Competition of Phytoplankton under Fluctuating Light

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ABSTRACT: Light is an essential resource for phytoplankton and fluctuates on a wide range of timescales. To understand how light fluctuations affect phytoplankton community structure and diversity, we have studied a set of simple models using a combination of analytical and numerical techniques. Light fluctuations can affect community structure when species exhibit the gleaner-opportunist trade-off between competitive ability and ability to reach carrying capacity quickly. Fast fluctuations can switch the competitive dominant from a gleaner to an opportunist; slow fluctuations can cause this switch and also lead to stable coexistence. Coexistence is easiest between species that are highly differentiated along the gleaner-opportunist trade-off. Our results remain qualitatively unchanged when more realistic light fluctuations such as daily and seasonal changes in irradiance and the presence of a spatial gradient in light are considered. Seasonal change in day length may be one of the factors driving the seasonal succession of phytoplankton, from opportunist species dominant under shorter day lengths (spring and autumn) to gleaner species dominant under longer day length (summer). These results illustrate how resource fluctuations can have an important role in structuring ecological communities.

Keywords: coexistence, competition, light fluctuations, phytoplankton, temporal heterogeneity.

Nonequilibrium conditions prevail in nature. Environmental factors and resources, as well as population densities, fluctuate in both time and space. Dynamic environmental conditions are an important structuring force in ecological systems (Nisbet and Gurney 1982; DeAngelis and Waterhouse 1987; Chesson 1988). Environmental fluctuations are likely to have a significant effect on com-

munities in aquatic ecosystems because of close coupling of physical forcing and biota (Steele 1985). Hutchinson suggested that nonequilibrium environmental conditions may explain the coexistence of many species of phytoplankton in a seemingly homogeneous environment, the so-called paradox of the plankton (Hutchinson 1961). General analytical models demonstrate that nonequilibrium resource supply can promote coexistence and enhance diversity (Armstrong and McGehee 1976, 1980; Levins 1979), supporting Hutchinson's ideas. Hsu (1980) showed that seasonally varying nutrient can allow coexistence of two species growing, according to Monod kinetics. Hale and Somolinos (1983) extended Hsu's results to a multispecies community and more general growth dependence. These theoretical results showing that resource fluctuations can allow coexistence were confirmed experimentally for phytoplankton competing for ammonia or phosphorus (Turpin and Harrison 1979; Sommer 1984, 1985; Grover 1991).

The coexistence of two or more species under variable resource supply is possible when species exhibit a gleaner-opportunist trade-off. A gleaner species grows better at low resource levels as a result of a low minimum resource requirement. An opportunist species is one that can take advantage of high resource levels. Traditionally an opportunist is thought to be one with a high maximum growth rate (Grover 1997). We show that, when competing species have different mortality rates, it is the ratio of the maximum growth rate to the mortality rate that determines whether a species is an opportunist.

Light is a major resource for phytoplankton and has a complex pattern of variability both in time and space. The effects of spatial heterogeneity in light supply on competition of phytoplankton have been investigated by Britton and Timm (1993) and Huisman and Weissing (1994). The vertical gradient in light availability in a well-mixed water column is not sufficient for more than one species to occur at equilibrium (Huisman and Weissing 1994). Britton and Timm (1993) demonstrated, however, that a spatial gradient in light distribution with depth coupled with diffusion of algal cells through the water column may allow coexistence of many species of phytoplankton as well as their vertical segregation. Huisman et al. (1999a, 1999b) also showed that

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incomplete mixing may lead to coexistence of competing species, although the coexistence region is small. The investigation of the effects of temporal heterogeneity of light supply on phytoplankton competition and coexistence lags behind (Grover 1997). Our goal in this article is to investigate how the presence of temporal heterogeneity in light supply may affect competition and coexistence of phytoplankton. We use a simple model of light competition where light is attenuated exponentially by phytoplankton biomass. Previous studies of nonequilibrium resource supply have concentrated on the effects of fluctuating nutrients, where the dynamics of the resource is described by a separate differential equation with a periodically varying term (Hsu 1980; Hale and Somolinos 1983). In contrast, light here is characterized algebraically.

We use invasibility criteria to determine the outcome of competition. If each species can invade a monoculture of the other species (the growth rate of an invader averaged over a period is >0), long-term stable coexistence is possible (Armstrong and McGehee 1980; Smith and Waltman 1995). If neither species can invade a monoculture of the other (growth rate of invader is <0), the outcome of competition depends on initial conditions. If only one of the two species is able to invade successfully, we say that one species outcompetes the other. Namba (1984, 1986; Namba and Takahashi 1993) has used a Lotka-Volterra competition model with periodically fluctuating coefficients to show that species may coexist, even though one cannot invade a monoculture of the other. This depends on the existence of multiple attractors, and such coexistence is not stable against large environmental fluctuations. Because we have not found any cases of multiple attractors in our model, we have operationally defined the competitive dominant to be a species that can invade a monoculture of the other but whose monoculture cannot be invaded.

Light fluctuations in nature occur over a wide range of temporal scales, from fast fluctuations as a result of surface waves (on the order of $10\ \mathrm{s}^{-1}$) to seasonal changes in irradiance ($10^{-8}\ \mathrm{s}^{-1}$); different types of fluctuations are superimposed on each other, complicating the consideration of the potential effects. We start with simple square wave fluctuations that capture some general features of light variability and still allow analytical treatment. Because light distribution is spatially heterogeneous, we investigate how adding spatial heterogeneity (a vertical gradient in a well-mixed column) to temporal variation in irradiance may affect competition. We also look at how more realistic light regimes, including diel and seasonal changes in irradiance influence competitive interactions. We extend our results to the case when species compete for another essential resource under fluctuating light. Thus, in this study, we address several important aspects of the interaction between dynamic light regimes and phytoplankton competition.

The Basic Model

We use a model where species growth is limited by light availability only:

$$\frac{dB_i}{dt} = B_i\left(\mu_i \frac{I}{I + K_i} - m_i\right),\qquad(1)$$

where B_i is the biomass of species i ($i = 1, 2$) and I is the incident irradiance. The growth rate is a saturating function of incident irradiance, described by a Monod function with maximum growth rate per unit biomass μ_i and half-saturation constant K_i. Biomass loss as a result of respiration, grazing, sedimentation, and washout occurs at rate m_i. The ratio of the maximum growth rate to the loss rate is an important parameter we will call $R = \mu/m$.

The incident light is determined by incoming light, which is attenuated by phytoplankton biomass according to Lambert-Beer's law (Kirk 1994):

$$I = I_{\mathrm{in}}e^{-(a_1 B_1 + a_2 B_2)},\qquad(2)$$

where I_{in} is the intensity of the incoming light and a_i is the light attenuation coefficient of species i. Light absorption by background turbidity is incorporated into I_{in}. To isolate the effect of temporal heterogeneity on the outcome of competition, we do not include a spatial gradient in light distribution here and assume that all cells in the mixture experience the same light level. The presence of a spatial gradient can alter phytoplankton competition for light under constant irradiance (Britton and Timm 1993; Huisman and Weissing 1994). We will address the effect of a vertical gradient on light competition under fluctuating light in a later section.

The increase of biomass leads to a decrease in the incident light experienced by cells; therefore, species compete for light by shading. Each species is able to increase when the incident light is above its minimum resource requirement, I_i^*, given by

$$I_i^* = \frac{K_i}{R_i - 1}.\qquad(3)$$

In accordance with resource competition theory (Tilman 1982), under constant conditions, the species with the lowest I^* displaces all others by reducing the incident light below the break-even light level I^* of the other species. At equilibrium, the biomass of the superior competitor is

$$B_i^* = \frac{\log (I_{in}/I_i^*)}{a_i}. \tag{4}$$

To provide a concrete example, we often use model parameters obtained experimentally for the diatom *Nitzschia* sp. and the green alga *Sphaerocystis schroeteri* (Litchman 2000; table 1). *Sphaerocystis* has a lower I^* and therefore outcompetes *Nitzschia* under constant light. *Sphaerocystis* also has a higher maximum growth rate, μ, but because its mortality rate is lower, *Nitzschia* has a greater R than *Sphaerocystis*. Thus, these species exhibit the generalized gleaner-opportunist trade-off, with *Sphaerocystis* the gleaner and *Nitzschia* the opportunist, and their growth-irradiance curves intersect (fig. 1).

We begin our analysis with the simplest fluctuating light regime, where incoming light alternates periodically between light and dark. Each fluctuation regime can be characterized by the incoming irradiance when light is on (I_{in}), the proportion of each period when light is on (p), and the fluctuation period (T). First, we determine the conditions for a single species to persist by itself; then we consider interspecific competition. In general, competition under equations (1) and (2) cannot be treated analytically under fluctuating light levels. However, we can determine the outcome of competition under two contrasting limits: the limit of infinitely fast fluctuations ($T \to 0$) and the limit of infinitely slow fluctuations ($T \to \infty$). The biological interpretation and conclusions of each limiting case are given below; mathematical details are given in the appendixes. Because the difference between the real model and the approximations goes to 0 as T approaches 0 or infinity, these limiting cases provide reasonable approximations for a range of finite (sufficiently short or long) periods. We use numerical techniques to determine the behavior of the system for intermediate periods and to verify the validity of our analytical approximations.

