

COMPETITIVE EXCLUSION IN PHYTOPLANKTON COMMUNITIES IN A EUTROPHIC WATER COLUMN

ROBERT STEPHEN CANTRELL

Department of Mathematics
University of Miami
Coral Gables, FL 33146, USA

KING-YEUNG LAM*

Department of Mathematics
The Ohio State University
Columbus, OH 43210, USA

ABSTRACT. We analyze a reaction-diffusion system modeling the competition of multiple phytoplankton species which are limited only by light. While the dynamics of a single species has been well studied, the dynamics of the two-species model has only begun to be understood with the recent establishment of a comparison principle. In this paper, we show that the competition of N similar phytoplankton species, for any number N , generically leads to competitive exclusion. The main tool is the theory of a normalized principal bundle for linear parabolic equations.

1. Introduction. In this paper we analyze a reaction-diffusion model of the growth of multiple phytoplankton species in a eutrophic, vertical water column. In such environments nutrients are in abundance and the different phytoplankton species are typically limited by, and competing for, light only. Consider a water column with unit cross-sectional area and with N phytoplankton species, for some $N \geq 2$. Let x denote the depth within the water column where x varies from 0 (the water surface) to L (the bottom), and let $u_i(x, t)$ denote the population density of the i -th species at the location x and time t . The following model was proposed by Huisman et al [4, 5, 6].

$$\partial_t u_i = \mu_i \partial_{xx} u_i - \alpha_i \partial_x u_i + u_i [g_i(I(x, t)) - d_i] \quad \text{for } 0 < x < L, t > 0, \quad (1)$$

for $i = 1, \dots, N$, and with no-flux boundary conditions

$$\mu_i \partial_x u_i - \alpha_i u_i = 0 \quad \text{for } x = 0, L, t > 0, i = 1, \dots, N, \quad (2)$$

and initial data

$$u_i(x, 0) = u_{i,0}(x) \quad \text{for } 0 \leq x \leq L, i = 1, \dots, N. \quad (3)$$

2020 *Mathematics Subject Classification.* Primary: 35B51, 35K57, 47H07; Secondary: 92D25.

Key words and phrases. phytoplankton, competition, nonlocal reaction-diffusion systems, asymptotic behavior, multiple species.

RSC is partially supported by NSF grant DMS-1853478; KYL is partially supported by NSF grant DMS-1853561.

* Corresponding author: K.-Y. Lam.

Here $\mu_i > 0$ is the diffusion coefficient caused by turbulence, $\alpha_i \in \mathbb{R}$ is the sinking (if $\alpha_i < 0$) or buoyant (if $\alpha_i > 0$) velocity, $d_i > 0$ is the loss rate. The water column has vertical depth $L > 0$ and we denote $x = 0$ to be the water surface and $x = L$ to be the bottom. The term $g_i(I)$ represents the specific growth rate of the i -th phytoplankton species, which depends on the light intensity $I(x, t)$. By the Lambert-Beer law, the light intensity $I(x, t)$ takes the form

$$I(x, t) = I_0 e^{-k_0 x} \exp \left(-k_0 x - \sum_{j=1}^N k_j \int_0^x u_j(y, t) dy \right), \quad (4)$$

where $I_0 > 0$ is the incident light intensity, $k_0 > 0$ is the background turbidity, k_i is the absorption coefficient of the i -th phytoplankton species.

The system (1)-(4) is intended to model a eutrophic water column, where nutrient is in abundance, and phytoplankton species compete for light via shading. The integral appearing in (4) is due to the fact that the light is able to reach to depth x only after being absorbed by water and the biomass population at depth between 0 and x . In other words, the competition for light is nonlocal. The functions g_i are smooth and satisfy

$$g_i(0) = 0, \quad g'_i(I) > 0 \quad \text{for } I > 0 \quad \text{and } g_i \in L^\infty([0, \infty)). \quad (5)$$

Typical examples of g_i include

$$g_i(I) = \frac{m_i I}{a_i + I} \quad \text{and} \quad g_i(I) = \frac{m_i}{a_i} (1 - e^{-a_i I}),$$

where m_i, a_i are positive constants.

The dynamics of the single species model is well-understood, thanks to the order-preserving property that is satisfied by the cumulative distribution function $u^*(x, t) = \int_0^x u(y, t) dy$. This was first observed by Shigesada and Okubo [19] in the special case of ($k_0 = 0$), when the cumulative distribution function actually satisfies a closed equation without any nonlocal terms. This fact was exploited by Ishii and Takagi [12] to show that the flow retains the natural order in u^* , and derive the existence and global attractivity of the positive equilibrium. In the case with background turbidity ($k_0 > 0$), the global attractivity to equilibrium was first proved by Du and Hsu [2]. See also [15, 18] for the case with time-periodic forcing.

When there is no background turbidity ($k_0 = 0$), it can be shown [14] that the single phytoplankton species can persist in any finite water column. When there is background turbidity ($k_0 > 0$), Ebert et al. [3] illustrated the existence of a critical water column depth beyond which the single species cannot persist. This and related notions, such as critical diffusion rate and critical sinking rate, were subsequently analyzed by Hsu and Lou [11].

For multi-species competition, it was predicted by Huisman and Weissing [4, 5] that competitive exclusion occurs in well mixed environments. This is opposed to the apparent diversity of phytoplankton communities in nature, which is called the paradox of plankton [10]. For $N = 2$, the existence of a positive steady state and a uniform persistence result were established in [2]. In [13], a comparison principle was established for the two-species case, and competitive exclusion results were established. For $N \geq 3$, only the existence of positive steady state has been proved [16].

In this paper, we will introduce a method that is not contingent on the order-preserving property of the semiflow. As a result, we are able to determine the

global dynamical property of (1)-(4) for N species when $N \geq 3$. Our results say that competitive exclusion generically occurs for any number of species, provided that they are sufficiently similar. As an application, we generalize the results in [13] to N species. Mathematically, it is interesting that the global dynamics of arbitrarily many species can sometimes be determined. This is possible thanks to a novel result concerning the normalized principal bundle (see Proposition 2) which is proved in [1].

Biologically interpreted, the results in this paper and [13] suggest that an eutrophic environment in and of itself does not promote coexistence of phytoplankton species, and other factors, such as nutrient limitation, predation and seasonal forcing, might be important.

