Lecture 4: Competition of phytoplankton population in water column

[Ishii-Takagi (1983)] [Huisman et al. (1999)]

$$\begin{cases} u_t = \mu_1 u_{xx} - \alpha_1 u_x + u(g_1(I(x,t)) - d_1 u) & x \in (0,L),\ t>0, \\ v_t = \mu_2 v_{xx} - \alpha_2 v_x + v(g_2(I(x,t) - d_2 v) & x \in (0,L),\ t>0, \\ \partial_n u = \partial_n v = 0 & x = 0, L,\ ,\ t>0, \\ u(x,0) = u_0(x), \quad v(x,0) = v_0(x) & x \in (0,L). \end{cases}$$

where $\mu_j > 0$ are diffusion rates (due to turbulence); $\alpha_j \in \mathbb{R}$ are buoyancy/sinking rates; $d_j > 0$ are death rates,

$$g_j(s) = \frac{a_j s}{K_j + s} \qquad \text{(Michaelis-Menton)}$$

$$I(x,t) = \exp\left(- \int_0^x (k_0 + u(y,t) + v(y,t)\, dy \right) \qquad \text{(Lambert–Beer law).}$$

Here k_0 models background attenuation and $u+v$ models shading by the phytoplankton.

Referece: [Jiang-L.-Lou-Wang, SIAM J. Appl. Math., 2019].

0.1 Single population

Let $X \in C([0, L])$ and $X_+ = C([0, L]; \mathbb{R}_+)$.

$$\begin{cases} u_t = \mu u_{xx} - \alpha u_x + u(g_1(I(x,t)) - d_1 u) & x \in (0, L),\ t > 0, \\ \partial_n u = 0 & x = 0, L,\ ,\ t > 0. \\ I(x,t) = \exp\left(- \int_0^x (k_0 + u(y,t)\, dy\right) & x \in (0, L),\ t > 0, \\ u(x, 0) = u_0(x) & x \in (0, L). \end{cases} \tag{0.1}$$

This nonlocal PDE generates a semiflow in $\Phi_t : X_+ \to X_+$ which is strongly positive according to the special cone

$$\mathcal{K} = \{\phi \in X : \int_0^x \phi(y)\, dy \geq 0 \quad \text{for all } 0 \leq x \leq L\}.$$

