Phytoplankton nutrient competition under dynamic light regimes

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Abstract

   Many physiological processes in phytoplankton, including nutrient uptake, vary on a number of temporal scales. Experiments show that the daily cycle in irradiance affects nutrient uptake rates. We used a Droop-based model of resource competition to investigate how diel variability in nutrient uptake influences phytoplankton competition and community structure. The analytical approximation we derive shows that if nutrient uptake is light dependent, the minimum nutrient requirements and, hence, nutrient competitive abilities depend on light regime in a species-specific way. Consequently, daily variations in irradiance may slow rates of competitive exclusion or reverse the identity of the superior competitor but not allow stable coexistence. Irradiance-induced fluctuations in the maximum nutrient uptake rate of the superior competitor can lead to fluctuations in ambient nutrient concentration and an increase in the average nutrient concentration compared to constant light conditions. This can enhance nutrient use by inferior competitors. These results may be applicable to bacteria–phytoplankton nutrient competition as well. Depending on the costs and benefits of maintaining nutrient uptake in the dark, different strategies of nutrient use are optimal under different light regimes. Our results suggest that by mediating limiting nutrient use, fluctuations in irradiance may alter the structure of phytoplankton communities.

   In aquatic systems, physical forcing and biotic responses are tightly coupled (Steele and Henderson 1994). Major ecological interactions such as competition and predation are affected by environmental fluctuations. Light is an important environmental factor and an essential resource for phytoplankton that fluctuates on multiple temporal scales. Previously we have demonstrated that daily and seasonal light fluctuations significantly affect phytoplankton competition for light (Litchman and Klausmeier 2001). However, in many aquatic systems phytoplankton compete not for light but for nutrients. A substantial body of literature indicates that nutrient uptake rates depend on many environmental factors including light. It is, therefore, likely that light fluctuations can mediate nutrient competition among phytoplankton. Here we explore how variation in the uptake rates of the limiting nutrient modifies resource competition in phytoplankton.

   Numerous experimental studies have shown that uptake of many essential nutrients by phytoplankton depends on irradiance. Frequently, the uptake rates are lower in the dark. Riegman et al. (2000) showed that nitrogen (N) uptake of *Emiliania huxleyi* in the dark was 30% of the uptake rate in the light. Phosphorus (P) uptake in the dark was also lower than in the light, and the greatest difference between the uptake rates was for the lowest growth rate.

   The maximum nutrient uptake rate (V_{max}) usually exhibits a much stronger light dependence than the half-saturation constant of uptake. Anderson and Roels (1981) showed that in the diatom *Chaetoceros curvisetus* the maximum uptake rate for N, V_{max}, was clearly a function of irradiance, while the K_s did not depend on irradiance.

   The dependence of nutrient uptake on irradiance was observed for both cultures and natural phytoplankton communities. MacIsaac (1978) reported a cyclic pattern in N uptake for both nitrate and ammonium in a *Gonyaulax*-dominated natural community. Maximum uptake was centered at noon, and minimum uptake was around midnight. Cochlan et al. (1991) observed strong diel periodicity in nitrate and ammonium uptake in the subarctic Pacific and off the coast of British Columbia, with higher uptake rates during the day. A nighttime decrease in nitrate uptake was more pronounced than the decrease in ammonium uptake (15–16% and 30–36% of the daylight rates, respectively). Iron uptake may also be highly light dependent: the diatom *Phaeodactylum tricornutum* had higher iron uptake rates during the light period (Soria-Dengg et al. 2001).

   The degree of the uptake dependence on light appears to be different for different nutrients. Nutrients that require more energy to be assimilated, e.g., nitrate versus ammonium (Syrett 1981), may show stronger uptake dependence on light, as was observed in several studies (Kudela et al. 1997; Mulholland et al. 1999). The dependence of nutrient uptake on light often weakens with increasing nutrient limitation (Healey 1977; Syrett 1981).