1.1. Main results. We make two assumptions to simplify our problem. The first main assumption is that the N species are sufficiently similar and are organized by a trade-off curve, in the sense that

$$\mu_i = \mu(z_i), \quad \alpha_i = \alpha(z_i), \quad d_i = d(z_i)$$

for some smooth functions $\mu(z), \alpha(z)$ and $d(z)$ depending on a trait parameter $z \in \mathbb{R}$ and $(z_i)_{i=1}^N$ is a strictly increasing sequence. For example, we will consider the case when $\mu = z$ varies across species, while $\alpha = \alpha_0$ and $d = d_0$ are constant; see Theorems 1.2–1.4. The second assumption is that the growth function $g(\cdot)$ is the same for all species. Next, by replacing $g(I_0 \cdot)$ by $g(\cdot)$ and u_i by u_i/k_i , we obtain the modified system

$$\begin{cases} \partial_t u_i = \mu_i \partial_{xx} u_i - \alpha_i \partial_x u_i + u_i [g(I(x, t)) - d_i] & \text{for } 0 < x < L, t > 0, 1 \leq i \leq N, \\ I(x, t) = \exp(-k_0 x - \sum_{j=1}^N \int_0^x u_j(y, t) dy) & \text{for } 0 < x < L, t > 0, \\ \mu_i \partial_x u_i - \alpha_i u_i = 0 & \text{for } x = 0, L, t > 0, 1 \leq i \leq N, \\ u_i(x, 0) = u_{i,0}(x) & \text{for } 0 \leq x \leq L, 1 \leq i \leq N, \end{cases} \quad (6)$$

where we assume

$$g(0) = 0, \quad g(+\infty) < +\infty, \quad g'(s) > 0 \quad \text{for } s \geq 0,$$

and

$$d^* < g(e^{-k_0 L}), \quad \text{where} \quad d^* = \sup_{z \in I} d(z). \quad (7)$$

Moreover, there exists $C_0 > 0$ such that

$$\frac{1}{C_0} \leq \mu(z) \leq C_0, \quad |\alpha(z)| \leq C_0, \quad 0 < d(z) \leq C_0 \quad \text{for all } z. \quad (8)$$

Condition (7) means that, in the absence of phytoplankton, the growth rate is everywhere positive, down to the bottom of the water column. This is used to prove Lemma 2.3, that the trivial equilibrium is repelling in some uniform sense.

We will prove that, in general, competitive exclusion takes place when the N species are similar. To state our theorem, we will introduce some notions from adaptive dynamics. Consider the single species problem

$$\begin{cases} \partial_t \theta = \mu(z) \partial_{xx} \theta - \alpha(z) \partial_x \theta + [g(I(x, t)) - d(z)] \theta & \text{for } 0 < x < L, t > 0, \\ \mu(z) \partial_x \theta - \alpha(z) \theta = 0 & \text{for } x = 0, L, t > 0, \\ u(x, 0) = u_0(x) & \text{for } x \in [0, L]. \end{cases} \quad (9)$$

Under the assumption (7), it is well-known [2, 15, 18] that, for each z , (9) has a unique positive equilibrium $\theta_z(x)$ that is globally asymptotically stable among all

positive solutions of (9). Suppose a species with trait value $\hat{z}$ is at equilibrium. A natural question is whether a species with a different trait $z \neq \hat{z}$ can invade this resident equilibrium when rare. The answer can be given in terms of the sign of the principal eigenvalue $\lambda(z, \hat{z})$ of the problem:

$$\begin{cases} \mu(z)\phi''(x) - \alpha(z)\phi'(x) + [g(\sigma^*(x)) - d(z)]\phi(x) + \lambda\phi(x) = 0 & \text{for } 0 < x < L, \\ \sigma^*(x) = \exp(-k_0x - \int_0^x \theta_{\hat{z}}(y) dy) & \text{for } 0 < x < L, \\ \mu(z)\phi'(x) - \alpha(z)\phi(x) = 0 & \text{for } x = 0, L. \end{cases} \quad (10)$$

The quantity $\lambda(z, \hat{z})$ is called the invasion exponent. When $\lambda(z, \hat{z}) < 0$, the rare invader with trait z can invade the resident with trait $\hat{z}$ successfully. When $\lambda(z, \hat{z}) > 0$, the invasion fails. Note that when $z = \hat{z}$, then the invasion exponent vanishes, as the equilibrium solution $\theta_{\hat{z}}$ is a positive eigenfunction corresponding to the zero eigenvalue. In particular, for $z \approx \hat{z}$, the invasion depends on the first derivative $\partial_z \lambda(z, \hat{z})|_{z=\hat{z}}$, which is called the selection gradient.

Theorem 1.1. *Suppose*

$$\partial_z \lambda(z, \hat{z})|_{z=\hat{z}} > 0 \quad \text{for some } \hat{z}. \quad (11)$$

Then there exists $\varepsilon > 0$ such that for arbitrary N and arbitrary increasing sequence $(z_i)_{i=1}^N \subset (\hat{z} - \varepsilon, \hat{z} + \varepsilon)$, every positive solution $(u_i)_{i=1}^N$ of (6) converges to the equilibrium $E_1 = (\theta_{z_1}, 0, \dots, 0)$ as $t \rightarrow \infty$.

Remark 1. The case $\partial_z \lambda(z, \hat{z})|_{z=\hat{z}} < 0$ can be transformed to $\partial_z \lambda(z, \hat{z})|_{z=\hat{z}} > 0$, by replacing z with $-z$. One can then argue similarly to show the global asymptotic stability of the equilibrium $E_N = (0, \dots, 0, \theta_{z_N})$.

As applications, we present three sufficient conditions in which the condition (11) is verified. The first result says that, other things held constant, then the most buoyant species wins.

Theorem 1.2. *Suppose*

$$\mu(z) = \mu_0 > 0, \quad \alpha(z) = z, \quad d(z) = d_0.$$

Then for each $\hat{z} \in \mathbb{R}$, there exists $\varepsilon > 0$ such that for any N and increasing sequence $(z_i)_{i=1}^N \subset (\hat{z} - \varepsilon, \hat{z} + \varepsilon)$, every positive solution of (6) converges to the equilibrium $E_1 := (\theta_{z_1}, 0, \dots, 0)$.

