Resource Competition and the Ecological Success of Phytoplankton

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Phytoplankton are major primary producers in the aquatic realm, responsible for almost half of global net primary production (Field *et al*. 1998). Their abundance and community structure directly impact higher trophic levels and key biogeochemical cycles. Phytoplankton are an extremely diverse, polyphyletic group that includes both prokaryotic and eukaryotic forms. What makes phytoplankton so successful? Several fundamental processes, such as photosynthesis, growth, resource acquisition, and grazer avoidance, to a large degree define ecological niche of phytoplankton. The success of phytoplankton depends on how efficiently they acquire resources, transform them into growth, and avoid being eaten or infected. Diverse selective pressures on phytoplankton increase the efficiency of these processes and allow species to persist under changing conditions. Resource competition is one of the key ecological processes that controls species composition, diversity, and succession of phytoplankton communities. In this chapter I discuss the role of resource competition in structuring past, present, and future phytoplankton communities.

I. RESOURCE ACQUISITION AND MEASURES OF COMPETITIVE ABILITY

The resources that phytoplankton need include carbon, light, macro- and micronutrients such as nitrogen, phosphorus, and iron, and certain vitamins. The ability to utilize these resources effectively will give a phytoplankton species a competitive advantage over other members of the community and thus contribute to its overall fitness. I briefly review how the utilization of resources such as nutrients and light is described and how competitive ability for these resources is defined.

A. Nutrients

Nutrients are dissolved in the aquatic medium and taken up through the cellular surface. The rate of nutrient uptake, V, is often described as a saturating function of nutrient, R (Michaelis–Menten kinetics). The key parameters that characterize the efficiency of nutrient uptake are the maximum uptake rate, V_{max}, and half-saturation constant for uptake, K.

$$V = V_{max} \frac{R}{K + R} \qquad (1)$$

Acquired resource is then used for growth and, consequently, growth, μ, depends on the internal nutrient concentration or cellular quota, Q, as follows:

$$\mu = \mu_\infty \left(1 - \frac{Q_{min}}{Q} \right) \qquad (2)$$

where μ_∞ is the growth rate of species at an infinite quota, Q is the internal nutrient concentration (nutrient quota), and Q_{min} is the minimum quota (when growth rate equals 0). Equation 2 is known as the Droop model (Droop 1968, 1973). Equations 1 and 2 are widely used to describe phytoplankton nutrient uptake and growth. A similar model of phytoplankton growth based on internal nutrient concentration was proposed by Caperon (1968). Droop and other internal stores models have been shown to be more accurate than models of growth based on the external nutrient concentration (e.g., Monod model), especially under fluctuating nutrient supply (Turpin and Harrison 1979; Turpin 1988; Grover 1991a). However, even these internal stores models with a separate Michaelis–Menten equation for uptake still oversimplify nutrient uptake and growth processes. A more detailed overview of nutrient uptake in phytoplankton is given in Raven (1980) and Riebesell and Wolf-Gladrow (2002). Examples of more mechanistic models of phytoplankton growth can be found in Kooijman and others (Kooijman *et al*. 2004; Vrede *et al*. 2004).

How do these different traits that affect nutrient uptake and requirements combine to determine the outcome of nutrient competition?

Resource competition theory shows that the species that reduces the limiting resource to the lowest concentration in monoculture is the best competitor at equilibrium in a well-mixed system (Tilman 1982). This critical concentration is termed R^*. It is, therefore, possible to predict the outcome of competition by measuring R^*s in monocultures for different species for a given nutrient. It is also possible to derive R^* from a particular model of nutrient uptake and growth. Given Droop model (Equations 1 and 2), the break-even nutrient concentration, R^*, can be expressed as follows:

$$R^* = \frac{K\mu_\infty Q_{min} m}{V_{max}(\mu_\infty - m) - \mu_\infty Q_{min} m}, \qquad (3)$$

where symbols are as in Equations 1 and 2 and m is mortality. Thus R^* integrates many physiological parameters into a synthetic metric of competitive ability. Figure 1 shows how R^* depends on the individual parameters of nutrient uptake and growth.

Resource competition theory has been successfully used to determine the outcome of laboratory experiments (Tilman 1977) and to explain the distribution of species along resource supply gradients (Tilman et al. 1982) and patterns of species diversity in different lakes (Interlandi and Kilham 2001). A review by Tilman and colleagues provides a more detailed introduction into the theory of resource competition, as applied to phytoplankton (Tilman et al. 1982).

It must be stressed that this theory is based on well-mixed and equilibrium conditions. Deviations from spatial and temporal homogeneity may alter the selective value of physiological traits and can open up new mechanisms for species coexistence (see Section II).

B. Light

Light, another essential resource, has a complex pattern of spatial and temporal variability (Falkowski 1984; Ferris and Christian 1991). The unavoidable vertical light gradient makes the dynamics of light competition more complex than those of nutrient competition. Recent work of Huisman and colleagues showed that light-dependent growth of monocultures can be used to predict the outcome of competition for light, similar to nutrient competition (Huisman and Weissing 1994; Weissing and Huisman 1994; Huisman et al. 1999a). Phytoplankton growth is modeled as a function of light availability at a given depth (we use the original notation of Huisman et al.):

$$\frac{d\omega_i}{dt} = \frac{1}{z}\int_0^z P_i[I(s)]\omega_i ds - D\omega_i$$

where ω_i is the biomass and $p_i(I)$ is the specific production rate of species i as an increasing function of light intensity, $I(s)$ is the light intensity as a decreasing function of depth s, z is the total depth of the water column, and D is the loss rate.

Light is attenuated exponentially by phytoplankton biomass and background turbidity:

$$I(s) = I_{in}\exp\left(-\left[\sum_{j-1}^{n} k_j\omega_j s + K_{bg}s\right]\right)$$

