Competition dynamics of phytoplankton species in eutrophic water columns

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December 17, 2021

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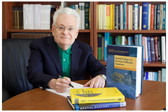
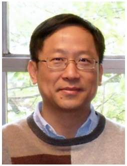


Steve Cantrell (Miami)



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Phytoplankton

- Phytoplankton are any photosynthetic microbiota found in lakes and oceans.
  - cyanobacteria, diatom, dinoflagellate, green algae, cocolithophores
- Account for half of global photosynthetic carbon fixation, and over half of global oxygen production
- They require nutrients and light (typically) for growth.
- Varying size and densities. Some gain buoyancy through gas vacuoles, or flagella.
- Many produce toxins, although the reasons are unclear.

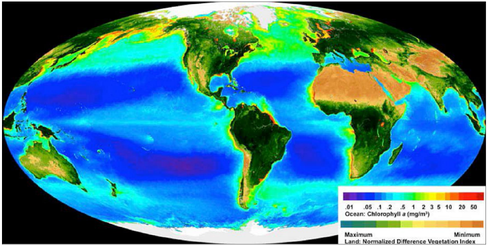

Figure: Global image of the Earth's biosphere as seen by SeaWiFS. (Image credit: NASA)

Huisman's model for Eutrophic Water Column

Following [Huisman et al.], we make the following assumptions.

- A eutrophic water column: the growth rate g of all organisms only depends on light availability, and is not limited by other nutrients.
- Competition by shading: There is no direct interference between different species, there are no toxic interactions.
- Consider a vertical water where $x = 0$ is top and $x = L$ is bottom.

$$\begin{cases} \partial_t u_i = D_i \partial_{xx} u_i - \alpha_i \partial_x u_i + g(I(x,t))u_i - d_i u_i & \text{for } 0 \leq x \leq L,\ t > 0, \\ D_i \partial_x u_i - \alpha_i u_i = 0 & \text{for } x = 0,\ L,\ t > 0, \end{cases}$$

where D_i is turbulent diffusion, α_i is the sinking velocity, d_i is death rate. The light intensity $I(x,t)$ satisfies the Lambert-Beer law:

$$I(x,t) = \exp\left(-k_0 x - \sum_{i=1}^{N} \int_0^x u_i(y,t)\, dy \right).$$

The case of a single species was first studied by Shigesada and Okubo in 1981, in the case $k_0 = 0$ (the self-shading case):

$$\begin{cases} \partial_t u = D\partial_{xx}u - \alpha\partial_x u + g(\exp(-\int_0^x u(y,t)\,dy)u - du & \text{for } 0 \le x \le L,\ t > 0, \\ D\partial_x u - \alpha_i u = 0 & \text{for } x = 0,\ L,\ t > 0, \end{cases}$$

When $k_0 = 0$, They observed that the cumulative distribution

$$U(x,t) = \int_0^x u(y,t)\,dy$$

satisfies a single reaction-diffusion equation

$$\partial_t U = D\partial_{xx}U - \alpha\partial_x U + h(U) - dU,$$

where $h'(s) = g(e^{-s})$.

J. Math. Biology (1981) 12: 311 – 326

Journal of Mathematical Biology

Analysis of the Self-Shading Effect on Algal Vertical Distribution in Natural Waters*

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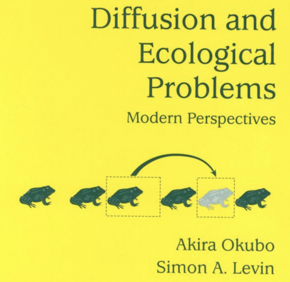
Abstract. Self-shading of light by algae growing in a column of water plays an