Single Species Persistence

For a species to persist by itself, it must be able to invade the empty system. To determine this, we average its growth rate over a period when the species is sufficiently rare so that the incident light is given by the incoming light. When the invasion rate is positive, the species can persist in monoculture (Smith and Waltman 1995):

$$\int_0^T \frac{dB}{Bdt} dt = \int_0^{pT} \left(\mu \frac{I_{in}}{I_{in} + K} - m \right) dt$$
$$- \int_{pT}^T mdt > 0, \tag{5}$$

Table 1: Parameters used in simulations

	Nitschia (opportunist)	*Sphaerocystis* (gleaner)
μ (d^{-1})	1.31	1.44
m (d^{-1})	.41	.77
K (μmol photons m^{-2} s^{-1})	34.5	6.0
I^* (μmol photons m^{-2} s^{-1})	15.72	6.90
$R = \mu/m$	3.195	1.870

Note: Values for *Nitzschia* and *Sphaerocystis* were determined empirically (Litchman 2000); mortality rates include a dilution rate of 0.17 d^{-1}; $I_{in} = 1,400$ μmol photons m^{-2} s^{-1} and $a = 0.04$, unless otherwise noted.

integrating

$$p\mu \frac{I_{in}}{I_{in} + K} - m > 0, \tag{6}$$

and rearranging

$$p > p_{min} = \frac{m}{\mu[I_{in}/(I_{in} + K)]} = \frac{1}{R}\left(1 + \frac{K}{I_{in}}\right). \tag{7}$$

For $I_{in} \gg K$,

$$p_{min} \approx \frac{1}{R}. \tag{8}$$

These results hold regardless of the period, T. Under a typical midday irradiance of $I_{in} = 1,400$ μmol photons m^{-2} s^{-1}, p_{min} of *Nitzschia* is 0.321 and p_{min} of *Sphaerocystis* is 0.537.

Competition under Fast Fluctuations

As period T decreases to 0, species average their growth rates over the period (app. A). The minimum light requirement, $I_i^*(p)$, depends on the proportion of light in a period, p, as well as the characteristics of the species:

$$I_i^*(p) = \frac{K_i}{pR_i - 1}, \tag{9}$$

where $I_i^*(p)$ represents the minimum incoming light, I_{in}, which will allow species i to persist with light on for p proportion of each period. In competition, the species with the lowest I^* displaces all others, but since I^* is now a function of p, the outcome of competition also depends on p. Coexistence is impossible, but the competitive dominance may be reversed from the case of constant light. Figure 2 shows that the I^* curves of *Nitzschia* and *Sphaerocystis* intersect once at $p_{switch} = 0.629$. For $p < 0.629$,

Nitzschia wins competition, and for $p > 0.629$, *Sphaerocystis* wins (fig. 3*A*). In general, the I^* curves of two species intersect if and only if $I_{gl}^* < I_{op}^*$ and $R_{op} > R_{gl}$; that is, they must show the gleaner-opportunist trade-off. The value of p where they intersect is

$$p_{\text{switch}} = \frac{K_{op} - K_{gl}}{R_{gl}K_{op} - R_{op}K_{gl}}. \tag{10}$$

Thus, the nonlinear dependence of the minimum light requirements on the temporal pattern of light supply may reverse the outcome of competition from that under constant light.

Competition under Slow Fluctuations

As the period T increases to infinity, the environment remains constant for longer times. The dynamics consists of rapid jumps between the vicinities of equilibrium points, the carrying capacities of the populations and zero, each of which is approached asymptotically. At the beginning of each period, both species are quite rare and grow exponentially near their maximum rates of increase. The opportunist nears its monoculture equilibrium while the gleaner is still of negligible density. The opportunist remains near its equilibrium while the gleaner continues to grow, at a slower rate because of the shade of the opportunist. At some time, the gleaner nears its monoculture equilibrium and displaces the opportunist. When $t = pT$, the light turns off and both species die exponentially to become rare again at the start of the next period (fig. 3*B*). Stable coexistence
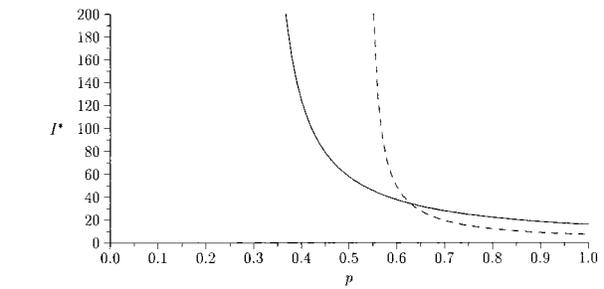

Figure 2: Minimum light requirements, $I^*(p)$ of *Nitzschia* (*solid line*) and *Sphaerocystis* (*dashed line*) as a function of the proportion of light in each period, p.

between a gleaner and an opportunist can be proven possible under slow fluctuations.

Stable coexistence between two competitors occurs when each species can invade a monoculture of the other (Smith and Waltman 1995). In appendix B, we show that the growth rate of a species invading a monoculture is

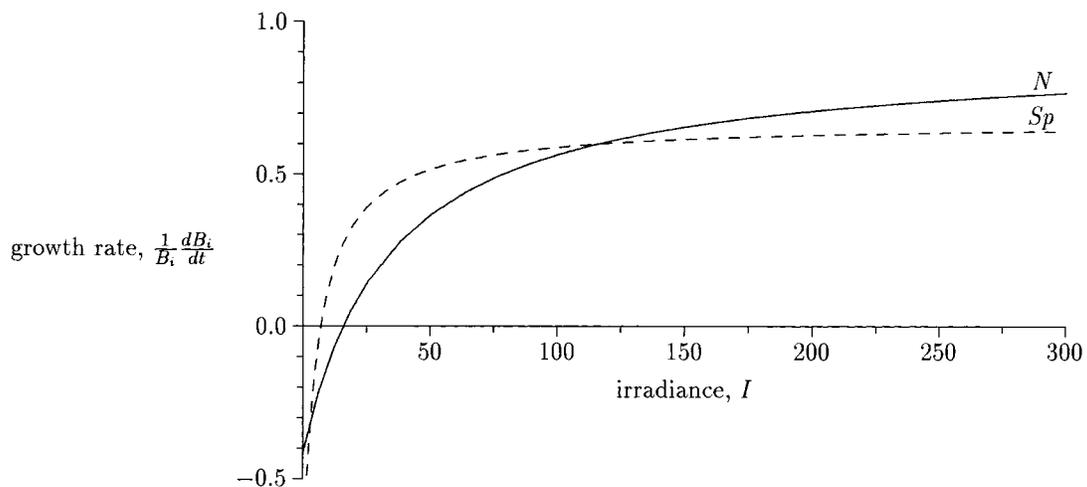$$g_{\text{inv}} = g_1 + g_2 + g_3, \tag{11}$$

with

Figure 1: Growth-irradiance curves used in the model. Solid line is the diatom *Nitzschia*, and dashed line is the green alga *Sphaerocystis*. Parameters are given in table 1.
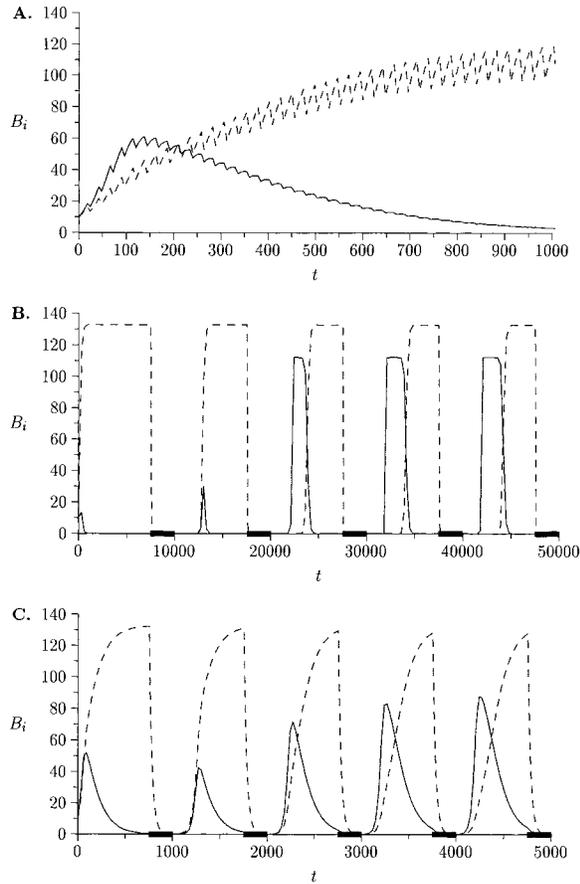
Figure 3: Numerical solution of equations (1) and (2) for light : dark fluctuations ($p = 0.75$) of three periods: (*A*) $T = 24$ h, (*B*) $T = 10{,}000$ h, and (*C*) $T = 1{,}000$ h. The solid line is *Nitzschia*, and the dashed line is *Sphaerocystis*. The black bars represent dark periods. Parts *B* and *C* are examples of stable coexistence.