The second result says that, if all the species are buoyant with the same buoyancy velocity, then the slowest diffusing species wins.

Theorem 1.3. *Suppose*

$$\mu(z) = z, \quad \alpha(z) = \alpha_0, \quad d(z) = d_0.$$

If $\alpha_0 \leq 0$, then for each $\hat{z} > 0$, there exists $\varepsilon > 0$ such that for any N and increasing sequence $(z_i)_{i=1}^N \subset (\hat{z} - \varepsilon, \hat{z} + \varepsilon)$, every positive solution of (6) converges to the equilibrium $E_1 := (\theta_{z_1}, 0, \dots, 0)$.

The third result says that, if all the species are sinking with the same velocity, and that velocity is large enough, then the fastest diffusing species wins.

Theorem 1.4. *Suppose*

$$\mu(z) = z, \quad \alpha(z) = \alpha_0, \quad d(z) = d_0.$$

If $\alpha_0 \geq [g(1) - d_0]L$, then for each $\hat{z} > 0$, there exists $\varepsilon > 0$ such that for any N and increasing sequence $(z_i)_{i=1}^N \subset (\hat{z} - \varepsilon, \hat{z} + \varepsilon)$, every positive solution of (6) converges to the equilibrium $E_N := (0, \dots, 0, \theta_{z_N})$.

Remark 2. In [13], the case $N = 2$ was considered and the conclusion of Theorems 1.2-1.4 hold without the smallness condition on ε .

The rest of the paper is organized as follows: In Section 2, we derive some uniform bounds for positive solutions to the time-dependent problem (6). In Section 3, we use the smallness of ε to show that for any positive solutions $(u_i)_{i=1}^N$ of (6), the total population $\sum_{i=1}^N u_i$ eventually enters a neighborhood of the positive equilibrium of the single species problem. In Section 4, we introduce the notion of normalized principal bundle, which is a generalized notion of principal eigenvalue for elliptic or periodic-parabolic operators. In Section 5, we prove a general exclusion criterion and then give the proof of Theorem 1.1. Finally, we illustrate our main result by proving Theorems 1.2-1.4 in Section 6.

2. A priori estimates. Define

$$G(s) = \int_0^s g(e^{-\tau}) d\tau - d_* s, \quad \text{where } d_* = \inf_{z \in I} d(z). \quad (12)$$

Then $G(0) = 0$, $G'(s) = g(e^{-s}) - d_*$, and, since $G'(+\infty) = -d_* < 0$, there exists $M_1 > 0$ such that

$$G(s) < 0 \quad \text{for } s \geq M_1. \quad (13)$$

In the following we will also denote

$$\hat{u}(x, t) = \sum_{i=1}^N u_i(x, t), \quad U_i(x, t) := \int_0^x u_i(y, t) dy \quad \text{and} \quad \hat{U}(x, t) = \sum_{i=1}^N U_i(x, t).$$

Lemma 2.1. Let $(u_i)_{i=1}^N$ be a non-negative solution of (6) such that

$$\sum_{i=1}^N \|u_i(x, 0)\|_{L^1([0, L])} \leq M,$$

then

$$\begin{cases} \sup_{t \geq 0} \sum_{i=1}^N \|u_i(x, t)\|_{L^1([0, L])} \leq \max\{M, M_1\}, \\ \limsup_{t \rightarrow \infty} \sum_{i=1}^N \|u_i(x, t)\|_{L^1([0, L])} \leq M_1. \end{cases} \quad (14)$$

Proof. Integrating (6) with respect to x from 0 to L , and adding i from 1 to N , we obtain

$$\begin{aligned} \frac{d}{dt} \hat{U}(L, t) &= \int_0^L \sum_{i=1}^N [g(\exp(-k_0 x - \hat{U}(x, t))) - d_i] u_i(x, t) dx \\ &\leq \int_0^L [g(\exp(-\hat{U}(x, t))) - d_*] \partial_x \hat{U}(x, t) dx \\ &= \int_0^L \partial_x [G(\hat{U}(x, t))] dx = G(\hat{U}(L, t)), \end{aligned}$$

where we used $G(0) = 0$ and $\hat{U}(0, t) = 0$ in the last equality. Since $G(s) < 0$ for $s \geq M_1$, it is not difficult to deduce (14) from the above differential inequality. $\square$

Lemma 2.2. *There exists C_1 such that for any N and any $(z_i)_{i=1}^N \subset I$, every positive solution $(u_i)_{i=1}^N$ (6) satisfies*

$$\limsup_{t \rightarrow \infty} \sum_{i=1}^N \|u_i(x, t)\|_{C^{2+\alpha, 1+\alpha/2}([0, L] \times [t, t+1])} \leq C_1, \quad (15)$$

where C_1 depends on C_0 from (8), but does not depend on the number N and the initial data.

Proof. Fix an arbitrary positive solution $(u_i)_{i=1}^N$ of (6). By Lemma 2.1,

$$\limsup_{t \rightarrow \infty} \sum_{i=1}^N \|u_i\|_{L^1([0, L] \times [t, t+3])} \leq 3M_1,$$

so there exists $T_0 > 0$ such that

$$\sum_{j=1}^N \|u_j\|_{L^1([0, L] \times [t, t+3])} \leq 4M_1 \quad \text{for } t \geq T_0.$$

Observe that the equation of u_i can be regarded as a linear parabolic equation with non-autonomous coefficients:

$$\partial_t u_i - \mu_i \partial_{xx} u_i - \alpha_i \partial_x u_i = \tilde{\sigma}_i(x, t) u_i, \quad (16)$$

where

$$\tilde{\sigma}_i(x, t) = g(\exp(-k_0 x - \hat{U}(x, t))) - d_i \in L^\infty([0, L] \times [0, \infty)).$$

We can apply the uniform Harnack inequality [8, Theorem 2.5] to deduce that

$$\sup_{0 < x < L} u_i(x, t) \leq C_H \inf_{0 < x < L} u_i(x, t) \quad \text{for } t \geq 1. \quad (17)$$

where C_H does not depend on i and the initial data. Then, we have

$$\|u_i\|_{L^\infty([0, L] \times [t, t+3])} \leq C \|u_i\|_{L^1([0, L] \times [t, t+3])} \leq C \quad \text{for } t \geq 1. \quad (18)$$

