

Algal games: The vertical distribution of phytoplankton in poorly mixed water columns

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Abstract

Phytoplankton often face the dilemma of living in contrasting gradients of two essential resources: light that is supplied from above and nutrients that are often supplied from below. In poorly mixed water columns, algae can be heterogeneously distributed, with thin layers of biomass found on the surface, at depth, or on the sediment surface. Here, we show that these patterns can result from intraspecific competition for light and nutrients. First, we present numerical solutions of a reaction-diffusion-taxis model of phytoplankton, nutrients, and light. We argue that motile phytoplankton can form a thin layer under poorly mixed conditions. We then analyze a related game theoretical model that treats the depth of a thin layer of phytoplankton as the strategy. The evolutionarily stable strategy is the depth at which the phytoplankton are equally limited by both resources, as long as the layer is restricted to the water column. The layer becomes shallower with an increase in the nutrient supply and deeper with an increase in the light supply. For low nutrient levels, low background attenuation, and shallow water columns, a benthic layer occurs; for intermediate nutrient levels in deep water columns, a deep chlorophyll maximum occurs; and for high nutrient levels, a surface scum occurs. These general patterns are in agreement with field observations. Thus, this model can explain many patterns of algal distribution found in poorly mixed aquatic ecosystems.

The distribution of phytoplankton in lakes and oceans is highly heterogeneous, both vertically and horizontally (Reynolds 1984; Neill 1994). The most prominent vertical aggregations of algae are deep chlorophyll maxima (DCMs), benthic layers, and surface scums, where up to 90% of total biomass is concentrated in a relatively thin layer (Zohary 1989; Gasol et al. 1993). DCMs have been observed in small and large lakes (Fee 1976; Moll and Stoermer 1982; Abbott et al. 1984) and in the oceans (Cullen 1982; Takahashi et al. 1989). Vertically heterogeneous distributions of phytoplankton are usually associated with poorly mixed conditions, when mixing of the whole water column is prevented by a density gradient or when the source of turbulent kinetic energy is small (Lindholm 1992; Reynolds 1992). However, poor mixing alone is not sufficient for producing vertical patterns in phytoplankton distribution: contrasting gradients in light and nutrients are thought to play an important role (Cullen 1982; Davey and Heaney 1989; Reynolds 1992).

Different taxa of phytoplankton can form vertically heterogeneous distributions. Often, these are species that can choose their position in the water column by actively swimming (flagellates) or regulating their buoyancy (cyanobacteria) (Lindholm 1992). DCMs can also consist of diatoms (Fahnenstiel and Glime 1983; Davey and Heaney 1989), some of which have been shown to be able to decrease their

sinking velocity in nutrient-rich water (Tilman and Kilham 1976; Davey and Heaney 1989). Surface blooms are usually dominated by positively buoyant cyanobacteria (Reynolds 1984; Brock 1985). The thickness of DCMs ranges from several centimeters to tens of meters, depending on degree of mixing (Coon et al. 1987; Lindholm 1992).

In this paper, we present a model of light and nutrient competition under poorly mixed conditions. First, we demonstrate that motile phytoplankton can form a thin layer under poorly mixed conditions. Under the assumption of a thin layer, competition for light from above and nutrients from below can be thought of as a game, with the depth of the phytoplankton layer as the strategy. The evolutionarily stable strategy (ESS) is a depth that prevents growth in the rest of the water column (Maynard Smith and Price 1973; Geritz et al. 1998). We determine the ESS depth and equilibrium biomass and examine how they depend on parameters characterizing the phytoplankton species and the chemistry and physics of the environment.

The model

Consider a one-dimensional water column, where depth is indexed by $0 \leq z \leq z_b$, with $z = 0$ at the surface and $z = z_b$ at the bottom of the water column. Our model consists of equations for the depth profiles of phytoplankton biomass, b ; nutrient, R ; and light, I .

The change in phytoplankton biomass at depth z results from three processes: growth, loss, and movement. The functions $f_I(I)$ and $f_R(R)$ are the phytoplankton growth rate as a function of I or R when that resource is limiting. In numerical solutions we use the Michaelis-Menten form for these functions, $f_I(I) = rI/(I + K_I)$ and $f_R(R) = rR/(R + K_R)$, where r is the maximum growth rate and the K s are half-saturation constants, but our results hold for any bounded, strictly increasing functions. Following Liebig's law of the minimum for essential resources, the gross phytoplankton growth rate is given by $\min(f_I(I), f_R(R))$. Biomass is lost at

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density-independent rate m , representing respiration, death, and grazing. We define $g(z) = \min(f_R(R(z)), f_I(I(z))) - m$ to be the net per capita growth rate at depth z . Two important composite parameters are the break-even light and nutrient levels, $I^* = f_I^{-1}(m)$ and $R^* = f_R^{-1}(m)$, respectively (Tilman 1982; Grover 1997). Net growth is possible ($g(z) > 0$) only when $R > R^*$ and $I > I^*$.

Passive movement due to turbulence is modeled by eddy diffusion, with diffusion coefficient D_b (Okubo 1980; Imboden and Wüest 1995). For simplicity we assume that the diffusion coefficient is uniform with depth. Active movement is modeled by a taxis term (Keller and Segel 1971; Okubo 1980). Biologically, phytoplankton should move up if conditions are better above than below, down if conditions are better below than above, and not move if conditions are worse above and below. To model this, we have phytoplankton move at velocity $v(\cdot)$, which is a function of the gradient in growth rate, $\partial g/\partial z$. Positive v is oriented upward, in the direction of negative z . We assume that $v(\cdot)$ is an odd decreasing function that approaches v_{\max} as $\partial g/\partial z$ approaches negative infinity, approaches $-v_{\max}$ as $\partial g/\partial z$ approaches positive infinity, and $v(0) = 0$. In numerical solutions we use a step function, with $v = v_{\max}$ for $\partial g/\partial z < 0$, $v = -v_{\max}$ for $\partial g/\partial z > 0$, and $v = 0$ for $\partial g/\partial z = 0$.