where I_{in} is the incident light intensity, k_j is the specific light attenuation coefficient of species j, K_{bg} is the total background turbidity due to nonphytoplankton components, and n is the total number of phytoplankton species. The model predicts that each species has a critical light intensity I_{out} at which its biomass remains constant. A species with the lowest critical light intensity is the best light competitor, as it is able to reduce I_{out} below the critical intensities of other species (Huisman and Weissing 1994; Huisman et al. 1999a). The I_{out} as the measure of light competitive ability is similar to the R^* measure of the nutrient competitive ability; the key difference is, however, that I_{out} depends on the incoming light (Huisman and Weissing 1994), while R^* is independent of nutrient inflow (Tilman 1982).
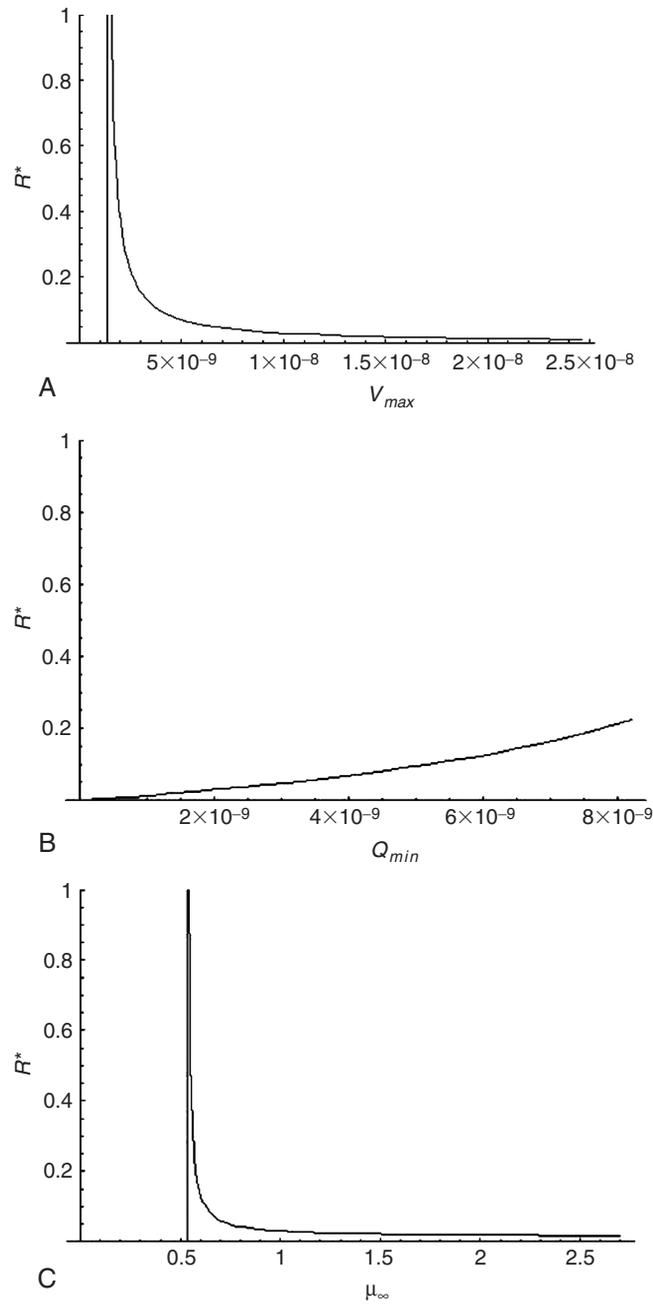
FIGURE 1. The dependence of R^* on major physiological parameters, as in Equation 3. R^* as a function of **(A)** V_{max}, **(B)** Q_{min}, **(C)** μ_∞,
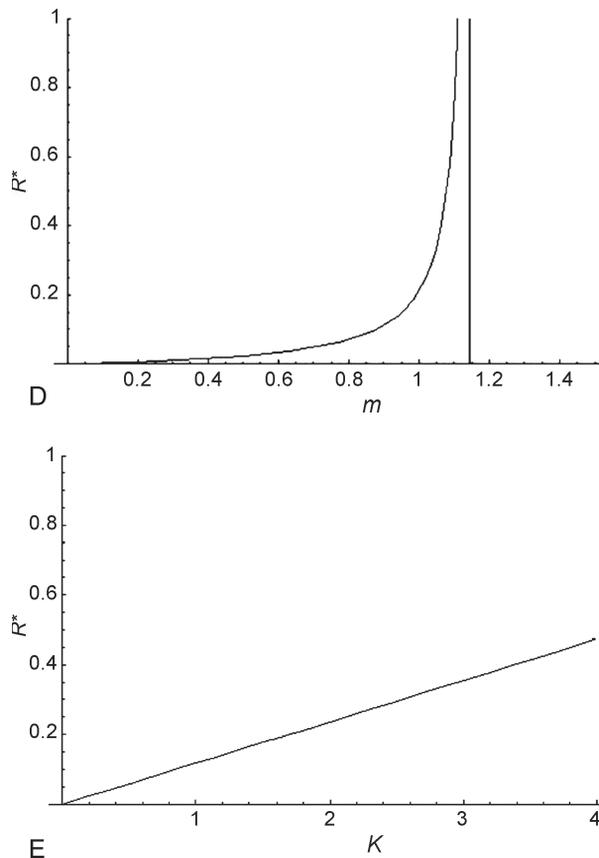
(Continued)

FIGURE 1. Cont'd (D) *m,* and (E) *K*. Parameter values are as follows: $V_{max} = 1.23^*10^{-8}$ µmol nutrient cell^{-1} day^{-1}, $Q_{min} = 1.64^*10^{-9}$ µmol nutrient cell^{-1}, $\mu_\infty = 1.35$ day^{-1}, m = 0.5 day^{-1}, and $K = 0.2$ µmol nutrient L^{-1}.

II. THE ROLE OF SPATIAL AND TEMPORAL HETEROGENEITY IN RESOURCE COMPETITION IN PHYTOPLANKTON

In aquatic ecosystems, the effects of spatial and temporal heterogeneity are especially strong, as physical forcing and biological processes are tightly coupled due to similar characteristic time scales of physical forcing and biological responses (Steele 1985). Major resources for phytoplankton are heterogeneously distributed in space, both along the vertical and horizontal dimensions and in time. Here I discuss the implications of the vertical heterogeneity in resource distribution: a vertical gradient in light, with irradi-

ances decreasing exponentially with depth and an opposing gradient in nutrient concentration (increase with depth) (Figure 2). Phytoplankton also often exhibit vertically heterogeneous distributions that can be both the cause and the consequence of the vertical heterogeneity in light and nutrients.

A. Heterogeneity in Nutrient Distribution

Low nutrient concentrations in the euphotic zone are due to biological uptake and often lead to severe nutrient limitation of phytoplankton during the periods of high water-column stability. However, a number of physical processes episodically supply
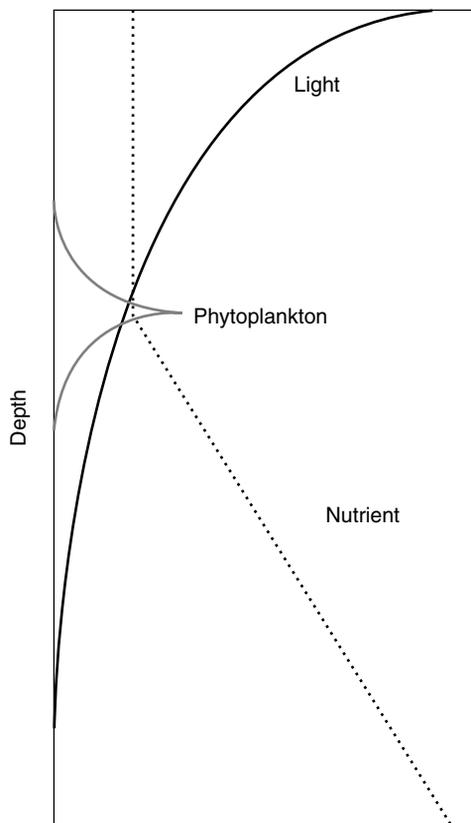
FIGURE 2. Typical heterogeneous distributions of light, a limiting nutrient, and a subsurface chlorophyll maximum in the water column.

nutrients to the upper water column, thus causing a temporal heterogeneity in resource supply. Turbulent eddies may entrain nutrient-rich waters from the pycnocline, leading to higher rates of primary productivity in the upper mixed layer (Falkowski *et al.* 1991; Garcon *et al.* 2001). If nutrient concentrations are elevated in the deeper water, increased nutrient fluxes will occur to the upper mixed layer due to mixing created by internal waves (Holligan *et al.* 1985). Upwelling brings nutrients from the nutrient-rich deep waters into the euphotic zone, where uptake by phytoplankton can lead to enhanced growth. Similarly, Ekman transport and pumping near the coast creates upwelling conditions that distribute more nutrients to the euphotic zone (Bauer *et al.* 1991). Such nutrient pulses occur at multiple temporal

scales; for example, extremely slow Rossby waves with periods of ca. 3 months were shown to inject nitrate into the upper water column, increasing productivity and shifting phytoplankton community structure to fast-growing species of haptophytes and pelago-phytes (Sakamoto *et al.* 2004). Long-lived baroclinic eddies (life span of ca. 150 days) were shown to increase nitrate concentrations up to eightfold and promote growth of large phytoplankton (Vaillancourt *et al.* 2003). Understanding how episodic mesoscale physical processes in the ocean such as eddies (Falkowski *et al.* 1991; McGillicuddy *et al.* 1998), localized upwelling (Martin *et al.* 2002), and others influence phytoplankton production, and community structure, and thus the rest of the food web, is an active area of research. There are also much faster processes that can lead to nutrient injections into the upper part of the water column, such as Langmuir circulation and small-scale turbulent processes (Thorpe 2004a, b).

