

SIMONS COLLABORATION ON COMPUTATIONAL BIOGEOCHEMICAL MODELING OF MARINE ECOSYSTEMS
WORKSHOP ON MODELING PRIMARY PRODUCTION, NEW YORK, 4TH - 6TH MARCH 2025

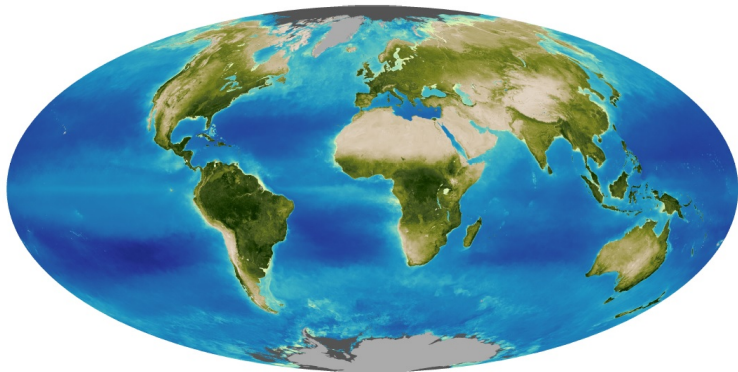
HISTORY OF PRIMARY PRODUCTION MODELS

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The hardest thing to predict is the **past**.

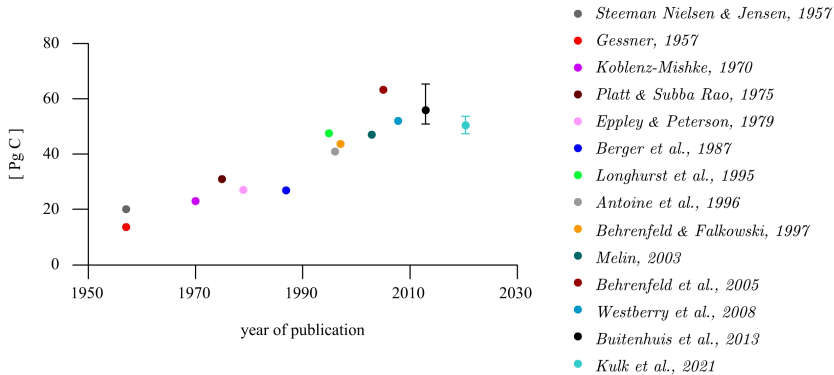
Where we are now



Anthropogenic carbon emissions per year 10 Gt C
Carbon assimilated by the biosphere per year 100 Gt C
Carbon assimilated by phytoplankton 50% of total
Phytoplankton biomass 1% of total land biomass

How we got here

Global annual marine primary production from the literature



Adopted from Buitenhuis et al. (2013)

Approaches to studying primary production

In situ

Incubation at sea under natural light conditions.

(Steemann Nielsen, 1952)

In vitro

Incubation under controlled light conditions.

(Platt i Jassby, 1976)

In silico

Computer implementation of primary production models.

(Gentleman, 2002)

In silico

Time evolution of phytoplankton biomass B in the ocean is modelled as:

$$\frac{\partial B}{\partial t} = \text{production} - \text{losses} + \text{advection} + \text{mixing}$$

Change in biomass is a result of **production**, **losses** and **transport**.

Mathematical description of the problem

$$\frac{\partial B}{\partial t} + w \frac{\partial B}{\partial z} = \left(P^B(I) - L^B \right) B + M \frac{\partial^2 B}{\partial z^2}$$

$$I(z, t) = I_0(t) \exp \left(- \int_0^z \left(K_w + k_B B(z', t) \right) dz' \right)$$

With respect to light I the problem has all the qualities one seeks in physics:

nonlinear + **nonlocal** + **nonautonomous**

Many competitors

$$\frac{\partial B_i}{\partial t} + w_i \frac{\partial B_i}{\partial z} = \left(P_i^B(I) - L_i^B \right) B_i + M \frac{\partial^2 B_i}{\partial z^2}$$

$$I(z, t) = I_0(t) \exp \left(- \int_0^z \left(K_w + \sum_i k_{B,i} B_i(z', t) \right) dz' \right)$$

With respect to light I the problem has all the qualities one seeks in physics:

nonlinear + **nonlocal** + **nonautonomous**

What effect does turbulence have on photosynthesis?

Going back to 1935!

...vertical movements of the water must favour new growth of phytoplankton through the mixing which carries nutritive substances to the illuminated zone from deep waters.

On the other hand a series of facts observed in recent years indicates that vertical mixing, besides having a favourable effect, may have an unfavourable influence on the growth of the phytoplankton, because it prevents the living cells from accumulating in the illuminated zone where they may utilize the light for photosynthesis, and the nitrates and phosphates for growth and propagation.

(Gran & Braarud, 1935)

Sverdrup, Johnson & Fleming (1942)

It is obvious that the compensation point is determined by physiological characteristics of the plants and may, therefore, be somewhat different for different species, just as the optimum light intensity is not the same for all species. The compensation point is independent of the time during which photosynthesis and respiration have been measured if the oxygen production per unit time remains proportional to the light intensity and the oxygen consumption per unit time remains constant. On these assumptions, the oxygen production dP in the short time interval dt equals $aIdt$, where a is a constant and I is the light intensity, and the oxygen consumption dR equals bdt where b is another constant. The compensation point, I_c , is defined by

$$dP = dR, \quad \text{giving} \quad I_c = \frac{b}{a}.$$

The values of oxygen production P and consumption R in the time T are

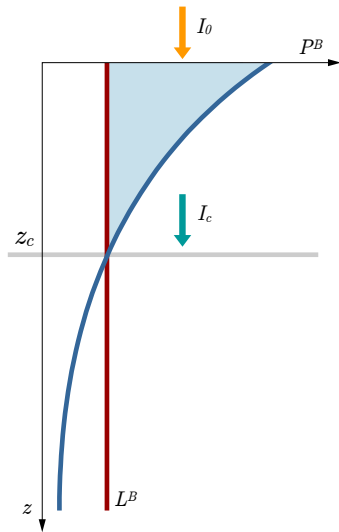
$$P = a \int_0^T Idt, \quad R = bT.$$

The average light intensity in the time T is

$$\bar{I} = \frac{1}{T} \int_0^T Idt.$$

Therefore, if $P = R$, it follows that

$$\bar{I}_c = \frac{b}{a} = I_c;$$



Riley, Stommel & Bumpus (1949)

In considering the remainder of the problem, it is apparent that equation (1) does not represent the rate of change of the plankton at any particular depth in the presence of such phenomena as vertical turbulence and sinking. Methods of handling such problems were discussed by Sverdrup, Johnson, and Fleming (1942: 159–160), and an equation was proposed in which the “local time change of concentration equals effects of diffusion minus advection plus biological processes.” In the present case their equation is presented in the form

