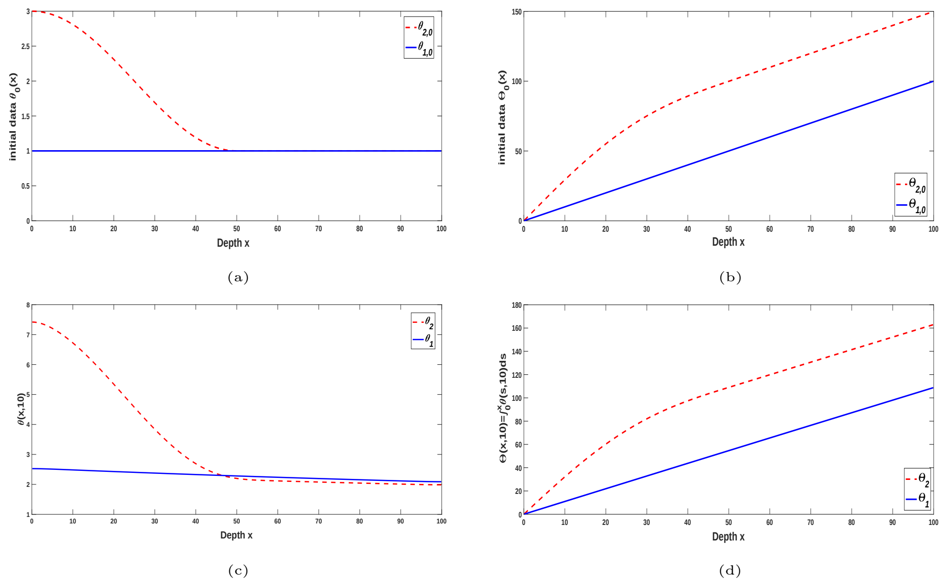

FIG. 1. *Numerical solution of (3.21), with $D_1 = 1$, $\alpha_1 = 0$, $L = 100$, $f_1(x,t,\Theta,0) = g(\exp(-k_0x - k_1\Theta))$, where $g(I) = \frac{I}{10+I}$ and $k_0 = k_1 = d = 0.001$, and initial condition $\theta_{1,0} = \chi_{[0,L/2]}(\cos(2\pi x/L) + 1) + 1$ and $\theta_{2,0} = 1$. Panels* (a) *and* (c) *are the population densities $\theta_i(x,t)$ $(i = 1,2)$ at times $t = 0$ and $t = 10$ resp.; Panels* (b) *and* (d) *are the initial cumulative distribution functions of population densities $\Theta_i(x,t) = \int_0^x \theta_i(s,t)\,ds$ $(i = 1,2)$ at times $t = 0$ and $t = 10$. The first (resp. second) species is represented by the red/dotted line (resp. blue/solid line).*

Remark 3.10. By choosing $u_i(\cdot,0) = \theta_{i,0}$ for $i = 1,2$, and $v_1(\cdot,0) \equiv v_2(\cdot,0) \equiv \epsilon$, then $(u_1(\cdot,0), v_1(\cdot,0)) \leq_P (u_2(\cdot,0), v_2(\cdot,0))$. However, it follows from the above result and continuous dependence on initial data that $(u_1(\cdot,t), v_1(\cdot,t)) \not\leq_P (u_2(\cdot,t), v_2(\cdot,t))$ for some $t > 0$.

As a consequence of monotone dynamical systems theory, one can show the uniqueness and global asymptotic stability of positive equilibria (in the case of autonomous semiflow) or positive periodic solution (in the case of time-periodic semiflow). We will show the latter here, as the former follows as an easy consequence.

The following eigenvalue problem will be useful for our later purposes:

$$(3.23)\qquad \begin{cases} \varphi_t = (D_1\varphi_x - \alpha_1\varphi)_x + f_1(x,t,0,0)\varphi + \mu\varphi, & 0 < x < L,\ 0 < t < T, \\ D_1\varphi_x - \alpha_1\varphi = 0, & x = 0, L,\ 0 < t < T, \\ \varphi(x,0) = \varphi(x,T), & 0 \leq x \leq L, \\ \varphi(x,t) > 0, & 0 \leq x \leq L,\ 0 \leq t \leq T. \end{cases}$$

It is well known (see, e.g., [11]) that (3.23) has a principal eigenvalue, denoted by μ_1, with the corresponding positive eigenfunction.

PROPOSITION 3.11. *Assume that f_1 satisfies* (**H**), *and let D_1, α_1, f_1 be T-periodic in t, and there exists $M_1 > 0$ such that*

$$(3.24)\qquad \sup_{[0,L]\times[0,T]} f_1(x,t,M_1,0) < 0 \quad \text{and} \quad \|f_1(\cdot,\cdot,\cdot,0)\|_{L^\infty([0,L]\times[0,T]\times[0,\infty))} \leq M_1.$$

Let μ_1 be the principal eigenvalue of (3.23)*.*

(a) *If $\mu_1 \geq 0$, then every solution of* (3.21) *converges to zero;*

(b) *If $\mu_1 < 0$, then* (3.21) *has a unique positive T-periodic solution. Furthermore, it attracts all non-negative, non-trivial solutions of* (3.21)*.*

In case $f_1(x,t,p,0) = g(I_0 \exp(-k_0 x - k_1 p)) - d(x,t)$ where $g(\cdot)$ satisfies (1.5), the condition (3.24) is clearly satisfied, and the above result generalizes all previous results [5, 7, 28, 31, 32]. Our main contribution is a short proof of the boundedness of trajectories, which has not been proven when all coefficients vary periodically with time. This allows the use of the concept of subhomogeneity to show the existence, uniqueness and global stability of positive steady state simultaneously.

Proof of Proposition 3.11. We will apply [37, Theorem 2.3.4] to prove this proposition. Let $\tilde{Q}_T$ be the Poincaré map of time T, generated by the T-periodic equation (3.21). It is obvious that the Poincaré map $\tilde{Q}_T$ is monotone by Corollary 3.8, and compact in $C([0,L])$ by parabolic estimate. Therefore, we need only to verify that every positive orbit of $\tilde{Q}_T$ in $C([0,L];\mathbb{R}_+)$ is bounded, $\tilde{Q}_T$ is strongly subhomogeneous, and the Fréchet derivative $\mathcal{D}\tilde{Q}_T(0)$ is compact and strongly positive.

Claim 1. The semiflow is point dissipative, i.e. there exists $M > 0$, independent of initial data, such that

$$\limsup_{t\to\infty} \|\theta(\cdot,t)\|_{C([0,L])} \leq M.$$

By the fact that $f_1(x,t,p,0)$ is uniformly bounded in L^∞, Harnack inequality [19, Theorem 2.5] applies, so that there is a uniform positive constant $C' > 0$ such that

$$\sup_{0<x<L} \theta(x,t) \leq C' \inf_{0<x<L} \theta(x,t) \qquad \text{for all } t \geq 1.$$

By (3.24), it is possible to choose a small constant $\delta_2 > 0$ such that

$$(3.25) \quad C' \int_0^{\delta_2} \max\{f_1(x,t,0,0), 0\}\, dx + \int_{\delta_2}^L f_1(x,t,M_1,0)\, dx < 0 \qquad \text{for } 0 \leq t \leq T.$$

It suffices to show that $\limsup_{t\to\infty} \int_0^L \theta\, dx \leq \max\{M_1, C'LM_1/\delta_2\}$. To this end, it is enough to show the following claim.