Theoretical and experimental studies of phytoplankton nutrient competition show that dynamics and outcome of competition strongly depend on frequency of nutrient pulses (Turpin and Harrison 1979; Grover 1991c; Stolte and Riegman 1996; Tozzi *et al.* 2004). Under high-frequency nutrient pulses (e.g., daily), the conditions are similar to the continuous nutrient supply, and species that win in a constant nutrient environment (species with the lowest R^*) dominate in such a regime as well, as fast fluctuations are physiologically averaged out (Grover 1991c). In contrast, under low-frequency nutrient pulses (with a several day period) species that may be inferior competitors under constant nutrient supply may gain competitive advantage (Grover 1991c; Stolte and Riegman 1996). Such species may have superior storage abilities through high maximum nutrient uptake rate and/or a large maximum nutrient quota, and thus be non-equilibrium strategists (Grover 1991c; Stolte and Riegman 1996). Assuming that diatoms are better adapted to store nitrate, a limiting nutrient, compared to coccolithophores,

Tozzi *et al*. (2004) showed with a simulation model that pulsed nutrient regimes favor diatoms over coccolithophores.

Hutchinson (1961) proposed that nonequilibrium conditions could explain the paradox of the plankton in which many species of phytoplankton limited by few resources coexist in a seemingly homogeneous environment, whereas according to the competitive exclusion principle, the number of coexisting species cannot exceed the number of limiting resources (Gause 1934; Hardin 1960). Theoretical studies show that fluctuations in limiting resources (e.g., nutrients) may allow coexistence of more than one species on a single limiting resource, while under constant resource supply a species capable of reducing the resource concentration to the lowest level would competitively displace other species (Armstrong and McGehee 1976, 1980; Levins 1979; Hsu 1980). The dynamics and outcome of competition may also depend on how predictable fluctuation regimes are: Generally, under more randomly fluctuating conditions, the advantage of non-equilibrium specialists decreases (Grover 1991c).

B. Heterogeneity in Light Distribution

Light, another essential resource for phytoplankton, also fluctuates on a wide range of temporal scales with different amplitudes. Due to a vertical gradient in light distribution and different mixing patterns phytoplankton experience temporal fluctuations in light supply on a wide range of time scales. Many of the hydrodynamic processes that alter nutrient regimes (see previous section) also cause light fluctuations for phytoplankton. Turbulent eddies in the upper mixed layer change the light exposure of phytoplankton on time scales of minutes to hours (Denman and Gargett 1983). Contracting and expanding internal waves can move phytoplankton tens of meters up and down through the vertical light gradient (Denman and Gargett 1983).

Light fluctuations may significantly change phytoplankton photosynthesis and primary productivity (e.g., Marra 1978; Falkowski and Wirick 1981; Mallin and Paerl 1992). Moreover, our own studies show that fluctuating light may also alter growth rates in a species-specific way, delay competitive exclusion, promote coexistence, and change community composition (Litchman 1998, 2000; Litchman and Klausmeier 2001). We found that fast light fluctuations may change competitive outcome and lead to a dominance by nonequilibrium specialists, species that are inferior competitors under constant light but have high maximum growth rates (Litchman and Klausmeier 2001). In addition, slow light fluctuations could lead to stable coexistence of multiple species and thus increase diversity (Litchman and Klausmeier 2001). In general, fluctuating conditions select for fast-growing species, whereas constant environments select for best equilibrium competitors (Grover 1991c; Litchman and Klausmeier 2001).

Light fluctuations may also mediate competition for a limiting nutrient due to the light-dependent nutrient uptake (Macisaac and Dugdale 1972; Litchman *et al*. 2004). Depending on the costs and benefits of maintaining nutrient uptake in the dark, different strategies of nutrient use are optimal under different light regimes: If the cost of maintaining nutrient uptake in the dark is high and algae experience short periods of darkness or low light (shallow mixing and/or long day length), the optimal strategy is not to take up nutrient in the dark. In contrast, if the periods of low light or darkness are long (deep mixing or short day length), the optimal strategy would be to maintain some uptake in the dark, despite the costs (Litchman *et al*. 2004). It may be that different functional groups of phytoplankton are more adapted to a particular strategy, depending on the physical conditions they are associated with and other physiological adaptations. Diatoms often dominate under low water-column stability (Li 2002), that is, deep mixing conditions, and thus may experience prolonged periods of low light or darkness. Some studies suggest that diatoms are more efficient at maintaining

nitrate uptake in the dark compared to flagellates (Clark *et al.* 2002).

The composite measure of competitive abilities, R^*, depends nonlinearly on resource fluctuations, and it is possible in some cases to derive such a relationship analytically to predict the outcome of resource competition under different fluctuation regimes (Litchman and Klausmeier 2001; Litchman *et al.* 2004).

C. Vertical Heterogeneity in Phytoplankton Distribution

Vertical gradients in the distribution of limiting nutrients may lead to the diversification of nutrient acquisition strategies (Troost *et al.* 2005a). Similarly, vertical gradient in irradiance allows for niche separation and coexistence of different strategies of light utilization under stratified conditions: High-light–adapted species grow in the upper part of the water column, whereas low-light–adapted species inhabit greater depths, often forming subsurface chlorophyll maxima (Reynolds 1997).

There is an emerging literature on modeling the vertical distribution of phytoplankton, begun by Riley *et al.* in 1949. Lande and Lewis (1989) did not consider population dynamics but rather the effect of mixing on the vertical distribution of a physiological state, photoadaptation. Early models of population dynamics (Shigesada and Okubo 1981; Britton and Timm 1993) focused on mathematical proofs and treated competition phenomenologically. Huisman and Weissing (1994, 1995; Weissing and Huisman 1994) developed a mechanistic model of phytoplankton growth and competition in perfectly well-mixed water columns. The assumption of total mixing allowed them to integrate over the water column to arrive at a simpler, nonspatial model. They found that although there is an inevitable light gradient, the competitive exclusion principle still holds, allowing one species when competing for light and two when competing for light and nutrients. Later, Huisman *et al.* (1999a, b) relaxed the assumption of

perfect mixing by considering a reaction-diffusion model of growth and competition in incompletely mixed water columns. Considering light limitation only (no nutrients), they showed that incomplete mixing can allow two species to coexist on one limiting resource but only over a narrow range of parameter values (Huisman *et al.* 1999b). Phytoplankton sinking has been considered by Huisman *et al.* (2002), Diehl (2002), and Yoshiyama and Nakajima (2002).

Yoshiyama and Nakajima (2002) made a step toward physical realism by considering vertical heterogeneity in mixing rates, placing a well-mixed layer above a poorly mixed one. They considered a single species, limited by light and nutrients. They found that under low nutrients, a heterogeneous distribution of phytoplankton arose in the deep layer; under high nutrients, the biomass was uniformly distributed throughout the surface mixed layer; and in between, multiple stable states were possible (although this may depend on the assumption that phytoplankton and nutrients have different diffusion coefficients across the thermocline).

Klausmeier and Litchman (2001) investigated the vertical distribution of a single species of phytoplankton in poorly mixed water columns, with light- and nutrient-dependent growth. Light is supplied at the top of the water column and nutrients are supplied at the bottom, diffusing across the sediment-water interface. They included a novel feature not found in the other models reviewed so far: phytoplankton behavior in the form of active movement up gradients in potential growth rate. Direct numerical solution of the reaction-diffusion-advection model showed that phytoplankton could form thin layers of biomass when mixing is weak and swimming is strong. The width of the layer is determined by the ratio of the turbulent diffusion coefficient and the swimming speed.