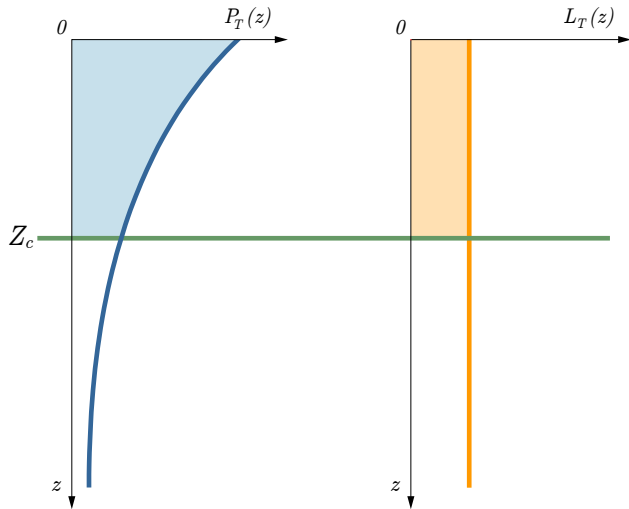
$$\frac{\partial p}{\partial t} = p(p_h - r - wh) + \frac{\partial}{\partial z} \cdot \frac{A}{\rho} \cdot \frac{\partial p}{\partial z} - \frac{V\mu_0}{\mu_T} \cdot \frac{\partial p}{\partial z}. \quad (9)$$

Sverdrup (1953) argument

In order that the vernal blooming of phytoplankton shall begin it is necessary that in the surface layer the production of organic matter by photosynthesis exceeds the destruction by respiration. On certain assumptions a “critical depth” is defined. The depth of a mixed surface layer must be less than this critical depth if the phytoplankton population of the mixed layer shall increase.

$$\frac{\alpha^B I_T}{K} (1 - e^{-KZ_c}) = L_T^B Z_c$$

The classical Critical Depth Criterion (Sverdrup, 1953)



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Introduction to the Themed Section: ‘*Revisiting Sverdrup’s Critical Depth Hypothesis*’

Introduction

Revisiting Sverdrup’s critical depth hypothesis

Shubha Sathyendranath^{1*}, Rubao Ji², and Howard I. Browman³

Kierstead & Slobodkin (1953)

THE SIZE OF WATER MASSES CONTAINING PLANKTON BLOOMS¹

By

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*Brown University
Providence, Rhode Island*

AND

L. BASIL SLOBODKIN

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New Haven, Connecticut*

ABSTRACT

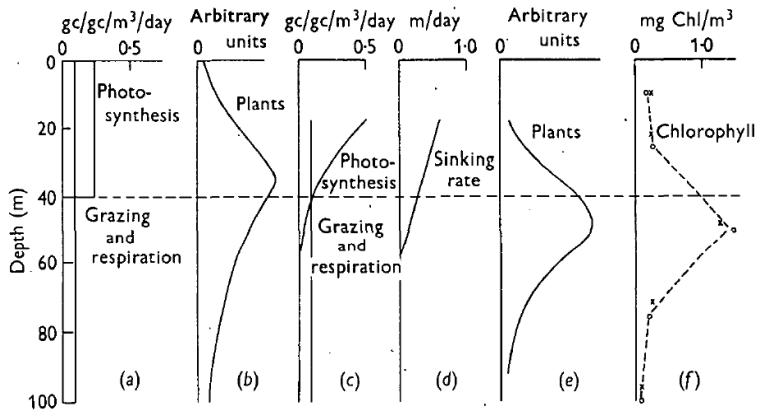
If a phytoplankton population is assumed to be increasing logarithmically in a mass of water surrounded by water which is unsuitable for the survival of the population, it can be shown that there is a minimum critical size for the water mass below which no increase in concentration of phytoplankton can occur. In a one-dimensional water mass with leakage at both ends, this size, after a time of the order of $L^2/8\pi^2D$, is given by

$$L_c = \pi \sqrt{\frac{D}{K}},$$

where L_c is the length of the water mass, D the diffusion, and K the rate of increase of the population. The corresponding size in a cylindrical water mass is given by

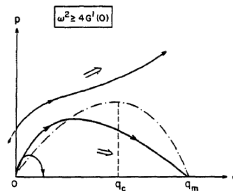
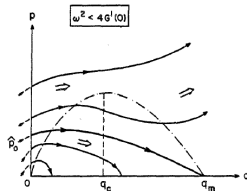
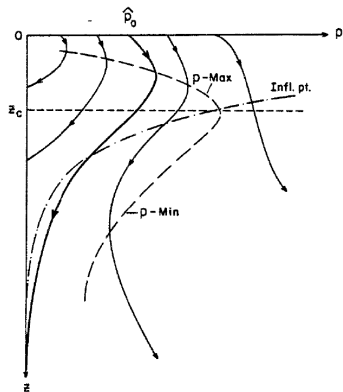
What effect does sinking have on photosynthesis?

Steele & Yentsch (1960) Journal of the Marine Biological Association of the UK



Such features are normally explained by the sinking of plants and a sinking rate constant with depth is used in the mathematical models of Riley, Stommel & Bumpus (1949) to explain some observed patterns of vertical distribution. However, *on the basis of their model, the chlorophyll maximum must occur above the compensation depth.*

Shigesada & Okubo (1981) Journal of Mathematical Biology



Self-shading of light by algae growing in a column of water plays an important role in the dynamics of algal blooms. Thus without self-shading the algal concentration would increase more rapidly, making the nutrient limitation too strong. Apart from the practical importance of self-shading, its *inherent nonlinearity in the growth dynamics leads to an interesting mathematical problem...*

There are numerous mathematical papers on the topic...

It is clear that $z(0) \leq 0$. By (4.5),

$$z'(s) = y(s+1) - y(s) \leq -\lambda \left(\int_s^{s+1} y(t) dt - \frac{C}{\lambda \omega} \right) \leq -\lambda z(s).$$

Therefore we have

$$z(s) \leq z(0)e^{-\lambda s} \leq 0,$$

that is,

$$\int_s^{s+1} \int_{\mathbb{R}_+} v(x, t)^2 e^{-\omega x} dx dt \leq 2M \quad \text{for all } s \geq 0. \quad (4.8)$$

We see from (4.8) that for each $t \geq 1$, there exists $t_0 \in [t-1, t]$ such that

$$\int_{\mathbb{R}_+} v(x, t_0)^2 e^{-\omega x} dx \leq 2M$$

and hence by putting $T = t$, $s = t_0$ in (4.5),

$$\int_{\mathbb{R}_+} v(x, t)^2 e^{-\omega x} dx \leq 2 \left(M + \frac{C}{\omega} \right).$$

Thus we have (4.6) and therefore (4.7) by (4.5).