Claim 3.12. *The differential inequality*

$$\frac{d}{dt}\int_0^L \theta(x,t)\, dx \leq -\delta_3 \int_0^L \theta(x,t)\, dx$$

holds whenever $\int_0^L \theta(x,t)\, dx > \max\{M_1, C'LM_1/\delta_2\}$.

Now, denote $\theta_*(t) = \inf_x \theta(x,t)$ and $\theta^*(t) = \sup_x \theta(x,t)$, then

$$M_1 < \frac{\delta_2}{C'L}\int_0^L \theta(x,t)\, dx \leq \frac{\delta_2}{C'}\theta^*(t) \leq \delta_2 \theta_*(t).$$

Integrating the equation of θ over $(0,L)$, we obtain

$$
\begin{aligned}
&\frac{d}{dt}\int_0^L \theta(x,t)\,dx \\
&= \int_0^L f_1\left(x,t,\int_0^x \theta(s,t)\,ds,0\right)\theta(x,t)\,dx \\
&\le \int_0^L f_1(x,t,x\theta_*(t),0)\theta(x,t)\,dx \\
&\le \int_0^{\delta_2} f_1(x,t,0,0)\theta(x,t)\,dx + \int_{\delta_2}^L f_1(x,t,M_1,0)\theta(x,t)\,dx \\
&\le \theta^*(t)\int_0^{\delta_2} \max\{f_1(x,t,0,0),0\}\,dx + \int_{\delta_2}^L f_1(x,t,M_1,0)\,dx\,\theta_*(t) \\
&\le \left(C'\int_0^{\delta_2} \max\{f_1(x,t,0,0),0\}\,dx + \int_{\delta_2}^L f_1(x,t,M_1,0)\,dx\right)\theta_*(t) \\
&\le \left(C'\int_0^{\delta_2} \max\{f_1(x,t,0,0),0\}\,dx + \int_{\delta_2}^L f_1(x,t,M_1,0)\,dx\right)\frac{1}{C'L}\int_0^L \theta(x,t)\,dx\,.
\end{aligned}
$$

This proves the point dissipativity.

Claim 2. The Poincaré map is strongly subhomogeneous.

We will show that $\tilde{Q}_T$ is strongly subhomogeneous, i.e.

$$
\tilde{Q}_T(\lambda\theta_0) \gg_{\mathcal{K}_1} \lambda\tilde{Q}_T(\theta_0) \quad \text{for all } \theta_0 >_{P_1} 0 \text{ and } \lambda \in (0,1). \tag{3.26}
$$

Let $\theta(x,t)$ be solution to (3.21) with initial condition θ_0. For $(x,t) \in (0,L)\times[0,T]$,

$$
\begin{aligned}
(\lambda\theta)_t &= (D_1(\lambda\theta)_x - \alpha_1(\lambda\theta))_x + f_1(x,t,\int_0^x \theta(s,t)\,ds,0)(\lambda\theta) \\
&< (D_1(\lambda\theta)_x - \alpha_1(\lambda\theta))_x + f_1(x,t,\int_0^x \lambda\theta(s,t)\,ds,0)(\lambda\theta).
\end{aligned}
$$

i.e. $\lambda\theta$ is a subsolution to the (3.21) with initial condition $\lambda\theta_0$. Since the above inequality is strict, $\lambda\theta$ is not identically equal to the solution of (3.21) with initial condition $\lambda\theta_0$. By Corollary 3.8 and evaluate at time $t=T$, we deduce (3.26).

Claim 3. The Fréchet derivative $\mathcal{D}\tilde{Q}_T(0)$ is compact and strongly positive.

This follows directly from the fact that $\mathcal{D}\tilde{Q}_T(0) = Z(T)$, where $Z(t)$ is the analytic semigroup generated by the linearized system of (3.21) at $\theta = 0$:

$$
\begin{cases}
\theta_t = (D_1\theta_x - \alpha_1\theta)_x + f_1(x,t,0,0)\theta, & 0<x<L,\ t>0, \\
D_1\theta_x - \alpha_1\theta = 0, & x=0,L,\ t>0, \\
\theta(x,0) = \theta_0 \geqslant, \not\equiv 0, & 0<x<L.
\end{cases} \tag{3.27}
$$

That $Z(T)$ is strongly positive follows from standard parabolic maximum principle. Moreover, by standard parabolic L^p estimate, $Z(T)$ is a bounded map from $C([0,L])$ to $C^2([0,L])$. The map $Z(T)$ is thus compact, by the Arzelà-Ascoli Theorem.

If $\mu_1 \ge 0$, then $r(\mathcal{D}\tilde{Q}_T(0)) = \exp(-\mu_1 T) \le 1$. By [37, Theorem 2.3.4(a)], every solution of (3.21) converges to zero. If $\mu_1 < 0$, then $r(\mathcal{D}\tilde{Q}_T(0)) = \exp(-\mu_1 T) > 1$. By [37, Theorem 2.3.4(b)], the map $\tilde{Q}_T$ has a unique positive fixed point $\tilde{\vartheta}$ such that every positive orbit with non-negative, non-trivial, continuous initial data converges to $\tilde{\vartheta}$. This means that system (3.21) has a unique positive T-periodic solution $\tilde{\theta}$, determined by $\tilde{\theta}(\cdot,0) = \tilde{\theta}(\cdot,T) = \tilde{\vartheta}$, which attracts all non-negative and non-trivial solutions of (3.21). ∎

Remark 3.13. Within the context of a single species, we improved previous results in [28] by showing a strong maximum principle (which implies strong monotonicity of the semiflow) for super- and subsolutions (which satisfies only differential inequalities), and by allowing the coefficients to be space-time heterogeneous.

4. Global Dynamics for the Nonlocal Two-species Model. It is well known that diffusion and advection rates have significant effects on the outcome of competition. In this section, we apply Theorem 4.1 to analyze the global dynamics of two-species competition system. To obtain qualitative results, we restrict ourselves for the remainder of the paper to consider the autonomous case (1.1) - (1.3), when D_i, α_i, d_i are constants. In the introduction, the light intensity $I(x,t)$ is given by (1.4), where the shading coefficients of the two species are given by k_1, k_2. However, by transforming $(\tilde{u},\tilde{v}) = (k_1 u, k_2 v)$ and $\tilde{g}_i(I_0\cdot) = g_i(\cdot)$, and by observing that k_1, k_2 do not affect the dynamics qualitatively, we may assume $k_1 = k_2 = 1$ and $I_0 = 1$ without loss of generality, so that the light intensity (1.4) can be simplified to

$$I(x,t) = \exp\Big(-k_0 x - \int_0^x [u(s,t)+v(s,t)]ds\Big). \tag{4.1}$$

We focus on the following three different cases:

(i) $D_1 = D_2$, $\alpha_1 < \alpha_2$;

(ii) $D_1 < D_2$, $\alpha_1 = \alpha_2 \geq [g(1) - d]L > 0$;

(iii) $D_1 < D_2$, $\alpha_1 = \alpha_2 \leq 0$.