Taken together, these assumptions above growth, loss, and movement result in

$$\begin{aligned} \frac{\partial b}{\partial t} &= \min(f_I(I), f_R(R))b - mb + D_b \frac{\partial^2 b}{\partial z^2} + \frac{\partial}{\partial z} \left[v \left(\frac{\partial g}{\partial z} \right) b \right] \\ &= [\text{Growth}] - [\text{Loss}] + [\text{Passive movement}] \\ &\quad + [\text{Active movement}] \end{aligned} \quad (1a)$$

No-flux boundary conditions at $z = 0$ and $z = z_b$ specify that phytoplankton do not enter or leave the water column

$$\left[D_b \frac{\partial b}{\partial z} + v \left(\frac{\partial g}{\partial z} \right) b \right] \Big|_{z=0} = \left[D_b \frac{\partial b}{\partial z} + v \left(\frac{\partial g}{\partial z} \right) b \right] \Big|_{z=z_b} = 0 \quad (1b)$$

Nutrients in the water column are mixed by eddy diffusion with diffusion coefficient D_R and are consumed by phytoplankton. Also, ε proportion of the nutrients in dead phytoplankton is immediately recycled

$$\begin{aligned} \frac{\partial R}{\partial t} &= -\frac{b}{Y} \min(f_I(I), f_R(R)) + D_R \frac{\partial^2 R}{\partial z^2} + \varepsilon m \frac{b}{Y} \\ &= -[\text{Uptake}] + [\text{Mixing}] + [\text{Recycling}] \end{aligned} \quad (1c)$$

Y describes the yield of phytoplankton biomass per unit nutrient consumed. Nutrients do not leave the top of the water column but are supplied at the bottom. Nutrients in the sediments are fixed at concentration R_{in} , while the nutrient concentration at the bottom of the water column is $R(z_b)$. Nutrients diffuse across the sediment-water interface at a rate proportional to the concentration difference across the interface.

$$\frac{\partial R}{\partial z} \Big|_{z=0} = 0, \quad \frac{\partial R}{\partial z} \Big|_{z=z_b} = h(R_{\text{in}} - R(z_b)) \quad (1d)$$

The parameter h describes the permeability of the interface:

as $h \rightarrow 0$ the boundary condition approaches a no-flux boundary condition, and as $h \rightarrow \infty$ it approaches the Dirichlet boundary condition $R(z_b) = R_{\text{in}}$.

Light at the surface is I_{in} ; light at depth z is determined by Lambert-Beer's law with phytoplankton attenuation coefficient a and background attenuation coefficient a_{bg} :

$$I(z) = I_{\text{in}} \exp \left\{ - \int_0^z [ab(Z) + a_{\text{bg}}] dZ \right\} \quad (1e)$$

Equations 1a–1e are our model.

Numerical solutions and dimensional analysis

To develop intuition about the solution to Eq. 1, we first present the equilibrium distributions of nutrients, light, and biomass determined from numerical solutions of the model (Fig. 1A–1E). The computer program used to solve the model uses a simple explicit finite difference scheme, with centered-in-space differencing for the diffusion term and up-wind differencing for the taxis term (Press et al. 1992). Mass is conserved, the scheme was stable for the time steps we used, and any numerical diffusion was insignificant compared to the actual diffusion terms. The program is available from the first author. We use the biologically reasonable parameter values given in Table 1, choosing phosphorus as the nutrient because it is a common limiting nutrient in lakes. Swimming velocity v_{\max} increases from Fig. 1A to Fig. 1E. In these simulations, phytoplankton are most uniformly distributed when they do not actively move (Fig. 1A). As v_{\max} increases, the phytoplankton become increasingly concentrated in a thin layer (Fig. 1E).

Dimensional analysis shows that the width of a layer of phytoplankton swimming toward a preferred depth and mixed by turbulent diffusion is proportional to D/v_{\max} . Order of magnitude estimates of both parameters are available. Swimming velocity v_{\max} ranges from 10^1 to 10^2 m d⁻¹ (Reynolds 1984), and typical eddy diffusion coefficients are $D = 10^1$ m² d⁻¹ in poorly mixed hypolimnia of stratified water columns and $D = 10^3$ m² d⁻¹ in well-mixed water columns (Imboden 1990). These imply that the thickness of a layer under poorly mixed conditions is on the order of 0.1–1 m and under mixed conditions is 10–100 m. Thus, the assumption of thin layers is plausible for poorly mixed waters and unreasonable for well-mixed waters. We will exploit the fact that phytoplankton can concentrate in a thin layer to analyze the model using a game theoretical approach.

Game theoretical approach

The field observations of thin layers of phytoplankton in poorly mixed water columns and the above results suggest that we may approximate the distribution of phytoplankton by an infinitely thin layer. For our game theoretical results, we assume that the phytoplankton form an infinitely thin layer at depth z_l by letting $b(z) = B\delta(z_l)$, where $\delta(z_l)$ is a Dirac delta function and B is the total depth-integrated biomass; that is,

