Review in Advance first posted online
on September 10, 2008. (Minor changes may
still occur before final publication
online and in print.)

Trait-Based Community Ecology of Phytoplankton

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Key Words

marine, freshwater, resources, trade-offs, functional groups

Abstract

Trait-based approaches are increasingly used in ecology. Phytoplankton communities, with a rich history as model systems in community ecology, are ideally suited for applying and further developing these concepts. Here we summarize the essential components of trait-based approaches and review their historical and potential application to illuminating phytoplankton community ecology. Major ecological axes relevant to phytoplankton include light and nutrient acquisition and use, natural enemy interactions, morphological variation, temperature sensitivity, and modes of reproduction. Trade-offs between these traits play key roles in determining community structure. Freshwater and marine environments may select for a different suite of traits owing to their different physical and chemical properties. We describe mathematical techniques for integrating traits into measures of growth and fitness and predicting how community structure varies along environmental gradients. Finally, we outline challenges and future directions for the application of trait-based approaches to phytoplankton ecology.

1. INTRODUCTION

Phytoplankton are an extremely diverse, polyphyletic group of microscopic photosynthetic protists (algae) and cyanobacteria. The first phytoplankton (marine cyanobacteria) probably appeared almost 3 billion years ago (Hedges et al. 2001). Since then, phytoplankton oxygenated Earth's atmosphere, have undergone dramatic diversification (including founding the lineage of terrestrial plants) and numerous extinction events, and conquered the freshwater realm. Today they account for approximately half of Earth's primary productivity (Falkowski et al. 2004, Field et al. 1998, Katz et al. 2004). Phytoplankton community composition profoundly affects the biogeochemical cycling of many elements, such as carbon, nitrogen, and phosphorus, because major functional groups have different requirements and modes of acquisition of these elements (Falkowski et al. 2004). Many cyanobacteria are able to fix atmospheric nitrogen and increase nitrogen availability in the water column (Capone et al. 1997, Herrero & Flores 2008, Howarth et al. 1988). Diatoms have a greater efficiency of carbon sequestration into the deep ocean, because their heavy silica frustules make them sink faster than other groups of phytoplankton (Smetacek 1999), with a direct effect on global climate (Falkowski et al. 1998). Phytoplankton groups also differ in their edibility and nutritional value for higher trophic levels (Sterner & Elser 2002). Finally, many phytoplankton species can produce toxins that negatively affect water quality and higher trophic levels (Anderson et al. 1998, Huisman et al. 2005).

Because phytoplankton community composition impacts the functioning of aquatic ecosystems and global climate, it is important to understand what factors govern phytoplankton community assembly and dynamics. Human-induced global change will likely rapidly alter phytoplankton community structure (Huisman et al. 2005, Le Quéré et al. 2005, Litchman et al. 2006) and, therefore, the need to understand phytoplankton community reorganizations in the changing climate becomes even more pressing.

Beyond these practical concerns, many fundamental questions in ecology have been formulated and answered using phytoplankton as a model system. Hutchinson's (1961) "paradox of the plankton" asked why many species of phytoplankton could coexist on just a few resources, contrary to the competitive exclusion principle. Phytoplankton were one of the first applications of resource competition theory (Tilman 1977, 1982; Tilman et al. 1982). Fundamental principles of food web interactions such as predator-prey or keystone predator have also been frequently addressed in phytoplankton (Leibold 1996). Major advances in ecological stoichiometry were made using a freshwater phytoplankton-zooplankton system (Sterner & Elser 2002). Phytoplankton are an excellent model system to address such fundamental ecological questions because of their small size, short generation times, large population numbers, and ease of manipulation in controlled laboratory conditions.