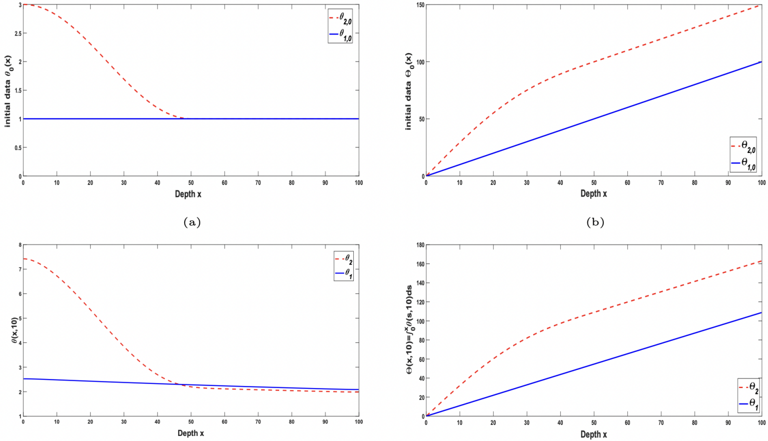


Single Species Dynamics

Subsequently, [Ishii and Takagi 1982] show that the semiflow retains the natural order in U:

$$\int_0^x u(y,0)\,dy \le \int_0^x \tilde{u}(y,0)\,dy \quad \forall x \quad \Longrightarrow \quad \int_0^x u(y,t)\,dy \le \int_0^x \tilde{u}(y,t)\,dy \quad \forall x,\, t>0$$

However, the semiflow does not retain the order in u. [Jiang-L.-Lou-Wang, 2019]



(a) (b)

Globally Attractive Equilibrium

Based on the order-preserving property, one can apply the abstract theory of monotone dynamical systems to prove the following.

Theorem

There exists a unique positive equilibrium $\theta(x)$ such that every positive solution u of the single species model satisfies

$$u(x,t) \to \theta(x) \quad \text{as } t \to \infty.$$

- $k_0 = 0$ [Ishii-Takagi JMB 1982]
- $k_0 > 0$ [Du-Hsu SIAP 2010]
- Time-periodic envionment [Ma-Ou JDE 2017], [Jiang et al. SIAP 2019]

This sets the scene for studying the competition of multiple species.

Single Species Dynamics

Question (Huismann et al. Limnol. Ocean. 1999)

How does the depth (L), turbulent diffusion rate D, sinking/buoyant velocity α, death rate d affect the persistence of the population?

Based on the results in [Hsu-Lou SIMA 2010], when other parameters being fixed, there is...

- one critical death rate d^*
- one critical sinking velocity α^*
- one critical depth L^*
- <u>one or more</u> critial diffusion rate

How about water stratification, in which the diffusion is fast in the surface, and slow in the bottom of the water column? We have the following conjecture:

- If nutrient is abundant and $\alpha > 0$ (sinking), then stratification promotes persistence.
- However, if nutrient is limiting, then stratification prevents nutrient cycling and promotes extinction.

Competitive exclusion principle

Two species that compete for the exact same resources cannot stably coexist at the same location.

Two-species competition – Order-Preserving Property

Let (u_1,u_2) and $(\tilde{u}_1,\tilde{u}_2)$ be two solutions of the two-species competition model:

$$\begin{cases} \partial_t u_1 = D_1 \partial_{xx} u_1 - \alpha_1 \partial_x u_1 + g_1(\exp(-k_0 - \sum_{i=1}^2 \int_0^x u_i(y,t)\,dy)u_1 - d_1 u_1 & \text{for } 0 \le x \le L,\ t > 0, \\ \partial_t u_2 = D_2 \partial_{xx} u_2 - \alpha_2 \partial_x u_2 + g_2(\exp(-k_0 - \sum_{i=1}^2 \int_0^x u_i(y,t)\,dy)u_2 - d_2 u_2 & \text{for } 0 \le x \le L,\ t > 0, \end{cases}$$

with no-flux boundary conditions at $x = 0,\ L$.

Theorem (Jiang-L.-Lou-Wang SIAP 2019)

The competitive order is retained by the semiflow. Namely, if

$$\int_0^x u_1(y,0)\,dy \le \int_0^x \tilde{u}_1(y,0)\,dy \quad \text{and} \quad \int_0^x u_2(y,0)\,dy \ge \int_0^x \tilde{u}_2(y,0)\,dy \quad \forall x$$

then the same inequalities holds for all $t > 0$.