$$g_1 = \frac{\mu_{\text{inv}}[I_{\text{in}}/(I_{\text{in}} + K_{\text{inv}})] - m_{\text{inv}}}{\mu_{\text{res}}[I_{\text{in}}/(I_{\text{in}} + K_{\text{res}})] - m_{\text{res}}} m_{\text{res}}(1 - p),$$

$$g_2 = \left(\mu_{\text{inv}} \frac{I^*_{\text{res}}}{I^*_{\text{res}} + K_{\text{inv}}} - m_{\text{inv}}\right)$$
$$\times \frac{p\mu_{\text{res}}[I_{\text{in}}/(I_{\text{in}} + K_{\text{res}})] - m_{\text{res}}}{\mu_{\text{res}}[I_{\text{in}}/(I_{\text{in}} + K_{\text{res}})] - m_{\text{res}}}, \qquad (12)$$

$$g_3 = -m_{\text{inv}}(1 - p).$$

These g_i's correspond to the exponential growth or decline rate of the invader during each phase of the resident's dynamics. We can find the values of p that bound the region of stable coexistence by setting (11) equal to 0 and solving for p using each species as resident and invader. For *Nitzschia* and *Sphaerocystis* and $I_{\text{in}} = 1{,}400$ μmol pho-

tons m^{-2} s^{-1}, this predicts dominance by *Nitzschia* for $p < 0.683$, coexistence for $0.683 < p < 0.810$, and dominance by *Sphaerocystis* for $p > 0.810$. The range of p that allows coexistence increases with incoming light I_{in} (fig. 4). When $I_{\text{in}} \gg K_{\text{res}}$ and $I_{\text{in}} \gg K_{\text{inv}}$, the invasibility criterion can be approximated by

$$g_1 = \frac{\mu_{\text{inv}} - m_{\text{inv}}}{\mu_{\text{res}} - m_{\text{res}}} m_{\text{res}}(1 - p),$$

$$g_2 = \left(\mu_{\text{inv}} \frac{I^*_{\text{res}}}{I^*_{\text{res}} + K_{\text{inv}}} - m_{\text{inv}}\right) \frac{p\mu_{\text{res}} - m_{\text{res}}}{\mu_{\text{res}} - m_{\text{res}}}, \qquad (13)$$

$$g_3 = -m_{\text{inv}}(1 - p).$$

Using (11) and (13), we find that species coexist for intermediate p:

$$\frac{1}{R_{\text{gl}}} + \frac{K_{\text{gl}}}{K_{\text{op}} - K_{\text{gl}}}\left(\frac{R_{\text{op}}}{R_{\text{gl}}} - 1\right)$$
$$< p < \qquad (14)$$
$$\frac{1}{R_{\text{op}}} + \frac{K_{\text{op}}}{K_{\text{op}} - K_{\text{gl}}}\left(1 - \frac{R_{\text{gl}}}{R_{\text{op}}}\right).$$

Figure 5 summarizes the posttransient successional dynamics over a period in the slow fluctuation limit for all p, assuming I_{in} large. As p decreases from 1, the gleaner rises to high density later in the period. Below $p = 0.815$, the opportunist enters the community and precedes the gleaner in each period. When the jumps between equilibria occur is determined by solving equations (B8). As p decreases, the opportunist rises to high density earlier,
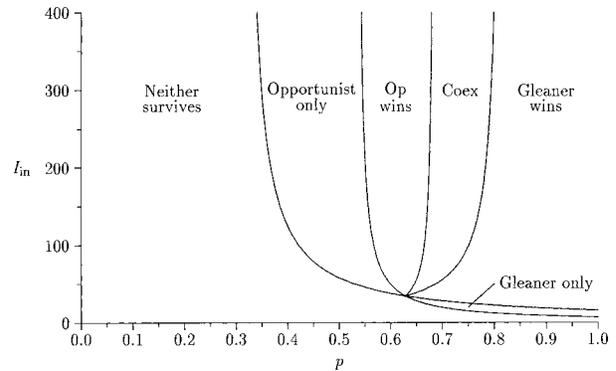

Figure 4: Outcome of competition between the gleaner *Sphaerocystis* and the opportunist *Nitzschia* under slowly fluctuating light as a function of p, the proportion of light in a period, and I_{in}, the incoming light level.
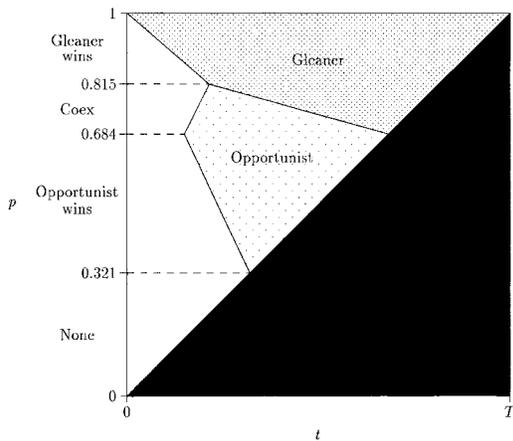
Figure 5: Successional dynamics within a period under slowly fluctuating light as a function of p. The white region represents the phase when both species are rare and light is on, the shaded regions represent time when one species is dominant, and the dark region represents time when the light is off.

and the switch to the gleaner happens later until, at $p = 0.684$, the gleaner is excluded. As p decreases further, the opportunist declines until, at $p = 0.321$, it is excluded and neither species can survive.

The range of p for which stable coexistence occurs becomes larger as one species becomes a better competitor (more extreme gleaner) and the other species increases its ratio of the maximum growth rate to mortality rate (becomes a more extreme opportunist). Let w be the width of the coexistence region under high incoming light defined by (14):

$$w = \frac{1}{R_{op}} - \frac{1}{R_{gl}} + \frac{K_{op}}{K_{op} - K_{gl}} \left(1 - \frac{R_{gl}}{R_{op}} \right)$$

$$- \frac{K_{gl}}{K_{op} - K_{gl}} \left(\frac{R_{op}}{R_{gl}} - 1 \right). \qquad (15)$$

It can be shown that w approaches its maximum possible value of 1 when $R_{op}, R_{gl} \to \infty$, such that $R_{gl}/R_{op} \to 0$ and either $K_{op} \to \infty$ or $K_{gl} \to 0$ (app. C). Coexistence in the slow fluctuation limit becomes easier as the competing species become more differentiated along the gleaner-opportunist axis.

Intermediate Fluctuations

The analytical expressions derived above are exact only for infinitely fast ($T \to 0$) or slow ($T \to \infty$) fluctuations. We

used numerical techniques to determine the extent of their applicability to fluctuating regimes of finite periods (T) by systematically sampling the T-p parameter space and determining the outcome of competition. We numerically solved (1) and (2) for each species in monoculture until it reached its monoculture periodic solution. We then determined whether the other species could invade this monoculture by computing its growth rate averaged over a period (Smith and Waltman 1995),

$$g_{inv} = \frac{1}{T} \int_0^T \left[\mu_{inv} \frac{I(\tau)}{I(\tau) + K_{inv}} - m_{inv} \right] d\tau, \qquad (16)$$

where the incident light level I is determined by the resident population. If each species can invade a monoculture of the other species ($g_{inv} > 0$), stable coexistence is possible. If only one species is able to invade the other, the competitive exclusion occurs. If neither species invades the monoculture of the other, the winner is determined by initial conditions.

Numerical solutions using the parameters of *Nitzschia* and *Sphaerocystis* confirm the predictions of the analytical approximations for both fast and slow fluctuations. The predictions based on the fast fluctuation approximation hold for periods $T < 20$ h, and the predictions based on the slow fluctuation approximation hold for periods $T > 2,000$ h (fig. 6A). When algae spend too much time in the dark (low p), neither species can survive (eqq. [7], [8]). *Nitzschia* is able to grow at lower proportions of light than *Sphaerocystis* (fig. 6A). As p increases, both species are able to grow in monoculture, with *Nitzschia* being the dominant competitor. For larger values of p, there is a region of stable coexistence of negligible width for $T < 20$ h and of greater width as T increases. For larger p, up to $p = 1$, *Sphaerocystis* outcompetes *Nitzschia*. Although the region of true coexistence where the mutual invasibility criterion is met is narrow at short fluctuation periods, there is a much wider range of values of p where the time for competitive exclusion of one of the two species is extremely long. These times to exclusion can exceed several months, a common timescale for phytoplankton succession in temperate waters. Thus, the region where both species persist for a long although finite time (neutral coexistence sensu Grover 1997) can be much wider than the region of true coexistence.