2. TRAIT-BASED APPROACHES TO PHYTOPLANKTON COMMUNITIES

There has been a recent interest in trait-based approaches in ecology, particularly in plant ecology (Lavorel & Garnier 2002, McGill et al. 2006, Westoby & Wright 2006), because these approaches hold the potential of increasing our ability to explain the organization of ecological communities and predict their reorganizations under global change. The major components of trait-based approaches are traits, environmental gradients, species interactions, and performance currencies (McGill et al. 2006). Despite recent advances in trait-based approaches, significant hurdles exist in realizing their full potential, at least partly because in many systems it is difficult to determine what traits define the ecological niches of organisms and to measure those traits. We argue that
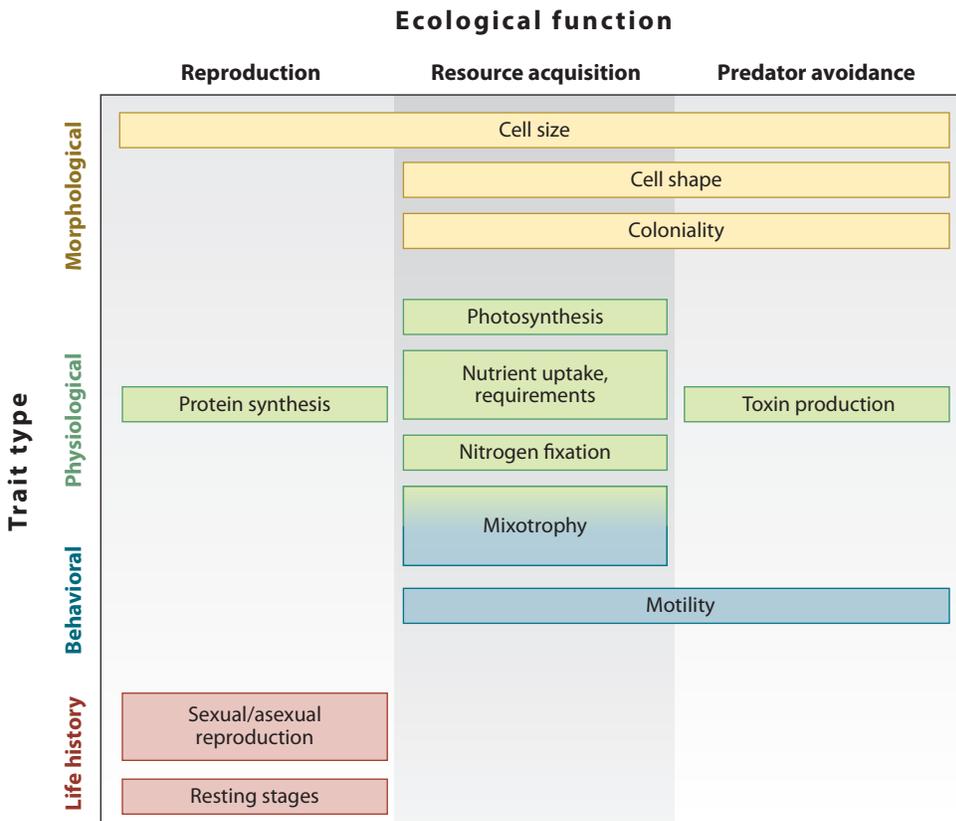
Ecological function

Figure 1

A typology of phytoplankton functional traits.

phytoplankton provide an ideal system to test trait-based approaches because of their relative simplicity and the well-defined traits that determine their ecological niche (**Figure 1**).

Using traits to predict community composition along environmental gradients is not novel in phytoplankton ecology. Spanish ecologist and oceanographer Ramon Margalef (1978) pioneered such approaches by using the responses of different taxonomic/functional groups of phytoplankton to nutrients and turbulence to predict their occurrence along these environmental gradients. These ideas are summarized in his elegant "mandala," where different groups occupy different quadrants of the nutrient-turbulence space. British phytoplankton ecologist Colin Reynolds (Reynolds 1984a,b, 2006; Reynolds et al. 2002) developed a detailed classification of different functional groups of phytoplankton based on their morphological and physiological traits, similar to the Grime's (1977) CSR (competitors, stress tolerators, and ruderals) scheme for terrestrial plants.

The goal of this review is to continue to lay the foundation of a trait-based approach to phytoplankton community ecology. First we review the most ecologically relevant traits to phytoplankton, then discuss trade-offs between them. We then look at statistical and mathematical methods to use traits to predict community structure. Finally, we suggest areas for future development. Other reviews relevant to these themes cover general background on phytoplankton ecology (Falkowski & Raven 2007, Litchman 2007, Reynolds 2006, Sandgren 1988, Sommer 1989, Tilman

et al. 1982), trait-based approaches to ecology (Westoby & Wright 2006; Westoby et al. 2002), resource competition (Grover 1997), and game theory (McGill & Brown 2007).