Global dynamics can be accertained by invoking a result in [Munther-Lam 2016], and based on earlier works by [Hess-Lazer 1991] [Hsu-Smith-Waltman 1996]:

Theorem

If the two-specie competition system has no coexistence equilibrium solutions, then exactly one of the following holds:

- *All positive solutions satisfies $(u,v) \to (\theta_1, 0)$ as $t \to \infty$,*
- *All positive solutions satisfies $(u,v) \to (0, \theta_2)$ as $t \to \infty$,*

where θ_i is the positive equilibrium of the respective single species problem.

Two-species Model

The following is proved in [Jiang-L.-Lou-Wang SIAP 2019]:

Theorem

- *(Selection for buoyancy) If* $\alpha_1 < \alpha_2$ *and other parameters held constant, then* $(\theta_1, 0)$ *attracts all solutions.*
- *(Selection for slow diffuser)If* $\alpha_1 = \alpha_2 \le 0$ *(buoyant), and* $D_1 < D_2$*, then* $(\theta_1, 0)$ *attracts all solutions.*
- *(Selection for fast diffuser) If* $\alpha_1 = \alpha_2 \ge [g(1) - d]L$ *(sinking), and* $D_1 < D_2$*, then* $(0, \theta_2)$ *attracts all solutions.*

SIAM J. APPL. MATH.
Vol. 79, No. 2, pp. 716–742

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

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Diversity of the plankton

Some of the results are generalized to N-species model [Cantrell-L. DCDS-B 2021].

DISCRETE AND CONTINUOUS
DYNAMICAL SYSTEMS SERIES B
Volume **26**, Number **4**, April **2021**

doi:10.3934/dcdsb.2020361

pp. **1783–1795**

COMPETITIVE EXCLUSION IN PHYTOPLANKTON COMMUNITIES IN A EUTROPHIC WATER COLUMN

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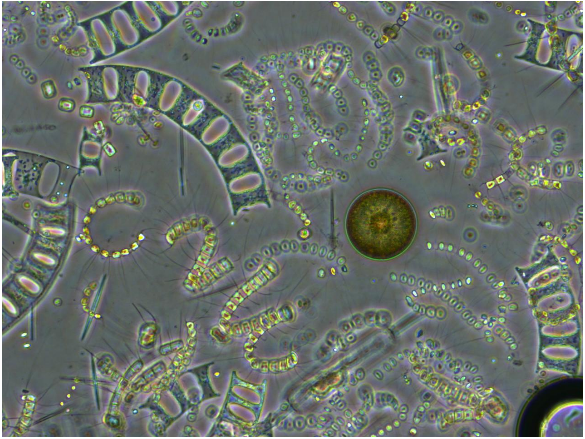
Conclusion:
It seems that exclusion is prevalent, consistent with the prediction of competition theory. Since light forms a single resource, and other nutrients are not limiting.

Diversity of the plankton

But exclusion isn't always the case:



Paradox of the Plankton

G.E. Hutchinson noticed that phytoplankton seemingly violate the competitive exclusion principle. That is, there is typically a large variety of coexisting phytoplankton species supported by a limited amount of resource, mainly nutrient and light. Some explanations:

- Symbiotic relationships
- Chaotic water turbulence, or spatial heterogeneity (patchiness)
- Predation preference (phytoplankton-zooplankton interaction)
- Seasonal climate conditions
- Long transient dynamics

Paradox of the Plankton

G.E. Hutchinson noticed that phytoplankton seemingly violate the competitive exclusion principle. That is, there is typically a large variety of coexisting phytoplankton species supported by a limited amount of resource, mainly nutrient and light. Some explanations:

Niche Differentiation (in conjunction with vertical gradient)

A competition model

- Water column is NOT well mixed.
- Phytoplankton diffuse, and sink or float (advection) vertically.
- Assume sufficient nutrient, and competition for light.
- Light availability follows the Lambert-Beer law
- growth depends on light availability

$$\begin{cases} \partial_t u = D_u \partial_x^2 u - \alpha_u \partial_x u + [\tilde{g}_u(x,t) - d_u]u & \text{for } 0 < x < L, t > 0, \\ \partial_t v = D_v \partial_x^2 v - \alpha_v \partial_x v + [\tilde{g}_v(x,t) - d_v]v & \text{for } 0 < x < L, t > 0, \\ D_i \partial_x u_i(x,t) - \alpha_i u_i(x,t) = 0 & \text{for } x = 0, L, t > 0, i = u,v, \\ u_i(x,0) = u_{i,0}(x), & \text{for } 0 < x < L, i = u,v. \end{cases}$$