but not the usual cone

$$K = \{\phi \in X : \phi(x) \geq 0 \quad \text{for all } 0 \leq x \leq L\}.$$

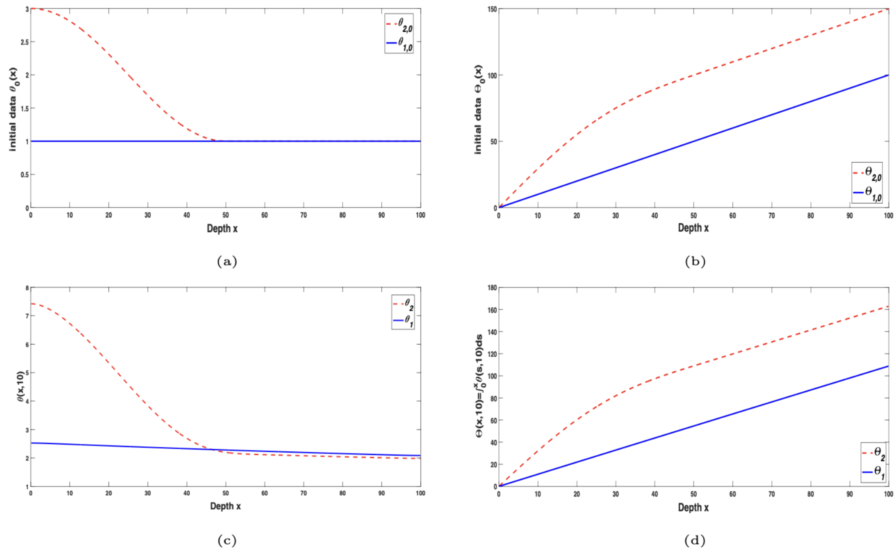

FIG. 1. *Numerical solution of* (3.21)*, with* $D_1 = 1$*,* $\alpha_1 = 0$*,* $L = 100$*,* $f_1(x, t, \Theta, 0) = g(\exp(-k_0 x - k_1 \Theta))$*, where* $g(I) = \frac{I}{10+I}$ *and* $k_0 = k_1 = d = 0.001$*, and initial condition* $\theta_{1,0} = \chi_{[0,L/2]}(\cos(2\pi x/L) + 1) + 1$ *and* $\theta_{2,0} = 1$*. 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).*

Exercise!

$$\text{Int}(\mathcal{K}) = \left\{ u_0 \in X \ :\ u_0(0) > 0 \quad \text{and} \quad \int_0^x u_0(y)\, dy > 0 \ \text{ for all } x \in (0, L]. \right\}$$

Definition 1. For $u_0, \tilde{u}_0 \in X$,

$$u_0 \leq_{\mathcal{K}} \tilde{u}_0 \qquad \Longleftrightarrow \qquad \tilde{u}_0 - u_0 \in \mathcal{K}.$$

$$u_0 <_{\mathcal{K}} \tilde{u}_0 \qquad \Longleftrightarrow \qquad \tilde{u}_0 - u_0 \in \mathcal{K} \setminus \{0\}.$$

$$u_0 \leq_{\mathcal{K}} \tilde{u}_0 \qquad \Longleftrightarrow \qquad \tilde{u}_0 - u_0 \in \mathrm{Int}(\mathcal{K}).$$

Theorem 2. *The nonlocal PDE generates a semiflow in $\Phi_t : X_+ \to X_+$ which is strongly positive according to the special cone $\mathcal{K}$, i.e.*

$$u_0 <_{\mathcal{K}} \tilde{u}_0 \qquad \Longleftrightarrow \qquad u(\cdot, t) \ll_{\mathcal{K}} \tilde{u}(\cdot, t) \quad \text{for } t > 0,$$

where $u(x,t) = \Phi_t(u_0)$ and $\tilde{u}(x,t) = \Phi_t(\tilde{u}_0)$.

This is equivalent to establishing a strong maximum principle (modulo an approximation argument).

Observation: $U(x,t) := \int_0^x u(y,t)\,dy$, so that $\boxed{U_x = u}$, and note that

$$U_t = \mu U_{xx} - \alpha U_x + F(x, U(x,t)) - \int_0^x F_x(y, U(y,t))\,dy$$

where $F(x,s) = \int_0^s \big(g(e^{-k_0 x - s}) - d\big)\, dz.$

Lemma 3. *Let*

$$\begin{cases} (u_2)_t \geq D(u_2)_{xx} - \alpha(u_2)_x + [g(e^{-k_0 x - \int_0^x u_2}) - d]u_2 & x \in [0, L],\ t > 0, \\ \mu(u_2)_x - \alpha u_2 \geq 0 & x = 0, L,\ t > 0, \end{cases}$$

and the reverse inequality holds for $u_1(x,t)$.
Suppose $\exists t^* > 0$ such that

$$\begin{cases} u_1 \leq_K u_2 & \text{for } 0 \leq t \leq t^* \\ u_2 - u_1\big|_{t=t^*} \notin \mathrm{Int}(\mathcal{K}), \end{cases}$$

then $u_2(x,t) \equiv u_1(x,t)$ for $x \in [0, L]$ and $t \in [0, t^*]$.

Proof. Let $U_i(x,t) = \int_0^x u_i(y,t)\,dy$, then $U_1 \leq U_2$ for $[0,L] \times [0,t^*]$.and one of the following holds at $t = t^*$:

(A) $U_1(x^*, t^*) = U_2(x^*, t^*)$ for some $x^* \in (0, L]$, or

(B) $(U_1 - U_2)_x(0, t^*) = 0$.

(A) $U_1(x^*,t^*) = U_2(x^*,t^*)$ for some $x^* \in (0,L]$, or

(B) $(U_1 - U_2)_x(0,t^*) = 0$.