3. MAJOR ECOLOGICAL AXES AND ASSOCIATED TRAITS

The major ecological axes that define ecological niches of phytoplankton are physical environment, resources, and natural enemies (grazers and parasites) (Margalef 1978; Reynolds 1984b, 1994, 2006; Tilman et al. 1982). For each of these axes a whole hierarchy of traits exists, from the subcellular to population level, that allow phytoplankton to survive and reproduce in the environment. It is beyond the scope of this review to discuss all these traits. Instead, we will focus on those functional traits that significantly affect fitness (Violle et al. 2007) and are frequently measured and used to define major functional groups in phytoplankton (Le Quéré et al. 2005, Litchman et al. 2006).

3.1. Light

Light is an essential resource for phytoplankton, and is heterogeneous in space and time. In aquatic environments, light is strongly attenuated by the medium, dissolved substances, and suspended particles, including phytoplankton, resulting in a pronounced vertical gradient in intensity and spectral distribution (Kirk 1994). Phytoplankton possess a multitude of traits that allow efficient capture and utilization of vastly different intensities and diverse spectral domains of light. All phytoplankton are photoautotrophic and, thus, traits that characterize photosynthetic performance are among the key resource acquisition traits (Richardson et al. 1983).

Many models of light-dependent photosynthesis and growth incorporate a range of physiological detail (reviewed in Zonneveld 1998). Static models simply relate photosynthesis or growth to irradiance. Dynamic models capture the dynamics of photoadaptation and photoinhibition, making them more appropriate for fluctuating light regimes. Under constant light, dynamic models reduce to static ones, but with parameters that correspond to more fundamental processes (Zonneveld 1997).

There are two common relationships between photosynthesis and irradiance (P-I curves). In the first, photosynthesis increases linearly with irradiance at low levels with slope α but saturates at high irradiance at a maximum rate of photosynthesis, P_{max} (**Figure 2a**). Cellular chlorophyll concentration is a key trait that contributes to both α and P_{max}. In the second, there is an optimal irradiance, I_{opt}, where P_{max} is reached, photosynthesis is inhibited beyond I_{opt} (Falkowski & Raven 2007, Kirk 1994) (**Figure 2b**). These parameters, α, P_{max}, I_{opt}, and cellular chlorophyll content, can be considered light-acquisition traits. The simplest treatment of growth-irradiance (μ-I) curves assumes a constant C:cell ratio and therefore mirrors P-I curves; more complex models include a variable C:cell ratio (Zonneveld 1997).

These traits are inherently plastic: Depending on the environment and acclimation history, they can assume vastly different values in the same species or genetic strain. In low-light environments, phytoplankton often exhibit high slopes of the P-I and μ-I curves but greater sensitivity to photoinhibition (Falkowski 1980). Nutrient limitation often decreases the efficiency of photosynthesis and light-dependent growth and increases sensitivity to photoinhibition (Litchman et al. 2002, 2003; Young & Beardall 2005). Cellular chlorophyll concentration is greater at low irradiances, which maximizes photon capture, and decreases with increasing light (Falkowski 1980).

Despite this trait plasticity, major taxonomic groups differ in the mean values and ranges of these light utilization traits. Diatoms, dinoflagellates, and cyanobacteria have greater α's than other groups, allowing for more efficient utilization of low light; green algae, in contrast, have lower
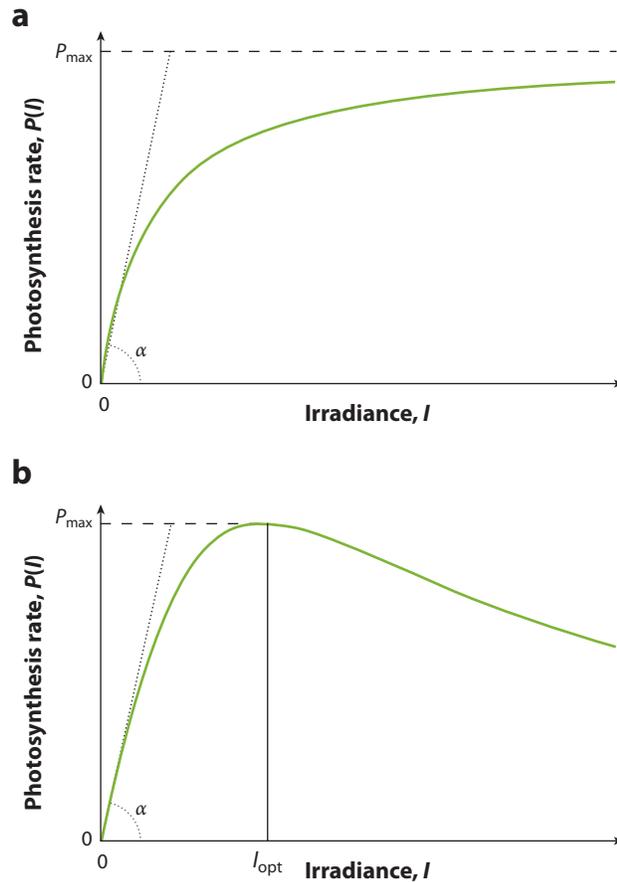
Figure 2