First attempt

$$\begin{cases} \partial_t u = D_u \partial_x^2 u - \alpha_u \partial_x u + [\tilde{g}_u(x,t) - d_u]u & \text{for } 0 < x < L, t > 0, \\ \partial_t v = D_v \partial_x^2 v - \alpha_v \partial_x v + [\tilde{g}_v(x,t) - d_v]v & \text{for } 0 < x < L, t > 0, \\ D_i \partial_x u_i(x,t) - \alpha_i u_i(x,t) = 0 & \text{for } x = 0, L, t > 0, i = u, v, \\ u_i(x,0) = u_{i,0}(x), & \text{for } 0 < x < L, i = u, v. \end{cases}$$

where

$$I(x,t) = I_0 exp(-k_{bg}x - \int_0^x (k_u u(s,t) + k_v v(s,t))ds).$$

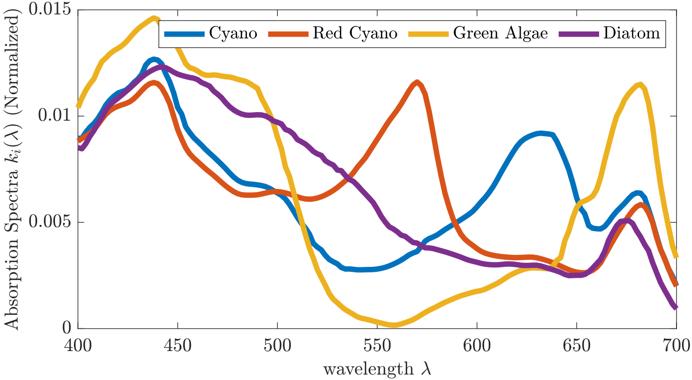
and light dependent growth:

$$\tilde{g}_u = \frac{g_{max,u} k_u I(x,t)}{\gamma_u + k_u I(x,t)}$$

where I_0 is the incident light intensity, k_{bg} is the background light attenuation, k_u, k_v are the light absorption of the species.

Different adsorptions

Light utilization varies between phytoplankton species:



Model

[Stomp et al., Ecol. Lett., 2007] Light acts as a continuous resource

$$I(\lambda,x,t) = I_{\text{in}}(\lambda,t)\exp\left[-K_{BG}(\lambda)x - \int_0^x (k_u(\lambda)u(y,t) - k_v(\lambda)v(y,t))dy\right].$$

$$I_i(x,t) = \int_{400}^{700} k_i(\lambda)I(\lambda,x,t)d\lambda$$

and growth function

$$g_i = \frac{g_{max,i}I_i(x,t)}{\gamma_i + I_i(x,t)}$$

$$\begin{cases} \partial_t u = D_u\partial_x^2 u - \alpha_i\partial_x u + uf_u(x,t,\int_0^x u,\int_0^x v) & \text{for } 0<x<L, t>0,\\ \partial_t v = D_v\partial_x^2 v - \alpha_v\partial_x v + vf_v(x,t,\int_0^x u,\int_0^x v) & \text{for } 0<x<L, t>0,\\ D_i\partial_x u_i(x,t) - \alpha_i u_i(x,t) = 0 & \text{for } x=0,L, t>0, i=u,v,\\ u_i(x,0) = u_{i,0}(x), & \text{for } 0<x<L, i=u,v, \end{cases}$$

where

$$f_i(x,t,p_1,p_2) = g_i\left(\int_{400}^{700} k_i(\lambda)I_{\text{in}}(\lambda,t)\exp\left[-K_{BG}(\lambda)x - \sum_{j=1}^{2} k_j(\lambda)p_j\right]d\lambda\right) - d_i$$

Results

- Note that $x \mapsto f_i(x,t,p_1,p_2)$ is decreasing in x, so the results in [Jiang et al. 2019] says that the system is a monotone dynamical system of two competing species.
- We can similarly establish conditions for the existence of semitrivial solutions $E_1 = (\bar{u},0)$ and $E_2 = (0,\bar{v})$, and whether the two species coexist.