Due to the strongly monotonicity proved in Theorem 2.1, to a large extent, its dynamics can be determined by the stability/instability of the semi-trivial solution of the stationary problem [2,12,15,25,34,37]. For the convenience of the readers, we state the precise abstract theorem here.

THEOREM 4.1 ([15, Theorem B] and [25, Theorem 1.3]). *If the system* (1.1)-(1.4) *has no positive steady states, and the semi-trivial steady state* $(0,\tilde{v})$ (resp. $(\tilde{u},0)$) *is linearly unstable, then* $(\tilde{u},0)$ (resp. $(0,\tilde{v})$) *is globally asymptotically stable among all non-negative, non-trivial solutions.*

Remark 4.2. Our setting is slightly more general than that outlined in [15]. In particular, the semiflow Q_t generated by (3.1) is defined in $Y^+ = Y_1^+ \times Y_1^+$, where $Y_1^+ = C([0,L];\mathbb{R}_+)$, but the semiflow only preserve the order generated by the weaker cone $\mathcal{K} = \mathcal{K}_1 \times (-\mathcal{K}_1)$, with $Y_1^+ \subsetneq \mathcal{K}_1$. However, it is straightforward to observe that [15, Propositions 2.1 and 2.4] are independent of the above assumption, and that the proofs of [15, Theorem B] and [25, Theorem 1.3] both stand in our setting. Therefore, we omit the proof of Theorem 4.1 here.

In preparation to apply Theorem 4.1, we will demonstrate that the equation

$$\begin{cases} \theta_t = D\theta_{xx} - \alpha\theta_x + [g(e^{-k_0 x - \int_0^x \theta(s,t)\,ds}) - d]\theta = 0, & 0 < x < L, \\ D\theta_x - \alpha\theta = 0, & x = 0, L, \\ \theta(x,0) = \theta_0(x) \geq 0, & 0 \leq x \leq L, \end{cases} \tag{4.2}$$

has a unique positive steady state $\tilde{\theta}$, which is always linearly stable, and then characterize the stability of the two semi-trivial steady states in terms of two standard principal eigenvalue problems.

4.1. An Eigenvalue Problem for the Single Species Model. For constants $D > 0$, $\alpha \in \mathbb{R}$ and $h \in C([0, L])$, consider the following standard eigenvalue problem:

$$\begin{cases} D\phi_{xx} - \alpha\phi_x + h(x)\phi + \lambda\phi = 0, & 0 < x < L, \\ D\phi_x - \alpha\phi = 0, & x = 0, L. \end{cases} \tag{4.3}$$

By setting $\psi = e^{-(\alpha/D)x}\phi$, the problem (4.3) can be transformed into a self-adjoint problem

$$\begin{cases} -D(e^{(\alpha/D)x}\psi_x)_x - h(x)e^{(\alpha/D)x}\psi = \lambda e^{(\alpha/D)x}\psi, & 0 < x < L, \\ \psi_x(0) = \psi_x(L) = 0. \end{cases} \tag{4.4}$$

Therefore, all eigenvalues of (4.4) (and thus (4.3)) are real, and we can denote the smallest eigenvalue by $\lambda_1(D, \alpha, h)$. Define

$$d_* = -\lambda_1(D, \alpha, -g(e^{-k_0 x})).$$

It is easy to show that d_* is positive. In fact, d_* is the critical death rate.

THEOREM 4.3 ([5, Theorem 2.1], [13, Theorem 3.1]). *If $0 < d < d_*$, then (4.2) has a unique positive steady state, denoted by $\tilde{\theta}(x)$. If $d \geq d_*$, then zero is the only nonnegative steady state of (4.2).*

We linearize (4.2) at $\tilde{\theta}$ to obtain the following eigenvalue problem:

$$\begin{cases} D\phi_{xx} - \alpha\phi_x + [g(\sigma) - d]\phi - \tilde{\theta}\sigma g'(\sigma)\int_0^x \phi(s)\,ds + \mu\phi = 0, & 0 < x < L, \\ D\phi_x - \alpha\phi = 0, & x = 0, L, \end{cases} \tag{4.5}$$

where $\sigma = e^{-k_0 x - \int_0^x \tilde{\theta}(s)\,ds}$.

Our result says that $\tilde{\theta}$ is linearly stable. In fact, there is a real eigenvalue of (4.5) which is strictly less than the real part of all other eigenvalues of (4.5).

THEOREM 4.4. *Let $\tilde{\theta}$ be the unique positive steady state of (4.2). The eigenvalue problem (4.5) admits a real, simple eigenvalue μ_1 and an eigenfunction $\phi \gg_{\mathcal{K}_1} 0$, such that $\mu_1 < \operatorname{Re}\mu$ for all eigenvalues $\mu \neq \mu_1$. It is characterized as the unique eigenvalue of (4.5) with the eigenfunction $\phi >_{\mathcal{K}_1} 0$. Furthermore, $\mu_1 > 0$.*

Proof. Assume $\tilde{\theta}(x)$ is a positive steady state of (4.2), and let $\theta_0 \in C([0, L]; \mathbb{R})$. Then $\theta(\cdot, t) = \hat{\Phi}_t(\theta_0)$, where $\hat{\Phi}_t$ denotes the continuous semiflow generated by (4.2). Then $z(x, t) = \mathcal{D}\hat{\Phi}_t(\tilde{\theta})[\theta_0](x)$ satisfies the linear equation

$$z_t + \mathcal{L}z = 0, \quad z(0) = \theta_0. \tag{4.6}$$

where the unbounded operator

$$\mathcal{L} = -D\partial_{xx} + \alpha\partial_x - [g(\sigma) - d] + \tilde{\theta}\sigma g'(\sigma)\Big(\int_0^x \cdot\Big)$$

is defined on the domain

$$\mathrm{Dom}(\mathcal{L}) = \{z \in C^2((0, L)) \cap C^1([0, L]) : \mathcal{L}z \in C([0, L]), Dz_x - \alpha z\big|_{x=0,L} = 0\}.$$

According to [30, Proposition 3.1.4], the linear equation (4.6) generates an analytic semigroup $e^{-\mathcal{L}t}$ on $C([0, L])$. Thus $\mathcal{D}\hat{\Phi}_t(\tilde{\theta}) = e^{-\mathcal{L}t}$.

For $\theta_0 \in \mathcal{K}_1$, $\epsilon > 0$, the monotonicity of $\hat{\Phi}_t$ with respect to cone $\mathcal{K}_1$ implies

$$\frac{\theta(\cdot,t;\tilde{\theta}+\epsilon\theta_0)-\theta(\cdot,t;\tilde{\theta})}{\epsilon} = \frac{\hat{\Phi}_t(\tilde{\theta}+\epsilon\theta_0)-\hat{\Phi}_t(\tilde{\theta})}{\epsilon} \geqslant_{\mathcal{K}_1} 0.$$

Upon taking the limit as $\epsilon \to 0$, we get $\mathcal{D}\hat{\Phi}_t(\tilde{\theta})[\theta_0] \geqslant_{\mathcal{K}_1} 0$. In other words, $e^{-\mathcal{L}t} = \mathcal{D}\hat{\Phi}_t(\tilde{\theta})$ is a positive operator with respect to the order generated by cone $\mathcal{K}_1$ in the sense that $\mathcal{D}\hat{\Phi}_t(\tilde{\theta})\mathcal{K}_1 \subset \mathcal{K}_1$ holds for $t \geq 0$.