Typical shapes of photosynthesis-irradiance curves and their defining parameters: (*a*) saturating and (*b*) with photoinhibition. P_{max}, maximum rate of photosynthesis; I_{opt}, optimal irradiance; α, slope.

α's and saturate growth at higher irradiances, but tend to be less susceptible to photoinhibition (Richardson et al. 1983; A. Schwaderer, K. Yoshiyama & E. Litchman, unpublished data). The degree of plasticity in cellular chlorophyll under different light or nutrient conditions may also vary across taxonomic groups (Falkowski 1980, Geider et al. 1998, Richardson et al. 1983). Consequently, these functional groups are often associated with contrasting light environments. Diatoms and cyanobacteria frequently dominate under low-light conditions that result from either deep mixing (diatoms) or high light attenuation coefficients due to high algal biomass (cyanobacteria) (Reynolds 1984b).

Another trait that allows motile phytoplankton species to optimize light capture is their behavioral response to light: swimming/floating toward the light if light-limited, or away if light-inhibited (Clegg et al. 2003, Kamykowski et al. 1998, Klemer et al. 1982, Wallace & Hamilton 1999). Because light is a resource, the growth of a species reduces light availability for the given species and its competitors. An important trait that characterizes light utilization is the specific light attenuation coefficient, which determines how much light is attenuated per unit biomass (Huisman & Weissing 1994, Kirk 1994). Different species and groups of phytoplankton vary not only in the absolute values of this trait, but also in its plasticity (Agawin et al. 2007). It is

competitively advantageous to have a high specific light attenuation coefficient to consume a greater fraction of light, at the added expense of light-absorbing pigments.

3.1.1. Light spectrum. Phytoplankton possess a diverse set of pigments to capture different parts of the spectrum within the visible range. The main photosynthetic pigment is chlorophyll, which comes in different configurations (chlorophyll *a*, *b*, *c*, and *d*; Falkowski & Raven 2007). Several accessory pigments (phycobilins and carotenoids) increase the range of the usable spectral range, absorbing light in the wavelengths complementary to chlorophyll absorbance (Falkowski & Raven 2007, Kirk 1994). Pigment composition differs in major groups of phytoplankton and reflects their evolutionary origin (Falkowski & Raven 2007), as different groups arose as a result of primary, secondary, or even tertiary endosymbiotic events (Hackett et al. 2007). Moreover, even closely related species may differ not only in their light intensity requirements, but also in their pigment composition and, consequently, their ability to utilize different parts of the visible spectrum (Rocap et al. 2003, Stomp et al. 2004, Ting et al. 2002). In the case of closely related species, differences in light requirements and spectral utilization patterns are likely a result of adaptive diversification by differential retention of ancestral pigment genes or new gene acquisition through duplication or lateral transfer (Rocap et al. 2003). Some phytoplankton species can regulate what parts of the spectrum they utilize by adjusting their pigment composition, depending on the availability of different wavelengths of light (Stomp et al. 2004, Ting et al. 2002). Pigment composition is an important trait that separates ecological niches of different species and functional groups along the spectral gradient often associated with depth and/or different water color (Kirk 1994; Stomp et al. 2004, 2007). Differences in spectral use of light can provide opportunities for species coexistence (Stomp et al. 2004, 2007).