We determined the dependence of the outcome of competition on p and T in numerical simulations for a wide range of the incoming light, I_{in}. The results are robust and do not depend greatly on the I_{in} when $I_{in} \gg K_i$ (fig. 4). The presence of a spatial gradient, however, makes the outcome a function of the incoming light (Huisman and
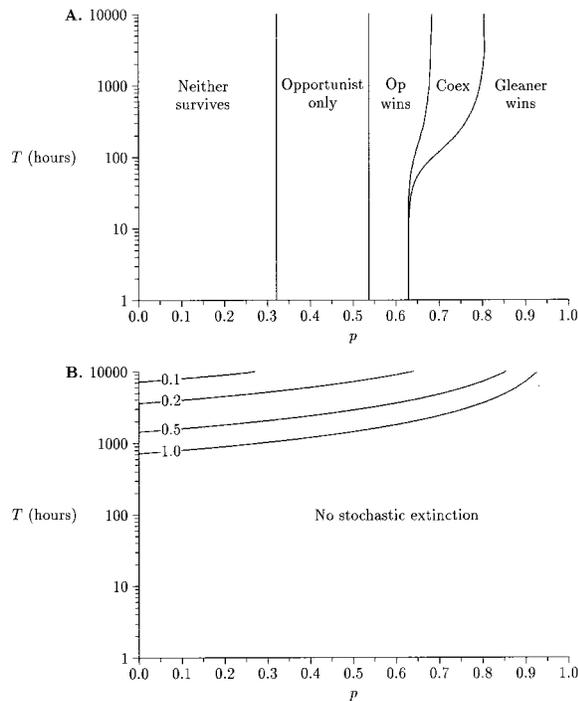
Figure 6: *A*, Outcome of competition between the gleaner, *Sphaerocystis*, and the opportunist, *Nitzschia*, under different fluctuation regimes determined by *p* and the period *T*. Slow fluctuations of intermediate *p* promote stable coexistence. *B*, Approximate range of validity of our deterministic approach computed with (17). Contours represent different mortality rates, m (d^{-1}). Stochastic extinction is likely above each contour. As an order-of-magnitude estimate of $\hat{B}$, we let $\hat{B} = 10^4$ cells/mL $\times$ 10^6 mL/m^3 $\times$ 10^5 m^3/lake = 10^{15}/lake = 10^{15} cells/lake; for the minimum viable population size, we let $B_{min} = 10^2$ cells/lake.

Weissing 1994); the effect of this gradient on competition under fluctuating light is discussed below.

Range of Validity of Deterministic Approach

Under slow fluctuations, the biomasses of both species are greatly reduced during the dark phase (fig. 3*B*, 3*C*). Because our model is deterministic, such low abundances are tolerated, but in reality, if the time spent in the dark is too great, one or both species may go extinct as a result of demographic stochasticity. Here, we determine an approximate range of *p* and *T* for which stochastic extinction is avoided and our deterministic approach is valid.

We can estimate the reduction in biomass over the dark period as

$$B(T) = \hat{B}e^{-m(1-p)T}. \qquad (17)$$

This is valid for either species in monoculture or the

gleaner when species coexist; the analogous formula for the opportunist while coexisting with the gleaner is more complicated because the opportunist also dies exponentially when the gleaner is near its carrying capacity. We use equation (17) to determine the range of parameters under which our deterministic approach is valid by setting a minimum viable population size, B_{min}, and requiring $B(T) > B_{min}$. Phytoplankton mortality rates range from practically 0 to $m = 0.8$ d^{-1} and are usually <0.1 d^{-1} (Reynolds 1984). Figure 6*B* shows that stochastic extinction will not be a problem for the typical phytoplankton species during an annual cycle (10^4 h). The example parameters for *Nitzschia* and *Sphaerocystis* we use (table 1) are at the high end of the mortality rates reported in the literature. Coexistence of these species is still possible for periods from 100 to 1,000 h, but decreased mortality through resting stages (Reynolds 1984) or decreased respiration in the dark (Jochem 1999) would be required for the annual persistence of these species.

Effect of Vertical Gradient in Light

In the previous section, we showed that light fluctuations may reverse the competitive outcome of the constant light conditions or lead to stable coexistence. Our treatment did not consider the vertical light gradient found in all real systems. Huisman and Weissing (1994) modeled competition for constant light, assuming a well-mixed water column but including the effect of this spatial gradient. The major effect of such a gradient on competition for constant light is that the outcome depends on the incoming light, I_{in}. The species that reduces light at the bottom of the water column, I_{out}^*, to the lowest level wins competition. The outcome of competition can be predicted by comparing the I_{out}^* of monocultures of species at equilibrium. How does incorporating spatial gradient affect our qualitative conclusions concerning light fluctuations?

To answer this question, we used Huisman and Weissing's model of competition for light and included fluctuations in light supply:

$$\frac{dB_i}{dt} = \frac{a_i B_i}{a_1 B_1 + a_2 B_2} \frac{\mu_i}{a_i z} \log\left(\frac{K_i + I_{in}}{K_i + I}\right) - m_i B_i, \qquad (18)$$

where *z* is the depth of the water column. Using similar techniques as we used above for fast fluctuations, we can find I_{out}^* as a function of *p* and now I_{in}, though it can be determined only numerically. Figure 7 shows I_{out}^* as a function of *p* for three different light levels of incoming light I_{in} under light : dark fluctuations. For low I_{in}, a switch in dominance occurs (fig. 7*A*); for higher I_{in}, the value of *p* at which this switch occurs is greater (fig. 7*B*); as I_{in} is

increased further, the I_{out}^* curves do not cross and one species wins for all values of p (fig. 7C). Figure 8 shows the outcomes for finite periods. When a vertical spatial gradient is added to the simple model of light competition under fluctuating light (as in the constant light case), the outcome of competition depends on the incoming light, I_{in}, as well as on p and T. The qualitative results we found by neglecting the spatial light gradient continue to hold; that is, fast fluctuations can shift dominance from a gleaner to an opportunist, and stable coexistence is possible under slow fluctuations (fig. 8). Han et al. (1999) have also considered the Huisman-Weissing model under daily changing irradiance and similarly found the possibility for a switch in competitive dominance and the lack of coexistence for fluctuations of a 24-h period.

More Realistic Light Regimes

Daily Changes in Irradiance

So far we have considered a simple square wave function fluctuation in irradiance. The most prominent feature of natural light regimes is the day-night cycle, with varying irradiance throughout the light period. In this section, we investigate the effects of diel changes in irradiance on the outcome of competition of *Nitzschia* and *Sphaerocystis*. We can describe the incoming irradiance by a truncated sinusoidal function (Kirk 1994):

$$I_{in} = \max\left[0, I_{max}\left(c_1 - c_2 \cos\frac{2\pi t}{24}\right)\right], \qquad (19)$$

where I_{max} is the maximum irradiance (at noon), c_1 and c_2 are functions of the Julian day and latitude, and t is time measured in hours. We used Spencer's approximation (Kirk 1994) to calculate the values of c_1 and c_2:

$$c_1 = \sin\gamma\sin\delta, \text{ and } c_2 = \cos\gamma\cos\delta, \qquad (20)$$

where γ is the latitude and δ is the solar declination on the given day:

$$\delta = 0.39637 - 22.9133\cos\phi + 4.02543\sin\phi$$
$$- 0.3872\cos 2\phi + 0.052\sin 2\phi, \qquad (21)$$

with $\phi = 2\pi\text{day}/365$ ("day" is the Julian day). First, we treat c_1 and c_2 as constants.

Numerical simulations of competition under daily cycle of irradiance show that the outcome of competition is sensitive to the day length or, in our notation, p, the proportion of light in a period, which is similar to the step function fluctuation regimes. The switch from *Nitzschia*'s
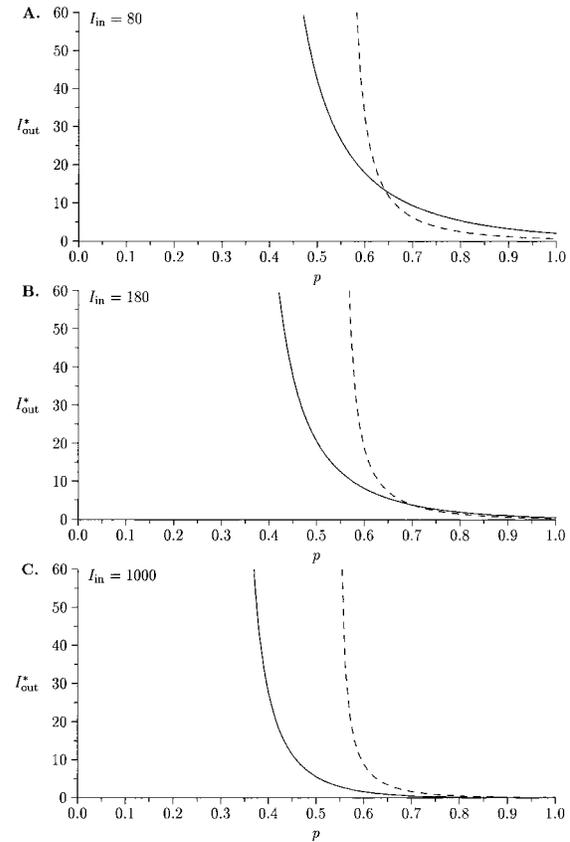
Figure 7: Dependence of $I^*(p)$ of *Nitzschia* (*solid line*) and *Sphaerocystis* (*dashed line*) on p for different I_{in} in the presence of a spatial gradient in light distribution. *A*, $I_{in} = 80$ μmol photons m^{-2} s^{-1}. *B*, $I_{in} = 180$ μmol photons m^{-2} s^{-1}. *C*, $I_{in} = 1,000$ μmol photons m^{-2} s^{-1}.

dominance to *Sphaerocystis*'s dominance occurred around $p_{switch} = 0.68$, compared to $p_{switch} = 0.629$ for light : dark fluctuations of a step function form with the same 24-h period. This shift of p_{switch} to a higher value is due to a lower daily irradiance dose under the sinusoidally changing irradiance compared to the step function form. Thus our results are qualitatively unchanged by the exact form of light supply function.