Define $W = U_2 - U_1$, then

$$\begin{aligned} &W_t - \mu W_{xx} + \alpha W_x \\ &\geq F(x,U_2(x,t)) - F(x,Y_1(x,t)) + \int_0^x [F_x(y,U_1(y,t)) - F_x(y,U_2(y,t))]\, dy \\ &= h(x,t)W + \int_0^x \left(\int_{U_1(y,t)}^{U_2(y,t)} k_0 e^{-k_0 y - z} g'(e^{-k_0 y - z}) dz \right) dy \\ &\geq h(x,t)W. \end{aligned}$$

Case (A). $W(x^*,t^*) = 0$ for some $x^* \in (0,L]$, then by classical strong maximum principle applied to W,

$$W(L,t^*) = 0 \quad \text{which implies} \quad W_t(L,t^*) \leq 0.$$

Note also that $\mu W_{xx} - \alpha W_x(L,t^*) = 0$. Hence,

$$\int_0^L \left(\int_{U_1(y,t)}^{U_2(y,t)} k_0 e^{-k_0 y - z} g'(e^{-k_0 y - z}) dz \right) dy = 0 \quad \text{i.e.} \quad U_1 \equiv U_2.$$

Case (B). $W_x(0,t^*) = (U_1 - U_2)_x(0,t^*) = 0$.
If $\exists t_j \nearrow t^*$ such that Case (A) holds, then done.
Otherwise, assume also

$$W = U_2 - U_1 > 0 \quad \text{in } (0,L] \times (0,t^*].$$

By Hopf's boundary lemma, $W_x(0,t^*) > 0$, which is a contradiction. □

Proof: Φ_t is strongly positive. On board. □

Theorem 4 (Du-Hsu SIMA (2010))**.** *Let λ_1 be pev of*

$$\mu\psi_{xx} - \alpha\psi_x + (g(e^{-k_0 x}) - d)\psi + \lambda_1\psi = 0 \quad \textit{in } \Omega, \qquad \mu\psi_x - \alpha\psi = 0 \quad \textit{on } \partial\Omega.$$

(a) *If $\lambda_1 \geq 0$, then $u(x,t) \to 0$ as $t \to \infty$ for any $u_0 \geq, \not\equiv 0$.*

(b) *If $\lambda_1 < 0$, then there exists a unique positive equilibrium $\theta(x)$, and*

$$u(x,t) \to \theta(x) \quad \textit{as } t \to \infty \quad \textit{for any } u_0 \geq, \not\equiv 0.$$

Proof. For (a) and if $\lambda_1 > 0$, use the supersolution $\overline{u}(x,t) := e^{-\lambda_1 t}\psi(x)$:

$$\overline{u}_t \geq \mu\overline{u}_{xx} - \alpha\overline{u}_x + [g(e^{-k_0 x - \int_0^x \overline{u}}) - d]\overline{u}$$

For (b), we use the other important result from Monotone Dynamical Systems.

Fact 1: Suppose (i) 0 is linearly unstable, and (ii) here exists $M > 0$ such that

$$\limsup_{t\to\infty} \|u(\cdot,t)\|_X \le M.$$

Then there exists at least one positive equilibrium.

Fact 2: If there exists at least one positive equilibrium, and that every positive equilibrium is locally asymptotically stable, then there exists a unique positive equilibrium which is globally attractive.

(eventual boundedness) Since $\lambda_1 < 0$, the trivial equilibrium is linearly unstable. For boundedness, observe that since

$$-d \le g(e^{-k_0 - \int_0^x u(y,t)\,dy}) - d \le \sup g$$

is uniformly L^∞ bounded, it follows that Harnack inequality holds, i.e.,

$$u(y,t) \le Cu(x,t) \quad \text{for } x, y \in [0,L],\ t \ge 1.$$

Hence, one use analogy with ODE to prove eventual boundedness. Then we can use Fact 1 to conclude the existence of at least one positive equilibrium $\theta(x)$.