Theorem

(Exclusion) If E_1 and E_2 both exist, and there is no coexistence equilibria, then one of E_1 or E_2 is globally attracting.

Theorem

(Coexistence) If E_1 and E_2 both exist, but are unstable, (corresponding decoupled eigenvalue problems have negative eigenvalues) then at least one coexistence solution exists and is stable.

Competitive advantage

Assuming $k_u(\lambda) = k_v(\lambda)$ we have a good undertanding of competitive advantages based on diffusion and advection.

Theorem

Let $D_1 = D_2$, $\alpha_1 < \alpha_2$, $d_1 = d_2$. If both E_1,E_2 exist, then the first species u_1 drives the second species u_2 to extinction, regardless of initial condition.

Theorem

Let $D_1 < D_2$, $\alpha_1 = \alpha_2 \geq \alpha^*$, $f_1 = f_2$, $d_1 = d_2$. If both E_1,E_2 exist, then the faster species u_2 drives the slower species u_1 to extinction, regardless of initial condition.

Theorem

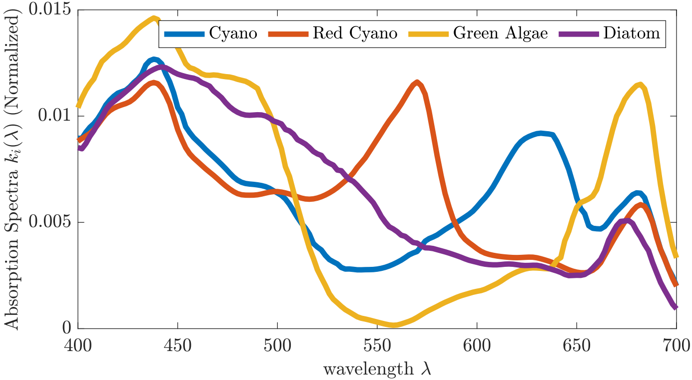
Let $D_1 < D_2$, $\alpha_1 = \alpha_2 \leq 0$, $f_1 = f_2$, $d_1 = d_2$. If both E_1,E_2 exist, then the slower species u_1 drives the faster species u_2 to extinction, regardless of initial condition.

Jiang, D. et al. SIAM J. Appl. Math. (2019).

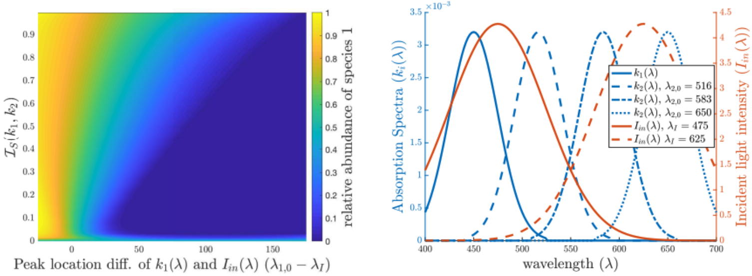
Goals

- Explore coexistence through two main mechanisms.
- 1) Coexistence through niche differentiation.
- 2) Coexistence through specialist vs. generalist competition.
- 3) multiple species.
- 4) real life scenarios.

Mechanism 1: Niche differentiation

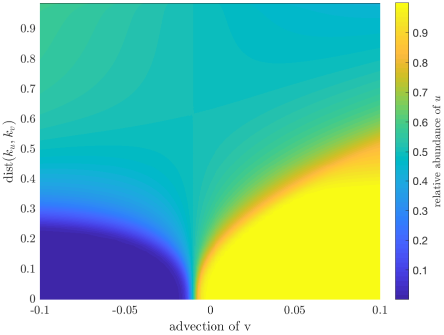


Mechanism 1: Niche differentiation and incident light



- If the peak of incident light is between the respective peak of k_u and k_v, then they coexist.
- Otherwise, there is competitive exclusion.

Mechanism 1: Niche differentiation and advection advantage



- When $I_S(k_1,k_2) = 0$, the buoyant species is selected.
- When $I_S(k_1,k_2) > 0$, coexistence is promoted.