Seasonal Changes in Irradiance

As demonstrated in the previous sections, the outcome of competition depends on the day length. Because the time to competitive exclusion is comparable to seasonal changes in the day length (one to several months), it is likely that seasonal changes in the day length will affect the dynamics and outcome of competition. Here we investigate how competition between *Nitzschia* and *Sphaerocystis* over a season is mediated by a seasonally changing day length. The in-
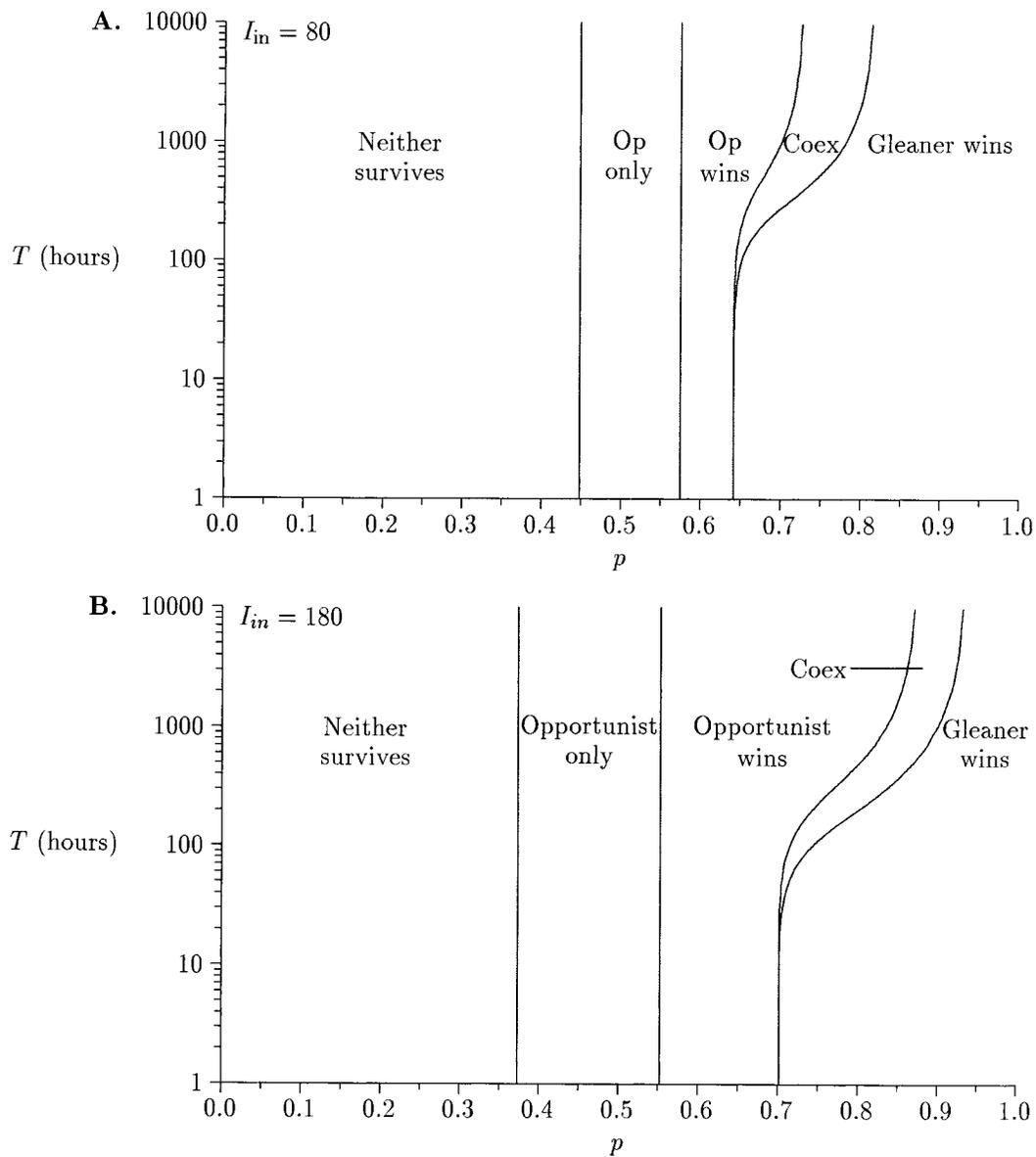
Figure 8: Competitive outcomes in the presence of a vertical gradient in irradiance for different values of I_{in}. *A*, I_{in} = 80 μmol photons m^{-2} s^{-1}. *B*, I_{in} = 180 μmol photons m^{-2} s^{-1}.

coming light changes sinusoidally during the day as in (19), but c_1 and c_2 now vary with the day of the year according to (20) and (21).

Figure 9 shows the competitive dynamics of *Nitzschia* and *Sphaerocystis* for growing seasons of different durations. In both cases, species were able to coexist stably. The seasonally changing day length (fig. 9C) favors either *Nitzschia* (when $p < 0.68$) or *Sphaerocystis* ($p > 0.68$), which, along with the nutrient depletion and stability of the water col-

umn, may contribute to the waxing and waning of their population densities over the growing season. The longer growing season (fig. 9B) allows the development of two peaks in the abundance of *Nitzschia*. Notice that in our simulations, *Nitzschia* is more abundant in the spring and in the fall (shorter day length), while *Sphaerocystis* peaks in abundance in midsummer, consistent with a typical seasonal succession sequence in temperate lakes (Reynolds 1984). The season is cut off after 160 or 180 d to mimic the end
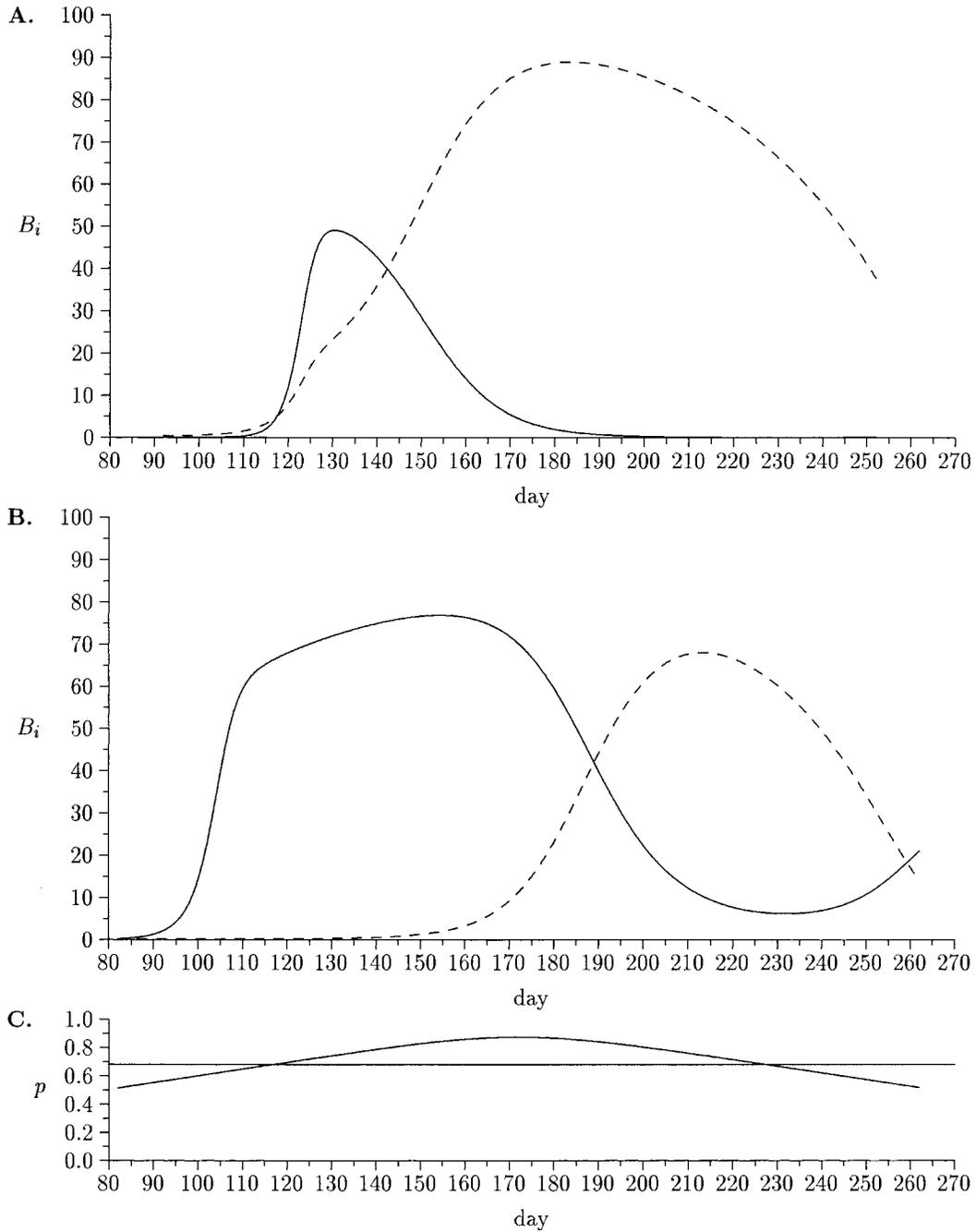
Figure 9: Dynamics of *Nitzschia* (*solid line*) and *Sphaerocystis* (*dashed line*) under seasonally changing day length at 65°N. No mixing was included. Biomasses were cut to 1% of their end-of-the-year value to begin each growing season. *A*, Growing season of 160 d. *B*, Growing season of 180 d. *C*, Daily value of p over the season. The horizontal line represents $p = 0.68$, above which *Sphaerocystis* is dominant and below which *Nitzschia* is dominant.

of the growing season. Stable coexistence of these species is not possible without truncating the season because $p > p_{switch}$ only from day 118 to 227. Not truncating the season results in the exclusion of *Sphaerocystis* since most of the year *Nitzschia* would win competition on a given day. For other parameter combinations, multiyear coexistence is possible without truncation.