3.2. Nutrients

Macro- and micronutrients such as nitrogen, phosphorus, iron, molybdenum, zinc, and others are essential resources for phytoplankton. Diatoms and silicoflagellates also require silica. Several physiological traits characterize nutrient uptake and utilization and their values directly affect the performance of species. The dependence of growth rate on a given nutrient is often described as a function of the internal nutrient concentration and uptake is described as a function of the external nutrient concentration (Droop 1973, Grover 1991b):

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

$$\text{uptake} = v(R) = v_{\max} \frac{R}{K + R}, \qquad\qquad 1.$$

where μ_∞ is the growth rate of species at an infinite quota (d^{-1}), Q is the internal nutrient concentration (nutrient quota) (μmol nutrient cell^{-1}), $Q_{\min}$ is the minimum quota (when growth rate equals 0), $v_{\max}$ is the maximum nutrient uptake rate (μmol nutrient cell^{-1} d^{-1}), K is the half-saturation constant for nutrient uptake (μmol nutrient L^{-1}), and R is the external nutrient concentration (μmol nutrient L^{-1}) (**Figure 3**).

These traits (μ_∞, $Q_{\min}$, $v_{\max}$, and K) are frequently measured in diverse species of phytoplankton and, despite considerable intraspecific plasticity in response to nutrient and light conditions (Harrison et al. 1989, Litchman et al. 2004, Morel 1987, Rhee & Gotham 1981a), differ significantly across species and major taxonomic groups (Litchman et al. 2007, Shuter 1978, Smayda 1997). Sommer (1984) proposed three major strategies of nutrient acquisition in phytoplankton: velocity-adapted species with high maximum nutrient uptake rates ($v_{\max}$) and high maximum
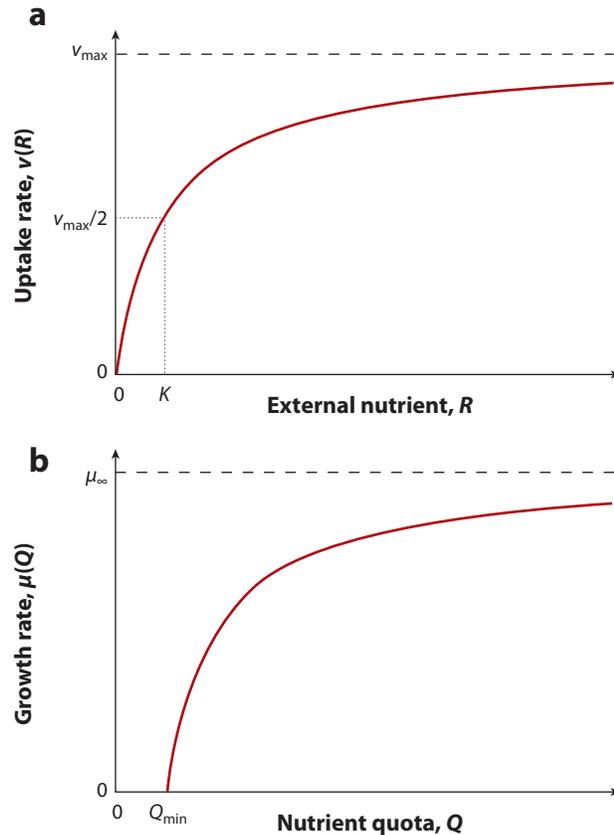
Figure 3

Functions that describe nutrient uptake and use: (*a*) Michaelis-Menten uptake and (*b*) Droop's growth function. v_{max}, maximum nutrient uptake rate; K, half-saturation constant for nutrient uptake; μ_∞, growth rate of species at an infinite quota; Q_{min}, minimum quota.

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}, and affinity-adapted species with low half-saturation constants for nutrient uptake (K) that are advantageous under nutrient limitation. The ratio of v_{max} to K, called nutrient uptake affinity, is frequently used to characterize nutrient uptake abilities (Healey 1980) and is analogous to α from *P-I* curves. Another trait that can be important, especially in fluctuating nutrient environments, is the maximum cellular nutrient concentration Q_{max}, which characterizes a storage capacity (Grover 1991b). Under a relatively low frequency of the limiting nutrient supply, large storage capacity may increase species' competitive ability, whereas under high-frequency fluctuations other traits such as the asymptotic maximum growth rate μ_∞, maximum nutrient uptake rate v_{max}, and/or half-saturation constant for uptake K have a greater influence on realized growth rates and competitive abilities (Grover 1991b, Stolte & Riegman 1996).