Next, we show that the analytic semigroup $e^{-\mathcal{L}t} = \mathcal{D}\hat{\Phi}_t(\tilde{\theta})$ is strongly positive with respect to the order generated by $\mathcal{K}_1$. To prove this, we only need to show that $\int_0^x z(s,t)\,ds > 0$ and $z(0,t) > 0$ for all $t > 0$. Since $e^{-\mathcal{L}t} = \mathcal{D}\hat{\Phi}_t(\tilde{\theta})$ is a positive operator with respect to cone $\mathcal{K}_1$, then $\int_0^x z(s,t)\,ds \geq 0$. Therefore, if $\int_0^x z(s,t)\,ds > 0$ does not hold, then there exists some $(x_0,t_0) \in (0,L] \times (0,\infty)$ such that $\int_0^{x_0} z(s,t_0)\,ds = 0$.

Let $\int_0^x z(s,t)\,ds = Z(x,t)$. Using the relation

$$[g(\sigma)-d]z - \tilde{\theta}\sigma g'(\sigma)Z = [(g(\sigma)-d)Z]' + k_0 g'(\sigma)\sigma Z,$$

we may integrate (4.6) over $(0,x)$ to obtain the differential inequality

$$Z_t - DZ_{xx} + \alpha Z_x - [g(\sigma)-d]Z = k_0\int_0^x g'(\sigma)\sigma Z\,ds \geq 0\,. \tag{4.7}$$

Since $\theta_0 \not\equiv 0$ and $Z(\cdot,0) \not\equiv 0$, then the strong maximum principle implies $Z(x,t) > 0$ for all $x \in (0,L)$ and $t > 0$, i.e., $x_0 = L$ and $Z(L,t_0) = 0$. Then $Z_t(L,t_0) \leq 0$, and by the boundary condition, we deduce $DZ_{xx}(L,t_0) - \alpha Z_x(L,t_0) = Dz_x(L,t_0) - \alpha z(L,t_0) = 0$. It follows from (4.7) that

$$0 \geq Z_t(L,t_0) = k_0\int_0^L g'(\sigma)\sigma Z\,ds. \tag{4.8}$$

Since $k_0 > 0$, $\sigma > 0$, $g'(\sigma) > 0$, then $Z(x,t_0) \equiv 0$ for all $x \in [0,L]$. Contradiction.

Hence, $Z(x,t) = \int_0^x z(s,t)\,ds > 0$ for all $t > 0$ and $x \in (0,L]$. Since $Z(0,t) \equiv 0$ and $Z(x,t)$ satisfies (4.7) for all $t > 0$, then $z(0,t) = Z_x(0,t) > 0$ for all $t > 0$ by the Hopf boundary lemma.

Therefore, for each $t > 0$, the operator $e^{-\mathcal{L}t}$ is compact and strongly positive on $C([0,L])$ with respect to the order generated by $\mathcal{K}_1$. It follows by standard arguments in [34, Ch. 7] that the elliptic eigenvalue problem (4.5) has a principal eigenvalue $\mu_1 \in \mathbb{R}$ with all the stated properties, except for $\mu_1 > 0$.

To show $\mu_1 > 0$, we suppose to the contrary that $\mu_1 \leq 0$ and use $\phi_1 \gg_{\mathcal{K}_1} 0$ to get

$$\tilde{\theta}\sigma g'(\sigma)\int_0^x \phi_1(s)\,ds > 0 \quad \text{for} \quad x \in (0,L].$$

Then (4.5) yields that

$$D\phi_{1,xx} - \alpha\phi_{1,x} + [g(\sigma)-d]\phi_1 + \mu_1\phi_1 > 0 \quad \text{for } 0 < x < L.$$

Next, we use the facts $\int_0^x \phi_1(s)\,ds > 0$ and $\tilde{\theta} > 0$ for $x \in [0,L]$, to obtain the constant $c > 0$ such that $\min_{[0,L]}(c\tilde{\theta} - \phi_1) = 0$. Then $\varphi = c\tilde{\theta} - \phi_1$ satisfies

$$\begin{cases} D\varphi_{xx} - \alpha\varphi_x + [g(\sigma)-d]\varphi + \mu_1\varphi < \mu_1 c\tilde{\theta} \leq 0 & \text{for } 0 < x < L, \\ D\varphi_x = \alpha\varphi & \text{for } x = 0, L, \\ \min_{[0,L]}\varphi = 0\,. \end{cases}$$

By the strict differential inequality and non-negativity of φ we must have $\varphi > 0$ in $(0, L)$ and that $\varphi(x_0) = 0$ for some $x_0 \in \{0, L\}$. But the Hopf boundary lemma says $\varphi_x(x_0) \neq 0$, which contradicts the boundary condition $\varphi_x(x_0) = \frac{\alpha}{D}\varphi(x_0) = 0$. ∎

4.2. Eigenvalue Problems for the Two-species Model. In this subsection, we study the linear eigenvalue problem of the two-species model associated with the stability of semi-trivial steady states.

We assume the parameters are chosen so that system (1.1)-(1.4) has two semi-trivial steady states $(\tilde{u}, 0)$ and $(0, \tilde{v})$ (e.g. if the death rates d_i are not too large). The associated linearized eigenvalue problem at $(\tilde{u}, 0)$ is

(4.9)
$$\begin{cases} D_1\phi_{xx} - \alpha_1\phi_x + [g_1(\sigma_1) - d_1]\phi - \tilde{u}\sigma_1 g_1'(\sigma_1)[\int_0^x \phi(s)\,ds + \int_0^x \varphi(s)\,ds] + \Lambda\phi = 0, \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad 0 < x < L, \\ D_2\varphi_{xx} - \alpha_2\varphi_x + [g_2(\sigma_1) - d_2]\varphi + \Lambda\varphi = 0, \qquad 0 < x < L, \\ D_1\phi_x - \alpha_1\phi = D_2\varphi_x - \alpha_2\varphi = 0, \qquad x = 0, L, \end{cases}$$

where $\sigma_1(x) = e^{-k_0 x - \int_0^x \tilde{u}(s)\,ds}$.

We shall exploit the fact that the second equation is decoupled from the first. Consider the following eigenvalue problem:

$$\text{(4.10)} \qquad \begin{cases} D_2\varphi_{xx} - \alpha_2\varphi_x + [g_2(\sigma_1) - d_2]\varphi + \lambda\varphi = 0, & 0 < x < L, \\ D_2\varphi_x - \alpha_2\varphi = 0, & x = 0, L. \end{cases}$$

As already discussed, (4.10) admits a real principal eigenvalue, denoted by $\lambda_u = \lambda_1(D_2, \alpha_2, g_2(\sigma_1) - d_2)$, which is simple, and its corresponding eigenfunction φ_1 does not change sign, and $\lambda_u < \lambda$ for all $\lambda \neq \lambda_u$. The stability properties of $(\tilde{u}, 0)$ are determined by the sign of λ_u, as the next result shows.