A novel analytical approach was developed by Klausmeier and Litchman (2001) to determine the location and biomass of the phytoplankton layer under poor mixing and rapid swimming. By treating the dis-

tribution of phytoplankton as an infinitely thin layer, they could solve for the optimal depth of the layer as an evolutionarily stable strategy, using methods from evolutionary game theory. Competition for nutrients and light in a poorly mixed water column could result in three different kinds of vertically heterogeneous distributions: at low nutrient and background attenuation levels, a benthic layer forms; at high nutrient levels, a surface scum forms; and at intermediate nutrient levels, a deep chlorophyll maximum (DCM) occurs (Klausmeier and Litchman 2001). The opposing gradients of light and a limiting nutrient may lead to stable coexistence of multiple species at different depths if those species exhibit a trade-off in nutrient versus light competitive ability (Klausmeier *et al*. unpublished).

Phytoplankton in the DCM may exhibit population fluctuations and chaotic behavior because sinking of phytoplankton and the upward diffusion of nutrients occur on different time scales: Phytoplankton sinking out of the optimal irradiance decline and do not completely utilize upward diffusing nutrients. When the upward diffusing nutrients reach depth with adequate irradiance, phytoplankton growth is stimulated (Huisman *et al*. 2006). Seasonal changes in irradiance may also facilitate chaotic oscillations in phytoplankton density; these oscillations, in turn, may promote coexistence of multiple species in the DCM (Huisman *et al*. 2006).

III. PHYSIOLOGICAL TRADE-OFFS

The ability of phytoplankton to acquire and utilize resources can be characterized by key physiological parameters that differ among species. These differences in physiological traits arise from physical and chemical constraints on physiological functions. These constraints define various trade-offs in resource utilization in all organisms, and these trade-offs lie at the heart of niche-based nonneutral theories explaining species diversity (Tilman 2000; Bohannan *et al*. 2002).

A trade-off occurs when a trait that confers an advantage for performing one function simultaneously confers a disadvantage for performing another function (Bohannan *et al*. 2002). I discuss some relevant trade-offs in phytoplankton and illustrate how such trade-offs can promote species coexistence and diversity.

A lower R^* can be achieved by increasing the maximum nutrient uptake rate, V_{max}, growth rate at infinite nutrient quota, μ_{∞}, by decreasing half-saturation constant for uptake, K, minimum nutrient quota, Q_{min}, and/or mortality, m. An evolutionary pressure to increase nutrient competitive ability, that is, to lower the R^*, may act on all these parameters simultaneously. Interestingly, the dependence of R^* on individual physiological parameters is nonlinear for all parameters except for the half-saturation constant for uptake, K (see Figure 1). This means that for certain ranges of these parameters a change in parameter value could lead to a greater change in competitive ability than for other parameter ranges. In addition, the influence of these parameters on the R^* may be unequal, so that a relatively similar change in one parameter compared to another may lead to a much greater change in R^* (see Figure 1).

If these parameters were independent, it would be possible to select for a "superspecies" with all the parameters at values that would lead to the lowest R^* possible. However, as our recent work indicates, key parameters of nutrient uptake and growth are correlated with each other, and these correlations may represent real physiological trade-offs (Litchman *et al*. submitted). For example, we found significant positive correlations between V_{max} and K and between Q_{min} and V_{max} (Litchman *et al*. submitted). Such trade-offs are likely to preclude the evolution of a superspecies and, instead, can promote diversity of eco-physiological strategies of resource utilization. A consideration of physiological trade-offs in an ecological context that defines selective pressures should improve our understanding of the mechanisms structuring past, present, and future phytoplankton communities.

A. Nutrient Utilization Trade-Offs

Various physiological trade-offs that lead to distinct ecological strategies of nutrient utilization in phytoplankton can be explained mechanistically. For example, a positive correlation between the maximum uptake rate and half-saturation constant for nitrate uptake can be explained based on the model of nutrient uptake by Aksnes and Egge (1991). Briefly, a limited surface area used for uptake of a particular nutrient could be partitioned into uptake sites in at least two contrasting ways: large number of uptake sites with a smaller active area of individual sites or fewer uptake sites with a larger area of individual uptake sites (Litchman *et al*. submitted). According to the formulas of Aksnes and Egge (1991), the former strategy would result in high *Vmax* and high *K*, whereas the latter strategy would lead to low *Vmax* and low *K* (Litchman *et al*. submitted).

Data suggest that there may also be trade-offs in the utilization of and competitive abilities for different nutrients. Oceanic centric diatoms have lower iron requirements than coastal species (Brand *et al*. 1983; Maldonado and Price 1996). However, there may be a trade-off in requirements for iron and another micronutrient, copper. Peers *et al*. (2005) showed that oceanic diatoms have significantly higher requirements for copper (necessary for iron utilization and growth) compared to coastal forms, demonstrating a trade-off between iron and copper requirements (Peers *et al*. 2005). Classic work by Tilman and colleagues revealed trade-offs in competitive ability for silicon versus phosphorus among freshwater diatoms (Tilman 1977; Tilman *et al*. 1982). It is unknown, however, how universal such trade-offs are.

B. Light Utilization Trade-Offs

There are also various physiological trade-offs in light utilization. Often, species that can grow at very low irradiances have their growth saturated or inhibited at lower irradiances, compared to species that cannot grow at low irradiances (Ryther 1956; Falkowski 1980; Richardson *et al*. 1983). For example, green algae have significantly higher irradiances at which minimum and maximum growth is achieved, compared to other major taxonomic groups (Richardson *et al*. 1983). Experimental work by Stomp and colleagues (Stomp *et al*. 2004) demonstrated that a trade-off in utilization of different parts of the light spectrum in algae can lead to species coexistence. Two isolates of unicellular cyanobacteria of the genus *Synechococcus* differ in their accessory pigment composition: an isolate BS4 contains phycocyanin and hence is capable of absorbing light in the orange-red part of the spectrum, whereas the isolate BS5 contains phycoerythrin and is able to absorb photons in the green-yellow part of the spectrum. When the two isolates were competing for light, the phycocyanin-containing isolate won under red light. Conversely, the phycoerythrin-containing cyanobacterium won under green light. Competition under white light did not result in competitive exclusion, as the two isolates were utilizing different parts of the spectrum and were able to coexist (Stomp *et al*. 2004).

C. Trade-Offs in Nutrient Competitive Ability Versus Light Competitive Ability

Another important trade-off is that between nutrient and light competitive ability (Leibold 1997). An elegant study by Strzepek and Harrison (2004) demonstrated a trade-off between iron requirements and light utilization in marine diatoms: the open ocean species have significantly lower iron requirements compared to coastal species due to changes in photosynthetic apparatus. By lowering their cellular iron content, open ocean diatoms compromise their ability to utilize rapidly fluctuating light; this ability is, however, less relevant in the open ocean than in coastal environment where fast light fluctuations occur due to tidal mixing (Strzepek and Harrison 2004). A higher

minimum quota for nitrogen at low irradiance (Rhee and Gotham 1981) represents another example of a physiological trade-off between light and nutrient competitive abilities and is probably due to higher chlorophyll concentration to increase light utilization at low light.