Now we note that u satisfies

$$u_t = u_{xx} - U(u)u \quad \text{in } \mathbb{R}_+ \times \mathbb{R}_+, \quad (4.9)$$

$$u_x(0, t) = \frac{\omega}{2} u(0, t), \quad \lim_{x \rightarrow \infty} u(x, t) = 0 \quad \text{for } t \in \mathbb{R}_+. \quad (4.10)$$

Using these and putting $C_1 = -\min\{\omega^2/4 + f(0)\}$, we have

$$\begin{aligned} \frac{1}{2} \frac{d}{dt} \int_{\mathbb{R}_+} u^2 dx &= \int_{\mathbb{R}_+} (u_{xx} - U(u)u) u_x dx \\ &\leq [u_x u_x]_0^\infty - \int_{\mathbb{R}_+} u_x^2 dx - 2 \int_{\mathbb{R}_+} u_x u_{xx} dx + C_1 \int_{\mathbb{R}_+} u^2 dx \\ &\leq -\frac{\omega}{2} u(0, t)^2 - \frac{1}{2} \int_{\mathbb{R}_+} u_x^2 dx + 2 \int_{\mathbb{R}_+} u^2 dx + C_1 \int_{\mathbb{R}_+} u^2 dx. \end{aligned}$$

Integrating this over $[s, T]$ with $0 \leq s < T$ and then letting $n \rightarrow \infty$, we get

$$\frac{1}{2} \int_{\mathbb{R}_+} u(x, T)^2 dx + \frac{1}{2} \int_s^T \int_{\mathbb{R}_+} u_x^2 dx dt \leq \frac{1}{2} \int_{\mathbb{R}_+} u(x, s)^2 dx + C_1 \int_s^T \int_{\mathbb{R}_+} u^2 dx dt \quad (4.11)$$

if the right-hand side is finite. By (4.7), the second term on the right-hand side of (4.11) is finite for any $0 \leq s < T$, and the first term is finite for $s = 0$. Therefore we see from (4.11) with $s = 0$ that $\int_{\mathbb{R}_+} u(x, t)^2 dx < \infty$ for all $t > 0$. We see thus that (4.11) is valid for all $0 \leq s < T$. By the same argument as the deduction of (4.6) and

(4.7) from (4.5) and (4.8), we see from (4.7) and (4.11) that (4.1) and

$$\sup_{s \in \mathbb{R}_+} \int_s^{s+1} \int_{\mathbb{R}_+} u^2 dx dt < \infty \quad (4.12)$$

are valid.

By (4.9) and (4.10), we get

$$\begin{aligned} \int_{\mathbb{R}_+} (u_t + U(u)u) u_x dx &= \int_{\mathbb{R}_+} u_{xx} u_x dx \\ &= [u_x u_x]_0^\infty - \int_{\mathbb{R}_+} u_x u_{xx} dx - 2 \int_{\mathbb{R}_+} u_x u_{xx} dx \\ &\leq -\frac{1}{2} \frac{d}{dt} \left(\frac{\omega}{2} u(0, t)^2 + \int_{\mathbb{R}_+} u_x^2 dx \right) \\ &\quad + \frac{1}{4} \int_{\mathbb{R}_+} u_x^2 dx + 4 \int_{\mathbb{R}_+} u^2 dx. \end{aligned}$$

Using that

$$-U(u)u u_x \leq C_2 |u u_x| \leq \frac{1}{4} u_x^2 + C_2^2 u^2,$$

where $C_2 = \max\{\omega^2/4 + \lambda, C_1\}$, from the above inequality we get

$$\begin{aligned} \int_{\mathbb{R}_+} u_x^2 dx + \frac{d}{dt} \left(\frac{\omega}{2} u(0, t)^2 + \int_{\mathbb{R}_+} u_x^2 dx \right) \\ \leq 8 \int_{\mathbb{R}_+} u_x^2 dx + 2C_2^2 \int_{\mathbb{R}_+} u^2 dx. \end{aligned}$$

Multiply this by $(t-s)$ with $s \geq 0$, integrate over $[s, T]$ with $T > s$, and let $n \rightarrow \infty$ to obtain

$$\begin{aligned} \int_s^T \int_{\mathbb{R}_+} (t-s) u_t^2 dx dt + (T-s) \left(\frac{\omega}{2} u(0, T)^2 + \int_{\mathbb{R}_+} u_x^2 dx \right) \\ \leq \frac{\omega}{2} \int_s^T u(0, t)^2 dt + \int_s^T \int_{\mathbb{R}_+} u_x^2 dx dt + 2C_2^2 \int_s^T \int_{\mathbb{R}_+} (t-s) u^2 dx dt. \quad (4.13) \end{aligned}$$

We note that $u(x, t) \rightarrow 0$ as $x \rightarrow \infty$ since $p \in L^\infty(Q_T) \cap C(\bar{Q}_T)$ and hence that by (4.10)

$$u(0, t)^2 = -2 \int_{\mathbb{R}_+} u u_x dx \leq \int_{\mathbb{R}_+} u^2 dx + \int_{\mathbb{R}_+} u_x^2 dx.$$

Therefore, substituting $T = s+1$ and $T = s+2$ into (4.13), we get (4.2) and (4.3), respectively, in view of (4.7) and (4.12). Q.E.D.

Proof of Theorem 2.3, Assertion (i). Denoting $u(x, t) = e^{-\omega x/2} p(x, t)$ and recalling (4.9) and (4.10), we compute that

To this end we fix $\delta \in (0, h)$. Integrating the equation for $\hat{p}_\delta := \hat{p}_{D_\delta}$, namely, (3.9), over $[0, h]$ we obtain

$$\int_0^h [g_\sigma(x) - d] \hat{p}_\sigma(x) dx = 0.$$

By lemma 3.4, as $n \rightarrow \infty$,

$$\int_0^h \hat{p}_n(x) dx \rightarrow \frac{1}{\sigma}, \quad \int_0^h \hat{p}_\sigma(x) dx \rightarrow 0,$$

and

$$\int_0^h g_\sigma(x) \hat{p}_\sigma(x) dx \leq g(1) \int_0^h \hat{p}_\sigma(x) dx \rightarrow 0.$$

Therefore we have

$$\begin{aligned} \frac{d}{\sigma} &= \int_0^h g_\sigma(x) \hat{p}_\sigma(x) dx + o(1) \\ &= \int_0^h g[e^{-k_0 x - k_\tau \int_0^x \hat{p}_\sigma(s) ds}] \hat{p}_\sigma(x) dx + o(1) \\ &= \frac{1}{k_\tau} \int_{k_0 h + k_\tau \int_0^h \hat{p}_\sigma(s) ds}^{k_0 h + k_\tau \int_0^h \hat{p}_\sigma(s) ds} g(e^{-\tau}) d\tau - \frac{k_0}{k_\tau} \int_0^h g_\sigma(x) dx + o(1) \end{aligned} \quad (3.12)$$

Since $0 < g_\sigma(x) \leq g(1)$ for all n and $x \in [0, h]$, we may assume, by passing to a subsequence, $g_\sigma(x) \rightarrow g_*(x)$ weakly in $L^2([0, h])$ with $\|g_*\|_\infty \leq g(1)$. Hence letting $n \rightarrow \infty$ in (3.12), we obtain

$$\frac{d}{\sigma} = \frac{1}{k_\tau} \int_{k_0 h}^{k_0 h + k_\tau \int_0^h g_*(s) ds} g(e^{-\tau}) d\tau - \frac{k_0}{k_\tau} \int_0^h g_*(x) dx.$$

Letting $\delta \rightarrow h$, we obtain

$$\frac{dk_\tau}{\sigma} = \int_{k_0 h}^{k_0 h + k_\tau \int_0^h g_*(s) ds} g(e^{-\tau}) d\tau.$$

That is,

$$d = \int_0^1 g(e^{-k_0 h - k_\tau x / \sigma}) dx.$$

Since τ_* is uniquely determined this way, we have

$$\tau_D \rightarrow \tau_* \quad \text{as } D \rightarrow 0.$$

This finishes the proof. $\square$

Summing up the above discussion, we have the following result.