   The dependence of nutrient uptake on irradiance appears to differ among taxonomic groups (Eppley et al. 1971; Wheeler et al. 1983). Uptake of nitrate and ammonium was much higher in the light than in the dark in *Skeletonema costatum* and was more uniform for *Emiliania huxleyi* (Eppley et al. 1971). Dinoflagellates seem to have relatively high N uptake rates in the dark, at least under N-limiting conditions, compared to diatoms (Dortch and Maske 1982). It is possible that different ecological strategies with respect to nutrient uptake in the dark may be advantageous under different mixing and hence different irradiance conditions.

The taxonomic differences in the dependence of the limiting nutrient uptake on light may lead to different dynamics and outcome of nutrient competition among phytoplankton under different light regimes.

In oligotrophic P-limited systems, phytoplankton may compete with heterotrophic bacteria for inorganic P (Thingstad and Pengerud 1985; Cotner and Biddanda 2002). It is likely that nutrient uptake by bacteria has a different, possibly weaker, dependence on light than nutrient uptake by phytoplankton because heterotrophic bacteria do not directly depend on light as an energy source. Therefore, different light regimes resulting from daily, seasonal variations in irradiance or from different mixing patterns may affect competition for inorganic nutrients between phytoplankton and bacteria. We use analytical techniques and simulations to determine how the dependence of nutrient uptake on light affects nutrient competition and coexistence and what strategies of nutrient uptake are optimal under contrasting light regimes.

Model

To investigate the effects of variable nutrient uptake resulting from light fluctuations, we used a simple model of competition for a nutrient. Previous studies have shown that the Monod model is inadequate under variable conditions (Grover 1991). Therefore, we used a model of nutrient competition where uptake and growth are described by separate equations (Droop 1974). Within this type of model, there are several formulations with different degrees of detail (Morel 1987; Grover 1991). We used the following formulation where nutrient uptake depends only on the external nutrient concentration:

$$\frac{dB_i}{dt} = \mu_{\infty,i} B_i \frac{Q_i - Q_{\min,i}}{Q_i} - m_i B_i$$

$$\frac{dQ_i}{dt} = V_{\max,i} \frac{R}{K_i + R} - \mu_{\infty,i}(Q_i - Q_{\min,i})$$

$$\frac{dR}{dt} = a(R_{in} - R) - \sum_{i=1}^{N} B_i V_{\max,i} \frac{R}{K_i + R} \quad (1)$$

where B_i is the biomass of species i, $\mu_{\infty,i}$ is the growth rate of species i at infinite quota, $Q_{\min,i}$ is the minimum quota, m_i is mortality rate, $V_{\max,i}$ is the maximum nutrient uptake rate, K_i is the half-saturation constant for nutrient uptake, R is the external resource concentration, a is a dilution rate, and R_{in} is the resource concentration in the inflow.

The equilibrium value for a resource, i.e., the break-even nutrient concentration, in monoculture of species i can be determined easily:

$$R_i^* = \frac{K_i \mu_{\infty,i} Q_{\min,i} m_i}{V_{\max,i}(\mu_{\infty,i} - m_i) - \mu_{\infty,i} Q_{\min,i} m_i} \quad (2)$$

Under constant nutrient supply, the species with the lowest requirements for the limiting nutrient, R^*, wins competition (Tilman 1982). Under fluctuating light regimes the minimum resource requirements become dependent on the light regime in a species-specific way (Litchman and Klausmeier 2001).

Here we use an analytical approximation similar to that derived earlier (Litchman and Klausmeier 2001) to determine how nutrient competitive abilities and hence the dynamics and outcome of competition depend on light regime.