Niche differentiation is enough to overcome a competitive advantage.

Mechanism 1

Definition

Index of spectrum differentiation

$$I_S(k_1,k_2) = \frac{\|k_1 - k_2\|_{L^1}}{\|k_1\|_{L^1} + \|k_2\|_{L^1}}.$$

Theorem

- *If $I_S(k_1,k_2) = 0$, then competitive exclusion holds.*
- *If $I_S(k_1,k_2) = 1$, then exclusion equilibria are unstable, and the two species persist.*

Conjecture

There exists a critical value, D^* (dependent on model parameters), such that

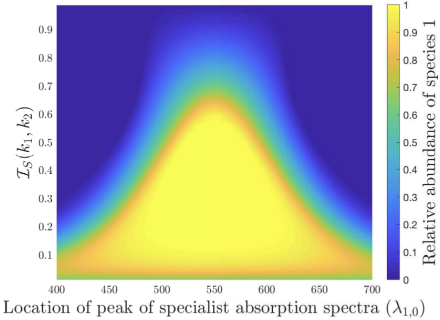
- *If $I_S(k_1,k_2) < D^*$, then competitive exclusion holds.*
- *If $I_S(k_1,k_2) > D^*$, then exclusion equilibria are unstable, and the two species persist.*

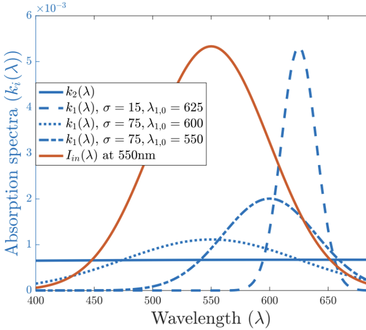
Mechanism 2: Specialist vs. Generalist

Specialist: can thrive only in a narrow range of environmental conditions or has a limited diet

Generalist: able to thrive in a wide variety of environmental conditions and can make use of a variety of different resources.

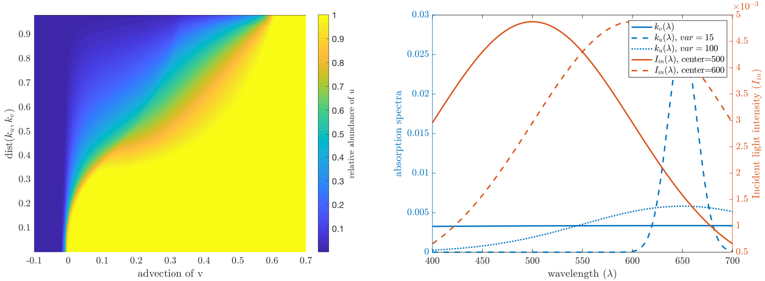
Mechanism 2: Specialist vs. Generalist





- v is the generalist, u is the specialist.
- Mean and variance of k_u are varied.

Mechanism 2: Specialist vs. Generalist



- v is the generalist, u is the specialist.
- Advection of v and variance of k_u are varied.

Coexistence can occur if the specialist becomes too specialized.

Mechanism 2

Proposition

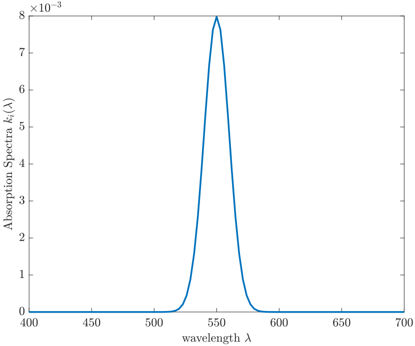
Sufficient condition for coexistence is given by:

$$\int_0^T \int_0^L e^{\alpha_u x/D_u} g_u \left(\int_{400}^{700} a_u(\lambda) k_u(\lambda) I_{\text{in}}(\lambda,t) e^{-K_{BG}(\lambda)x - k_v(\lambda)\frac{MD_v}{\alpha_v}(1-e^{-\alpha_v x/D_v})} \right) dxdt$$
$$> \int_0^T \int_0^L e^{\alpha_u x/D_u} d_u(x,t)\, dxdt \tag{1}$$