Next, we apply the Sobolev embedding theorem and the parabolic L^p estimate to the linear parabolic equation to improve the above estimate to

$$\begin{aligned} \|u_i\|_{C^{\alpha, \alpha/2}([0, L] \times [t+1, t+3])} &\leq C' \|u_i\|_{W^{2+p, 1+p}([0, L] \times [t+1, t+3])} \\ &\leq C \|u_i\|_{L^\infty([0, L] \times [t, t+3])} \leq C \|u_i\|_{L^1([0, L] \times [t, t+3])}. \end{aligned} \quad (19)$$

Then $\tilde{\sigma}_i(x, t)$ in (16) is Hölder continuous, so that by parabolic Schauder estimate, the above can then be improved to

$$\|u_i\|_{C^{2+\alpha, 1+\alpha/2}([0, L] \times [t+2, t+3])} \leq C \|u_i\|_{L^1([0, L] \times [t, t+3])}. \quad (20)$$

The desired conclusion follows by summing i from 1 to N , and taking supremum for $t \geq T_0$ to obtain

$$\sum_{j=1}^N \|u_j\|_{C^{2+\alpha, 1+\alpha/2}([0, L] \times [T_0+2, \infty))} \leq C \sup_{t \geq T_0} \sum_{j=1}^N \|u_j\|_{L^1([0, L] \times [t, t+3])} \leq 4CM_1.$$

Note that all the constants are independent of N and $(z_i)_{i=1}^N$, thanks to the assumption (8). This completes the proof. $\square$

Lemma 2.3. *There exists a constant $\delta_0 > 0$ such that for any positive solution $(u_i)_{i=1}^N$ of (6), we have*

$$\liminf_{t \rightarrow \infty} \left[\inf_{0 < x < L} \sum_{i=1}^N u_i(x, t) \right] \geq \delta_0.$$

Proof. Let $(u_i)_{i=1}^N$ be a positive solution of (6). Integrating (6) with respect to $x \in [0, L]$ and adding i from 1 to N , we have

$$\begin{aligned} \frac{d}{dt} \hat{U}(L, t) &\geq \int_0^L [g(e^{-k_0 x - \hat{U}(x, t)}) - d^*] \sum_{i=1}^N u_i(x, t) dx \\ &= \int_0^L \partial_x [\tilde{G}(k_0 x + \hat{U}(x, t)) - \tilde{G}(k_0 x)] dx \\ &\quad + k_0 \int_0^L [g(e^{-k_0 x}) - g(e^{-k_0 x - \hat{U}(x, t)})] dx \\ &\geq \tilde{G}(k_0 L + \hat{U}(L, t)) - \tilde{G}(k_0 L) \end{aligned} \quad (21)$$

where $\tilde{G}(s) = \int_0^s g(e^{-\tau}) d\tau - d^* s$. Note that the last inequality follows from the fact that $g'(s) > 0$ for $s > 0$.

Observe now that, by (7),

$$\tilde{G}'(k_0 L) = g(e^{-k_0 L}) - d^* > 0.$$

Hence there exists $\delta_1 > 0$ such that $\tilde{G}(k_0 L + s) - \tilde{G}(k_0 L) > 0$ for $s \in (0, \delta_1]$. Since the mapping $t \mapsto \hat{U}(L, t)$ satisfies the differential inequality (21), it follows that

$$\liminf_{t \rightarrow \infty} \sum_{i=1}^N \|u_i\|_{L^1[0, L]} = \liminf_{t \rightarrow \infty} \hat{U}(L, t) \geq \delta_1.$$

By applying Harnack inequality (17) once again, we can convert the above lower estimate of L^1 integral to the desired pointwise estimate. This proves the lemma. $\square$

3. A rough estimate.

Proposition 1. *For each $\eta > 0$, there exists $\varepsilon > 0$ such that for any $N \in \mathbb{N}$ and $(z_i)_{i=1}^N \in (\hat{z} - \varepsilon, \hat{z} + \varepsilon)$, any positive solution of (6) satisfies*

$$\limsup_{t \rightarrow \infty} \left\| \sum_{i=1}^N u_i(\cdot, t) - \theta_{\hat{z}}(\cdot) \right\|_{C([0, L])} < \eta. \quad (22)$$

Proof. Denote for simplicity $\hat{\mu} = \mu(\hat{z})$ and $\hat{\alpha} = \alpha(\hat{z})$. Let a positive solution $(u_i)_{i=1}^N$ of the time-dependent problem (6) be given. Our goal is to show (22).

Suppose to the contrary that there is $\eta_0 > 0$ such that for $k \in \mathbb{N}$, there exists $N_k \in \mathbb{N}$, and sequences $\{\mu_i^k\}_{i=1}^{N_k}$, $\{\alpha_i^k\}_{i=1}^{N_k}$ and a positive solution $(u_i^k)_{i=1}^{N_k}$ such that

$$\sup_i (|\mu_i^k - \hat{\mu}| + |\alpha_i^k - \hat{\alpha}|) < \frac{1}{k}, \quad \limsup_{t \rightarrow \infty} \left\| \hat{U}^k(x, t) - \theta_{\hat{z}}(x) \right\|_{C([0, L])} \geq \eta_0,$$

where $\hat{U}^k(x, t) = \sum_{i=1}^{N_k} u_i^k(x, t)$. We can infer that for each k , there exists $\{t_j^k\}_j \rightarrow \infty$ such that

$$\inf_{j \geq 1} \|\hat{U}^k(x, t_j^k) - \theta_{\hat{z}}\|_{C([0, L])} \geq \eta_0, \quad \text{for each } k \geq 1.$$

By the a priori estimate established in Lemma 2.2, we can pass to a subsequence so that

$$\hat{U}_j^k(x, t) := \hat{U}^k(x, t + t_j^k) \rightarrow \hat{U}_\infty^k(x, t) \quad \text{as } j \rightarrow \infty \text{ in } C_{loc}([0, L] \times \mathbb{R}),$$

where $\hat{U}_\infty^k$ is some entire solution of (6) satisfying

$$\|\hat{U}_\infty^k(x, 0) - \theta_{\hat{z}}(x)\|_{C([0, L])} \geq \eta_0, \quad (23)$$