Model results

We consider the simple case where two species have the same parameters, except for $V_{\max}$, which is a function of irradiance for species 1 (its maximum uptake rate is a constant in the light, and in the dark it is a fraction f [$0 \le f < 1$] of the uptake rate in the light) and is constant for species 2. We assume that $V_{\max,1}$ in the light is greater than $V_{\max,2}$, but $V_{\max,1}$ in the dark is less than $V_{\max,2}$. Such a scenario is also applicable to competition between phytoplankton (species 1) and bacteria (species 2) if we assume that bacterial uptake is not light dependent. Because species 1 has a higher $V_{\max}$ in the light and all other parameters are the same, its R^* in a constant light environment is lower than that of species 2, and thus species 1 is a better competitor during the light part of the period.

To determine how light fluctuations alter species competitive abilities, we consider light : dark fluctuations in the form of a step function with period T and the proportion of light in the period p. An averaging argument similar to the one that we used previously (Litchman and Klausmeier 2001) shows that under such fluctuations, the R^* of species 1 depends nonlinearly on the proportion of light in a period, p, and the degree of the dark uptake, f:

$$R_i^* = \frac{K_i \mu_{\infty,i} Q_{\min,i} m_i}{[p + (1-p)f]V_{\max,i}(\mu_{\max,i} - m_i) - \mu_{\max,i} Q_{\min,i} m_i} \quad (3)$$

Numerical solutions show that this approximation is valid for fast fluctuations ($T \le 24$ h). The R^* of species 2 is constant (Fig. 1). Figure 1A represents a case where species 1 completely ceases nutrient uptake in the dark ($f = 0$). Often, though, nutrient uptake in the dark is still a substantial fraction of the uptake in light (e.g., Riegman et al. 2000). Figure 1B represents a case where species 1 has the light-dependent maximum uptake rate (lower in the dark) and the $V_{\max}$ of species 2 does not depend on light.

In case of algal–bacterial competition, two competing species will likely have not only the different maximum cellular uptake rates (higher in algae under light; Cotner and Biddanda 2002) but different half-saturation constants for uptake as well (lower in bacteria; Cotner and Biddanda 2002). Such a scenario is represented in Fig. 1C. For the given cases, the R_1^* equals R_2^* at an intermediate value of p, p_{crit}, where a switch in competitive outcome occurs.