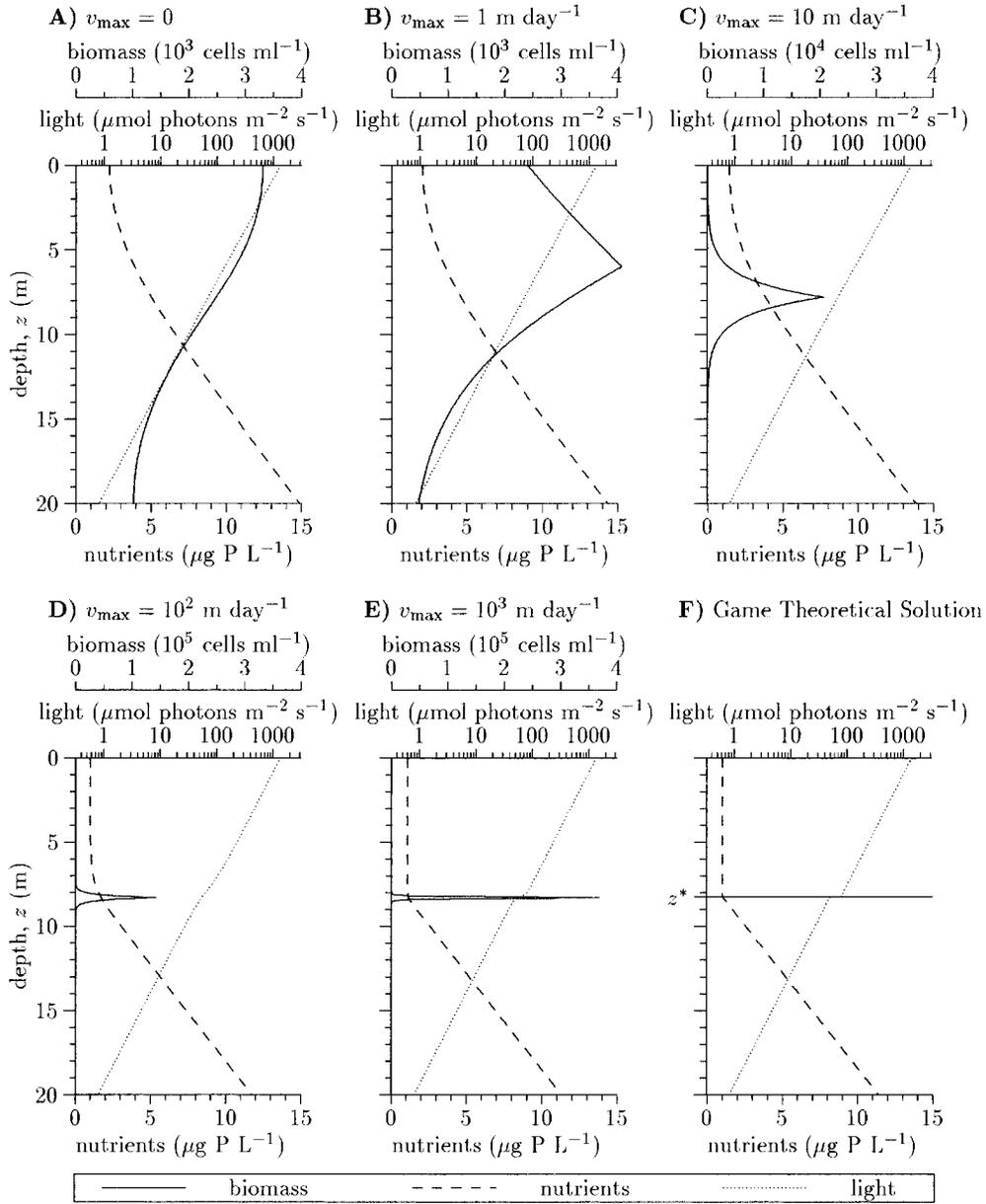


Fig. 1. Equilibrium vertical distributions of phytoplankton, nutrients, and light for varying v_{\max} determined by (A–E) numerical solution of Eq. 1 and (F) our game theoretical approach ($z^* = 8.25$ m from solving Eq. 4). Other parameters are given in Table 1. Note the changes in the biomass scale between parts.

$$b(z) = \begin{cases} \infty, z = z_l \\ 0, z \neq z_l \end{cases} \quad (2a)$$

and

$$\int_0^{z_b} b(z) dz = B \quad (2b)$$

Because we assume that active movement is sufficient to overcome biomass mixing ($D_b/v_{\max} \ll z_b$), we set $D_b = 0$.

The assumption of a thin layer allows us to investigate the model using a game theoretical approach. Given a layer

at z_l , we calculate the equilibrium biomass of phytoplankton and distribution of nutrients and light in the absence of movement. Then we determine whether net growth is possible above or below the layer at z_l . The ESS depth, z^* , is the depth of a layer that prevents phytoplankton from growing throughout the rest of the water column, that is $g(z) \leq 0$ for all z , either because there are insufficient nutrients ($R(z) \leq R^*$) or because there is insufficient light ($I(z) \leq I^*$). The ESS provides a stable equilibrium of the full model (Eq. 1) with $D_b = 0$ because $g(z) \leq 0$ for all z (no net growth occurs outside the layer) and $v(\partial g/\partial z|_{z^*}) = 0$ (no movement occurs). Small values of D_b blur this thin layer, but our qualitative results remain the same. Although we have not formally

Table 1. Parameters used in simulations unless otherwise noted.

Parameter	Meaning (units)	Value
z_b	water column depth (m)	20
R_{in}	sediment phosphorus concentration ($\mu\text{g P L}^{-1}$)	100
h	sediment-water column permeability (m^{-1})	10^{-2}
I_{in}	incoming light ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$)	1,400
a_{bg}	background attenuation coefficient (m^{-1})	0.35
a	algal attenuation coefficient (m^{-1} [cells ml^{-1}] $^{-1}$)	10^{-5}
$D_R = D_b$	eddy diffusion coefficient ($\text{m}^2 \text{d}^{-1}$)	10
v_{max}	swimming speed (m d^{-1})	100
r	maximum growth rate (d^{-1})	0.4
m	loss rate (d^{-1})	0.2
K_R	phosphorus half-saturation constant ($\mu\text{g P L}^{-1}$)	1.0
K_I	light half-saturation constant ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$)	50
Y	yield coefficient (cells ml^{-1} [$\mu\text{g P L}^{-1}$] $^{-1}$)	10^3
ε	recycling coefficient (dimensionless, $0 \leq \varepsilon < 1$)	0
R^*	minimum nutrient concentration ($\mu\text{g P L}^{-1}$)	1
I^*	minimum light level ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$)	50

demonstrated the connection between the full model (Eq. 1) and the game theoretical approach that follows, numerical results (compare Fig. 1C–1F) and intuition support the use of this approximation to gain insight into an otherwise difficult problem.

In the absence of phytoplankton ($b(z) = 0$), nutrients are uniformly distributed ($R(z) = R_{in}$) and light declines exponentially with depth due to background attenuation ($I(z) = I_{in}e^{-a_{bg}z}$). Depth-regulating phytoplankton can grow if $R_{in} > R^*$ and $I_{in} > I^*$; we assume these requirements are met. Background attenuation of light sets the maximum depth at which phytoplankton can grow,

$$z_{max} = \frac{\log(I_{in}/I^*)}{a_{bg}} \quad (3)$$

We assume $z_l \leq z_{max}$.