By Lemma 2.3 and by possibly taking a smaller η_0 , we may also assume that

$$\inf_{0 < x < L} \hat{U}_\infty^k(x, t) \geq \eta_0, \quad (24)$$

Now, since the estimate of Lemma 2.2 is independent of N , there is C_1 independent of k such that

$$\|\hat{U}_\infty^k\|_{C^{2+\alpha, 1+\alpha/2}([0, L] \times \mathbb{R})} \leq C_1 \quad (25)$$

Hence we can again pass to the limit to assume that, as $k \rightarrow \infty$, the sequence $\{\hat{U}_\infty^k\}_k$ converges in $C_{loc}([0, L] \times \mathbb{R})$ to some bounded entire solution U_∞ of the single species equation (9) with $z = \hat{z}$. Moreover, by (23) and (24), U_∞ satisfies

$$\|U_\infty(x, 0) - \theta_{\hat{z}}(x)\|_{C([0, L])} \geq \eta_0, \quad (26)$$

and

$$\inf_{0 < x < L} U_\infty(x, t) \geq \eta_0. \quad (27)$$

But this is in contradiction with the fact that the equilibrium solution $\theta_{\hat{z}}(x)$ attracts all positive solutions of (9). $\square$

4. The normalized principal bundle. In this section, we define the notion of a normalized principal bundle, which is a generalization of the notion of principal eigenfunction of an elliptic, or periodic-parabolic operator. We state a theorem concerning its smooth dependence on parameters.

4.1. The normalized principal bundle. Given three constants, $\mu, d > 0$, $\alpha \in \mathbb{R}$ and a function $h(x, t) \in C^{\beta, \beta/2}([0, L] \times \mathbb{R})$, we say that the pair $(\Psi_1(x, t), H_1(t))$ is the corresponding normalized principal bundle if it satisfies

$$\begin{cases} \begin{cases} \partial_t \Psi_1(x, t) - \mu \partial_{xx} \Psi_1(x, t) + \alpha \partial_x \Psi_1(x, t) - h(x, t) \Psi_1(x, t) + d \Psi_1(x, t) \\ \quad = H_1(t) \Psi_1(x, t) \end{cases} & \text{for } 0 < x < L, t \in \mathbb{R}, \\ \mu \partial_x \Psi_1(x, t) - \alpha \Psi_1(x, t) = 0 & \text{for } x \in \{0, L\}, t \in \mathbb{R}, \\ \int_D |e^{-\alpha x / \mu} \Psi_1(x, t)|^2 dx = 1 & \text{for } t \in \mathbb{R}, \\ \Psi_1(x, t) > 0 & \text{for } x \in [0, L], t \in \mathbb{R}. \end{cases} \quad (28)$$

Letting $\psi_1(x, t) := e^{-\alpha x / \mu} \Psi_1(x, t)$, the above problem can be transformed to

$$\begin{cases} \begin{cases} \partial_t \psi_1(x, t) - \mu \partial_{xx} \psi_1(x, t) - \alpha \partial_x \psi_1(x, t) - h(x, t) \psi_1(x, t) + d \psi_1(x, t) \\ \quad = H_1(t) \psi_1(x, t) \end{cases} & \text{for } 0 < x < L, t \in \mathbb{R}, \\ \partial_\nu \psi_1(x, t) = 0 & \text{for } x \in \{0, L\}, t \in \mathbb{R}, \\ \int_D |\psi_1(x, t)|^2 dx = 1 & \text{for } t \in \mathbb{R}, \\ \psi_1(x, t) > 0 & \text{for } x \in [0, L], t \in \mathbb{R}. \end{cases} \quad (29)$$

The existence and uniqueness of $(\psi_1(x, t), H_1(t))$ are proved in [17] (see also [8, 9] or [1, Theorem A1] for details).

Remark 3. By the uniform Harnack inequality (see [8, Theorem 2.5]) together with the normalization $\int_0^L |e^{-\alpha x / \mu} \Psi_1(x, t)|^2 dx = 1$ for $t \in \mathbb{R}$, it follows that for each $\delta > 0$ there is $C = C_\delta > 0$ such that if

$$\mu, d \in [\delta, 1/\delta], \quad |\alpha| + \|h(x, t)\|_{C([0, L] \times \mathbb{R})} \leq 1/\delta,$$

then

$$\frac{1}{C_\delta} \leq \Psi_1(x, t) \leq C_\delta \quad \text{in } [0, L] \times \mathbb{R}.$$

Remark 4. The notion of principal bundle is a natural generalization of the notion of principal eigenvalue and eigenfunction. If $h(x, t) = \hat{h}(x)$ for some time-independent function $\hat{h}$, then ψ_1 and H_1 are time-independent, i.e.

$$\Psi_1 = \hat{\psi}(x) \quad \text{and} \quad H_1 = \hat{\lambda}.$$

Moreover, $\hat{\psi}(x)$ and $\hat{\lambda}$ are the principal eigenfunction and principal eigenvalue of the elliptic problem

$$\begin{cases} -\mu\hat{\psi}''(x) + \alpha\hat{\psi}'(x) - (\hat{h}(x) - d)\hat{\psi}(x) = \hat{\lambda}\hat{\psi}(x) & \text{for } 0 < x < L, \\ \mu\hat{\psi}'(x) - \alpha\hat{\psi}(x) = 0 & \text{for } x = 0, L. \end{cases} \quad (30)$$

The main result of this section is the smooth dependence of the principal bundle on the coefficients.

Proposition 2. *The normalized principal bundle, as a mapping from*

$$\begin{aligned} (\mu, \alpha, d, h) &\mapsto (\Psi_1, H_1) \\ \mathbb{R}_+ \times \mathbb{R} \times \mathbb{R}_+ \times C^{\beta, \beta/2}([0, L] \times \mathbb{R}) &\rightarrow C^{2+\beta, 1+\beta/2}([0, L] \times \mathbb{R}) \times C^{1+\beta/2}(\mathbb{R}), \end{aligned}$$

is smooth.