Vertical Mixing

In addition to the daily cycle in irradiance, phytoplankton often experience superimposed light fluctuations as a result of the vertical mixing of the water column. Many types of vertical water movements with a wide range of temporal and spatial scales can subject phytoplankton to different irradiances, such as Langmuir spirals, gravity waves, turbulent mixing, and so forth (Denman and Gargett 1983; Imberger 1985). Although algal trajectories in the water column as a result of vertical movements and the resulting changes in irradiance may be quite complex, major vertical movements of cells cause fluctuations between high light and low light or darkness. Fluctuations resulting from mixing are more complex than the fluctuations we have considered: the proportion of light in a period is dynamic and depends on the biomass. However, simple fluctuations provide a heuristic description of an essential component of the irradiance changes experienced by cells traversing through the water column, that is, the alternation between high and low light or darkness.

Mixing causing light fluctuations of large enough amplitude (large mixing depth or high turbidity) would decrease p, the proportion of light in a period (algae would spend relatively more time in the dark) and thus may favor an opportunist such as *Nitzschia* over a gleaner such as *Sphaerocystis*. This result agrees well with the field observations on the dominance of diatoms including *Nitzschia* under the deep mixing conditions and *Sphaerocystis*'s intolerance of such conditions (Reynolds 1984). Huisman and Weissing (1994) developed and analyzed a model of competition for light in a perfectly mixed water column. They found that the outcome of competition may depend on the incoming light level, I_{in}. Specifically, they showed that two species with the gleaner-opportunist trade-off switch dominance, with the gleaner dominant under low I_{in} and the opportunist dominant under high I_{in} (see also our figs. 7, 8). This result can be explained by our results for fast fluctuations. A high I_{in} creates a wide range of light levels in the water column so that an alga experiences larger light fluctuations than under a low I_{in}. As we have shown, opportunist species are favored under fluctuating light. Thus, Huisman and Weissing's finding that the outcome of competition depends on I_{in} may be interpreted as resulting from the differential ability of species to use fluctuating light.

Nutrient Competition under Fluctuating Light

Often in natural systems, resources other than light limit phytoplankton growth: phosphorus in many temperate lakes, nitrogen and iron in marine systems, and carbon in highly productive lakes. Experimental studies have shown that light fluctuations of nonlimiting levels can mediate competition for nutrients and either reverse competitive outcome reached under constant light or lead to coexistence (van Gemerden 1974; Brzezinski and Nelson 1988). Our results can be extended to the situation where light and a nutrient are essential resources and light fluctuates.

Consider nutrient competition between two hypothetical species, where the nutrient-dependent growth of both species is described by a Monod equation. Resource is depleted as a result of species uptake and outflow but is replenished at a constant rate. We assume that growth and nutrient consumption (which is coupled to growth) occur only during the light part of a cycle; this is Liebig's law of the minimum. When light is on (p proportion of the time):

$$\frac{dB_i}{dt} = B_i\left(\mu_i\frac{r}{r + K_i} - m_i\right), \quad i = 1, 2,$$

$$\frac{dr}{dt} = \alpha(r_{in} - r) - B_1\mu_1\frac{r}{r + K_1} - B_2\mu_2\frac{r}{r + K_2}. \quad (22)$$

When light is off ($1 - p$ proportion of the time):

$$\frac{dB_i}{dt} = -m_iB_i, \quad i = 1, 2,$$

$$\frac{dr}{dt} = \alpha(r_{in} - r), \quad (23)$$

where B_i is the density of species i, r is the nutrient concentration, α is the rate of nutrient supply, and r_{in} is the nutrient concentration in the inflow; all other parameters are as above.

For fast light fluctuations, an averaging argument similar to that given in appendix A gives the following formula for r^* as a function of p, identical to (9):

$$r_i^*(p) = \frac{K_i}{pR_i - 1}. \quad (24)$$

For slow light fluctuations, an argument similar to that given in appendix B yields the same invasibility criterion as (11) and (12):

$$g_{inv} = g_1 + g_2 + g_3, \qquad (25)$$

with

$$g_1 = \frac{\mu_{inv}[r_{in}/(r_{in} + K_{inv})] - m_{inv}}{\mu_{res}[r_{in}/(r_{in} + K_{res})] - m_{res}} m_{res}(1 - p),$$

$$g_2 = \left(\mu_{inv} \frac{r^*_{res}}{r^*_{res} + K_{inv}} - m_{inv} \right)$$

$$\times \frac{p\mu_{res}[r_{in}/(r_{in} + K_{res})] - m_{res}}{\mu_{res}[r_{in}/(r_{in} + K_{res})] - m_{res}}, \qquad (26)$$

$$g_3 = -m_{inv}(1 - p).$$

The results are similar to those under fluctuating light of limiting levels because we can simplify the nutrient supply dynamics in both limiting cases, similar to light dynamics. Under fast fluctuations, the equilibrium nutrient level goes to the smallest $r^*(p)$ of the competing species. Under slow fluctuations, the nutrient level at the beginning of a period (which equals the nutrient level at the end of the previous period) becomes arbitrarily close to r_{in} as T increases to infinity (these parts of the period correspond to phases 1 and 3 from app. B). When the biomass of the resident is close to its carrying capacity (phase 2 of app. B), the nutrient level approaches r^*_{res}.

Numerical solution of this two-resource model showed very similar dependence of the outcome of competition on p and T as those given in figure 6A for fluctuating light and agreed with the fast and slow fluctuation approximations given above. As in the case of limiting light, fast light fluctuations can lead to a switch in competitive dominance and slow fluctuations in addition can lead to the stable coexistence of competitors.

Discussion

The results of this study suggest that temporal variability in light supply can have significant effects on the outcome of competition between phytoplankton species and thus on community structure. Fast fluctuations, including the daily irradiance cycle and fluctuations that result from change in cloud cover or mixing, can reverse competitive dominance and slow competitive exclusion. Slow fluctuations can change the identity of the competitive dominant and also lead to the stable coexistence of competitors. The reversal of competitive outcome and stable coexistence are possible only when the species show the gleaner-opportunist trade-off, that is, $I^*_{gl} < I^*_{op}$ and $R_{op} > R_{gl}$. Therefore, as predicted by other theoretical studies on nonequilibrium resource competition, trade-offs in the species responses to different resource levels are necessary for fluctuations to affect competition (Hsu 1980; Smith 1981; Chesson 1988). The trade-off between a low minimum resource requirement and a high maximum growth rate is known as the gleaner-opportunist trade-off (Grover 1997). We suggest that in the case of unequal mortalities, the gleaner-opportunist trade-off becomes a trade-off between a low minimum resource requirement (I^*) and a high ratio of maximum growth rate to mortality rate (R). The essence of the opportunist strategy is the ability to use occasionally high resource levels, either by having a greater maximum growth rate or by having a lower mortality rate. In the example we used here, *Nitzschia* (an opportunist) has a higher R than *Sphaerocystis* (a gleaner), allowing it to coexist with or displace *Sphaerocystis* under fluctuating light.

The presence or absence of coexistence regions and their position in the T-p space (eq. [14]) depends on the species parameters. Species coexist for the widest range of light regimes when they are highly differentiated along the gleaner-opportunist trade-off. Although we have discussed competition between only two species, slow light : dark fluctuations can allow coexistence of more species if they have the proper parameter values along the gleaner-opportunist trade-off. For example, figure 10 shows the stable coexistence of five competitors. An interesting extension of this work would be to examine the diversity and composition of an evolutionarily stable community structured by this mechanism given a particular parameterization of the trade-off between R and I^*. Our invasibility criterion (11) could be used as a fitness function to determine the location and nature of evolutionarily singular strategies (Brown and Vincent 1992; Geritz et al. 1998). Our preliminary investigations using this approach show that multiple species coexistence often emerges as an evolutionarily stable state. Thus, the coexistence of multiple species that we found in this article is robust with respect to evolution and successive invasion.