(every equilibrium $\theta(x)$ is linearly stable, if it exists) Suppose to the contrary that $\lambda \le 0$.

Let $\psi \gg_{\mathcal{K}} 0$ and λ be the pef and pev (apply Krein-Rutman with the special cone $\mathcal{K}$)

$$\begin{cases} \mu\psi_{xx} - \alpha\psi_x + [g(I_0) - d]\psi - \theta(x)g'(I_0)I_0(\int_0^x \psi(y)\,dy) + \lambda\psi = 0 & \text{in } [0,L], \\ \mu\psi_x - \alpha\psi = 0 & \text{for } x = 0, L. \end{cases}$$

where $I_0 = \exp(-k_0 - \int_0^x \theta(y)\,dy)$. We claim that $\lambda > 0$ (i.e. θ is stable).

Observe that $\theta(x)g'(I_0)I_0(\int_0^x \psi(y)\,dy) > 0$ in $(0,L]$, so that

$$\mu\psi_{xx} - \alpha\psi_x + [g(I_0) - d]\psi + \lambda\psi > 0 \quad \text{in } (0,L).$$

Since $\int_0^x \psi > 0$, we have $\sup \psi > 0$.

We can then touch ψ from above by $c\theta$, i.e. $\varphi = c\theta - \psi$ satisfies

$$c > 0 \quad \text{and} \quad \min_{[0,L]}(c\theta - \psi) = 0$$

and

$$\mu\varphi_{xx} - \alpha\varphi_x + [g(I_0) - d]\varphi + \lambda\varphi < \lambda c\theta \le 0.$$

Hence, $\varphi > 0$ in $(0,L)$ (strong MP) and by Hopf's lemma, either

$$\text{either} \quad \varphi_x(0) > 0 = \varphi(0) \quad \text{or} \quad \varphi_x(L) < 0 = \varphi(L).$$

This contradicts the boundary condition $\mu\varphi_x = \alpha\varphi$. □

Open Question: Addition of nutrient —- Here we assumed a eutrophic condition (where nutrient is abundant is not limiting).

0.2 Selection for more buoyant phytoplankton species

$$\begin{cases} u_t = \mu_1 u_{xx} - \alpha_1 u_x + u(g_1(I(x,t)) - d_1 u) & x \in (0,L),\ t > 0, \\ v_t = \mu_2 v_{xx} - \alpha_2 v_x + v(g_2(I(x,t) - d_2 v) & x \in (0,L),\ t > 0, \\ \partial_n u = \partial_n v = 0 & x = 0, L,\ ,\ t > 0, \\ u(x,0) = u_0(x), \quad v(x,0) = v_0(x) & x \in (0,L). \end{cases}$$

where

$$I(x,t) = \exp\left(-\int_0^x (k_0 + u(y,t) + v(y,t)\, dy\right) \qquad \text{(Lambert–Beer law)}.$$

Here k_0 models background attenuation and $u + v$ models shading by the phytoplankton.

Theorem 5. *The following was established in [Jiang-L.-Lou-Wang, 2019].*
(i) $\mu_1 = \mu_2$, $\alpha_1 < \alpha_2$ *then "more buoyant wins".*
(ii) $\mu_1 < \mu_2$, $\alpha_1 = \alpha_2 \geq [g(1) - d]L > 0$*; then "more diffusive wins".*
(iii) $\mu_1 < \mu_2$, $\alpha_1 = \alpha_2 \leq 0$*; then "less diffusive wins".*

Remark 6. These results can be generalized to N-species competition under additional assumptions [Cantrell-L. DCDS-B, 2021].

Open Question: For which $\alpha \in [0, [g(1) - d]L]$ can we find some $\hat{\mu} > 0$ such that

$$E_1 \text{ is locally asymptotically stable whenever } \ \mu_1 = \hat{\mu},\ \mu_2 \neq \hat{\mu}?$$

i.e. $\hat{\mu}$ is an evolutionarily stable strategy [Maynard Smith and Price, Nature, 1973].