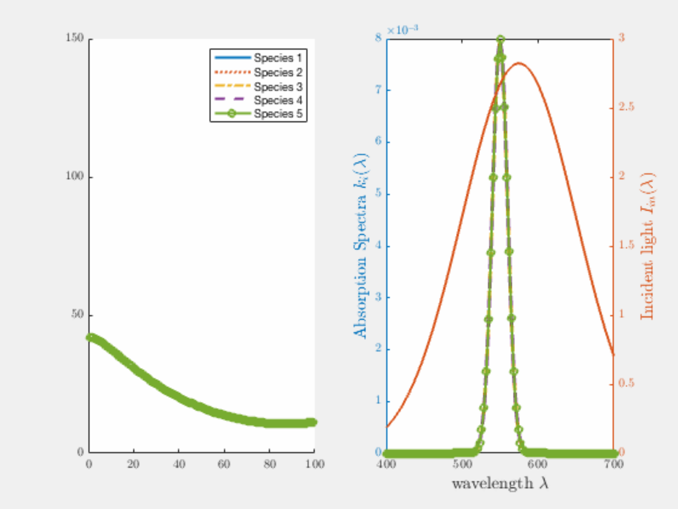
In essence, the overlap between species, and between the incident light is important for the coexistence outcome.

5 species competition

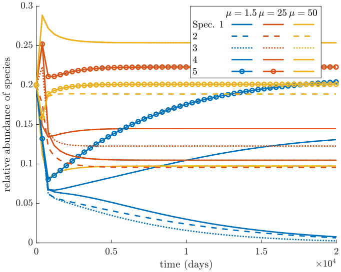
We know look at multiple species and their capabilities to coexist, assuming they are all specialized:

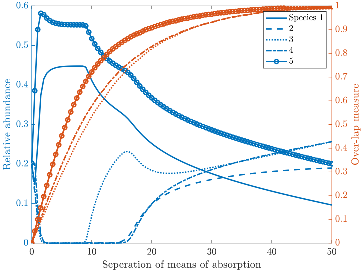


Only advantage through light

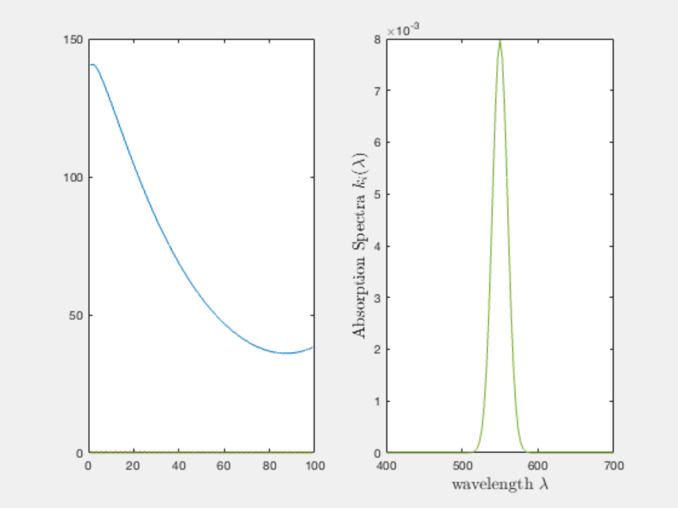


Only advantage through light



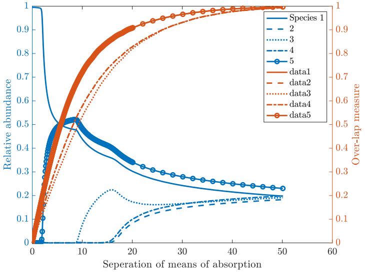


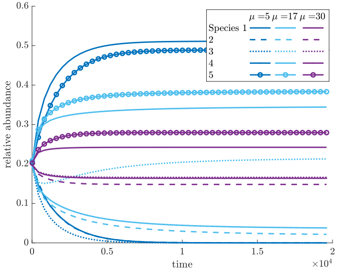
Add advection



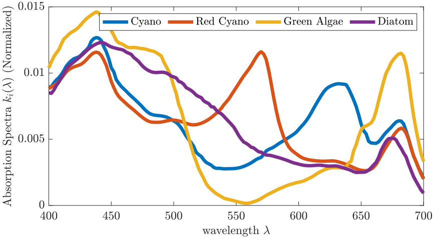
Now there may be two ways to gain advantage. But again, niche differentiation can enable coexistence.