PROPOSITION 4.5. *The problem* (4.9) *has a principal eigenvalue* $\Lambda_1 \in \mathbb{R}$*, in the sense that* $\Lambda_1 \leq \operatorname{Re}\Lambda$ *for all eigenvalues* Λ *of* (4.9) *and that the corresponding eigenfunction can be chosen in* $\mathcal{K} \setminus \{(0, 0)\}$*. Furthermore,* (*denote* $Y_1^+ = C([0, L]; \mathbb{R}_+)$)

(a) *If the principal eigenvalue* λ_u *of* (4.10) *is positive, then* $\Lambda_1 > 0$*.*

(b) *If the principal eigenvalue* λ_u *of* (4.10) *is non-positive, then* $\Lambda_1 = \lambda_u \leq 0$ *and the corresponding eigenfunction can be chosen in* $\operatorname{Int}\mathcal{K}_1 \times (-\operatorname{Int} Y_1^+)$*.*

Proof. By Theorem 2.1, the semiflow $\{Q_t\}_{t\geq 0}$, generated by the system (1.1)-(1.4) is strongly monotone with respect to the cone $\mathcal{K}$. As a result, the linear problem at any steady state generates a semigroup that is monotone with respect to the cone $\mathcal{K}$. Therefore, by standard arguments in [34, Ch. 7], we deduce that the elliptic problem (4.9), obtained by linearizing (1.1)-(1.4) at the steady state $(\tilde{u}, 0)$, has a principal eigenvalue Λ_1 with the stated properties. In particular, we can choose the eigenfunction corresponding to Λ_1 from within $\mathcal{K} \setminus \{(0, 0)\}$.

Now, consider the case when the principal eigenvalue λ_u of (4.10) is positive. Let $\Lambda_1 \in \mathbb{R}$ be the principal eigenvalue of (4.9) with eigenfunction $(\phi_1, \varphi_1) \in \mathcal{K} \setminus \{(0, 0)\}$. We claim that $\Lambda_1 > 0$. There are two cases to consider: (i) $\varphi_1 \not\equiv 0$; (ii) $\varphi_1 = 0$.

In Case (i), (Λ_1, φ_1) furnishes an eigenpair of problem (4.10), the latter of which as smallest eigenvalue $\lambda_u > 0$. Thus, $\Lambda_1 \geq \lambda_u > 0$.

In Case (ii), (Λ_1, ϕ_1) furnishes an eigenpair of

(4.11)
$$\begin{cases} D_1\phi_{xx} - \alpha_1\phi_x + [g_1(\sigma_1) - d_1]\phi - \tilde{u}\sigma_1 g_1'(\sigma_1)\int_0^x \phi(s)\,ds + \Lambda\phi = 0, & 0 < x < L, \\ D_1\phi_x - \alpha_1\phi = 0, & x = 0, L. \end{cases}$$

By Theorem 4.4, (4.11) has a positive principal eigenvalue μ_1, and μ_1 is always positive. Hence, we must have $\Lambda_1 \geq \mu_1 > 0$. This finishes the proof in case $\lambda_u > 0$.

Next, let $\lambda_u \le 0$ and let $\varphi_1 \in (-\operatorname{Int} Y_1^+) \subset (-\operatorname{Int}\mathcal{K}_1)$ be the corresponding principal eigenfunction of (4.10). It remains to construct $\phi_1 \in \operatorname{Int}\mathcal{K}_1$ such that λ_u is an eigenvalue of (4.9) with eigenfunction $(\phi_1, \varphi_1) \in \operatorname{Int}\mathcal{K}_1 \times (-\operatorname{Int} Y_1^+)$. To that end, define the operator $\mathcal{L}_1 = -D_1\partial_{xx} + \alpha_1\partial_x - [g_1(\sigma_1) - d_1] + \tilde{u}\sigma_1 g_1'(\sigma_1)(\int_0^x \cdot)$. By Theorem 4.4, the spectrum $\sigma(\mathcal{L}_1) \subset \{z \in \mathbb{C} : \operatorname{Re} z > 0\}$. And hence for $\lambda_u \le 0$, 0 is not an eigenvalue of $\mathcal{L}_1 - \lambda_u\mathcal{I}$, and the problem

$$\begin{cases} \mathcal{L}_1\phi - \lambda_u\phi = -\tilde{u}\sigma_1 g_1'(\sigma_1)\int_0^x \varphi_1(s)\,ds, & 0 < x < L, \\ D_1\phi_x - \alpha_1\phi = 0, & x = 0, L, \end{cases}$$

has a unique solution ϕ_1. In fact, let $f = -\tilde{u}\sigma_1 g_1'(\sigma_1)\int_0^x \varphi_1(s)\,ds$, then $f > 0$ and

$$\phi_1 = (\mathcal{L}_1 - \lambda_u)^{-1} f = \int_0^\infty e^{\lambda_u t} S_t f\,dt,$$

where $S_t = e^{-\mathcal{L}_1 t}$ is the analytic semigroup generated by $\mathcal{L}_1$ (see, e.g. [9, Theorem 3, Sect. 7.4]). From the proof of Theorem 4.4, S_t is strongly positive with respect to the order generated by cone $\mathcal{K}_1$. Therefore, $S_t f \gg_{\mathcal{K}_1} 0$ for all $t > 0$, and

$$\phi_1 \geqslant_{\mathcal{K}_1} \int_1^\infty e^{\lambda_u t} S_t f\,dt \gg_{\mathcal{K}_1} 0.$$

By construction, we conclude that $\lambda_u \le 0$ is an eigenvalue of (4.9) with eigenfunction $(\phi_1, \varphi_1) \in \operatorname{Int}\mathcal{K}_1 \times (-\operatorname{Int} Y_1^+)$. Hence $\Lambda_1 \le \lambda_u \le 0$. On the other hand, let $(\tilde{\phi}, \tilde{\varphi})$ be the eigenfunction of Λ_1, then $\tilde{\varphi} \not\equiv 0$, since otherwise $(\Lambda, \tilde{\phi})$ is an eigenpair of (4.11), whence $\Lambda \ge \mu_1 > 0$, contradictions. Therefore, $\tilde{\varphi} \not\equiv 0$ and $(\Lambda_1, \tilde{\varphi})$ furnishes an eigenpair of (4.10). Thus $\Lambda_1 \ge \lambda_u$ as well. This completes the proof. ∎

The linearized eigenvalue problem at semi-trivial steady state $(0, \tilde{v})$ is

(4.12)
$$\begin{cases} D_1\phi_{xx} - \alpha_1\phi_x + [g_1(\sigma_2) - d_1]\phi + \tilde{\Lambda}\phi = 0, & 0 < x < L, \\ D_2\varphi_{xx} - \alpha_2\varphi_x + [g_2(\sigma_2) - d_2]\varphi + \tilde{\Lambda}\varphi = \tilde{v}\sigma_2 g_2'(\sigma_2)[\int_0^x \phi(s)\,ds + \int_0^x \varphi(s)\,ds], & \\ & 0 < x < L, \\ D_1\phi_x - \alpha_1\phi = 0, & x = 0, L, \\ D_2\varphi_x - \alpha_2\varphi = 0, & x = 0, L, \end{cases}$$

where $\sigma_2(x) = e^{-k_0 x - \int_0^x \tilde{v}(s)\,ds}$. Let $\lambda_v = \lambda_1(D_1, \alpha_1, g_1(\sigma_2) - d_1)$ denote the principal eigenvalue of the eigenvalue problem

$$\begin{cases} D_1\phi_{xx} - \alpha_1\phi_x + [g_1(\sigma_2) - d_1]\phi + \lambda\phi = 0, & 0 < x < L, \\ D_1\phi_x - \alpha_1\phi = 0, & x = 0, L. \end{cases} \tag{4.13}$$

It follows analogously that the stability properties of $(0, \tilde{v})$ are determined by λ_v.