D. Trade-Offs in Growth Rate Versus Competitive Ability

Phytoplankton often exhibit a trade-off between the maximum growth rate and equilibrium competitive ability, a so-called gleaner-opportunist trade-off (Grover 1997) that is essentially a trade-off between the r and K strategies (Kilham and Kilham 1980; Sommer 1981). Under nonequilibrium or high resource conditions, species with high maximum growth rates, but not necessarily the lowest R^*, may win competition (Grover 1997). Due to trade-offs in biochemical allocation, high maximum growth rates are often associated with high cellular concentration of phosphorus-rich ribosomes enabling high growth rates (the growth rate hypothesis, Sterner and Elser 2002; Klausmeier *et al.* 2004). Species that are good competitors for nutrients or light invest heavily in nitrogen-rich uptake proteins or light-harvesting structures (chlorophyll complexes). These differences in investment (growth machinery, i.e., ribosomes, versus resource acquisition machinery) will lead to differences in cellular N:P stoichiometry (Klausmeier *et al.* 2004). If environmental conditions select for fast-growing species, the overall N:P stoichiometry of phytoplankton may be shifted to low N:P ratios and, conversely, if the conditions select for good competitors, phytoplankton N:P ratios will be higher (Klausmeier *et al.* 2004).

E. Trade-Offs in Grazing Resistance Versus Competitive Ability

Aside from acquiring resources and growing, the other important thing in the life of phytoplankton is to avoid being eaten. Good competitors in phytoplankton are often highly susceptible to grazing, whereas poor competitors are grazer-resistant, thus exhibiting the competitive ability–grazer resistance trade-off (Grover 1995). Given this trade-off, both generalist and specialist grazers can preclude competitive exclusion and maintain species diversity in phytoplankton (Armstrong 1994; Grover 1995; Leibold 1996; Grover and Holt 1998).

IV. ECOLOGICAL STRATEGIES OF RESOURCE UTILIZATION IN MAJOR FUNCTIONAL GROUPS

Major divisions of phytoplankton (taxonomic groups) such as diatoms, coccolithophores, dinoflagellates, chlorophytes (including prasinophytes), and cyanobacteria are often separated into distinct functional groups, as these taxonomic groups have unique biogeochemical signatures. Functional groups in phytoplankton are defined as groups of "organisms related through common biogeochemical processes" and are not necessarily phylogenetically related (Iglesias-Rodriguez *et al.* 2002a). Do these major functional groups have distinct strategies of nutrient utilization?

In his seminal article, Margalef (1978) classified marine phytoplankton according to their responses to the nutrient and turbulence fields. The so-called Margalef mandala includes diatoms, coccolithophorids, and dinoflagellates. Diatoms occupy the high-nutrient–high-turbulence corner of the nutrient–turbulence space, coccolithophorids are associated with intermediate nutrient concentrations and turbulence, and dinoflagellates cluster at low turbulence and high (red tide forms) or low nutrients. Later, Sommer (1984) proposed three major strategies of resource (nutrient) utilization in phytoplankton: "velocity-adapted" species with high maximum nutrient uptake rates (V_{max}) and high maximum growth rates (μ_{max}) that are able to utilize nutrient pulses and grow fast, "storage-adapted"

species with high V_{max} but lower μ_{max} that are able to acquire the limiting nutrient fast when it is available and store it for later use, and the "affinity-adapted" species with a low half-saturation constant for nutrient uptake (K) that is advantageous under severe nutrient limitation.

Early work on both marine and freshwater phytoplankton by Hutchinson, Eppley, Dugdale, and others indicated that different species exhibit contrasting strategies in utilizing major nutrients (Dugdale and Goering 1967; Hutchinson 1967; Eppley *et al*. 1969). Eppley *et al*. (1969) noted that species with high maximum growth rates tend to have low half-saturation constants (K) for uptake of nitrate and that oceanic species have lower K than coastal species. Dugdale (1967) hypothesized a positive association between the maximum nutrient uptake rate *Vmax* and half-saturation constant for uptake *K* and that species from oligotrophic environments would exhibit low values of both parameters and, conversely, species from eutrophic environments would have high values of both parameters. Dugdale's early ideas were fully supported by later studies.

Litchman *et al*. (2006, submitted) have recently compiled a database of key parameters of nutrient (nitrate, ammonium, and phosphate) uptake and growth for major groups of marine eukaryotic phytoplankton, diatoms, dinoflagellates, coccolithophores, and chlorophytes. Our data compilation revealed that major phytoplankton functional groups appear to differ in their parameters of nutrient uptake and growth.

A. Diatoms

Diatoms tend to have significantly higher maximum uptake rates of nutrients than any other group (Litchman *et al*. 2006). This, together with their relatively high maximum growth rates, makes diatoms good nutrient competitors in general (Figure 3) and the "velocity" specialists that are able to effectively utilize nutrient pulses. Large diatoms tend to have lower growth rates, as there is a negative correlation between the maximum growth rate and cell size (Banse 1976; Chisholm, 1992) but high maximum nutrient uptake rates, which would make large diatoms more "storage-adapted" (Sommer 1984). Coincidentally, large diatoms have disproportionately large vacuoles compared to smaller diatoms (Sicko-Goad *et al*. 1984) and because nitrate can be stored in vacuoles (Raven 1987), large diatom size leads to a "storage-adapted" strategy.

FIGURE 3. Competitive abilities (R^*s) of major taxonomic groups of marine phytoplankton for nitrate and phosphate, calculated according to Equation 3, using data from Litchman *et al*. (2006) and assuming mortality (m) of 0.1 day^{-1}. The lower R^* values indicate good competitive abilities at equilibrium.
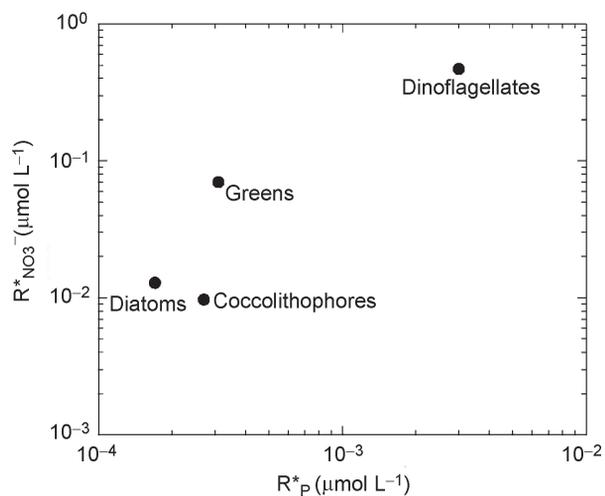
B. Coccolithophores

Coccolithophores also appear to be good nitrate, phosphorus, and iron competitors (see Figure 3), given their parameters for uptake of and growth on these nutrients (Sunda and Huntsman 1995; Riegman *et al.* 2000; Maldonado *et al.* 2001). In contrast to diatoms, they do not have particularly high maximum uptake rates but tend to have significantly lower half-saturation constants for nitrate uptake compared to other functional groups (Litchman *et al.* 2006, submitted) and are, thus, the affinity-adapted strategists. We should note, however, that this analysis is based on a single species of coccolithophorids, *Emiliania huxleyi,* as there are insufficient data on relevant parameters for other coccolithophores. Although *E. huxleyi* is not necessarily a typical coccolithophore (see de Vargas *et al.*, Chapter 12, this volume), it is an ecologically important species widely distributed in the world ocean (Iglesias-Rodriguez *et al.* 2002a, b).