The details of solving for the equilibrium distribution of nutrients, light, and biomass are given in the Web Appendix (http://www.aslo.org/lo/toc/vol46/issue_8/1998al.pdf). See also Fig. 1F. In summary, nutrients are constant above the layer and increase linearly with depth below the layer (Eq. A7). Light declines with depth exponentially due to background attenuation and drops a finite amount at the layer due to attenuation by phytoplankton (Eq. A8). Equilibrium biomass in the thin layer depends on whether the phytoplankton are nutrient limited (Eq. A13) or light limited (Eq. A15).

Now that we know the equilibrium profile of light and nutrients given a layer at z_l , we would like to find a depth at which a layer can prevent growth elsewhere in the water column ($g(z) \leq 0$). Net growth is positive below a nutrient-limited layer since $I > I^*$ there (Fig. 2A). Net growth is positive above a light-limited layer since $R > R^*$ there (Fig.

2B). Only a layer limited by both resources prevents growth throughout the rest of the water column (Fig. 2C). The depth at which this occurs can be found by equating Eq. A13 and Eq. A15 and solving for the ESS depth, z^* :

$$[\text{light-limited biomass}] = [\text{nutrient-limited biomass}]$$

$$\frac{\log(I_{in}/I^*)}{a} - \frac{a_{bg}}{a}z^* = \frac{YD_R(R_{in} - R^*)}{m(1 - \varepsilon)(z_b + 1/h - z^*)} \quad (4)$$

The above argument also shows that z^* is convergence stable (Eshel 1983; Geritz et al. 1998), that is, the ESS attracts solutions that do not start at the ESS. If $0 < z^* < z_b$, the layer occurs within the water column and corresponds to a DCM. If $z^* < 0$ or $z^* > z_b$, we restrict the algae to the water column. The first case corresponds to a light-limited surface layer at $z = 0$, and the second case corresponds to a nutrient-limited benthic layer at $z = z_b$.

The equilibrium biomass is

$$\hat{B} = \begin{cases} \frac{\log(I_{in}/I^*)}{a}, & z^* \leq 0 \quad (\text{surface layer}) \\ \frac{\log(I_{in}/I^*)}{a} - \frac{a_{bg}}{a}z^* = \frac{YD_R(R_{in} - R^*)}{m(1 - \varepsilon)(z_b + 1/h - z^*)}, & 0 < z^* < z_b \quad (\text{DCM}) \\ \frac{YD_R h}{m(1 - \varepsilon)}(R_{in} - R^*), & z^* \geq z_b \quad (\text{benthic layer}) \end{cases} \quad (5)$$

When the layer is on the surface, biomass increases logarithmically with light supply I_{in} but is independent of R_{in} : the layer is light limited. When the layer is on the bottom, biomass increases with nutrient supply R_{in} but is independent of I_{in} : the layer is nutrient limited.

Equation 4 can be solved for z^* , but the resulting algebraic expression is uninformative. The two limiting cases of no background attenuation ($a_{bg} = 0$) and no phytoplankton attenuation ($a = 0$) result in simpler expressions for z^* that can be more easily understood. After considering these limiting cases we will return to the general situation given by Eq. 4.

Phytoplankton attenuation only ($a_{bg} = 0$)—When $a_{bg} = 0$, the solution to Eq. 4 is

$$z^* = z_b + \frac{1}{h} - \frac{aYD_R(R_{in} - R^*)}{m(1 - \varepsilon)\log(I_{in}/I^*)} \quad (6)$$

What can Eq. 6 tell us? Nutrient supply is controlled by four parameters (R_{in} , h , D_R , and ε). Increasing each one decreases z^* , making the layer closer to the surface. Conversely, increasing light supply I_{in} increases z^* , leading to a deeper layer. Good nutrient competitors (low R^*) are found shallower in the water column (smaller z^*), and good light competitors (low I^*) are found deeper (larger z^*). If $z^* < 0$, the layer sits on the water surface and is light limited. This occurs when

$$R_{in} > R^* + \frac{m(1 - \varepsilon)\log(I_{in}/I^*)}{aYD_R} \left(z_b + \frac{1}{h} \right) \quad (7)$$

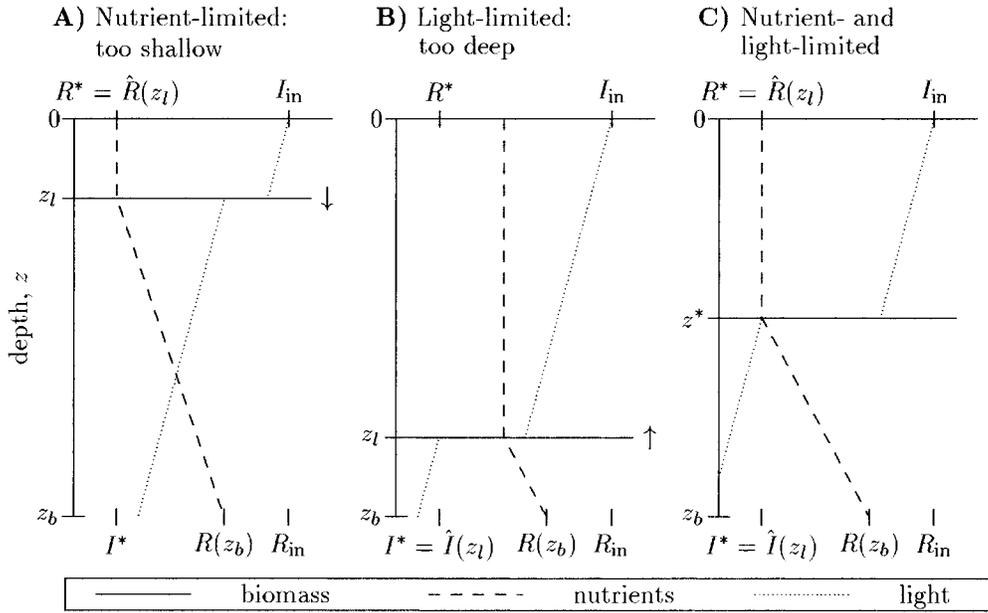


Fig. 2. Equilibrium distribution of nutrients and light, given layers at three depths z_l . (A) Growth is possible below a nutrient-limited layer because $I > I^*$. Motile phytoplankton would move down. (B) Growth is possible above a light-limited layer because $R > R^*$. Motile phytoplankton would move up. (C) An equally limited layer prevents growth throughout the water column; it is an ESS. Motile phytoplankton would stay at this depth.