Proof. We refer to [1, Proposition A.2] for details. $\square$

Corollary 1. *For given $\hat{z}, z \in I$, let $\lambda(z, \hat{z})$ and $\hat{\psi}(x; z, \hat{z})$ be the principal eigenvalue and eigenfunction of (10). Suppose $\partial_z \lambda(z, \hat{z})|_{z=\hat{z}} > 0$ (resp. $\partial_z \lambda(z, \hat{z})|_{z=\hat{z}} < 0$). There exists $\eta' > 0$ such that for any z and any function $h(x, t) \in C^{\beta, \beta/2}([0, L] \times \mathbb{R})$, if*

$$|z - \hat{z}| < \eta', \quad \text{and} \quad \|h(x, t) - \hat{h}(x)\|_{C^{\beta, \beta/2}([0, L] \times \mathbb{R})} < \eta', \quad (31)$$

where

$$\hat{h}(x) := g(\exp(-k_0 x - \int_0^x \theta_{\hat{z}}(y) dy)), \quad (32)$$

then the normalized principal bundle $(\Psi_1(x, t; z, h), H_1(t; z, h))$ of (28), corresponding to the choice $(\mu(z), \alpha(z), h(x, t))$, is a smooth function from $I \times C^{\beta, \beta/2}([0, L] \times \mathbb{R}) \rightarrow C^{1+\beta/2}(\mathbb{R})$. Furthermore, it satisfies

$$\partial_z H_1(t; z) \geq \eta' \quad (\text{resp. } \partial_z H_1(t; z) \leq -\eta') \quad \text{for all } t \in \mathbb{R}, z \in (\hat{z} - \eta', \hat{z} + \eta'),$$

where $\partial_z H_1(t; z, h)$ is the partial derivative of $H_1(t; z, h)$ with respect to the scalar parameter z .

Proof. Since the mappings $z \mapsto (\mu(z), \alpha(z), d(z))$, and $(\mu, \alpha, d, h) \mapsto (\Psi_1, H_1)$ are smooth, so is their composition $(z, h) \mapsto (\Psi_1, H_1)$. It remains to show the second part of the corollary.

Consider $\partial_z \lambda(z, \hat{z})|_{z=\hat{z}} > 0$. By Remark 4, we see that

$$(\Psi_1(x, t; z, \hat{h}), H_1(t; z, \hat{h})) = (\phi(x), \lambda(z, \hat{z}))$$

where $(\phi(x), \lambda(z, \hat{z}))$ is the principal eigenpair (10). By continuous dependence, there is $\varepsilon_1 > 0$ such that

$$\eta_0 := \inf_{z \in [\hat{z} - \varepsilon_1, \hat{z} + \varepsilon_1]} \frac{d}{dz} \lambda(z, \hat{z}) > 0.$$

Now it follows from the smooth dependence of (Ψ_1, H_1) on (z, h) that there exists $\eta' \in (0, \eta_0/2)$ such that if (31) holds, then

$$\begin{aligned} & \sup_{z \in [\hat{z} - \varepsilon_1, \hat{z} + \varepsilon_1]} \|\partial_z H_1(\cdot; z, h) - \partial_z H_1(\cdot; z, \hat{h})\|_{C^{\beta, \beta/2}([0, L] \times \mathbb{R})} \\ &= \|\partial_z H_1(\cdot; z, h) - \partial_z \lambda(z, \hat{z})|_{z=\hat{z}}\|_{C^{\beta, \beta/2}([0, L] \times \mathbb{R})} < \frac{\eta_0}{2}. \end{aligned}$$

Hence, for $z \in [\hat{z} - \varepsilon_1, \hat{z} + \varepsilon_1]$,

$$\partial_z H_1(t; z, h) > \partial_z \lambda(z, \hat{z})|_{z=\hat{z}} - \frac{\eta_0}{2} \geq \frac{\eta_0}{2} > \eta' \quad \text{for } t \in \mathbb{R}.$$

This proves the corollary. $\square$

5. A general exclusion criterion.

Proposition 3. *Suppose $\partial_z \lambda(z, \hat{z})|_{z=\hat{z}} > 0$ for some $\hat{z}$. There exists $\eta > 0$ such that if (22) holds, then for any N and any increasing sequence $(z_i)_{i=1}^N \subset (\hat{z} - \eta, \hat{z} + \eta)$, every positive solution $(u_i)_{i=1}^N$ of (6) converges to the equilibrium solution $E_1 = (\theta_{z_1}, 0, \dots, 0)$ as $t \rightarrow \infty$. i.e. The equilibrium E_1 is globally asymptotically stable among all positive solutions.*

Remark 5. By a change of variables $z \mapsto C - z$ and analogous arguments, it follows that if $\partial_z \lambda(z, \hat{z})|_{z=\hat{z}} < 0$, then there exists $\eta > 0$ such that if (22) holds, then for any N and any increasing sequence $(z_i)_{i=1}^N \subset (\hat{z} - \eta, \hat{z} + \eta)$, every positive solution of (6) converges to the equilibrium $E_N = (0, \dots, 0, \theta_{z_N})$.

Proof. Let the parameter $\hat{z}$ be given such that $\partial_z \lambda(z, \hat{z})|_{z=\hat{z}} > 0$, and let $\eta' > 0$ be as given in Corollary 1. We claim that there is $\varepsilon \in (0, \eta')$ such that for any N and any $(d_i)_{i=1}^N \subset (\hat{z} - \varepsilon, \hat{z} + \varepsilon)$,

$$\limsup_{t \rightarrow \infty} \max_{1 \leq i \leq N} \|h_i(x, t) - \hat{h}(x)\|_{C^{\beta, \beta/2}([0, L] \times [t, t+1])} < \eta', \quad (33)$$

where

$$h(x, t) = g(\exp(-k_0 x - \hat{U}(x, t))) = g(\exp(-k_0 x - \sum_{j=1}^N \int_0^x u_j(y, t) dy)), \quad (34)$$

and $\hat{h}(x)$ is given in (32). Indeed, in view of Proposition 1 and the *a priori* estimate (15), we can use interpolation to estimate

$$\|h(x, t) - \hat{h}(x)\|_{C^{\beta, \beta/2}([0, L] \times [t, t+1])} \leq C \left\| \sum_{i=1}^N u_i - \theta_{\hat{z}}(x) \right\|_{L^\infty([0, L] \times [t, t+1])}^\gamma$$

where $C > 1$ and $0 < \gamma < 1$ are some positive constants in the interpolation inequality. Hence, we deduce (33) upon taking η such that $C\eta^\gamma < \eta'$ and apply Proposition 1.