We use numerical solutions to verify the predictions from the analytical approximation (Eq. 3). Under constant light, as predicted by the minimum nutrient requirements of the two species, species 1 wins competition (Fig. 2A) and the equilibrium nutrient concentration equals R^* of species 1. The displacement of species 2 occurs after about 40 d (Fig. 2A). Under light : dark cycles with the proportion of light in a period less than 1 but greater than p_{crit}, species 2 is still displaced but at a slower rate. The nutrient concentration in the medium fluctuates with the light cycle around the $R^*(p)$
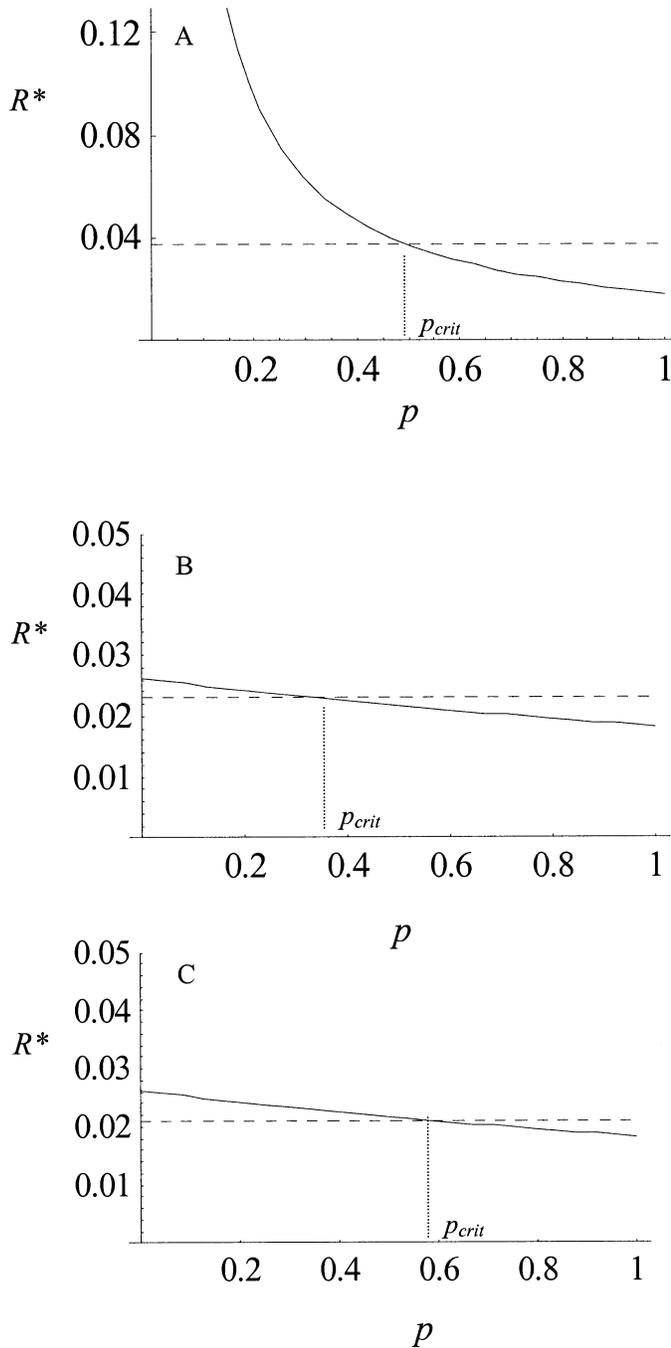
Fig. 1. The dependence of R^* on p, the proportion of light in a period for fast fluctuations. Species 1 (solid line) and species 2 (dashed line) are identical ($\mu_\infty = 0.8$ d^{-1}, $Q_{min} = 5 \times 10^{-9}$ μmol P cell^{-1}, $m = 0.25$ d^{-1}, $K = 2$ μmol L^{-1}) except V_{max}. (A) $V_{max1} = 2 \times 10^{-7}$ μmol P cell^{-1} d^{-1}, $f = 0$ (no uptake in the dark), and $V_{max2} = 1 \times 10^{-7}$ μmol P cell^{-1} d^{-1}; (B) species parameters as above, except $f = 0.7$ (fraction of the light uptake maintained in the dark by species 1) and $V_{max2} = 1.6 \times 10^{-7}$ μmol P cell^{-1} d^{-1}; (C) species parameters are as above, except $K_1 = 2$ μmol L^{-1}, $K_2 = 0.5$ μmol L^{-1}, $V_{max1} = 2 \times 10^{-7}$ μmol P cell^{-1} d^{-1}, $f = 0.7$, and $V_{max2} = 0.45 \times 10^{-7}$ μmol P cell^{-1} d^{-1}.
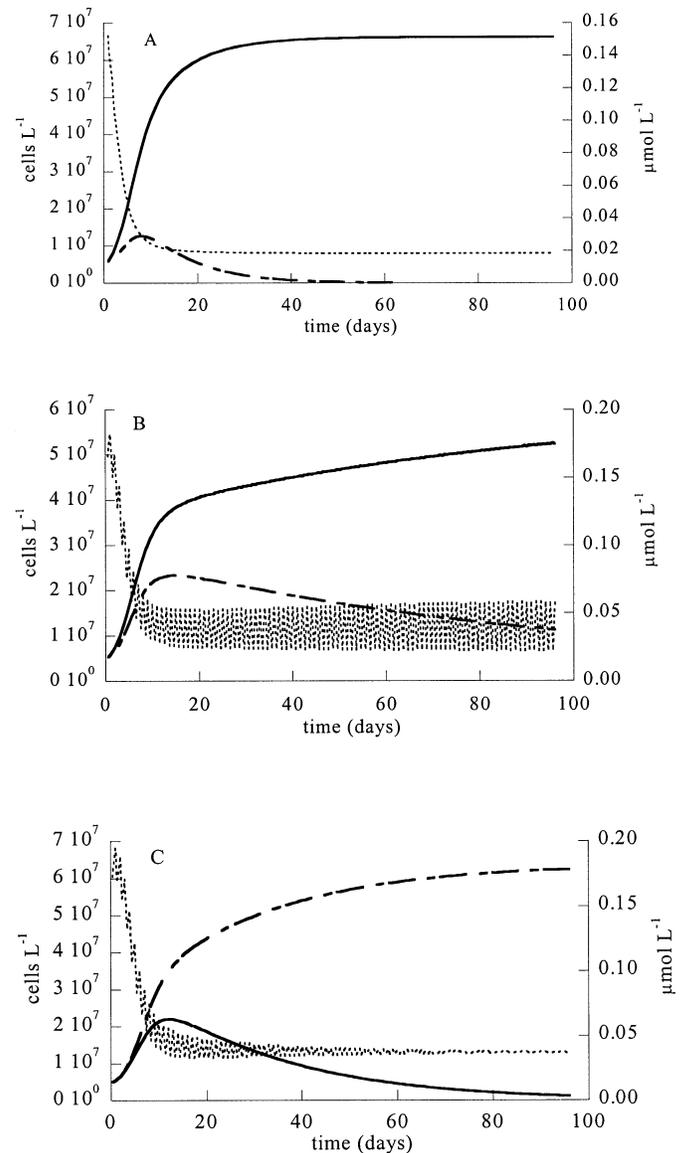