The distribution patterns of diatoms and coccolithophores correspond broadly to their strategies of nutrient utilization. Contrasting nutrient regimes are also associated with distinct patterns of the physical structure of the water column and irradiance regimes: low nutrient conditions arise under stratified conditions characterized by high water-column stability and high irradiance, whereas high nutrient concentrations are often associated with deep mixing, low average irradiance, and large amplitude fluctuations in irradiance. Both groups appear to be adapted to the whole suite of physicochemical conditions that are associated with contrasting nutrient regimes. Coccolithophores are well adapted not only to oligotrophic conditions but to high irradiance that is often associated with stratified, low nutrient conditions: they tend to have higher half-saturation constants of light-dependent growth and are resistant to photoinhibition (Nanninga and Tyrrell 1996). In contrast, diatoms have low half-saturation constants for irradiance-dependent growth

(Falkowski 1980; Richardson *et al.* 1983, Geider and Osborne 1989) and are, therefore, adapted to low light characteristic of the high mixing conditions. Thus, phytoplankton nutrient utilization strategies in conjunction with their responses to physical environment, such as turbulence and light, to a large extent define ecological niches of the two groups. Diatom relative abundance is positively correlated with nitrogen (and phosphorus) concentrations (Schiebel *et al.* 2004) and negatively correlated with stability of the water column (Li 2002). In contrast, the coccolithophorid abundance is greater at low nitrate and phosphate and high water-column stability and irradiance (Cavender-Bares *et al.* 2001; Haidar and Thierstein 2001).

C. Green Algae

Green algae, including prasinophytes, can be characterized by intermediate values of nutrient uptake and growth parameters, except for ammonium and, thus, have intermediate competitive abilities (see Figure 2). Our data compilation as well as the data by Reay *et al.* (1999) indicate that chlorophytes may have a disproportionately high affinity for ammonium over nitrate. Nutrient uptake affinity (Healey 1980), which is the ratio of the maximum uptake rate (V_{max}) and the half-saturation constant for uptake (K), is an important characteristic of nutrient acquisition. A high affinity indicates a superior ability to acquire the nutrient (Healey 1980). All microalgae tend to prefer ammonium over nitrate, as nitrate is more energetically costly to assimilate due to its oxidized state (Syrett 1981). In prasinophytes, however, this preference is around 10-fold greater than in other groups (Litchman *et al.* submitted). We hypothesized that this may be related to the conditions at the time of origin of prasinophytes (Litchman *et al.* submitted). Prasinophyte algae likely appeared around 1.5 billion years ago (Ga) (Hedges 2002; Hedges *et al.* 2004; Yoon *et al.* 2004) in mid-Proterozoic when lower pO_2

(Anbar and Knoll 2002) could have caused the reduced form of nitrogen (i.e., ammonium) to be prevalent (Stumm and Morgan 1981). Interestingly, cyanobacteria, the earliest oxygenic photoautotrophs, evolved under anoxic conditions (Anbar and Knoll 2002; Hedges 2002) and also appear to have a very strong preference for ammonium over nitrate (Herrero *et al.* 2001).

The suboxic conditions at the time of prasinophyte origin may have led to a whole suite of adaptations in this group enabling their success under such conditions. Several studies indicate that a prasinophyte *Tasmanites* may have been the dominant phytoplankter during the ocean anoxic events (OAEs) in the Mesozoic, for example, early Toarcian OAE in the lower Jurassic (Palliani and Riding 1999; Palliani *et al*. 2002; van de Schootbrugge *et al*. 2005). Low oxygen conditions likely increased ammonium availability directly due to a reducing potential and indirectly by stimulating nitrogen fixation by cyanobacteria (Figure 4). Nitrogen fixation may occur more readily under low oxygen condition because enzyme nitrogenase is sensitive to oxygen (Pienkos *et al*. 1983) and because low oxygen conditions increase availability of iron (Stumm and Morgan 1981), which is required for nitrogenase synthesis (Berman-Frank *et al*. 2001; Kustka *et al*. 2002). Increased iron availability may have also stimulated prasinophytes directly, as they may have high iron requirements (Quigg *et al*. 2003). In addition, low oxygen conditions may have reduced the abundance of grazers and that would increase *Tasmanites* densities, as prasinophytes (at least modern species) are effectively controlled by grazers (Boyd and Harrison 1999). Increased *Tasmanites* densities may lead to accumulation of organic matter that would promote anoxic conditions thus creating a positive feedback in the ecosystem (see Figure 4).
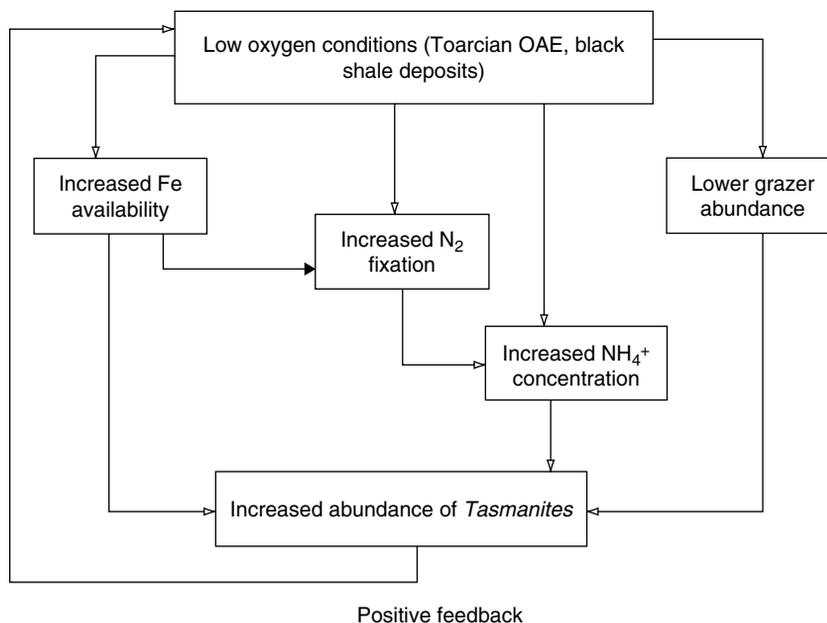

Positive feedback

FIGURE 4.   The hypothesized effects of anoxic conditions on *Tasmanites* dominance, including a possible positive feedback between *Tasmanites* dominance and anoxia. OAE, ocean anoxic event.

D. Dinoflagellates and the Role of Mixotrophy

Dinoflagellates have relatively unimpressive median values of key parameters of nutrient-dependent uptake and growth that result in poor competitive abilities for inorganic macronutrients (high R^*) (see Figure 3). For example, they have significantly higher half-saturation constants for nitrate uptake and significantly lower maximum uptake rates as well as lower maximum growth rates compared to diatoms and other functional groups of eukaryotic phytoplankton (Litchman *et al*. 2006 submitted). Dinoflagellates' ability to regulate their position in the water column by active swimming and a mixotrophic mode of nutrition likely contribute to their success in the ocean (Taylor 1987; Smayda 1997). Theoretical studies demonstrate that mixotrophy is advantageous in oligotrophic environments, whereas in more eutrophic environments an evolutionary specialization into autotrophs and heterotrophs occurs (Troost *et al*. 2005a, b). Phagotrophy in mixotrophs is more often a significant source of inorganic nutrients such as nitrogen, phosphorus, and iron rather than carbon, although at low light, prey ingestion may aid carbon acquisition as well (Raven 1997). A preliminary model study suggests that mixotrophy may also be advantageous in fluctuating environments (Litchman and Klausmeier unpublished).