PROPOSITION 4.6. *The problem* (4.12) *has a principal eigenvalue* $\tilde{\Lambda}_1 \in \mathbb{R}$, *in the sense that* $\tilde{\Lambda}_1 \le \operatorname{Re}\tilde{\Lambda}$ *for all eigenvalues* $\tilde{\Lambda}$ *of* (4.12) *and that the corresponding eigenfunction can be chosen in* $\mathcal{K}\backslash\{(0,0)\}$. *Furthermore, (denote* $Y_1^+ = C([0,L];\mathbb{R}_+)$*)*

(a) *If the principal eigenvalue* λ_v *of* (4.13) *is positive, then* $\tilde{\Lambda}_1 > 0$.

(b) *If the principal eigenvalue* λ_v *of* (4.13) *is non-positive, then* $\tilde{\Lambda}_1 = \lambda_v \le 0$ *and the corresponding eigenfunction can be chosen in* $\operatorname{Int} Y_1^+ \times (-\operatorname{Int}\mathcal{K}_1)$.

4.3. Auxilliary Eigenvalue Lemmas. In this subsection, we prove several useful lemmas concerning the principal eigenvalue $\lambda_1(D, \alpha, h)$ of (4.3) with positive eigenfunction ϕ_1. It can be shown that λ_1 and ϕ_1 are smooth functions of α and D (see, e.g., [1, Lemma 1.2]).

We will assume additionally the following:

(A) $h(x) \in C^1([0,L])$ such that $h'(x) < 0$ in $[0,L]$.

Set $\psi_1 = e^{-(\alpha/D)x}\phi_1$. Then ψ_1 satisfies

$$\begin{cases} D\psi_{1,xx} + \alpha\psi_{1,x} + h(x)\psi_1 + \lambda_1\psi_1 = 0, \quad 0 < x < L, \\ \psi_{1,x}(0) = \psi_{1,x}(L) = 0. \end{cases} \tag{4.14}$$

LEMMA 4.7. *If $h(x)$ satisfies* (A)*, then $\psi_{1,x} < 0$ in $(0,L)$.*

Proof. Multiplying (4.14) by $e^{(\alpha/D)x}$, we rewrite the resulting equation as

$$\begin{cases} D(e^{(\alpha/D)x}\psi_{1,x})_x + e^{(\alpha/D)x}\psi_1[h(x) + \lambda_1] = 0, \quad 0 < x < L, \\ \psi_{1,x}(0) = \psi_{1,x}(L) = 0. \end{cases} \tag{4.15}$$

Integrating (4.15) over $(0,L)$, we have

$$\int_0^L e^{(\alpha/D)x}\psi_1[h(x) + \lambda_1]\,dx = 0,$$

which implies that $h(x) + \lambda_1$ changes sign in $(0,L)$. Since $h(x)$ is strictly decreasing in $(0,L)$, then there exists a unique $x_0 \in (0,L)$ such that $h(x)+\lambda_1 > 0$ for $0 < x < x_0$ and $h(x) + \lambda_1 < 0$ for $x_0 < x < L$. Hence, by (4.15) we see that $(e^{(\alpha/D)x}\psi_{1,x})_x < 0$ for $0 < x < x_0$ and $(e^{(\alpha/D)x}\psi_{1,x})_x > 0$ for $x_0 < x < L$. That is, $e^{(\alpha/D)x}\psi_{1,x}$ is strictly decreasing in $(0,x_0)$, and strictly increasing in (x_0,L). Since $\psi_{1,x}(0) = \psi_{1,x}(L) = 0$, we have $\psi_{1,x} < 0$ in $(0,L)$. ∎

LEMMA 4.8. *If $h(x)$ satisfies* (A)*, then*

$$\frac{\partial\lambda_1}{\partial\alpha}(D,\alpha,h) > 0 \quad \text{for any } D > 0 \text{ and } \alpha \in \mathbb{R}.$$

The proof of Lemma 4.8 is similar to [13, Lemma 5.2], and we omit it here. The proof of the following Lemma 4.9 is similar to [13, Lemma 7.1] with some modifications. For the sake of completeness, we give the proof here in detail.

LEMMA 4.9. *If $h(x)$ satisfies* (A)*, then the following hold:*

(a) *$\frac{\partial\lambda_1}{\partial D}(D,\alpha,h) > 0$ for $D > 0$ and $\alpha \le 0$.*

(b) *If $\alpha \ge h(0)L$ and $\lambda_1(D^*,\alpha,h) = 0$ for some $D^* > 0$, then $\frac{\partial\lambda_1}{\partial D}(D^*,\alpha,h) < 0$.*

Proof. Recall that λ_1 and ψ_1 are smooth functions of D. For simplicity of notation, we denote $\frac{\partial\psi_1}{\partial D}$ by ψ_1', etc., where ψ_1 satisfies (4.14). Differentiating (4.14) with respect to D, we have

$$\begin{cases} D\psi'_{1,xx} + \psi_{1,xx} + \alpha\psi'_{1,x} + h(x)\psi_1' + \lambda_1'\psi_1 + \lambda_1\psi_1' = 0, \quad 0 < x < L, \\ \psi'_{1,x}(0) = \psi'_{1,x}(L) = 0. \end{cases} \tag{4.16}$$

Multiplying (4.16) by $e^{(\alpha/D)x}\psi_1$ and integrating the resulting equation in $(0,L)$, we have

$$\begin{aligned} &-D\int_0^L e^{(\alpha/D)x}\psi'_{1,x}\psi_{1,x}\,dx + \int_0^L e^{(\alpha/D)x}\psi_{1,xx}\psi_1\,dx + \int_0^L e^{(\alpha/D)x}h(x)\psi_1'\psi_1\,dx \\ &\quad +\lambda_1'\int_0^L e^{(\alpha/D)x}\psi_1^2\,dx + \lambda_1\int_0^L e^{(\alpha/D)x}\psi_1'\psi_1\,dx = 0. \end{aligned} \tag{4.17}$$

Similarly, multiplying (4.14) by $e^{(\alpha/D)x}\psi_1'$ and integrating it in $(0,L)$, we have

$$-D\int_0^L e^{(\alpha/D)x}\psi_{1,x}'\psi_{1,x}\,dx+\int_0^L e^{(\alpha/D)x}h(x)\psi_1'\psi_1\,dx+\lambda_1\int_0^L e^{(\alpha/D)x}\psi_1'\psi_1\,dx=0. \tag{4.18}$$