Thus, shallow (small z_b), eutrophic (large R_{in}) lakes can support a surface scum of algae. If $z^* > z_b$, the layer rests on the sediment and is nutrient limited. This occurs when

$$R_{in} < R^* + \frac{m(1 - \varepsilon)\log(I_{in}/I^*)}{haYD_R} \quad (8)$$

Because $R_{in} > R^*$ is required for the phytoplankton to grow at any depth, a benthic layer requires $h < \infty$ and is easiest when h is small and I_{in} is large. The equilibrium biomass is

$$\hat{B} = \begin{cases} \frac{\log(I_{in}/I^*)}{a}, & z^* < z_b \quad (\text{surface layer, DCM}) \\ \frac{YD_R h}{m(1 - \varepsilon)}(R_{in} - R^*), & z^* \geq z_b \quad (\text{benthic layer}) \end{cases} \quad (9)$$

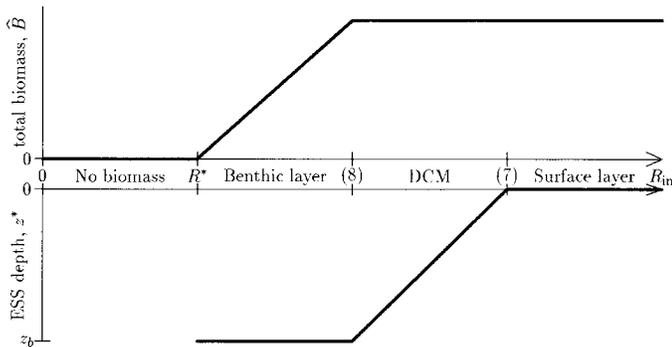


Fig. 3. The effect of nutrient supply concentration, R_{in} , when $a_{bg} = 0$. Depth is determined by Eq. 6, biomass by Eq. 9. The values of R_{in} that produce benthic and surface layers are given by Eq. 8 and Eq. 7, respectively.

Figure 3 illustrates the effect of nutrient enrichment on the equilibrium biomass and depth. In clear waters, nutrient enrichment does not affect equilibrium biomass of a DCM, but only decreases z^* .

Background attenuation only ($a = 0$)—When the phytoplankton do not affect the light level in the water column, the equilibrium depth is equal to the maximum depth set by background attenuation,

$$z^* = z_{max} = \frac{\log(I_{in}/I^*)}{a_{bg}} \quad (10)$$

Because $z^* > 0$, the existence of a surface scum of phytoplankton requires that phytoplankton contribute to light attenuation ($a \neq 0$). However, a benthic layer is still possible when $z^* > z_b$, or, equivalently,

$$a_{bg} < \frac{\log(I_{in}/I^*)}{z_b} \quad (11)$$

The equilibrium biomass is

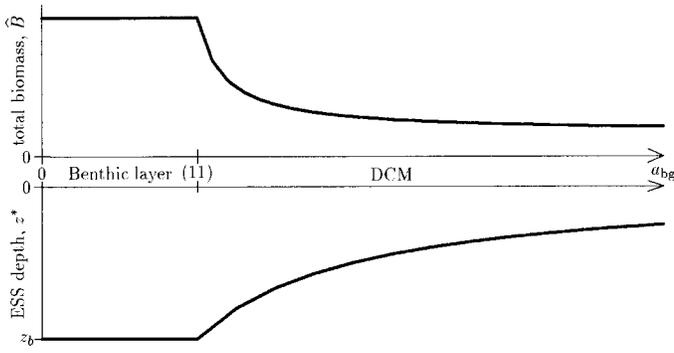


Fig. 4. The effect of background turbidity, a_{bg} , when $a_{bg} = 0$. Depth is determined by Eq. 10, biomass by Eq. 12. The values of a_{bg} that produces a benthic layer is given by Eq. 11.

$$\hat{B} = \begin{cases} \frac{YD_R(R_{in} - R^*)}{m(1 - \varepsilon)\left(z_b + \frac{1}{h} - \frac{\log(I_{in}/I^*)}{a_{bg}}\right)}, & 0 < z^* < z_b \quad (\text{DCM}) \\ \frac{YD_R h}{m(1 - \varepsilon)}(R_{in} - R^*), & z^* \geq z_b \quad (\text{benthic layer}) \end{cases} \quad (12)$$

Results that follow from Eq. 10 and 12: (1) The layer gets deeper with I_{in} increases, I^* decreases, and a_{bg} decreases. In this special case of no phytoplankton attenuation, layer depth is independent of nutrient supply parameters. This occurs because phytoplankton do not affect the light distribution so they reside as close as possible to the supply of nutrients. (2) Biomass increases with D_R , R_{in} , I_{in} , Y , and ε and decreases with a_{bg} , m , R^* , I^* , and z_b . Figure 4 illustrates the effect of background attenuation on the equilibrium biomass and depth. Increased background attenuation prevents a benthic layer and decreases the phytoplankton biomass.

Phytoplankton and background attenuation—When both phytoplankton and background attenuation are accounted for, the expression for z^* is complicated but the effects of varying parameters on z^* and \hat{B} can be determined by implicit differentiation in most cases (Table 2). In summary, increasing light levels (increasing I_{in} , decreasing attenuation coefficients a and a_{bg}) or increasing light competitive ability (decreasing I^*) moves the layer deeper; increasing nutrient supply (increasing R_{in} , D_R , h , ε) or increasing nutrient competitive ability (decreasing R^*) moves the layer toward the surface. Increasing the depth of the water column, z_b , moves the layer deeper, approaching the maximum possible depth set by background attenuation, z_{max} . Biomass of a DCM increases with competitive ability and the supply of both resources and decreases with the depth of the water column.