Having proved (33), after possibly a translation in time, we may assume without loss of generality that

$$\|h(\cdot, t) - \hat{h}\|_{C^{\alpha, \alpha/2}([0, L] \times [0, \infty))} < \eta'. \quad (35)$$

Extend $h(x, t)$ evenly in t , so that it is defined for $(x, t) \in [0, L] \times \mathbb{R}$. Since $(\hat{z} - \varepsilon, \hat{z} + \varepsilon) \subset (\hat{z} - \eta', \hat{z} + \eta')$, we have verified (31).

Let $\Psi_1(x, t; z, h)$ and $H_1(t; z, h)$ be the normalized principal bundle considered in the statement of Corollary 1. We have, for any $z \in [\hat{z} - \varepsilon, \hat{z} + \varepsilon]$,

$$\inf_{t \in \mathbb{R}} \partial_z H_1(t; z, h) \geq \eta' > 0. \quad (36)$$

For each i , we claim that there is $\bar{c}_i > \underline{c}_i > 0$ such that

$$\underline{c}_i e^{-\int_0^t H_1(s; z_i, h) ds} \Psi_1(x, t; z_i, h) \leq u_i(x, t) \leq \bar{c}_i e^{-\int_0^t H_1(s; z_i, h) ds} \Psi_1(x, t; z_i, h) \quad (37)$$

for $(x, t) \in [0, L] \times \mathbb{R}$.

Indeed, the left and right hand sides of (37) satisfy the same equation as u_i . Hence we can choose $\bar{c}_i$ large enough and $\underline{c}_i$ small enough to deduce (37) from the classical comparison theorem of linear parabolic equations. This proves (37).

By (36), we have

$$H_1(t; z_i, h) - H_1(t; z_1, h) \geq (z_i - z_1)\eta' > 0 \quad \text{for all } i > 1, \text{ and all } t \in \mathbb{R}.$$

Hence, we derive from (37) that, for $i > 1$,

$$\begin{aligned} \frac{u_i(x, t)}{u_1(x, t)} &\leq C \exp \left(- \int_0^t (H_1(s; z_i) - H_1(s; z_1)) ds \right) \frac{\Psi_1(x, t; z_i, h)}{\Psi_1(x, t; z_1, h)} \\ &\leq C \exp(-(z_i - z_1)\eta' t) \rightarrow 0 \quad \text{as } t \rightarrow \infty. \end{aligned}$$

Note that we have used Remark 3, which gives a constant $C > 0$ (that is independent of i) such that for $z \in (\hat{z} - \varepsilon, \hat{z} + \varepsilon)$,

$$\frac{1}{C} \leq \Psi_1(x, t; z, h) \leq C \quad \text{in } [0, L] \times \mathbb{R}.$$

Since we also have $\limsup_{t \rightarrow \infty} \sum_{i=1}^N \|u_i\| \leq C_1$ (by Lemmas 2.1 and 2.2), we deduce that $u_i \rightarrow 0$ uniformly for $i = 2, \dots, N$. Hence the semiflow generated by (6) is asymptotic to the single species model consisting of only the first species u_1 . Since the trivial solution is repelling (by Lemma 2.3), we deduce that $u_1 \rightarrow \theta_{z_1}$ uniformly as $t \rightarrow \infty$. $\square$

Proof of Theorem 1.1. Let η be given by Proposition 3. We can then choose $\varepsilon \in (0, \eta)$ by Proposition 1 such that for any N and $(z_i)_{i=1}^N \in (\hat{z} - \varepsilon, \hat{z} + \varepsilon)$, any positive solution $(u_i)_{i=1}^N$ of (6) satisfies (22). It then follows from the choice of η above and Proposition 3 that $E_1 = (\theta_{z_1}, 0, \dots, 0)$ is globally asymptotically stable among all positive solutions of (6). $\square$

6. Applications. We generalize several exclusion results in [13], involving only two species, to general N -species competition. First, we recall the following monotonicity property of the eigenvalues of some elliptic problems. For $\mu, d > 0$, $\alpha \in \mathbb{R}$ and $\hat{h} \in L^\infty([0, L])$, let $\Lambda_1(\mu, \alpha, d, \hat{h})$ be the principal eigenvalue of

$$\begin{cases} \mu \phi'' - \alpha \phi' + (\hat{h}(x) - d)\phi + \Lambda_1 \phi = 0 & \text{for } 0 < x < L, \\ \mu \phi' - \alpha \phi = 0 & \text{for } x = 0, L. \end{cases} \quad (38)$$

Lemma 6.1. *If $\hat{h} \in C^1([0, L])$ and satisfies $\hat{h}'(x) < 0$ in $[0, L]$, then the following assertions hold.*

- (a) $\partial_\alpha \Lambda_1(\mu, \alpha, d, \hat{h}) > 0$ for any $\mu, d > 0$ and $\alpha \in \mathbb{R}$.
- (b) $\partial_\mu \Lambda_1(\mu, \alpha, d, \hat{h}) > 0$ for any $\mu, d > 0$ and $\alpha \leq 0$.
- (c) If $\alpha \geq [\hat{h}(0) - d]L$ and $\Lambda_1(\mu^*, \alpha, d, \hat{h}) = 0$ for some $\mu^* > 0$, then

$$\partial_\mu \Lambda_1(\mu^*, \alpha, d, \hat{h}) < 0.$$

Proof. Let $\Phi(x) = e^{-\alpha x/\mu} \phi(x)$. Then (38) becomes

$$\begin{cases} \mu\Phi'' + \alpha\Phi' + (\hat{h}(x) - d)\Phi + \Lambda_1\Phi = 0 & \text{for } 0 < x < L, \\ \Phi' = 0 & \text{for } x = 0, L. \end{cases}$$

The proof of assertion (a) is similar to [11, Lemma 5.2] and we omit it here. The proofs of assertions (b) and (c) can be found in [13, Lemma 4.9]. $\square$

6.1. Proof of Theorems 1.2–1.4. First, we consider the case

$$\mu(z) = \mu_0 > 0, \quad \alpha(z) = z, \quad d(z) = d_0 > 0, \quad (39)$$

and prove Theorem 1.2.