Fig. 2. The dynamics of competition between two species under different light regimes. Species parameters are as in Fig 1. $p_{crit} = 0.5$. (A) Continuous light. (B) Light:dark fluctuations, $p = 0.6$. (C) Light:dark fluctuations, $p = 0.4$. Solid line is species 1, dashed line is species 2, and dotted line is the external nutrient concentration.

of species 1. As p approaches p_{crit}, the rate of displacement decreases. Under even shorter day lengths ($p < p_{crit}$), the competitive outcome is switched to dominance by species 2, which has equal uptake in the light and dark (Fig. 2C). The average nutrient concentration approaches the R^* of species 2, which is less than R^* of species 1 for a given p ($p < p_{crit}$). As in the case of competition for light (Litchman and Klausmeier 2001), fast fluctuations in irradiance do not lead to true coexistence where the invasibility criterion (Armstrong and McGehee 1980) is satisfied, but competitive exclusion may slow down considerably. For the case presented in Fig. 1B (nonzero dark uptake by species 2) and 1C (different half-saturation constants), the numerical simulations also agree with the analytical predictions (data not shown).

Ecological strategies—Maintaining a high uptake rate in the dark enhances species competitive abilities. However, nutrient uptake is often an energy-dependent process (Donald et al. 1997). Therefore, whether a species maintains nutrient uptake in the dark depends on the costs and benefits that can be different in different environments. Here we consider four characteristic cases when the cost of maintaining nutrient uptake in the dark is high or low and when the environment has short or long day length. We express the total metabolic cost of uptake as follows:

$$m_{tot} = m_{min} + m_f f \qquad (4)$$

where m_{tot} is the total metabolic cost of nutrient uptake, m_{min} is the cost of uptake in the light, and $m_f f$ is the cost of uptake in the dark with m_f being the cost of uptake in the dark and f being the dark uptake as the proportion of uptake in the light ($f = 0$ corresponds to no uptake in the dark, and $f = 1$ corresponds to the dark uptake rate equal the uptake rate in light). The optimal strategy is the one that minimizes R^*. Here we express R^* as a function of f, the dark uptake as the proportion of uptake in the light. Because of the tradeoff between the advantages of maintaining nutrient uptake in the dark and costs associated with it, different light regimes favor different nutrient use strategies. After substituting m_{tot} from Eq. 4 of p and f into Eq. 3, R^* becomes the following function of p and f:

$$R^*[p, f] = [K\mu_\infty Q_{min}(m_{min} + m_f f)]$$
$$\div \{[p + (1 - p)f]V_{max}[\mu_\infty - (m_{min} + m_f f)]$$
$$- \mu_\infty Q_{min}(m_{min} + m_f f)\}$$

where the parameters are as above. If the cost of nutrient uptake is high and the proportion of light in a period is high (e.g., long day length or shallow mixing conditions), then the optimal strategy is not to maintain nutrient uptake in the dark ($f = 0$) (Fig. 3A). When the proportion of light in a period decreases (under shorter day length or optically deeper mixing), it becomes advantageous to maintain some uptake in the dark (the lowest R^* corresponds to the intermediate value of f; Fig. 3B). When the cost of maintaining nutrient uptake in the dark is small, for low values of p, the optimal strategy (the lowest R^*) is to have high nutrient uptake rates in the dark ($f = 0$; Fig. 3C). Under high p the optimal strategy is not to maintain uptake in the dark ($f = 0$), even if the cost is not large (Fig. 3D). In such a case, however, the R^* difference among strategies, i.e., different values of f, is small.

Nutrient stoichiometry under dynamic light regimes—Because of the light dependence of nutrient uptake, varying light regimes are likely to alter nutrient stoichiometry of phytoplankton cells. According to the model, the concentration of the limiting nutrient increases in the end of the light period. The increase is more pronounced in the species with the light-dependent nutrient uptake. However, cellular nutrient content may fluctuate in the other species as well due to fluctuations in ambient nutrient concentrations caused by the first species.
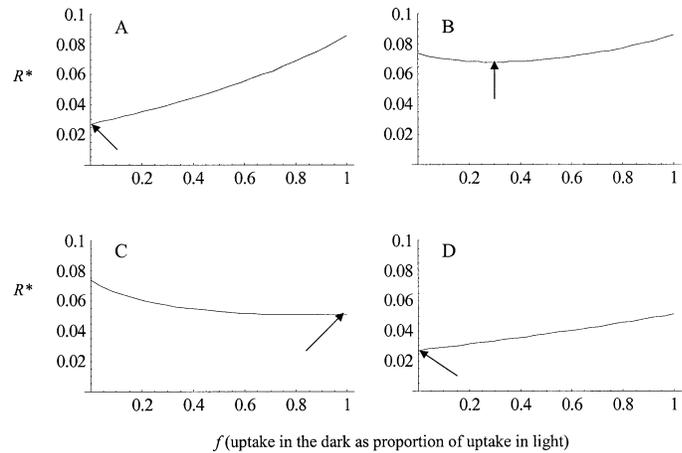

Fig. 3. Optimal ecological strategies for nutrient uptake in the dark. R^* as a function of the uptake in the dark. The optimal strategy has the lowest R^*, shown by the arrow. (A) High metabolic cost of uptake in the dark ($m_f = 0.25$) and high proportion of light in a period, p ($p = 0.8$); (B) high cost ($m_f = 0.25$) and low p ($p = 0.3$); (C) low cost ($m_f = 0.15$) and low p ($p = 0.3$); and (D) low cost ($m_f = 0.15$) and high p ($p = 0.8$).

Discussion

Competition and coexistence—Irradiance-induced variation in nutrient uptake can alter the competitive abilities of species: inferior competitors under continuous light capable of maintaining high uptake in the dark may have a competitive advantage under light:dark cycles. Our analytical approximation (Eq. 3) provides a useful tool for predicting the outcome of nutrient competition under different light regimes when nutrient uptake is light dependent. It may be applicable not only to competition among phytoplankton but to competition between phytoplankton and bacteria as well.