Theorem 3.8. *Let $d \in (0, g(e^{-k_0 h}))$. Then for all small $D > 0$, the unique positive solution $p_D(x)$ of (3.2) is strictly increasing in $[0, h]$. Moreover, as $D \rightarrow 0$,*

$$\max_{x \in [0, h - \frac{h}{2D}]} |p_D(x) - \tau^* D^{-1} e^{\sigma^*(x-h)/D}| \rightarrow 0, \quad (3.13)$$

and

$$\int_0^h p_D(x) dx \rightarrow \tau_*/\sigma, \quad (3.14)$$

where τ_* is uniquely determined by (3.11).

Proof. These conclusions follow directly from lemmas 3.1, 3.3, 3.4 and 3.7. We explain how (3.13) is obtained; the other conclusions are obvious.

From the definitions we obtain

$$p_D(x) = e^{-\frac{\sigma x}{2D}} \|u_D\|_\infty \tilde{u}_D(x) = \tau_D D^{-1} e^{-\frac{\sigma x}{2D}} \tilde{u}_D(x).$$

For $x \in [0, h - \frac{2D}{\sigma}] \ln D$, we have

$$D^{-1} e^{\sigma(x-h)/(2D)} \leq 1,$$

and hence (3.13) follows readily from lemmas 3.3 and 3.7. $\square$

Let us observe that (3.13) and (3.14) imply that for small D , $p_D(x)$ behaves like a δ -function concentrating at $x = h$.

3.2. The large diffusion case

By theorem 6 in [8], $d_D^* \rightarrow \frac{1}{\tau} \int_0^h g(e^{-k_0 x}) dx$ as $D \rightarrow \infty$. From our discussions in section 2, we know that for any fixed $d \in (0, \frac{1}{\tau} \int_0^h g(e^{-k_0 x}) dx)$, (3.2) has a unique positive solution $p_D(x)$ for every large D . We now show that the asymptotic profile of $p_D(x)$ is given by the following result.

Theorem 3.9. *As $D \rightarrow \infty$,*

$$p_D(x) \rightarrow c^* \quad \text{uniformly on } [0, h], \quad (3.15)$$

where c^* is uniquely determined by the equation

$$d = \frac{1}{h} \int_0^h g(e^{-k_0 x - k_\tau c^* x}) dx.$$

Proof. Setting $u_D(x) := p_D(x) \exp(-\frac{\sigma x}{2D})$, we have

$$\begin{cases} -u_D'' + \frac{\sigma^2}{4D^2} u_D = \frac{1}{D} [g(e^{-k_0 x - k_\tau \int_0^x u_D(s) \exp(\frac{\sigma s}{2D}) ds}) - d] u_D, & x \in (0, h), \\ u_D'(0) = \frac{\sigma}{2D} u_D(0), & u_D'(h) = \frac{\sigma}{2D} u_D(h). \end{cases} \quad (3.16)$$

Denote $\tilde{u}_D = u_D / \|u_D\|_\infty$. We then have

$$\begin{cases} -\tilde{u}_D'' + \frac{\sigma^2}{4D^2} \tilde{u}_D = \frac{1}{D} [g(e^{-k_0 x - k_\tau \int_0^x \tilde{u}_D(s) \exp(\frac{\sigma s}{2D}) ds}) - d] \tilde{u}_D, & x \in (0, h), \\ \tilde{u}_D'(0) = \frac{\sigma}{2D} \tilde{u}_D(0), & \tilde{u}_D'(h) = \frac{\sigma}{2D} \tilde{u}_D(h). \end{cases} \quad (3.17)$$

The right-hand side of the first equation of (3.17) is clearly uniformly bounded on $[0, h]$ for all large D . Hence $\tilde{u}_D$ and $\tilde{u}_D''$ are both uniformly bounded on $[0, h]$ for large D . Thus along any sequence of D going to ∞ , we can choose a subsequence, say D_{n_k} , such that $D_{n_k} \rightarrow \infty$, and $\tilde{u}_{n_k} := \tilde{u}_{D_{n_k}}$ converges in $C^1([0, h])$ to a function u_0 . Clearly u_0 satisfies (in the weak sense and hence classical sense)

$$u_0'' = 0 \quad \text{in } (0, h), \quad u_0'(0) = u_0'(h) = 0, \quad \|u_0\|_\infty = 1, \quad (3.18)$$

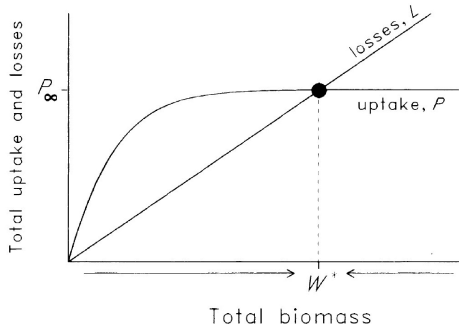
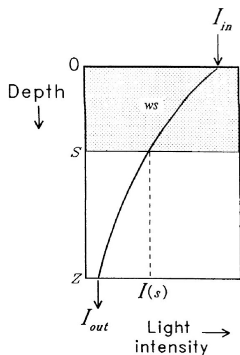
which implies $u_0 = 1$. It follows that $\tilde{u}_D \rightarrow 1$ in $C^1([0, h])$ as $D \rightarrow \infty$.

On the other hand, since $\tilde{u}_D$ satisfies (3.17), we can multiply the first equation of (3.17) by $\exp(\frac{\sigma x}{2D})$ and integrate it over $[0, h]$ to obtain

$$\int_0^h [g(e^{-k_0 x - k_\tau \int_0^x \tilde{u}_D(s) \exp(\frac{\sigma s}{2D}) ds}) - d] \tilde{u}_D(x) \exp(\frac{\sigma x}{2D}) dx = 0.$$

Many of those papers are not well known in the oceanographic community.

Huisman & Weissing (1994) and Weissing & Huisman (1994)



We argue that the crucial measure for phytoplankton growth **is not a critical depth but a critical light intensity** I_{out}^* . For each species I_{out}^* corresponds to the equilibrium light intensity at the bottom of a water column when the species is grown in monoculture.

Competition

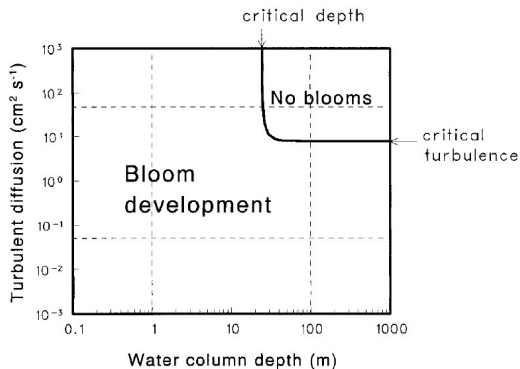
Imagine N phytoplankton species competing for light in the mixed layer.