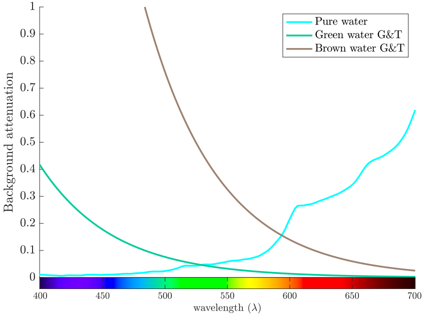
Add advection



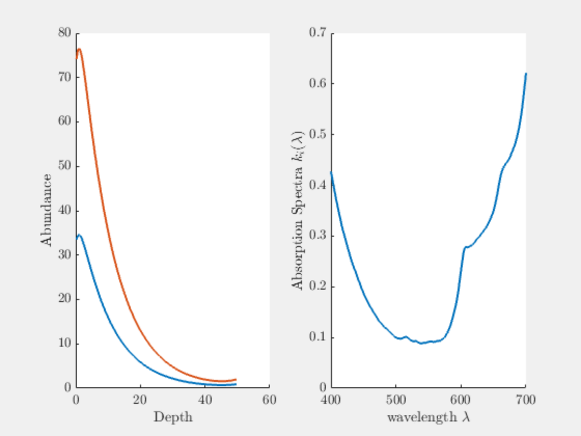


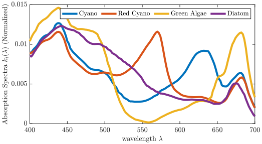
Realistic Scenarios



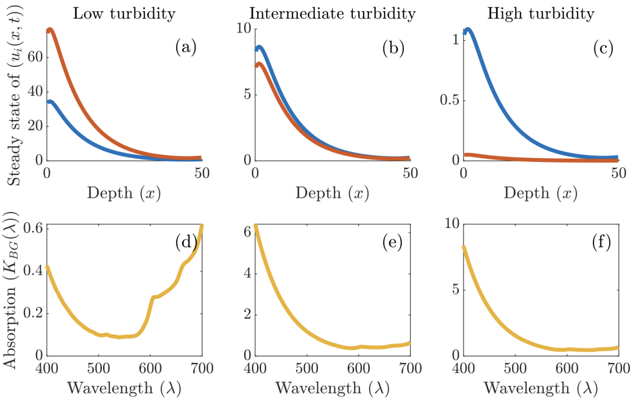


Green vs. Red


Abundance
Depth
Absorption Spectra $k_i(\lambda)$
wavelength λ


Cyano
Red Cyano
Green Algae
Diatom
Absorption Spectra $k_i(\lambda)$ (Normalized)
wavelength λ

Green vs. Red



- Vertical distribution of red and green cyanobacteria.
- Niche differentiation occurs
- Red dominate in less turbid case
- Green dominate in highly turbid case
- G&T: levels of gilvin and tripton (they absorb blue light).

Summary

Summary

- Analytical results of single and two-species models of phytoplankton populations.
- As opposed to the Lotka-Volterra model, the phytoplankton model does not satisfy a maximum principle.
- Nonethess, it preserves the competitive order of the cumulative distribution function

$$U(x,t) = \int_0^x u(y,t)\,dy \quad \Rightarrow \quad \text{It is a Monotone Dynamical System.}$$

- The paradox of the plankton through niche differentiation of light utilization.
- Showed how the different wavelength utilization can yeild coexistnece.
- Provided some insight to real scenarios.

Questions or Comments?

Acknowledgements

- Robert Stephen Cantrell (U Miami)
- Chris Heggerud (UC Davis)
- Danhua Jiang (Zhejiang U. Tech.)
- Yuan Lou (SJTU and Ohio State)
- Hao Wang (U Alberta)
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Thank you!

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Thank you for your participation to make this workshop possible!

Hope see you again in Columbus!