These findings suggest an interesting hypothesis regarding the origin of eukaryotic phytoplankton. Plastid acquisition in eukaryotic phytoplankton occurred through primary (chlorophytes), secondary (cryptophytes, haptophytes, and stramenopiles), or tertiary (dinoflagellates) endosymbioses (Yoon *et al*. 2004), when an ingested autotroph was retained and not digested. We may hypothesize that this plastid enslavement was possible in an environment that selected for mixotrophy rather than for pure autotrophy and heterotrophy: the environment characterized by oligotrophy and/or resource fluctuations. Brasier and Lindsay (1998) made a similar suggestion on nutrient limitation potentially triggering endosymbiotic event(s). Some estimates for the occurrence of primary and secondary endosymbioses put these respective events before 1558 million years ago (Ma) and around 1200 Ma, in the late Paleoproterozoic and early Mesoproterozoic, respectively (Yoon *et al*. 2004). Interestingly, at least at the time of secondary endosymbiosis, the conditions in the ocean may have been severely nutrient (nitrogen)-limited (Anbar and Knoll 2002), which would select for a mixotrophic strategy via secondary endosymbiosis. By late Mesoproterozoic, nitrogen availability may have increased (Anbar and Knoll 2002; Yoon *et al*. 2004), and this may have stimulated autotrophic specialization and algal diversification (Figure 5).
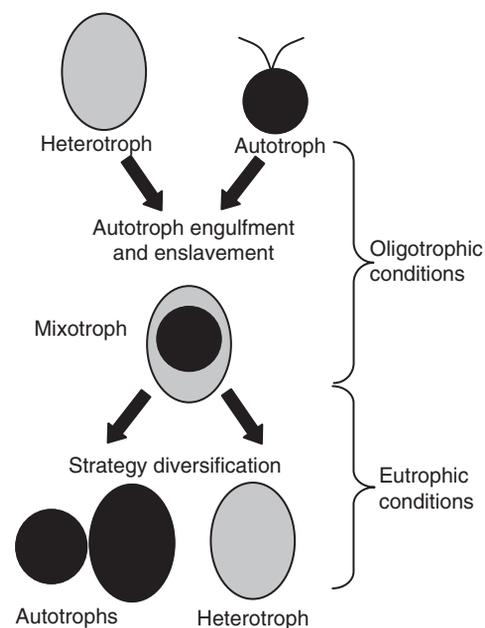

FIGURE 5. Hypothesis on the occurrence of endosymbiotic event under oligotrophic conditions that favor mixotrophy and the diversification of purely autotrophic and heterotrophic strategies under more eutrophic conditions.

E. The Role of Size

Key parameters of resource utilization and growth are correlated with cell size in phytoplankton (Eppley *et al*. 1969; Banse 1976; Shuter 1978; Smith and Kalff 1982; Finkel 2001 and Chapter 15, this volume; Litchman *et al*. submitted). Diffusion limitation of nutrient uptake increases with size (Munk and Riley 1952; Pasciak and Gavis 1974), and thus smaller cells should have a competitive advantage under nutrient-limited conditions. However, even in oligotrophic parts of the ocean where nutrient competition is severe, phytoplankton size spectra include not only extremely small-celled picoplankton but large diatoms as well (Hulburt 1967; Kilham and Kilham 1980; Gin *et al*. 1999; Venrick 1999). Why aren't large-celled species competitively displaced by small-celled species that are more effective nutrient competitors? First, a large cell size likely offsets the advantage of small-celled phytoplankton by affording an increased protection from grazing (Smetacek *et al*. 2004). Second, large size may be directly advantageous under fluctuating nutrient regimes: large-celled species, especially diatoms, have disproportionately large vacuoles that allow nutrient, nitrate in particular, to be stored until the next nutrient pulse while making it unavailable for smaller-sized species (Grover 1991c; Stolte and Riegman 1996). Third, large diatoms in oligotrophic gyres can migrate vertically: downward to reach nutrients at depths and upward to photosynthesize (Villareal *et al*. 1993, 1999), and the migration rate is positively correlated with cell size (Moore and Villareal 1996). This vertical migration can contribute significantly to new primary production in oligotrophic ocean (Villareal *et al*. 1999).

Cell size in different phytoplankton groups may evolve on long time scales due to selective pressures from changing physical environment such as sea level and the degree of turbulent mixing (Finkel *et al*. 2005 and Finkel this volume). Such long-term size changes may also significantly affect competitive abilities of phytoplankton on a geologic time scale.

F. Clonal Differences in Resource Utilization

There is an increasing body of evidence showing significant intraspecific genetic variation in phytoplankton, with different clones of the same species often having significantly different physiological parameters of growth, nutrient utilization, and, in case of toxic algae, toxin production (Medlin *et al*. 2000; Rynearson and Armbrust 2000, 2005; Carrillo *et al*. 2003). This genetic and physiological diversity within species allows adaptation to changing environments and, thus, species persistence. Genetic diversity in populations of phytoplankton is the basis for selection by biotic or abiotic selective forces and consequent rapid evolution. Grazing pressure on green alga *Chlorella vulgaris* selected for significantly more grazer-resistant cells (smaller cells) in just tens of generations (Yoshida *et al*. 2003). More grazer-resistant populations were also poorer competitors for nitrate, thus demonstrating a grazer-resistance–nutrient competitive ability trade-off (Yoshida *et al*. 2004). There is an intriguing indication that clonal diversity in phytoplankton may be maintained by algal viruses (Tarutani *et al.* 2000), and thus viruses may increase the ability of phytoplankton to adapt to changing environments.

V. FUTURE PHYTOPLANKTON COMMUNITIES

Phytoplankton clearly differ in their resource requirements, utilization strategies, and competitive abilities (e.g., Dugdale 1967; Margalef 1978; Sommer 1981, 1989; Reynolds 1984; Smayda 1997; Litchman *et al*. 2006). These differences underlie the immense diversity and both the short-term and long-term compositional changes of phytoplankton communities in nature. Predicting reorganization of phytoplankton communities under different global change scenarios is critical, as phytoplankton

significantly impact higher trophic levels and elemental cycles, yet the task remains challenging. Recent models of phytoplankton communities have started incorporating multiple functional groups such as diatoms, coccolithophores, dinoflagellates, cyanobacteria, and green algae, as well as multiple nutrients (e.g., Bissett *et al*. 1999; Moore *et al*. 2002; Gregg *et al*. 2003; Litchman *et al*. 2006). Parameterization of such parameter-rich models is usually based on just a few laboratory studies of individual species that increases the uncertainty of the predictions (Anderson 2005). A better way of parameterizing multiple functional groups of phytoplankton in such models may be to compile numerous data that would account for variation among species within taxa, physiological status, and measurement methods. Knowing physiological requirements of major groups is essential in predicting future dynamics of these groups.

In a multigroup multinutrient model of phytoplankton that was parameterized based on extensive literature compilation, Litchman *et al*. (2006) attempted to model community reorganizations under different global change scenarios such as altered mixed layer depth dynamics and changes in nitrogen, phosphorus, and iron concentrations. The predicted communities differed in total biomass and relative abundances of major functional groups, diatoms, coccolithophores, and prasinophytes. For example, an increased iron concentration is predicted to stimulate growth of diatoms and prasinophytes at the expense of coccolithophores because higher iron concentrations alleviate iron competition and diminish coccolithophores' competitive advantage (coccolithophores appear to be good iron competitors; Sunda and Huntsman 1995; Maldonado *et al*. 2001). Prolonged stratification and shallower mixing depths are predicted to result in more severe nutrient limitation and higher irradiance and would consequently increase densities of coccolithophores, as they appear to be adapted to low nutrient concentrations and high irradiances (Eppley *et al*. 1969; Nanninga and Tyrrell 1996; Litchman *et al*. 2006). However, other factors not included in the model may also be important: increased CO_2 will likely lower the pH of the ocean, and this may have a drastic effect on calcifying organisms, including coccolithophores (Orr *et al*. 2005). The rates of calcification and growth of the coccolithophore *E. huxleyi* decrease under high pCO$_2$ and may shift community dominance to noncalcifying phytoplankton (Engel *et al*. 2005).