Determining the effect of mortality rate, m , on the equilibrium depth is more difficult. Changing m alters both R^* and I^* , which have opposing effects on z^* . In every case we have investigated numerically, increasing m first increases z^* at low m , then decreases z^* at high m (Fig. 5). At low m , biomass is high and the depth of the layer is largely determined by algal attenuation. In this case, Eq. 6 shows that increasing m decreases z^* . Biologically, increasing m lowers biomass, which increases the light beneath the layer, allowing the phytoplankton to live deeper. At high m , biomass is low and the depth of the layer is largely determined by background attenuation. In this case, Eq. 10 shows that increasing m increases I^* , which decreases z^* . Biologically, higher m means more light is required to survive, so the phytoplankton must live at a shallower level. We have not been able to prove that equilibrium biomass, \hat{B} , decreases with increasing m , but numerical evaluations of Eqs. 4 and 5 support this statement (Fig. 5).

Figure 6A shows the layer depth z^* as a function of a_{bg} and R_{in} calculated by solving Eq. 4 subject to the constraint of $0 \leq z \leq z_b$, and Fig. 6B shows the equilibrium biomass given by Eq. 5 at the equilibrium depth. Except when $a_{bg} = 0$, biomass increases with R_{in} until the layer reaches the surface. Note that the value of R_{in} at which the layer reaches

Table 2. Effect of model parameters on equilibrium depth of a DCM (z^*) and biomass (\hat{B}) when layer is on the surface, a DCM, or a benthic layer. — indicates no effect. Results determined by implicitly differentiating Eq. 4 and 5, except those marked †, which indicates a result we have determined through numerical solution of Eq. 4 and 5.

Increase	z^*	$\hat{B}_{\text{surface layer}}$	\hat{B}_{DCM}	$\hat{B}_{\text{benthic layer}}$
I_{in}	Increases	Increases	Increases	—
I^*	Decreases	Decreases	Decreases	—
a	Decreases	Decreases	Decreases	—
Y	Decreases	—	Increases	Increases
D_R	Decreases	—	Increases	Increases
R_{in}	Decreases	—	Increases	Increases
R^*	Increases	—	Decreases	Decreases
z_b	Increases	—	Decreases	—
h	Decreases	—	Increases	Increases
a_{bg}	Decreases	—	Decreases	—
ε	Decreases	—	Increases	Increases
m	Increases (small m)†, Decreases (large m)†	Decreases	Decreases†	Decreases

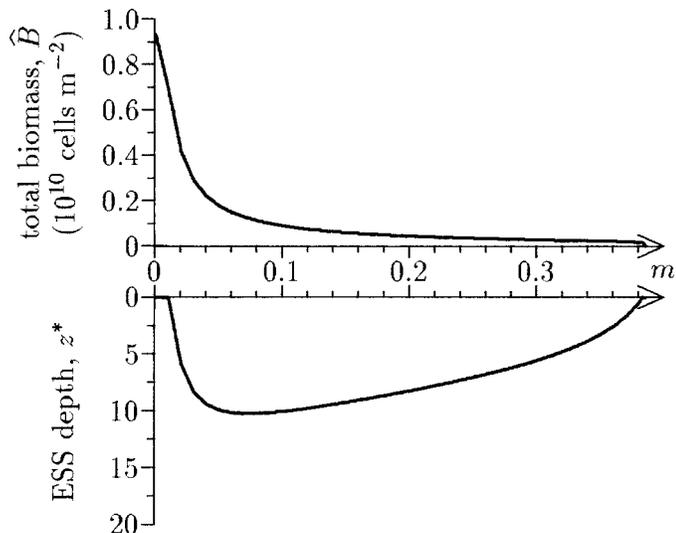


Fig. 5. The effects of mortality rate m . Depth is determined by numerically solving Eq. 4, biomass by substituting the equilibrium depth into Eq. 5. Parameters given in Table 1.

the surface is independent of a_{bg} , since $a_{bg}z^* = 0$ when $z^* = 0$. Thus, Eq. 7 holds for all values of a_{bg} . Figure 7 summarizes the model predictions as a function of R_{in} and a_{bg} : a benthic layer occurs for small R_{in} and a_{bg} , a DCM for intermediate R_{in} , and a surface scum for large R_{in} . DCMs are most likely in deep water columns, since increasing z_b shifts point (7) to the right and point (11) down, increasing the size of parameter space that leads to a DCM. Likewise, decreasing z_b decreases the size of parameter space that leads to a DCM, favoring benthic and surface layers.

Discussion

Model predictions—The model successfully replicates major vertical patterns of algal distribution under poorly mixed conditions such as surface scums, deep chlorophyll

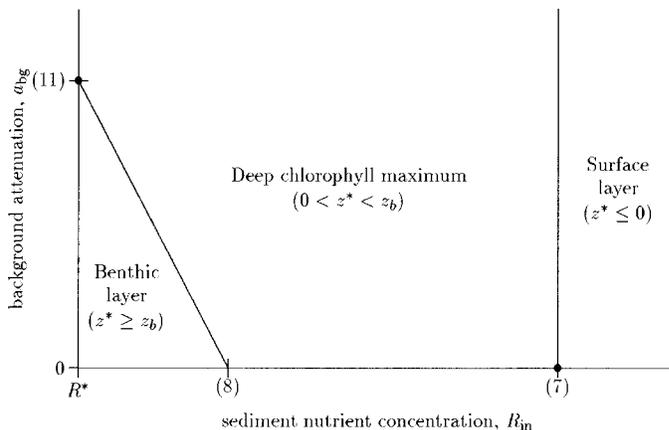


Fig. 7. Overview of how the location of primary producers depends on nutrient status, background turbidity, and water column depth. The locations of points (7), (8), and (11) are given by the equations with those numbers.

maxima, and benthic layers. A number of important relationships arise from the model. Some of these relationships are well documented for natural water bodies, while others provide new insights into the factors determining algal distribution and are amenable to testing. Below, we will discuss some of the major model predictions and their support by observations, as well as some relationships that to our knowledge have not been reported before but can provide new direction for future field studies in phytoplankton ecology. The predictions of the model explicitly relate physical and chemical parameters of a water body with vertical distribution of phytoplankton.