For both square wave and truncated sinusoidal fluctuations, p, the proportion of light in a period, is a key parameter determining the outcome of competition. Under light : dark fluctuations, lower values of p favor opportunists and higher values favor gleaners. One mechanism leading to changes in p is the seasonal variation in day length (fig. 9C). For temperate regions (45°N) during open water season, p varies from 0.56 in mid-April to 0.64 in mid-June and drops to 0.52 in mid-September; seasonal variation in p is even greater for higher latitudes. Our model predicts that the relatively short day length in the spring and autumn should favor fast-growing opportunist species such as diatoms, and the longer day length in summer should favor gleaner species such as green algae or cyanobacteria. A typical successional sequence in temperate lakes agrees well with the prediction (Reynolds 1984).
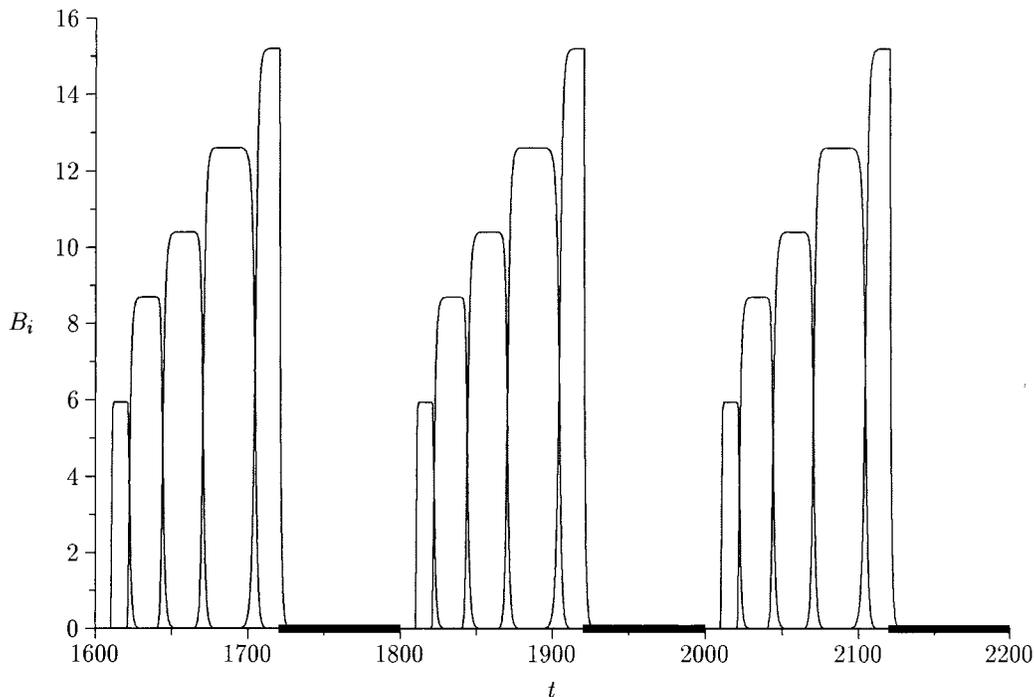
Figure 10: Stable coexistence of five species with the gleaner-opportunist trade-off. Species parameters: $\mu_1 = 1.8$, $K_1 = 0.002$; $\mu_2 = 2.5$, $K_2 = 0.05$; $\mu_3 = 5.0$, $K_3 = 0.3$; $\mu_4 = 10.0$, $K_4 = 15.0$; $\mu_5 = 20.0$, $K_5 = 500.0$. Other parameters: $a = 1.0$, $m = 1.0$, $p = 0.6$, and $T = 200$.

Thus, our model suggests that, in addition to water column stratification and nutrient depletion (Reynolds 1984), the seasonal change in day length may be one of the mechanisms driving the seasonal succession of phytoplankton in temperate lakes.

In addition to day length, the duration of the growing season can also influence phytoplankton dominance patterns and coexistence. The duration of a growing season can be interpreted as p for a fluctuation period $T = 1$ yr. As seen from figure 6, a short growing season favors opportunists and a long growing season favors gleaners. At the intermediate-length growing seasons, the two species would be able to coexist from year to year. In the beginning of the growing season an opportunist is the first to reach high density as a result of its large R. Thus, in the spring, opportunist species such as diatoms are favored for two distinct reasons: the relatively short day length (small p) and the nonlimiting light levels at the beginning of the season, which allow exponential growth.

In our analysis, we used the mutual invasibility criterion to determine regions of stable coexistence. Using Lotka-Volterra equations with periodically varying coefficients, Namba and Takahashi (1993) showed that the mutual invasibility criterion may not always reveal all coexistence cases in nonequilibrium systems. Although invasion of a

stable monoculture of a species by a small number of individuals of a second species can be unsuccessful, these species might still be able to coexist. The timing of invasion and the size of invading population affected the success of invasion. It is possible that introducing a larger inoculum at different times of the period may enlarge the region of parameters leading to coexistence. We have not found such examples of coexistence in our model, but they may exist.

Several experimental studies also demonstrate that light fluctuations can change the competitive outcome or promote coexistence (van Gemerden 1974; Brzezinski and Nelson 1988; Litchman 1998). However, experimental studies of the effects of resource fluctuations on competition and coexistence much more frequently consider fluctuating nutrient supplies. More experimental work is needed on competition under fluctuating light; the results of our model suggest a number of experiments. We suggest using light : dark fluctuations because the effects of resource variability are most pronounced. First, under fast fluctuations ($T < 30$ h), coexistence is impossible but the identity of the competitive dominant can change from a gleaner to an opportunist as p decreases. A straightforward test of this prediction would be to determine the parameters of two species then allow them to compete across a

range of p with $T = 24$ h. Second, we are unaware of any studies using a period longer than a day. However, our model predicts a significant region of true coexistence between a gleaner and an opportunist only under slow fluctuations ($T > 100$ h). Competition experiments under fluctuating light with $T > 100$ h could test whether seasonal successional patterns and long-term coexistence can be explained by the gleaner-opportunist trade-off.

Although this model is specific to light competition between phytoplankton, a number of our results apply quite generally to interspecific competition in a fluctuating environment. For example, the analytical approximations for fast and slow fluctuations can be applied to competition for other resources that are described algebraically. Our main results hold regardless of whether light is a limiting resource or whether it acts as a limiting factor affecting competition for a nutrient. In fact, the same results hold for any limiting factor that directly produces fluctuations in the growth rates of competing species. In all these cases, fast fluctuations can alter the competitive dominant but not allow true coexistence; slow fluctuations can both switch competitive dominants and allow stable coexistence of a gleaner and an opportunist. The analytical results for simple fluctuations qualitatively hold for other, more complex fluctuation types.

Using a simple model of light competition, we showed that light fluctuations over a wide range of temporal scales (from hourly to seasonal) may have a significant effect on species competition and coexistence. Our model does not include many important aspects of the light environment and phytoplankton responses to it such as the spectral distribution of light, a multidirectional light field, alternating mixing regimes, photoinhibition, photoacclimation, lags in phytoplankton responses to changing light, and so forth. In a well-mixed water column, the presence of a vertical gradient does not add more opportunities for coexistence (Huisman and Weissing 1994), but under stratified conditions, it can lead to increased coexistence (Britton and Timm 1993; Huisman et al. 1999a, 1999b). An explicit consideration of these and other factors could lead to an even greater variety of competitive outcomes and possibly to increased opportunities for coexistence.

Acknowledgments

APPENDIX A

Fast Fluctuations

Under fast light fluctuations, the dynamics of each species can be approximated by

$$\frac{dB_i}{dt} = B_i \frac{1}{T} \int_0^T \left(\mu_i \frac{I(\tau)}{I(\tau) + K_i} - m_i \right) d\tau, \qquad (A1)$$

where τ is a dummy variable and I is given by (2). The error in this approximation goes to 0 as T approaches 0 (Guckenheimer and Holmes 1983, chap. 4). Han et al. (1999) used a similar approach of averaging growth rates over the daily light cycle. Because incoming light alternates between light and dark, we can split the integral and simplify:

$$\frac{dB_i}{dt} = B_i \frac{1}{T} \left[\int_0^{pT} \left(\mu_i \frac{I}{I + K_i} - m_i \right) d\tau - \int_{pT}^T m_i d\tau \right]$$

$$= B_i \left(p\mu_i \frac{I}{I + K_i} - m_i \right). \qquad (A2)$$

We can solve for $I_i^*(p)$ as a function of the proportion of light in a period, p, by setting (A2) equal to 0:

$$I_i^*(p) = \frac{K_i}{pR_i - 1}. \qquad (A3)$$

Note the similarity between the expression for $I_i^*(p)$ under light : dark fluctuations, equation (A3), and the expression for I_i^* under constant light, equation (3). The value of $I_i^*(p)$ given by (A3) represents the minimum incoming irradiance that will support species i for a given p. In interspecific competition, the species with the smallest $I^*(p)$ will displace all others.

APPENDIX B

Slow Fluctuations

Under slow light fluctuations, we can approximate the periodic solution a monoculture follows. The error in this approximation goes to 0 as T approaches infinity. The knowledge of the dynamics of a single species allows us to calculate the growth rate of a second species invading that monoculture when rare. To calculate the dynamics of a single species, first note that, as the period increases, the

population spends a larger proportion of each period near an equilibrium. Choose an arbitrarily small ϵ. The time a population spends between $B = \epsilon$ and $B = \hat{B} - \epsilon$ is fixed; as T approaches infinity, the proportion of the period spent farther than ϵ from an equilibrium goes to 0. Thus, as the period approaches infinity, the dynamics comes to consist of rapid jumps between the vicinities of equilibria. During the transition between equilibria, there is a fixed error in our approximation, but the relative importance of this fixed error goes to 0 as T goes to infinity.