The attempts to predict composition and dynamics of future phytoplankton communities are in their infancy and the consideration of phytoplankton resource competition along with other ecological interactions is crucial for the success of such attempts.

VI. CHALLENGES AND FUTURE DIRECTIONS

Resource competition of phytoplankton is an area of ecology that has made significant advances over the last few decades and posed as well as answered many fundamental questions of ecology, such as the problem of competitive exclusion and species coexistence formulated in the Hutchinson's paradox of the plankton (Hutchinson 1961) and the concept of R^* as a measure of resource competitive ability (Tilman 1977, 1982; Tilman *et al*. 1982). Here, I briefly outline some challenges and promising directions in the area of phytoplankton resource competition that could lead to future advances in phytoplankton ecology and perhaps ecology in general.

A. Dynamic Regulation of Resource Utilization and Competitive Ability

Models of resource competition in phytoplankton generally assume constant parameter values for each species (e.g., Grover 1991c; Huisman and Weissing 1994; Ducobu *et al*. 1998). However, numerous experimental

studies show that various parameters that determine competitive ability, such as nutrient-dependent uptake and growth parameters (e.g., see Equation 3) depend on the growth conditions and hence are not simply a number but a distribution around a mean value. For example, the maximum rate of nutrient uptake, V_{max}, can change several-fold depending on the degree of nutrient limitation or irradiance (see Harrison *et al.* 1989); minimum nutrient quota, Q_{min}, for nitrogen also depends on irradiance levels (Rhee and Gotham 1981). Often, these dependencies not included in the model do not affect the dynamics, and outcome of competition and models with constant coefficients are sufficient for predicting competitive interactions (Tilman 1977; Huisman *et al.* 1999a). There are, however, cases in which simple models seem inadequate, fluctuating conditions may bring up physiological responses that are significant enough to cause a disagreement between models and experiments (e.g., Grover 1991a, b, c, 1992; Litchman 2003). The mechanisms of dynamic regulation of resource acquisition and utilization in phytoplankton are beginning to be addressed through genomic and metabolomic approaches (Armbrust *et al.* 2004; Allen 2005; Parker and Armbrust 2005). The up- or down-regulation of nutrient uptake transporters and photosynthetic machinery occurs rapidly under varying degree of resource limitation (e.g., Hildebrand and Dahlin 2000; Song and Ward 2004; Allen *et al.* 2005; Hildebrand 2005) and may alter species' competitive ability (Klausmeier *et al.* 2007). Understanding the dynamics of acclimation of phytoplankton to changing resource fields and determining how such acclimation may influence resource competitive ability and outcome of competition poses a new challenge and would improve our ability to predict phytoplankton dynamics in general.

B. Resource Interaction

Most models of resource competition often assume no interaction among resources and describe growth rate of phytoplankton as a minimum function of all potentially limiting resources (Liebig's law of the minimum or, more precisely referred to as Blackman limitation, if rates are considered, see Cullen 1991). The parameters of growth and uptake for each resource are assumed independent of other resources in the models. In reality, the physiology of relevant processes is more complex. Phytoplankton ecologists have long known that uptake of a nutrient depends on light and other nutrients, often in a species-specific way (e.g., Wheeler *et al.* 1983; Kudela and Cochlan 2000). The uptake of nitrate is inhibited by ammonium, and such inhibition may significantly alter nitrate utilization (Syrett 1981; Dortch 1990). The uptake rate of nitrate, phosphate, and other nutrients also depends on irradiance, and, because this dependence is species-specific, variations in light regime may mediate nutrient competition (Ahn *et al.* 2002; Litchman *et al.* 2004). Do we have to take into account such relationships among resources to adequately model competitive interactions? A model that included light-ammonium-nitrate interaction was used to successfully predict nitrate dynamics in a high-nutrient low-chlorophyll (HNLC) ocean, which suggests that such models may be more powerful in cases of resource colimitation (Armstrong 1999).

C. Evolution of Competitive Ability

Along with the short-term flexibility and plasticity of phytoplankton's ability to acquire and compete for resources, phytoplankton competitive ability likely evolves in response to changes in the environment, due to both biotic and abiotic selective forces. Because of their large population numbers, short generation times and clonal reproduction, phytoplankton can evolve on relatively fast time scales (Lynch *et al.* 1991; Yoshida *et al.* 2003, 2004). Mutants or clones with better competitive ability due to variation in ecophysiological parameters will be selected under given environmental conditions.

However, because of the trade-offs among various parameters as well as among competitive abilities for different resources and other fitness components such as grazer resistance, the evolution is likely to be constrained so that the emergence of a superspecies is improbable. Rapid evolution in competitive ability can alter the dynamics and outcome of resource competition and food web interactions (Yoshida *et al*. 2003, 2004). Very little is known of how fast competitive ability can evolve, and whether the rate of evolutionary change in competitive ability differs among taxonomic groups or for different resources. Laboratory experiments with green alga *Chlamydomonas* growing under elevated CO_2 showed lack of evolutionary adaptation to increased CO_2 over 1000 generations (Collins and Bell 2004), whereas over comparable number of generations in *Chlorella* zooplankton grazing pressure led to a selection of significantly more grazer-resistant clones with poor nutrient competitive ability (Yoshida *et al*. 2004). The experimental investigation of evolution of competitive ability in phytoplankton is a promising venue of research, especially as environmental conditions change rapidly due to anthropogenic perturbations.

Existing models of resource competition in phytoplankton do not take into account possible evolution of competitive ability and the appearance of new phenotypes and, therefore, may not be capable of realistically describing the dynamics of competitive communities. A promising approach to modeling evolution in an ecological context that accounts for complex species interactions is the adaptive dynamics approach, where fitness is a function of frequencies of interacting genotypes (Geritz *et al*. 1998; Waxman and Gavrilets 2005). This approach extends the methods of evolutionary game theory and can be used to investigate what new competitive strategies and evolutionary lineages may emerge under different environmental conditions (Doebeli and Dieckmann 2005; Kisdi and Gyllenberg 2005; Waxman and Gavrilets 2005).

D. Phylogenetic Relationships

Experimental data indicate that phytoplankton from major taxonomic groups differ in their competitive abilities for various resources (nutrients and light). Differences in competitive abilities and strategies among taxonomic groups may, in part, be explained by the environmental conditions at the time of their origin (Falkowski *et al*. 2004; Katz *et al*. 2004; Tozzi *et al*. 2004; Litchman *et al*. submitted). At the same time, molecular and physiological data indicate that within major taxa, species from marine versus freshwater environments differ in their strategies of nutrient utilization (Song and Ward 2004; Litchman *et al*. submitted). For example, nitrogen reductase transcription in marine green algae is regulated differently compared to freshwater green algae, which may be due to differences in the degree of limitation by nitrate in marine versus freshwater systems (Song and Ward 2004). Even genetically close clones inhabiting different depths may differ in their nutrient or light physiologies and competitive abilities (Moore *et al*. 1998; Rocap *et al*. 2003; Stomp *et al*. 2004). Understanding the influence of phylogenetic relationships versus ecological factors on phytoplankton competitive abilities poses exciting new challenges that require a synergism of genetic, physiological, and ecological approaches.

E. Concluding Remarks

Resource competition is a fundamental ecological process that structures phytoplankton communities. Significant theoretical and experimental advances have been made in the field of phytoplankton resource competition in the past several decades. However, we are just beginning to understand how differences in competitive strategies among major functional groups, as well as individual species, contribute to phytoplankton diversity and community shifts in nature. Diverse aspects of resource competition, such as mechanistic trade-offs in competitive abilities, as well as their flexibility and evolution, and competition under variable

conditions needs to be considered if we are to understand and/or predict the structure and function of the past, present, and future of phytoplankton communities.

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