For each species, I_{out}^* is the critical light intensity, which corresponds to the light intensity at the mixed layer base at steady state in monoculture.

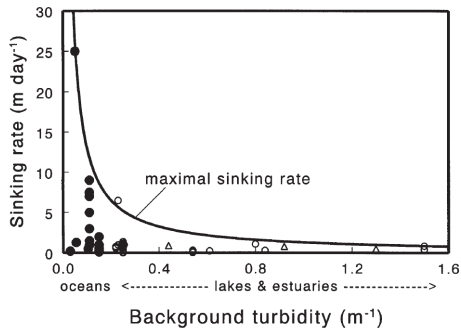
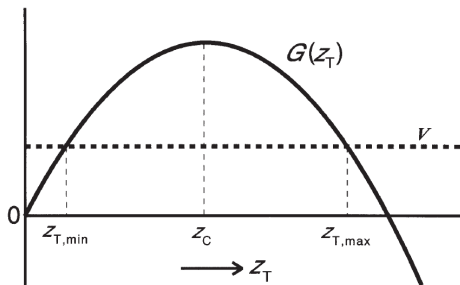
$$B(t) \rightarrow B_i^* \Big|_{\min I_{out}^*}$$

Following Huisman & Weissing (1994) and Weissing & Huisman (1994) the species with the lowest critical light intensity wins.

The competitive exclusion principle holds for light as a resource.



A turbulent diffusion model shows that *there are two different mechanisms for the development of phytoplankton blooms*. One of these mechanisms works in well-mixed environments and corresponds to the classical critical depth theory. The other mechanism is based on the rate of turbulent mixing. If turbulent mixing is less than a critical turbulence, phytoplankton growth rates exceed the vertical mixing rates, and a bloom develops irrespective of the depth of the upper water layer.



*... clear waters can sustain species with high sinking rates,
whereas turbid waters can sustain species with low sinking rates only.*

Some interesting exchanges

Behrenfeld (2010)

Abandoning Sverdrup's Critical Depth Hypothesis on phytoplankton blooms

Chiswell (2011)

Annual cycles and spring blooms in phytoplankton: don't abandon Sverdrup completely

Behrenfeld et al. (2013)

Annual cycles of ecological disturbance and recovery underlying the subarctic Atlantic spring plankton bloom

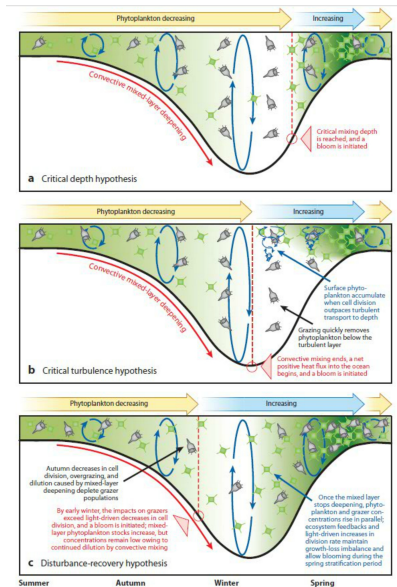
Chiswell (2013)

Comment on “Annual cycles of ecological disturbance and recovery underlying the subarctic Atlantic spring plankton bloom”

Behrenfeld et al. (2013)

Reply to a comment by Stephen M. Chiswell on: “Annual cycles of ecological disturbance and recovery underlying the subarctic Atlantic spring plankton bloom” by M. J. Behrenfeld et al. (2013)

Behrenfeld & Boss (2014) Annual Reviews of Marine Science



But all this time nobody actually solved Sverdrup's equation...

That is until Kovač et al. (2021) found the exact solution

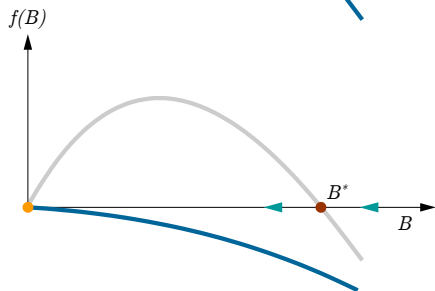
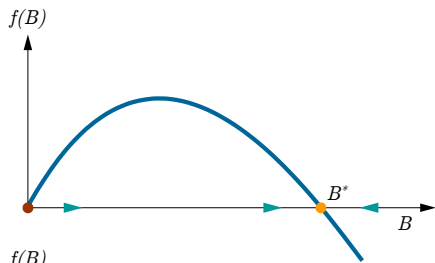
$$C = \frac{1}{K} \left(W_0 \left(-Ae^{-A} \right) + A \right)$$

$$B^* = \frac{K_w}{k_B} \left(\frac{C}{Z_m} - 1 \right)$$

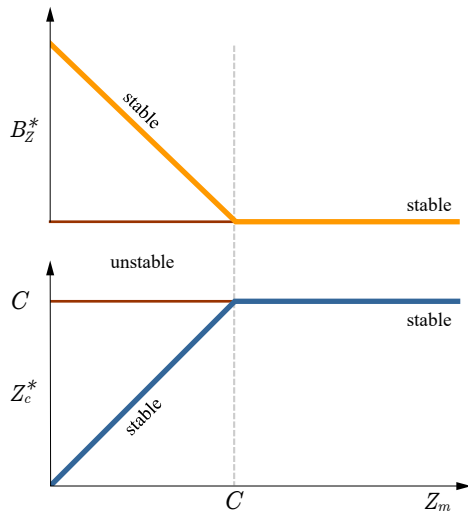
$$B_Z^* = \frac{K_w}{k_B} (C - Z_m)$$

These simple looking solutions opened up new unexpected avenues!

Bio-optical bifurcation



Bio-optical bifurcation



Competition

Imagine N phytoplankton species competing for light in the mixed layer.

The species with the deepest optically uncoupled critical depth wins!

$$B(t) \rightarrow B_i^* \Big|_{\max C_i} \qquad I(Z_m) \rightarrow I(C_i) \Big|_{\max C_i}$$

Following Huisman & Weissing (1994) and Weissing & Huisman (1994) the species with the lowest critical light intensity wins. This species also has the deepest optically uncoupled critical depth. Therefore the critical light argument is translated back to a critical depth argument.

Critical light and critical depth: Two sides, same coin.

Critical Depth Conservation Principle (Kovač et al., 2021)

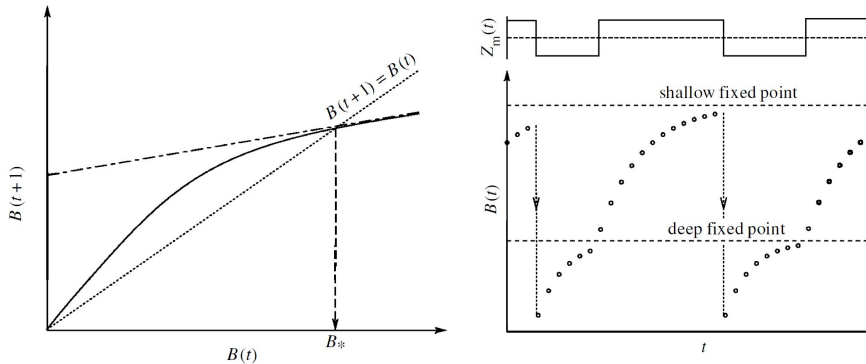
$$\frac{d(KZ_c)}{dt} = 0$$

The product KZ_c is a constant of motion!

$$\frac{d\zeta_c}{dt} = 0$$

When expressed as an optical depth the critical depth does not change over time.