Light dependence of nutrient uptake leads to fluctuations in nutrient availability and higher average nutrient concentration compared to constant light conditions. Light fluctuations may slow competitive exclusion and reverse the outcome reached under constant light but not permit stable coexistence. However, the time scales over which the slowing of competitive exclusion occurs are sufficiently long (ca. 2 months) to contribute effectively to phytoplankton diversity. A recent experimental study showed prolonged persistence of two species of cyanobacteria under fluctuating light and competitive exclusion of one of the species under constant light (Litchman 2003). These results on the role of light fluctuations on nutrient competition are similar to the effects of light fluctuations on competition for light (Litchman and Klausmeier 2001). A recent study (Ahn et al. 2002) showed that species-specific light-dependent nutrient uptake affects competitive dynamics in phytoplankton. Light fluctuations of longer time scales, e.g., due to changes in weather, were shown to promote diversity by altering competition for light (Litchman and Klausmeier 2001; Flöder et al. 2002). Similarly, we expect the slow light fluctuations to increase diversity by mediating nutrient competition.

Light-dependent nutrient uptake by phytoplankton causes fluctuations in ambient nutrient concentration that may in-

fluence competitive interactions among phytoplankton and bacteria. Kuipers et al. (2000) found that bacteria in the subtropical North Atlantic were limited by and competed with phytoplankton for N and P during the day but were limited by carbon during the night when N and P concentration increased and the organic carbon release by phytoplankton decreased.

In this paper we considered a simple case of the stepwise light–dark fluctuations; however, light fluctuations encountered by phytoplankton in nature are much more complex. V_{max} can also be a linear or nonlinear function of irradiance (MacIsaac and Dugdale 1972; Reshkin and Knauer 1979). It is likely, however, that the qualitative results would still hold even for a more complex pattern of light fluctuations, similar to the results on the effects of light fluctuations on competition for light (Litchman and Klausmeier 2001).

Ecological strategies—Both light regime and the metabolic expenses of maintaining nutrient uptake in the dark determine what nutrient uptake strategies are optimal. According to our analysis, for nutrients that require more energy to assimilate, dark uptake is less beneficial. Experimental studies support this: nitrate uptake often is much lower in the dark, while the uptake of ammonium occurs at comparable rates in both light and dark (Kudela et al. 1997; Mulholland et al. 1999). In the environments with substantial periods of low light or darkness (short day length or deep mixed layer), dark uptake of a limiting nutrient should occur more often. It is possible that different groups of phytoplankton dominating at different seasons or different mixing regimes may have contrasting strategies of nutrient use. Often diatoms dominate during deep mixing periods, while cyanobacteria are associated with stratified conditions (Reynolds 1984). These dominance patterns are likely related to the taxon-specific differences in sinking and buoyancy. We found that the diatom *Nitzschia* sp. maintained comparable uptake rates in light and dark, while the cyanobacterium *Phormidium luridum* had much lower uptake rates in the dark (Litchman et al. unpubl. data). These differences may reflect general taxon-specific strategies, but more species need to be surveyed.

The results of our analysis also imply that species or taxonomic groups capable of maintaining high uptake rates in the dark or low light would have a competitive advantage under the light regimes with a low proportion of light in a period. Extending this reasoning to the bacteria–phytoplankton interactions, we may hypothesize that bacteria could be more competitive in deeply mixed systems or under short day lengths. Cotner (2000) found a higher ratio of bacterial biomass to phytoplankton biomass in the Sargasso Sea when the mixed layer was deep. Greater competitive advantage of bacteria under these conditions may be one possible explanation for the higher ratio.

According to the model, cellular nutrient concentrations are likely to increase in the end of a light period. This agrees with the experimental studies where nutrient concentration was monitored (e.g., Eppley et al. 1971). Such an increase in cellular nutrient content and hence higher nutritional quality of phytoplankton can be beneficial for zooplankton migrating upward at the end of the day.

In summary, we showed that by affecting nutrient uptake, dynamic light regimes can modify nutrient competition among phytoplankton and possibly between phytoplankton and bacteria. Light fluctuations may slow competitive exclusion and reverse the competitive outcome reached under constant light. Contrasting light environments would favor different nutrient use strategies, and the optimal strategies depend on the cost of nutrient uptake.

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