Assuming the resident is on its monoculture periodic solution, each period can be broken into three phases. In the first phase, from $t = 0$ to t_1 (t_1 as yet undetermined), the initially sparse population grows exponentially, and $I \approx I_{in}$. In the second phase, from $t = t_1$ to pT, the population density is near its positive equilibrium, and $I \approx I_{res}^*$. In the third phase, from $t = pT$ to T, the population dies exponentially, and $I = 0$.

To determine when the first phase of exponential growth ends, note that the resident's growth rate averaged over a period must be 0. Thus,

$$\int_0^T \left[\mu_{res} \frac{I(t)}{I(t) + K_{res}} - m_{res} \right] dt = 0. \qquad (B1)$$

Splitting this integral into three pieces,

$$\int_0^{t_1} \left(\mu_{res} \frac{I_{in}}{I_{in} + K_{res}} - m_{res} \right) dt$$

$$+ \int_{t_1}^{pT} \left(\mu_{res} \frac{I_{res}^*}{I_{res}^* + K_{res}} - m_{res} \right) dt \qquad (B2)$$

$$- \int_{pT}^T m_{res} dt = 0.$$

The second integral equals 0 (the resident species is at its carrying capacity); integrating the other two and rearranging,

$$t_1 \left(\mu_{res} \frac{I_{in}}{I_{in} + K_{res}} - m_{res} \right) = m_{res}(1 - p)T. \qquad (B3)$$

The ecological interpretation of (B3) is that net growth during the first phase must balance losses during the third phase. Solving for t_1, we find

$$t_1 = \frac{m_{res}(1 - p)T}{\mu_{res}[I_{in}/(I_{in} + K_{res})] - m_{res}}. \qquad (B4)$$

Having calculated the periodic solution of the resident, we ask whether a rare invading species can increase over a complete period. We assume the invader is sufficiently rare that it does not affect the incident light level I or the resident. The dynamics of the invader is determined by the following equations: phase 1 ($0 \le t < t_1$),

$$\frac{dB_{inv}}{dt} = B_{inv} \left(\mu_{inv} \frac{I_{in}}{I_{in} + K_{inv}} - m_{inv} \right), \qquad (B5a)$$

phase 2 ($t_1 \le t < pT$),

$$\frac{dB_{inv}}{dt} = B_{inv} \left(\mu_{inv} \frac{I_{res}^*}{I_{res}^* + K_{inv}} - m_{inv} \right), \qquad (B5b)$$

phase 3 ($pT \le t < T$),

$$\frac{dB_{inv}}{dt} = -m_{inv} B_{inv}. \qquad (B5c)$$

Equations (B5a)–(B5c) each describe exponential growth; thus, the invader's growth rate averaged over a whole period is

$$g_{inv} = g_1 + g_2 + g_3, \qquad (B6a)$$

where the g_i's are the exponential growth or decline rates in the ith phase of the resident's dynamics multiplied by the proportion of each period spent in that phase (t_1 is given by [B4]):

$$g_1 = \frac{1}{T} \left(\mu_{inv} \frac{I_{in}}{I_{in} + K_{inv}} - m_{inv} \right) t_1$$

$$= \frac{\mu_{inv}[I_{in}/(I_{in} + K_{inv})] - m_{inv}}{\mu_{res}[I_{in}/(I_{in} + K_{res})] - m_{res}} m_{res}(1 - p),$$

$$g_2 = \frac{1}{T} \left(\mu_{inv} \frac{I_{res}^*}{I_{res}^* + K_{inv}} - m_{inv} \right)(pT - t_1) \qquad (B6b)$$

$$= \left(\mu_{inv} \frac{I_{res}^*}{I_{res}^* + K_{inv}} - m_{inv} \right)$$

$$\times \frac{p\mu_{res}[I_{in}/(I_{in} + K_{res})] - m_{res}}{\mu_{res}[I_{in}/(I_{in} + K_{res})] - m_{res}},$$

$$g_3 = -m_{inv}(1 - p).$$

The invader increases over the period if $g_{inv} = g_1 + g_2 + g_3 > 0$.

We can also construct the coexistence periodic solution

under slow fluctuations. Each period can be broken into four phases (fig. 3*B*): From $t = 0$ to t_{op}, both species grow exponentially, and $I \approx I_{in}$. From $t = t_{op}$ to t_{gl}, the opportunist is near its equilibrium, the gleaner grows exponentially in the shade of the opportunist, and $I \approx I_{op}^*$. From $t = t_{gl}$ to pT, the gleaner is near its equilibrium, the opportunist dies exponentially, and $I \approx I_{gl}^*$. From $t = pT$ to T, both species die exponentially, and $I = 0$.

To determine the times when the jumps between equilibria occur (t_{op} and t_{gl}), note that the growth rate of both species averaged over a period must be 0. Thus,

$$\int_0^T \left[\mu_{op} \frac{I(t)}{I(t) + K_{op}} - m_{op} \right] dt = 0, \quad (B7a)$$

$$\int_0^T \left[\mu_{gl} \frac{I(t)}{I(t) + K_{gl}} - m_{gl} \right] dt = 0. \quad (B7b)$$

Splitting these integrals into pieces and integrating as for a single species, t_{op} and t_{gl} are determined by the following equations:

$$\frac{t_{op}}{T} \left(\mu_{op} \frac{I_{in}}{I_{in} + K_{op}} - m_{op} \right) + \left(p - \frac{t_{gl}}{T} \right)$$

$$\times \left(\mu_{op} \frac{I_{gl}^*}{I_{gl}^* + K_{op}} - m_{op} \right) - (1 - p)m_{op} = 0, \quad (B8a)$$

$$\frac{t_{op}}{T} \left(\mu_{gl} \frac{I_{in}}{I_{in} + K_{gl}} - m_{gl} \right) + \left(\frac{t_{gl}}{T} - \frac{t_{op}}{T} \right)$$

$$\times \left(\mu_{gl} \frac{I_{op}^*}{I_{op}^* + K_{gl}} - m_{gl} \right) - (1 - p)m_{gl} = 0. \quad (B8b)$$

Since equations (B8) are linear in the unknowns t_{op} and t_{gl}, the coexistence periodic solution is unique in the slow fluctuation limit.

APPENDIX C

Parameters to Maximize Coexistence Region

Here we show that coexistence occurs for the widest range of p when species are highly differentiated along the gleaner-opportunist trade-off. To do this, we will find the combination of parameters that maximizes w, the width of the coexistence region,

$$w = \frac{1}{R_{op}} - \frac{1}{R_{gl}} + \frac{K_{op}}{K_{op} - K_{gl}} \left(1 - \frac{R_{gl}}{R_{op}} \right)$$

$$- \frac{K_{gl}}{K_{op} - K_{gl}} \left(\frac{R_{op}}{R_{gl}} - 1 \right). \quad (C1)$$

First, we maximize w with respect to the K's:

$$\frac{\partial w}{\partial K_{gl}} = \frac{K_{op}}{(K_{op} - K_{gl})^2} \left(2 - \frac{R_{op}}{R_{gl}} - \frac{R_{gl}}{R_{op}} \right) < 0, \quad (C2)$$

since

$$\frac{K_{op}}{(K_{op} - K_{gl})^2} > 0,$$

and

$$2 - \frac{R_{op}}{R_{gl}} - \frac{R_{gl}}{R_{op}} < 0.$$

$$\frac{\partial w}{\partial K_{op}} = \frac{K_{gl}}{(K_{op} - K_{gl})^2} \left(\frac{R_{op}}{R_{gl}} + \frac{R_{gl}}{R_{op}} - 2 \right) > 0, \quad (C3)$$

since

$$\frac{K_{gl}}{(K_{op} - K_{gl})^2} > 0,$$

and

$$\frac{R_{op}}{R_{gl}} + \frac{R_{gl}}{R_{op}} - 2 > 0.$$

Thus, K_{gl} must be minimized and K_{op} maximized. We will take either $K_{gl} = 0$ or $K_{op} = \infty$ to simplify our expression for w:

$$w = \frac{1}{R_{op}} - \frac{1}{R_{gl}} + 1 - \frac{R_{gl}}{R_{op}}. \quad (C4)$$

Now we maximize w with respect to the R's:

$$\frac{\partial w}{\partial R_{gl}} = R_{gl}^{-2} R_{op}^{-1}. \quad (C5)$$

When (C5) is set equal to 0 to find extrema,

$$R_{op} = R_{gl}^2. \tag{C6}$$

This is a maximum since

$$\frac{\partial^2 w}{\partial R_{gl}^2} = -2R_{gl}^{-3} < 0,$$

$$\frac{\partial w}{\partial R_{op}} = R_{op}^{-2}(R_{gl} - 1). \tag{C7}$$

When (C7) is set equal to 0, we find that

$$R_{gl} = 1, \tag{C8}$$

but this is a minimum since plugging (C6) and (C8) into (C5) gives $w = 0$. For $R_{gl} > 1$, (C7) shows that

$$\frac{\partial w}{\partial R_{op}} > 0,$$

so that R_{op} is to be maximized.

Therefore, the coexistence region is widest when $K_{gl} \to 0$, $K_{op} \to \infty$, $R_{op} \to \infty$, and $R_{gl} \to \infty$ such that $R_{gl}/R_{op} \to 0$. In these limits, the width of the coexistence region $w \to 1$.

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