The idea came from an observation made in a paper by Platt et al. (2003).



For a given mixed-layer depth, our analysis shows that *there will be a preferred value of biomass to which the simulated biomass will converge*. Moreover, this preferred value is bounded, such that if the initial biomass is less than this bound, the biomass will approach but not exceed it. On the other hand, if the initial biomass is above the preferred value, it will be reduced to it within a finite number of steps. *The magnitude of the preferred value for biomass is lower the greater the mixed-layer depth.*

Does this hold when mixing is not strong?

LETTERS

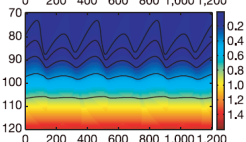
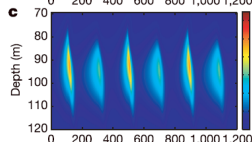
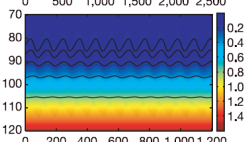
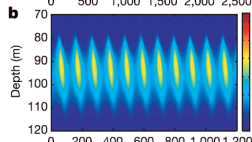
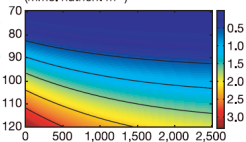
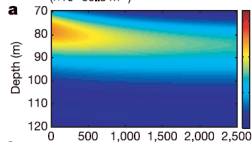
Reduced mixing generates oscillations and chaos in the oceanic deep chlorophyll maximum

Jef Huisman^{1*}, Nga N. Pham Thi^{2*}, David M. Karl³ & Ben Sommeijer²

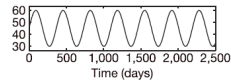
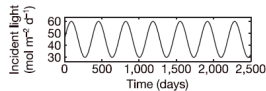
Constant environment

Population density of species
($\times 10^7$ cells m^{-3})

Nutrient concentration
($\text{mmol nutrient m}^{-3}$)

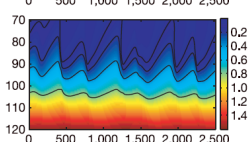
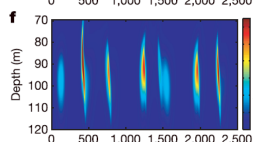
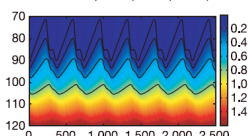
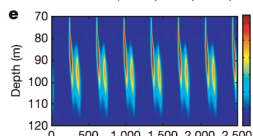
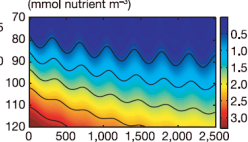
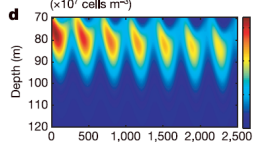


Seasonal environment



Population density of species
($\times 10^7$ cells m^{-3})

Nutrient concentration
($\text{mmol nutrient m}^{-3}$)



New results seem to indicate a positive answer!

As we have recently shown the compensation depth is governed by:

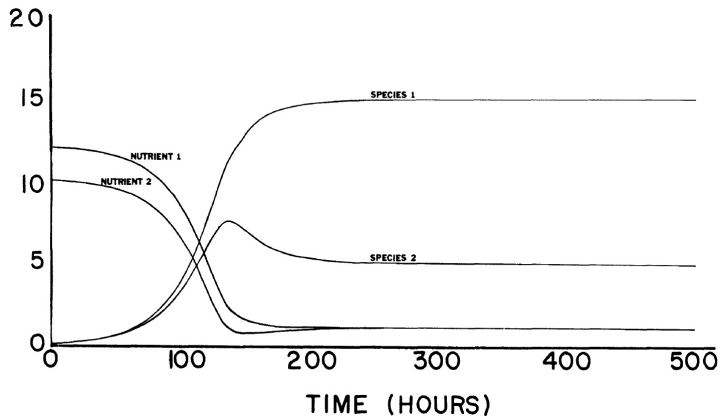
$$\frac{\partial z_c}{\partial t} = -\frac{k_B}{K_w + k_B B(z_c)} \int_0^{z_c} \frac{\partial B(z')}{\partial t} dz'$$

And has the following constant of motion:

$$\frac{d}{dt} I(z_c(t)) = 0$$

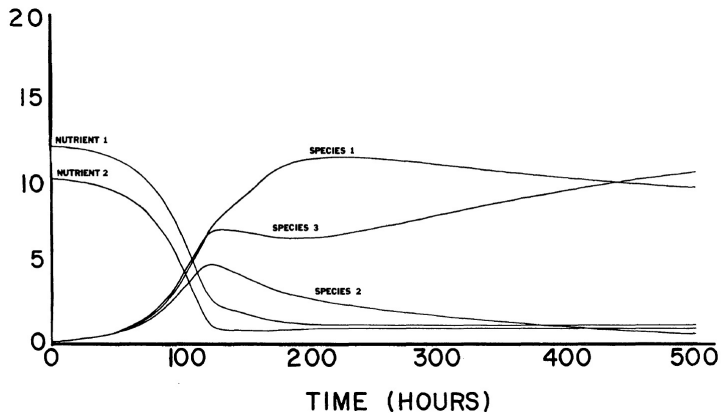
Time to mention nutrients?!

Petersen (1975) The American Naturalist

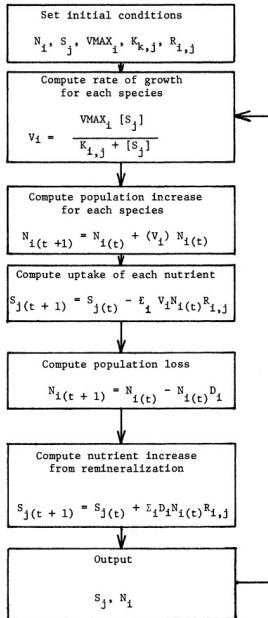


I suggest that several species of phytoplankton can coexist in a true competitive equilibrium if they are collectively restricted from further growth by an array of different nutrients.