It follows from (4.17) and (4.18) that

$$\lambda_1'=\frac{-\int_0^L e^{(\alpha/D)x}\psi_{1,xx}\psi_1\,dx}{\int_0^L e^{(\alpha/D)x}\psi_1^2\,dx}. \tag{4.19}$$

By Lemma 4.7, we have $\psi_{1,x}<0$ in $(0,L)$. Hence, if $\alpha\leqslant 0$, then

$$\begin{aligned}\int_0^L e^{(\alpha/D)x}\psi_{1,xx}\psi_1 dx&=-\int_0^L \psi_{1,x}(e^{(\alpha/D)x}\psi_1)_x\,dx\\&=-\int_0^L e^{(\alpha/D)x}\psi_{1,x}\Big[\psi_{1,x}+(\alpha/D)\psi_1\Big]\,dx<0.\end{aligned} \tag{4.20}$$

Thus $\lambda_1'>0$ for any $\alpha\le 0$ and $D>0$. This proves (a).

On the other hand, if $\lambda_1(D^*,\alpha,h)=0$ for some $D^*>0$, then the corresponding eigenfunction ψ_1 satisfies

$$\begin{cases} D^*\psi_{1,xx}+\alpha\psi_{1,x}+h(x)\psi_1=0, & 0<x<L,\\ \psi_{1,x}(0)=\psi_{1,x}(L)=0.\end{cases} \tag{4.21}$$

Multiplying (4.21) by $e^{(\alpha/D^*)x}$, and integrating over $(0,L)$, we have

$$\int_0^L h(x)\psi_1(x)e^{(\alpha/D^*)x}\,dx=0.$$

Thus the decreasing function h must change sign, i.e. $h'(x)<0, h(0)>0$. Combining with $\psi_{1,x}<0$, we have

$$\int_0^x h(s)\psi_1(s)\,ds<\int_0^x h(0)\psi_1(s)\,ds<h(0)\int_0^x\psi_1(0)\,ds<h(0)\psi_1(0)L.$$

Next, we integrate (4.21) in $(0,x)$, to get

$$D^*\psi_{1,x}(x)+\alpha\psi_1(x)=\alpha\psi_1(0)-\int_0^x h(s)\psi_1(s)\,ds>[\alpha-h(0)L]\psi_1(0)\ge 0,$$

provided that $\alpha\ge h(0)L$. By virtue of (4.20), we obtain

$$\int_0^L e^{(\alpha/D^*)x}\psi_{1,xx}\psi_1\,dx=-\frac{1}{D^*}\int_0^L e^{(\alpha/D^*)x}\psi_{1,x}(D^*\psi_{1,x}+\alpha\psi_1)\,dx>0.$$

It follows then from (4.19) that $\frac{\partial\lambda_1}{\partial D}(D^*,\alpha,h)<0$. This proves (b). ∎

4.4. The Case $D_1=D_2$, $\alpha_1<\alpha_2$. To investigate whether stronger or weaker advection is more beneficial for species to win the competition in the two-species phytoplankton model, we assume the only phenotypic difference between them is the advection rate. To be more precise, we assume $D_1=D_2\equiv D>0$, $\alpha_1<\alpha_2$. For the rest of this paper, we assume two phytoplankton species have the same growth rates and death rates, i.e., $g_1(\cdot)=g_2(\cdot)\equiv g(\cdot)$ and $d_1=d_2\equiv d$.

Proof of Theorem 2.2. By Theorem 4.1, it suffices to establish, for system (1.1)-(1.4) (and that $k_1 = k_2 = I_0 = 1$), the linear instability of $(0, \tilde{v})$, and the non-existence of postive steady states.

Step 1. $(0, \tilde{v})$ is linearly unstable.

Recall that $\tilde{v}$ is the unique positive solution to

$$\begin{cases} D\tilde{v}_{xx} - \alpha_2 \tilde{v}_x + [g(\sigma_2) - d]\tilde{v} = 0, & 0 < x < L, \\ D\tilde{v}_x - \alpha_2 \tilde{v} = 0, & x = 0, L, \end{cases}$$

where $\sigma_2(x) = e^{-k_0 x - \int_0^x \tilde{v}(s)\, ds}$. Since $\tilde{v} > 0$ is a positive eigenfunction of (4.3) with $\alpha = \alpha_2$ and $h(x) = g(\sigma_2) - d$, we have $\lambda_1(D, \alpha_2, g(\sigma_2) - d) = 0$.

It follows from Proposition 4.6 that the stability of $(0, \tilde{v})$ is determined by the sign of the principal eigenvalue $\lambda_1(D, \alpha_1, g(\sigma_2) - d)$. Since $\alpha_1 < \alpha_2$, we may apply Lemma 4.8 to yield

$$\lambda_1(D, \alpha_1, g(\sigma_2) - d) < \lambda_1(D, \alpha_2, g(\sigma_2) - d) = 0.$$

Thus $(0, \tilde{v})$ is linearly unstable.

Step 2. The system (1.1)-(1.4) has no co-existence steady states.

Suppose to the contrary that (u^*, v^*) be a co-existence steady state of (1.1)-(1.4), then we have

$$\begin{cases} Du^*_{xx} - \alpha_1 u^*_x + [g(\sigma^*(x)) - d]u^* = 0, & 0 < x < L, \\ Dv^*_{xx} - \alpha_2 v^*_x + [g(\sigma^*(x)) - d]v^* = 0, & 0 < x < L, \\ Du^*_x - \alpha_1 u^* = 0, \text{ and } Dv^*_x - \alpha_2 v^* = 0, & x = 0,\, L, \end{cases}$$

where $\sigma^*(x) = \exp(-k_0 x - \int_0^x [u^*(s) + v^*(s)]\, ds)$. Let $h(x) = g(\sigma^*(x)) - d$ so that $h'(x) < 0$. Since $u^*(x) > 0, v^*(x) > 0$, then

$$\lambda_1(D, \alpha_1, h) = \lambda_1(D, \alpha_2, h) = 0.$$

This is in contradiction with Lemma 4.8, which says that λ_1 is strictly monotone increasing in α. Therefore, the system (1.1)-(1.4) has no co-existence steady state. ∎

4.5. The Case $D_1 < D_2$, $\alpha_1 = \alpha_2 \geq [g(1) - d]L$. In this and the next subsection, we explore the effect of diffusion on the outcome of competition. According to Lemma 4.9, the monotonicity of the principal eigenvalue $\lambda_1(D, \alpha, h)$ with respect to D also depends on the advection rate α. Here, we first consider that both species have large sinking rates, i.e., $\alpha_1 = \alpha_2 \equiv \alpha \geq [g(1) - d]L > 0$. (Note that $g(\cdot)$ satisfies (1.5) and as we assume that the semi-trivial steady states exist, so we always have $g(1) - d > 0$.)

Proof of Theorem 2.3. By Theorem 4.1, it suffices to establish, for system (1.1)-(1.4), the linear instability of $(\tilde{u}, 0)$, and the non-existence of positive steady states.