Open Question: Find a criterion for two-species to coexist.

Open Question: Multiple trophic level — nutrient/phytoplankton, and zooplankton dynamics.

Proposition 7. *The competition system generates a strongly positive semiflow with respect to the cone:*

$$\mathcal{K}_c := \mathcal{K} \times (-\mathcal{K})$$

Proof. Omitted. □

0.2.1 Two eigenvalue lemmas

Definition 8. For $\mu > 0$, $\alpha \in \mathbb{R}$ and $h \in C([0, L])$, let $\lambda_1(\mu, \alpha, h(\cdot))$ and ψ be the pev and pef of

$$\mu\psi_{xx} + \alpha\psi_x + h(x)\psi + \lambda_1\psi = 0 \quad \text{in } (0, L), \quad \psi_x = 0 \quad \text{for } x = 0, L.$$

Lemma 9. *If h is strictly decreasing, then $\psi_x(x) < 0$ in $(0, L)$.*

Proof.

$$\mu(e^{\alpha x/\mu}\psi_x)_x + e^{\alpha x/\mu}[h(x) + \lambda_1]\psi = 0 \qquad \text{in } (0, L), \qquad \psi_x\big|_{x=0,L} = 0.$$

Integrate

$$\int_0^L e^{\alpha x/\mu}\psi[h(x) + \lambda_1]\, dx = 0 \quad \text{so} \quad h(x) + \lambda_1 \quad \text{change sign.}$$

i.e. there exists $x_0 \in (0, L)$ such that

$$(e^{\alpha x/\mu}\psi_x)_x < 0 \quad \text{in } (0, x_0), \qquad \text{and} \qquad (e^{\alpha x/\mu}\psi_x)_x > 0 \quad \text{in } (x_0, L),$$

□

Lemma 10. *If h is strictly decreasing, then $\partial_\alpha\lambda_1(\mu, \alpha, h) > 0$.*

Proof. Normalize $\int e^{\alpha x/\mu}\psi^2\, dx = 1$. Then $\psi' = \partial_\alpha\psi$ satisfies

$$\mu\psi'_{xx} + \alpha\psi'_x + \psi_x + (h + \lambda_1)\psi' = -\lambda_1'\psi \quad \text{and} \quad \psi'_x\big|_{x=0,L} = 0.$$

Multiply by $e^{\alpha x/\mu}$, and rewrite into self-adjoint form:

$$\mu(e^{\alpha x/\mu}\psi'_x)_x + e^{\alpha x/\mu}(h + \lambda_1)\psi' = -e^{\alpha x/\mu}\psi_x - e^{\alpha x/\mu}\lambda_1'\psi$$

Multiply by ψ, and integrate by parts,

$$0 = -\int e^{\alpha x/\mu}(\psi_x\psi + \lambda_1'\psi^2)\, dx$$

So $\lambda_1' = -\int e^{\alpha x/\mu}\psi\psi_x\, dx > 0$, □

Theorem 11. *Let $\mu_1 = \mu_2 = \mu$. If $\alpha_1 < \alpha_2$, and both semi-trivial equilibrium $E_1 = (\tilde{u}, 0)$ and $E_2(0, \tilde{v})$ exist, then the more buoyant species u drives the species v to extinction.*

Proof. Step 1. $E_2 = (0, \tilde{[}v)$ is unstable.

$$\lambda_1(\mu, \alpha_2, h_2) < \lambda_1(\mu, \alpha_1, h_2) = 0$$

where $h_2(x) = g(\exp(-k_0 x - \int_0^x \tilde{v}(y)\, dy)) - d$ is strictly decreasing in x.

Step 2. There is no positive equilibrium (u^*, v^*) such that $u^* > 0$ and $v^* > 0$.
Otherwise,

$$\lambda_1(\mu, \alpha_1, h^*) = 0 = \lambda_1(\mu, \alpha_2, h^*)$$

with $h^* = g(\exp(-k_0 x - \int -0^x(u^* + v^*)\, dy) - d$ being a strictly decreasing function. □