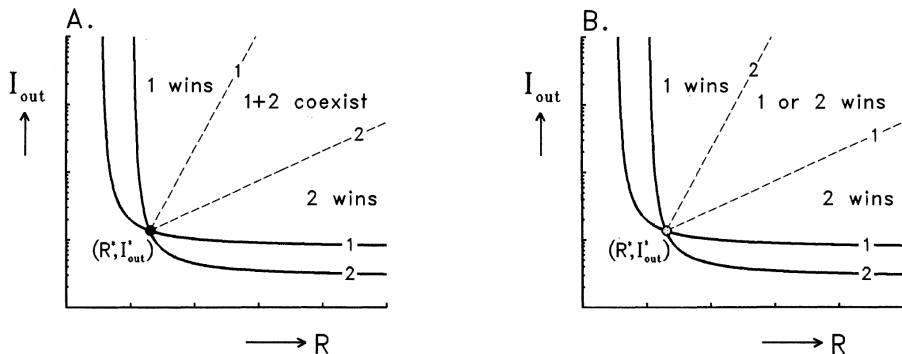
Petersen (1975) The American Naturalist



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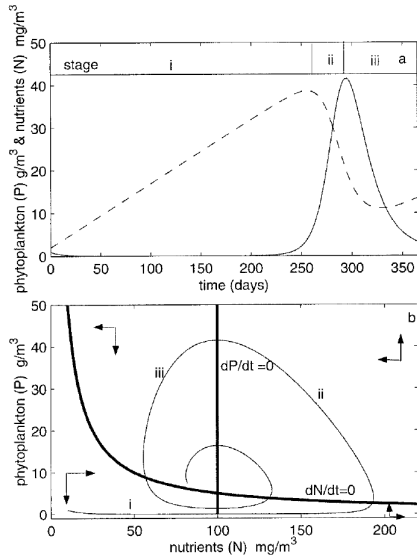


(Petersen, 1975)

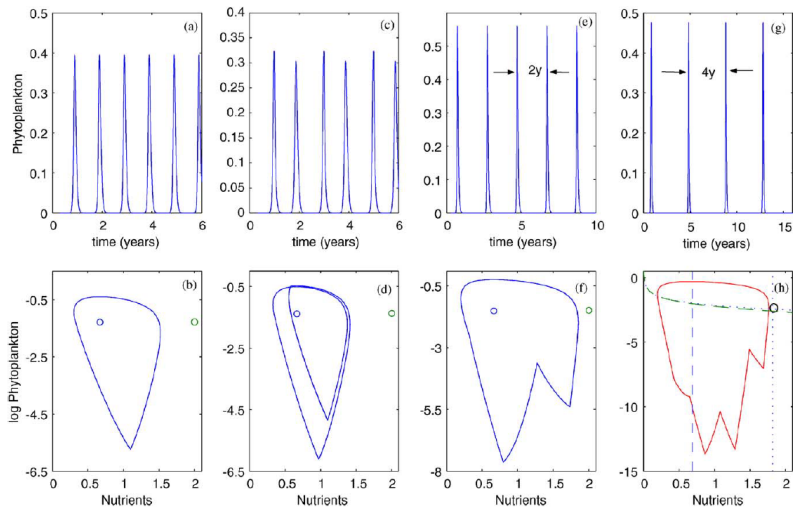


Still, our model predicts that at most two species can stably coexist in a mixed water column. Hence, the spatial heterogeneity imposed by a light gradient is not sufficient to solve Hutchinson's paradox of the plankton.

Huppert et al. (2002) The American Naturalist



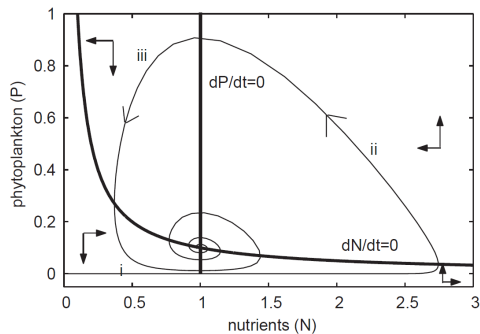
Huppert et al. (2005) Journal of Theoretical Biology



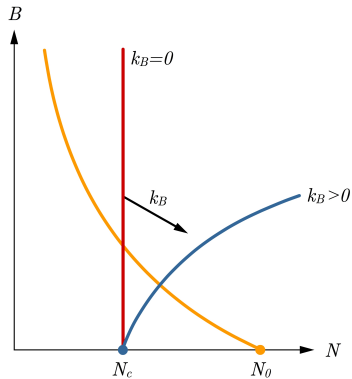
Huppert et al. (2005)

Unusually, despite the persistent seasonal forcing, it is extremely difficult to generate blooms that are both annually recurring and also chaotic or irregular (i.e. in amplitude) even though this characterizes many real time-series. Instead the model has a tendency to ‘skip’ with outbreaks often being suppressed from 1 year to the next.

Why is the nullcline vertical?



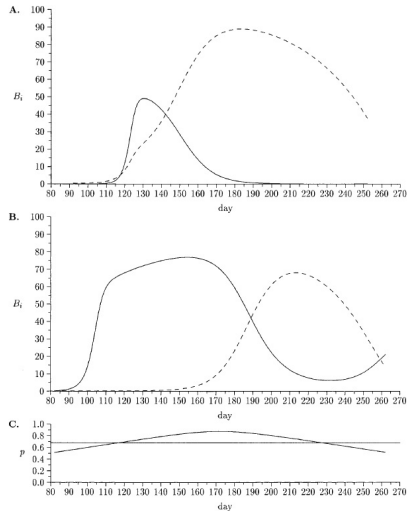
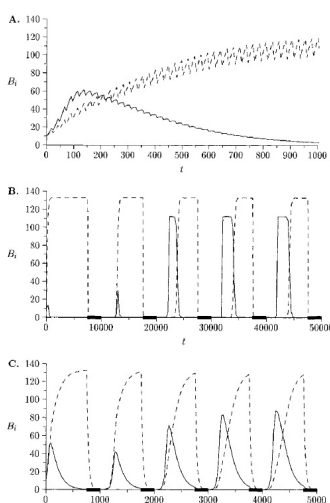
Huppert et al. (2005)



Kovač et al. (2020)

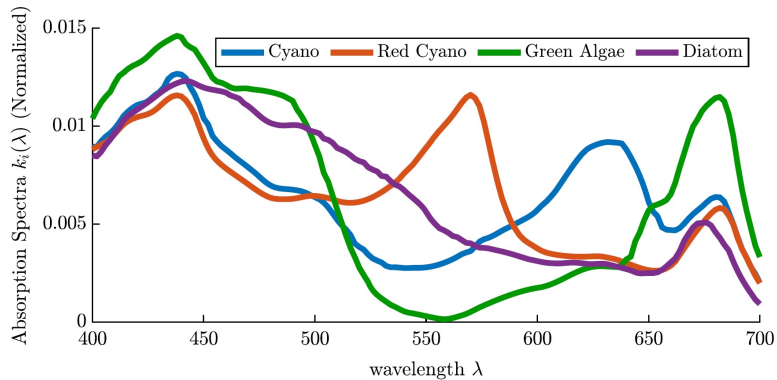
Can light effects alone be responsible for coexistence?