Step 1. $(\tilde{u}, 0)$ is linearly unstable.

First, we observe as before from the equation satisfied by $\tilde{u}$ that $\lambda_1(D_1, \alpha, g(\sigma_1) - d) = 0$, where $\sigma_1(x) = e^{-k_0 x - \int_0^x \tilde{u}(s)\, ds}$.

Since $D_1 < D_2$ and $\alpha \geq [g(1) - d]L$, we may apply Lemma 4.9(b) to yield

$$\lambda_1(D_2, \alpha, g(\sigma_1) - d) < \lambda_1(D_1, \alpha, g(\sigma_1) - d) = 0.$$

It follows from Proposition 4.5 that $(\tilde{u}, 0)$ is linearly unstable.

Step 2. The system (1.1)-(1.4) has no co-existence steady states.

Suppose to the contrary that (u^*, v^*) is a co-existence steady state of (1.1)-(1.4), then we deduce as before,

$$\lambda_1(D_1, \alpha, g(\sigma^*) - d) = \lambda_1(D_2, \alpha, g(\sigma^*) - d) = 0\,,$$

where $\sigma^*(x) = \exp(-k_0 x - \int_0^x [u^*(s) + v^*(s)]\, ds)$. But this is in contradiction with Lemma 4.9(b), which says that $D \mapsto \lambda_1(D, \alpha, g(\sigma^*) - d)$ has at most one positive root. Therefore, the system (1.1)-(1.4) has no co-existence steady state. ∎

4.6. The Case $D_1 < D_2$, $\alpha_1 = \alpha_2 \le 0$. This subsection is devoted to studying whether stronger or weaker diffusion is more beneficial when both species have buoyant rates. Precisely, we assume that $D_1 < D_2$, $\alpha_1 = \alpha_2 \equiv \alpha \le 0$.

Proof of Theorem 2.4. By Theorem 4.1, it suffices to establish, for system (1.1)-(1.4), the linear instability of $(0, \tilde{v})$, and the non-existence of positive steady states.
Step 1. $(0, \tilde{v})$ is linearly unstable.

First, we observe as before from the equation satisfied by $\tilde{v}$ that $\lambda_1(D_2, \alpha, g(\sigma_2) - d) = 0$, where $\sigma_2(x) = e^{-k_0 x - \int_0^x \tilde{v}(s)\, ds}$.

Since $D_1 < D_2$ and $\alpha \le 0$, we may apply Lemma 4.9(a) to yield

$$\lambda_1(D_1, \alpha, g(\sigma_2) - d) < \lambda_1(D_2, \alpha, g(\sigma_2) - d) = 0.$$

It follows from Proposition 4.6 that $(0, \tilde{v})$ is linearly unstable.
Step 2. The system (1.1)-(1.4) has no co-existence steady states.

We omit the details here as this is similar to Step 2 of the proofs of Theorems 2.3, where we use part (a) of Lemma 4.9 instead of part (b). This completes the proof. ∎

5. Discussion and Numerical Results. We investigate a nonlocal reaction-diffusion-advection system modeling the growth of two competing phytoplankton species in a eutrophic environment, where nutrients are in abundance and the species are limited by light only for their metabolism. We first demonstrate that the system does not preserve the competitive order in the pointwise sense (Remark 3.10). We introduce a special cone $\mathcal{K}$ involving cumulative distributions of the population densities, and a generalized notion of super- and subsolutions of (1.1)-(1.4), where the differential inequalities hold in the sense of the cone $\mathcal{K}$. A comparison principle is then established for the super- and subsolutions, which implies the monotonicity of the semiflow of (1.1)-(1.4) with respect to the cone $\mathcal{K}$ (Theorem 2.1). From a theoretical point of view, this paper introduces a new class of reaction-diffusion models with order-preserving property, which may be of independent interest [35].

A first application of the monotonicity result yields a simple proof of the existence and global attractivity of the unique positive steady state (or time-periodic solution) to the single species problem (Proposition 3.11). A second application concerns the dynamics of two competing phytoplankton species, as modeled by (1.1)-(1.4), in which sufficient conditions for local (Propositions 4.5 and 4.6) and global stability of semi-trivial steady states (Theorems 2.2-2.4) are obtained.

Consider system (1.1)-(1.4) and fix $D_1 < D_2$ and $\alpha_1 = \alpha_2 \equiv \alpha$. Theorems 2.3 and 2.4 say that $(\tilde{u}, 0)$ is globally asymptotically stable for $\alpha = 0$, and $(0, \tilde{v})$ is globally asymptotically stable for $\alpha = [g(1) - d]L$, which means there is an exchange of stability between the semi-trivial steady states as α varies from 0 to $[g(1) - d]L$. In this particular case, we conjecture that there exist two constants α_{min} and $\alpha_{\max}$ such that the following statements hold.

- When $\alpha \le \alpha_{min}$, the semi-trivial steady state $(\tilde{u}, 0)$ is globally asymptotically stable.

- When $\alpha_{min} < \alpha < \alpha_{max}$, there exists a unique positive steady state (u^*, v^*) which is globally asymptotically stable.
- When $\alpha \geq \alpha_{max}$, the semi-trivial steady state $(0, \tilde{v})$ is globally asymptotically stable.

In the following, we present some numerical result in support of this conjecture. See Figure 2.

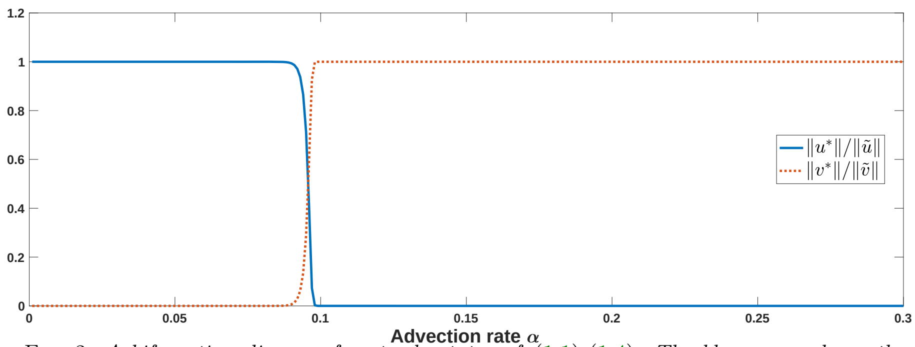

FIG. 2. *A bifurcation diagram for steady states of* (1.1)-(1.4). *The blue curve shows the ratio* $\|u^*\|_{L^1}/\|\tilde{u}\|_{L^1}$, *and the red curve shows the ratio* $\|v^*\|_{L^1}/\|\tilde{v}\|_{L^1}$ *as* α *varies from* 0 *to* 0.3, *where* (u^*, v^*) *is the stable steady state, and* $(\tilde{u}, 0)$ *and* $(0, \tilde{v})$ *are the two semi-trivial steady states. The parameters are chosen as* $D_1 = 1, D_2 = 5$, $d_1 = d_2 = 0.001$, $g_1(I) = g_2(I) = \frac{mI}{a+I}$, $m = 1$, $a = 10$, $I_0 = 1$, $k_0 = k_1 = k_2 = 0.001$, $L = 100$.

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