Proof of Theorem 1.2. For $z, \hat{z} \in \mathbb{R}$, the principal eigenvalue $\lambda(z, \hat{z})$ of (10) can be represented as

$$\lambda(z, \hat{z}) = \Lambda_1(\mu_0, z, d_0, h_A),$$

where $h_A(x) = g(\exp(-k_0x - \int_0^x \theta_{\hat{z}}(y) dy))$ and $\theta_{\hat{z}}$ is the positive equilibrium solution of the single species equation (9) with coefficients satisfying (39). It is easy to see that $h_A \in C^1([0, L])$ and $h'_A < 0$ in $[0, L]$. By Lemma 6.1(a), it follows that $\partial_z \lambda(z, \hat{z})|_{z=\hat{z}} > 0$. Hence, we may apply Theorem 1.1 to deduce the global asymptotic stability of E_1 among all positive solutions. $\square$

The proof of Theorem 1.3 is similar and we omit the details.

Next, we consider the case

$$\mu(z) = z, \quad d(z) = d_0 > 0, \quad \alpha(z) = \alpha_0 \geq [g(1) - d_0]L, \quad (40)$$

and prove Theorem 1.4.

Proof of Theorem 1.4. For $z, \hat{z} \in \mathbb{R}$, then the principal eigenvalue $\lambda(z, \hat{z})$ of (10) can be represented as

$$\lambda(z, \hat{z}) = \Lambda_1(z, \alpha_0, d_0, h_B),$$

where $h_B(x) = g(\exp(-k_0x - \int_0^x \theta_{\hat{z}}(y) dy))$, and $\theta_{\hat{z}}$ is the unique positive solution of

$$\begin{cases} \hat{z}\theta_{\hat{z}}'' - \alpha_0\theta_{\hat{z}}' + (g(\exp(-k_0x - \int_0^x \theta_{\hat{z}}(y) dy)) - d_0)\theta_{\hat{z}} = 0 & \text{for } 0 < x < L, \\ \mu_0\theta_{\hat{z}}' - \hat{z}\theta_{\hat{z}} = 0 & \text{for } x = 0, L. \end{cases}$$

It follows that $\Lambda_1(\hat{z}, \alpha_0, d_0, h_B) = 0$, since 0 is an eigenvalue admitting a positive eigenfunction $\theta_{\hat{z}}$. Also, observe that

$$\alpha_0 \geq [g(1) - d_0]L = [h_B(0) - d_0]L,$$

so that we can apply Lemma 6.1(c) to deduce that

$$\partial_z \lambda(z, \hat{z})|_{z=\hat{z}} = \partial_\mu \Lambda_1(\hat{z}, \alpha_0, d_0, h_B) < 0.$$

The desired conclusion now follows from Theorem 1.1 and Remark 1. $\square$

REFERENCES

- [1] R. S. Cantrell and K.-Y. Lam, On the evolution of slow dispersal in multi-species communities, 2020, [arXiv:2008.08498 \[math.AP\]](#)
- [2] Y. Du and S.-B. Hsu, On a nonlocal reaction-diffusion problem arising from the modeling of phytoplankton growth, *SIAM J. Math. Anal.*, **42** (2010), 1305–333.
- [3] U. Ebert, M. Arrayas, N. Temme, B. Sommeijer and J. Huisman, Critical condition for phytoplankton blooms, *Bull. Math. Biol.*, **63** (2001), 1095–1124.
- [4] J. Huisman and F.J. Weissing, Light-limited growth and competition for light in well-mixed aquatic environments: an elementary model, *Ecology*, **75** (1994), 507–520.
- [5] J. Huisman and F. J. Weissing, Competition for nutrients and light in a mixed water column: A theoretical analysis, *Am. Nat.*, **146** (1995), 536–564.
- [6] J. Huisman, P. van Oostveen and F. J. Weissing, Species dynamics in phytoplankton blooms: incomplete mixing and competition for light, *Am. Nat.*, **154** (1999), 46–67.
- [7] J. Hůska and P. Poláčik, The principal Floquet bundle and exponential separation for linear parabolic equations, *J. Dynam. Differential Equations*, **16** (2004), 347–375.
- [8] J. Hůska, Harnack inequality and exponential separation for oblique derivative problems on Lipschitz domains, *J. Differential Equations*, **226** (2006), 541–557.
- [9] J. Hůska, P. Poláčik and M. V. Safonov, Harnack inequalities, exponential separation, and perturbations of principal Floquet bundles for linear parabolic equations, *Ann. Inst. H. Poincaré Anal. Non Linéaire*, **24** (2007), 711–739.
- [10] G. E. Hutchinson, The paradox of the plankton, *Am. Nat.*, **95** (1961), 137–145.
- [11] S.-B. Hsu and Y. Lou, Single species growth with light and advection in a water column, *SIAM J. Appl. Math.*, **70** (2010), 2942–2974.
- [12] H. Ishii and I. Takagi, Global stability of stationary solutions to a nonlinear diffusion equation in phytoplankton dynamics, *J. Math. Biol.*, **16** (1982/83), 1–24.
- [13] D. Jiang, Y. Lou, K.-Y. Lam and Z. Wang, Monotonicity and global dynamics of a nonlocal two-species phytoplankton model, *SIAM J. Appl. Math.*, **79** (2019), 716–742.
- [14] T. Kolokolnikov, C. H. Ou and Y. Yuan, Phytoplankton depth profiles and their transitions near the critical sinking velocity, *J. Math. Biol.*, **59** (2009), 105–122.
- [15] M. J. Ma and C. H. Ou, Existence, uniqueness, stability and bifurcation of periodic patterns for a seasonal single phytoplankton model with self-shading effect, *J. Differential Equations*, **263** (2017), 5630–5655.
- [16] L. Mei and X. Zhang, Existence and nonexistence of positive steady states in multi-species phytoplankton dynamics, *J. Differential Equations*, **253** (2012), 2025–2063.
- [17] J. Mierczyński, Globally positive solutions of linear parabolic PDEs of second order with robin boundary conditions, *J. Math. Anal. Appl.*, **209** (1997), 47–59.
- [18] R. Peng and X.-Q. Zhao, A nonlocal and periodic reaction-diffusion-advection model of a single phytoplankton species, *J. Math. Biol.*, **72** (2016), 755–791.
- [19] N. Shigesada and A. Okubo, Analysis of the self-shading effect on algal vertical distribution in natural waters, *J. Math. Biol.*, **12** (1981), 311–326.

Received August 2020; revised October 2020.

E-mail address: rsc@math.miami.edu

E-mail address: lam.184@math.ohio-state.edu