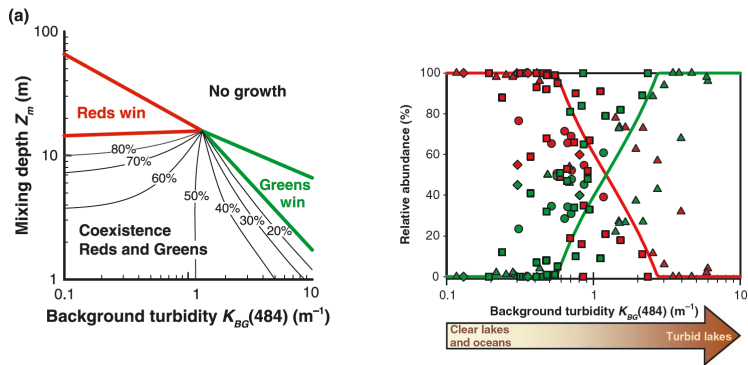
Lichtman & Klausmeier (2001) The American Naturalist



Seasonal change in daylength may be one of the factors driving the seasonal succession ...

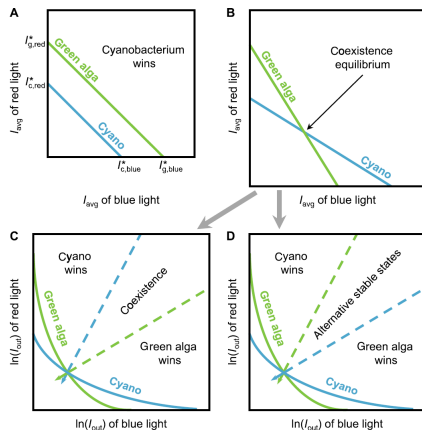
Heggerud et al. (2023) Mathematical Biology





Hutchinson's paradox of the plankton inspired many studies on the mechanisms of species coexistence. Recent laboratory experiments showed that **partitioning of white light allows stable coexistence** of red and green picocyanobacteria. Here, we investigate to what extent these laboratory findings can be extrapolated to natural waters. We predict from a parameterized competition model that the underwater light colour of lakes and seas provides ample opportunities for coexistence of red and green phytoplankton species.

Luimstra et al. (2020) Ecology



Can we advance ecological theory to predict how these differences in light-harvesting strategy affect competition between phytoplankton species? Here, we develop a new resource competition model in which the absorption and utilization efficiency of different colors of light are varied independently.

What about light and grazing?

ARTICLE

<https://doi.org/10.1038/s41467-019-09591-2>

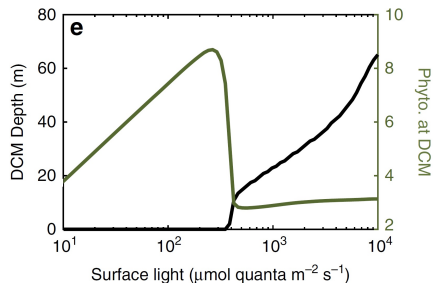
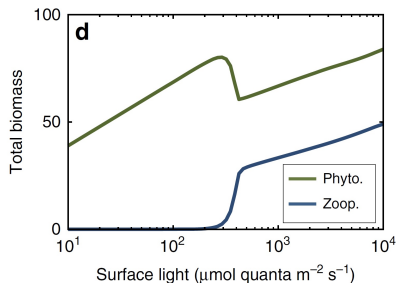
OPEN

Light-dependent grazing can drive formation and deepening of deep chlorophyll maxima

Holly V. Moeller¹, Charlotte Laufkötter^{2,3}, Edward M. Sweeney^{4,5} & Matthew D. Johnson⁶

$$\frac{\partial P}{\partial t} = P(z) \left[\frac{pI(z)}{H_P + I(z)} - l - \frac{gI(z)}{H_Z + I(z)} \cdot \frac{Z(z)}{H_A + P(z)} \right] + D \frac{\partial^2 P(z)}{\partial z^2}$$

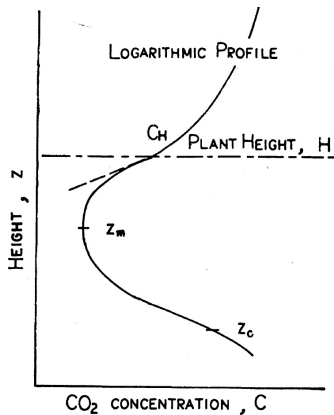
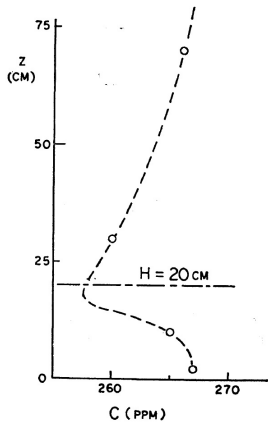
$$\frac{\partial Z}{\partial t} = Z(z) \left[\frac{egI(z)}{H_Z + I(z)} \cdot \frac{P(z)}{H_A + P(z)} - m \right] + D \frac{\partial^2 Z(z)}{\partial z^2}$$



Similar problems in other fields

Inoue (1965)

On the CO₂-Concentration Profiles within Crop Canopies



$$\frac{d}{dz} \left(K \frac{dC}{dz} \right) = (\epsilon I - r) F$$

Simillar problems in other fields

Spiers & Gurney (2001)

Population persistence in rivers and estuaries

Pachepsky et al. (2005)

Persistence, spread and the drift paradox

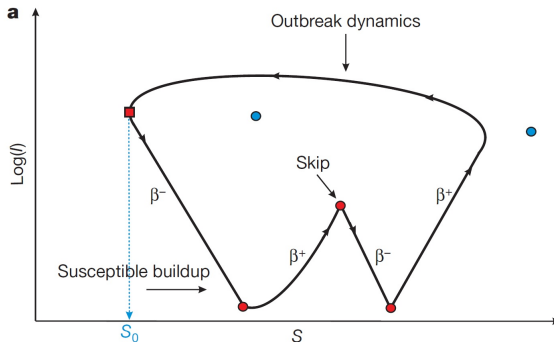
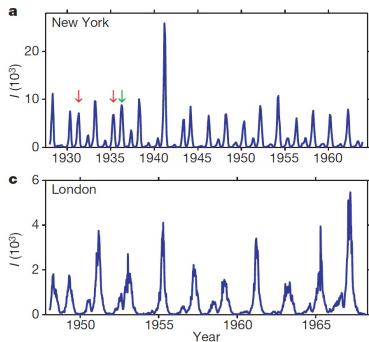
*Examples of such systems are found in **rivers and streams, marine currents, and areas with prevalent wind direction**. In streams, a long-standing question, dubbed **‘the drift paradox’**, asks why aquatic insects faced with downstream drift are able to persist in upper stream reaches.*

$$\frac{\partial n}{\partial t} = f(n)n - v \frac{\partial n}{\partial x} + D \frac{\partial^2 n}{\partial x^2}$$

Similar problems in other fields

Stone et al. (2007)

Seasonal dynamics of recurrent epidemics



Norbert Wiener's quote

*The most fruitful areas for the growth of the sciences were those which had been neglected as a **no-man's land between the various established fields**. Science has been increasingly the task of specialists, in fields which show a tendency to grow progressively narrower. Important work is delayed by the unavailability in one field of results that may have already become classical in the next field. **It is these boundary regions of science that offer the richest opportunities to the qualified investigator.***



PHOTOCLIM

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Thank you!