The first prediction is that depth-regulating phytoplankton can form a thin layer in a poorly mixed water column (Fig. 1). There is widespread empirical support for this result, which motivated our game theoretical approach. For example, DCMs consist of flagellates in Ontario’s Experimental Lakes Area (Fee 1976) and Antarctica’s ice-covered lakes (Spaulding et al. 1994), buoyancy-regulating cyanobacteria

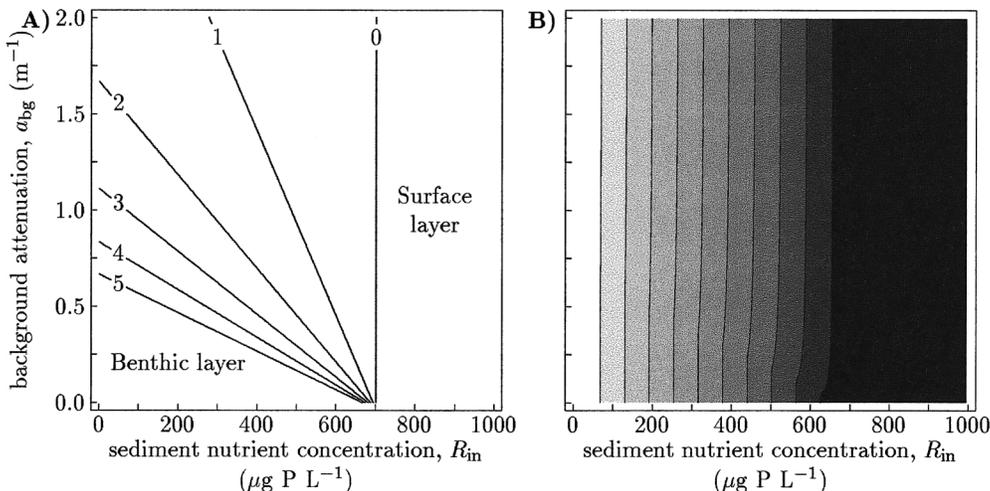


Fig. 6. (A) Equilibrium layer depth given by solving Eq. 4, with $z_b = 5$ m and other parameters given in Table 1. (B) Equilibrium biomass given by Eq. 5. Darker shades represent higher biomass.

in a small Minnesota lake (Walsby and Klemer 1974) and European lakes (Reynolds 1984), and diatoms in Lake Superior (Moll and Stoermer 1982). Our model predicts that the degree of turbulence determines the thickness of a DCM. Fee (1976) observed very narrow (from several to tens of centimeters) layers in small, very poorly mixed lakes (vertical eddy diffusion coefficients between 10^{-3} and 10^{-2} $\text{m}^2 \text{d}^{-1}$, among the lowest reported for lakes); in Lake Tahoe, where eddy diffusion coefficients were three to four orders of magnitude greater (10^1 $\text{m}^2 \text{d}^{-1}$), the thickness of the DCM layer was 10–20 m (Abbott et al. 1984).

The second prediction is that the concentration of the limiting nutrient should be low and constant above the phytoplankton layer and linearly increasing with depth below the layer. This pattern is seen in the distribution of nitrate and phosphate in Lake Tahoe (Holm-Hansen et al. 1976), dissolved silicate in Windermere (Davey and Heaney 1989), and dissolved inorganic nitrogen in Lake Carioca in Brazil (Reynolds et al. 1983). This is also consistent with the “typical tropical structure” of the tropical ocean (Herbland and Voituriez). As Cullen (1982) notes, “the chlorophyll maximum is found near the nitracline.” Our model shows that the DCM may in fact determine the location of the nitracline.

The third prediction is that the light level below a DCM or a surface layer is the break-even light level, I^* . This is a consequence of the ESS depth being where the phytoplankton are equally limited by light and nutrients. Because phytoplankton themselves can contribute appreciably to shading in eutrophic systems (Gasol et al. 1993; Kirk 1994), this is more than the trivial prediction that phytoplankton are found at the greatest depth at which background attenuation of light allows growth. Few studies directly compare light levels to species-specific break-even light levels. However, many studies note that DCMs occur where light levels are between 0.1% and 1% of surface irradiance. Given typical incoming irradiances (Kirk 1994), this is consistent with published values of I^* (Langdon 1988; Huisman et al. 1999a). Less has been published on the light level under a surface scum, except that it is greatly reduced by algal shading (Zohary 1989).

The fourth prediction is that the equilibrium depth of a layer is given by solving Eq. 4 and the equilibrium biomass by Eq. 5. Most generally, the model predicts a benthic layer in shallow (small z_b), oligotrophic (small R_{in}), clear (small a_{bg}) waters; a DCM in deep (large z_b) waters; and a surface scum in shallow, eutrophic (large R_{in}) waters (Fig. 7). These broad predictions are in agreement with field observations (Reynolds 1984; Zohary 1989; Lindholm 1992). Surface blooms of cyanobacteria are a characteristic feature of eutrophic lakes (Reynolds 1984; Brock 1985). A nice illustration of the relationship between nutrient status and the position of a thin layer is found in Klein and Chorus (1991): decreased nutrient loading replaced surface blooms with a DCM.

The effects of varying different parameters are summarized in Table 2. The model predicts that with increasing nutrient supply (R_{in} , h , and D_R), a layer moves closer to the surface and its biomass increases. Moll and Stoermer (1982) compared the DCMs in two Great Lakes, the oligotrophic

Lake Superior and the mesotrophic Lake Michigan, and reported that the depth of the DCM layer was greater and the biomass was lower in Lake Superior than in Lake Michigan. This is in agreement with our model predictions. Along with nutrient availability, light availability may influence the position and biomass of a phytoplankton layer. Under high light availability (high I_{in} or low a_{bg}), the layer deepens and in shallow lakes may reside on the bottom (Eq. 8 or Eq. 11). Schmitt and Nixdorf (1999) found that in a shallow eutrophic lake higher than usual light availability led to a dominance of benthic diatoms instead of a typical cyanobacterial bloom. In Lake Tahoe the DCM biomass was closely correlated with irradiance, and the depth of the layer was shallower in September than in July, possibly due to a decreasing total irradiance (Coon et al. 1987). A similar decrease in the DCM depth as the growing season progressed was observed for a metalimnetic *Cryptomonas* sp. population (Gasol et al. 1993), but not for the DCMs found in Ontario’s Experimental Lakes Area (Fee 1978).

The fifth prediction concerns the resource limitation of algae at different depths. The model analysis shows that a surface scum should be light limited, a benthic layer should be nutrient limited, and a DCM should be limited by both resources. A surface layer cannot be nutrient limited because the algae would then move deeper. When a benthic layer occurs, the model implies that the algae control the flux of nutrients from the sediments into the water column, which has been observed (Jansson 1980; Van Lujn et al. 1995; Woodruff et al. 1999).

Comparison with other models—Previous theoretical work on phytoplankton resource competition has not investigated the case of competition for light and nutrients supplied from the sediments in poorly mixed water columns. The inclusion of a directed movement term is also novel. Huisman and Weissing (1994, 1995) considered competition for nutrients and light in perfectly well-mixed water columns, where biomass and nutrients are assumed to be uniformly distributed but light declines exponentially with depth. In their model, the light level at the bottom of the water column, I_{out} , characterizes the light competitive ability of the phytoplankton. Unlike I^* , which characterizes the light competitive ability in our model, I_{out} depends on the light supply, I_{in} .

Huisman et al. (1999b) investigated the effect of incomplete mixing on the development of a phytoplankton bloom when light is the only limiting resource. They showed that in the absence of sinking, phytoplankton biomass must decrease with depth; only with sinking can biomass reach a maximum at depth. Britton and Timm (1993) came to similar conclusions using a model of competition for light and nutrients, which are perfectly recycled and treated implicitly. In contrast, our model does not require sinking to produce a DCM. However, our model also predicts a surface layer when phytoplankton are limited only by light.

Huisman et al. (1999b) found that poor mixing could allow phytoplankton to persist in deep water columns where they could not grow under strong mixing. Similarly, phytoplankton can survive in deep water columns in our model of poor mixing, where there is a critical depth in models of

competition for nutrients and light in well-mixed water columns (Huisman and Weissing 1995).

In this paper we treated mixing of the water column as homogeneous in space and time. In stratified lakes, a well-mixed layer lies above the thermocline and a poorly mixed hypolimnion (Imboden and Wüest 1995). Spatial variation in mixing could be incorporated in this modeling framework by letting the diffusion coefficients, D , vary with depth. One potentially illuminating special case would consider a perfectly well-mixed layer (Huisman and Weissing 1995) above a poorly mixed layer modeled as in this paper. Our preliminary results with such a model show that the predictions of Eqs. 4 and 5 are correct when the layer occurs in the hypolimnion, where the assumption of poor mixing is met. When Eq. 4 would predict the layer to lie in the well-mixed epilimnion, the assumption of poor mixing is invalid and the phytoplankton are evenly dispersed through the epilimnion. Thus, our model predictions are accurate as long as the poor mixing assumption is met at the depth of the phytoplankton layer. This also accounts for the fact that low wind, and therefore poor mixing, is a prerequisite for surface scums (Soranno 1997).

We have treated the light supply as constant, even though incoming light levels fluctuate over a wide range of temporal scales. Based on our analysis of the effect of light:dark fluctuations on resource competition in nonspatial models (Litchman and Klausmeier 2001), we conjecture that fast (daily) light fluctuations will only affect phytoplankton biomass and depth through the dependence of R^* and I^* on the light regime and that slow fluctuations would lead to more complicated dynamics.

We justified the assumption of a thin layer based on the ability of depth-regulating phytoplankton to overcome turbulent diffusion. Another potential mechanism that can counteract turbulent diffusion and produce DCMs is in situ growth (Cullen 1982). Indeed, numerical solutions of our general model (Eq. 1) with no active movement ($v_{\max} = 0$), low diffusivity ($D_R = D_b = 10^0 \text{ m}^2 \text{ d}^{-1}$), low background attenuation ($a_{\text{bg}} = 0.1 \text{ m}^{-1}$), and a deep water column ($z_b = 100 \text{ m}$) produce a 20 m wide DCM at $z = 27 \text{ m}$. Unfortunately, finding the width of the layer that results from the interplay of growth and diffusion is not straightforward. The resulting layer is often too wide for our game theoretical approach to be quantitatively accurate, although the qualitative results appear to be similar. A better understanding of the role of in situ growth in promoting DCMs would be useful, but may elude analytical results.

A generalization of the model presented here would be to relax the assumption of Liebig's law of the minimum, allowing interaction between nutrient and light limitation. We have performed a preliminary analysis of a model that replaces the minimum term of Eq. (1a,c) with a multiplicative term ($f_R(R)f_R(I)$). In this case, phytoplankton still aggregate in a thin layer, but the layer is not infinitely thin, even in the absence of biomass mixing ($D_b = 0$). This occurs because phytoplankton can be limited by both resources for a range of R and I . Although the equilibrium distribution of biomass is not a delta function, the qualitative ecological conclusions remain unchanged.

The model in this paper integrates a number of physical,

chemical, and biological processes that act together to determine the vertical distribution of phytoplankton. This model does not include many processes that affect the vertical distribution of phytoplankton. Oxygen status commonly changes with depth, with major effects on the biota and nutrient dynamics. Also not included are photoinhibition, variable quota and luxury uptake of nutrients, and depth-dependent herbivory. Further, nutrients are supplied only by mixing from the sediments or immediate recycling; in reality, nutrients can be supplied throughout the water column. Turbulent mixing of phytoplankton biomass also affects the distribution of phytoplankton (Fig. 1). Extensions of this model to include any of these processes would further develop our understanding of the vertical structure of phytoplankton communities.

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