Traits that characterize various aspects of nutrient acquisition and utilization (μ_∞, Q_{min}, v_{max}, and K) are often correlated (Grover 1991b, Litchman et al. 2007). These correlations may manifest trade-offs that arise from first principles, such as surface to volume ratio relations and enzyme kinetics: For example, v_{max} in diverse groups of marine phytoplankton is positively correlated with K, as predicted theoretically (Aksnes & Egge 1991, Litchman et al. 2007). Interestingly, different

functional/taxonomic groups appear to cluster along the physiological trade-off curves by having high v_{max} and K values (dinoflagellates and diatoms) or low v_{max} and K values (coccolithophores), thus adopting contrasting strategies of nutrient utilization (Litchman et al. 2007, Sommer 1984).

Some phytoplankton have adapted to extreme nutrient limitation by replacing the limiting nutrient with other elements in their biomolecules: Picocyanobacterium *Prochlorococcus* in the oligotrophic ocean uses sulfur instead of phosphorus in membrane lipids (Van Mooy et al. 2006). Such replacements may confer a competitive advantage over other phytoplankton under nutrient-limited conditions.

3.2.1. Nitrogen fixation. Nitrogen fixation is a key trait that enables acquisition of atmospheric nitrogen. Among phytoplankton, only cyanobacteria possess this ability (Herrero & Flores 2008). Consequently, this trait separates them from all other taxonomic divisions and makes N-fixers one of the major functional groups (Le Quéré et al. 2005). However, not all cyanobacteria are N-fixers. Among N-fixers, unicellular and filamentous forms exist. The filamentous forms may possess specialized cells, heterocysts, where N-fixation takes place, which separates N-fixation and photosynthesis and leads to higher rates of N-fixation, because the key N-fixation enzyme nitrogenase is sensitive to oxygen (Berman-Frank et al. 2007). However, heterocystous N-fixers occur primarily in freshwater and estuarine habitats and are absent in the open ocean, possibly because of their higher iron and phosphorus requirements compared with nonheterocystous N-fixers (Berman-Frank et al. 2007). Other groups of phytoplankton, e.g., oceanic diatoms, may harbor symbiotic cyanobacteria and thus have access to atmospheric nitrogen (Carpenter & Janson 2000, Carpenter et al. 1999).

3.2.2. Mixotrophy. An important trait that aids in nutrient and sometimes carbon acquisition in some phytoplankton is the ability to feed heterotrophically by engulfing prey cells (Raven 1997). Mixotrophy (presence of heterotrophic and autotrophic modes of nutrition) as a generalist strategy is advantageous under low nutrient conditions, whereas under more eutrophic conditions being a specialist may be a better strategy (Troost et al. 2005a,b). Many groups of phytoplankton exhibit mixotrophy; usually those groups are poor competitors for inorganic nutrients, such as dinoflagellates and cryptophytes (Laybourn-Parry et al. 2005, Litchman et al. 2007, Smayda 1997).

3.3. Grazers and Parasites

Although phytoplankton compete for resources, they also face strong selective pressures from the top down. After all, what good are nutrients after you've been eaten? A simple model that includes many salient aspects of the phytoplankton-grazer interaction is

$$\begin{bmatrix} \text{per } Z_j \text{ grazing rate on} \\ \text{phytoplankton } i \\ \text{by zooplankton } j \end{bmatrix} = f_{ij}(P_i) = \frac{c_{ij}P_i}{1 + \sum b_{ij}c_{ij}P_i}$$

$$\begin{bmatrix} \text{per } Z_j \text{ growth of} \\ \text{zooplankton } j \end{bmatrix} = g_j(P_1, P_2, \ldots, P_n) = \min\left(\sum e_{ij}f_{ij}(P_i) - r_j, \frac{\sum e_{ij}f_{ij}(P_i)Q_i}{q_j}\right).$$

2.

This model combines a multispecies type-II functional response with the possibility of nutrient limitation of grazer growth (Hall 2004, Sterner 1997). Here P_i denotes phytoplankton species i and Z_j denotes zooplankton species j. c_{ij} is the encounter rate, b_{ij} is the handling time, e_{ij} is the edibility of phytoplankton i for zooplankton j, Q_i is the nutrient quota of phytoplankton i, q_j is the nutrient quota of zooplankton j, and r_j is the C respiration rate of zooplankton j.

This model illustrates four traits of phytoplankton that affect their interaction with grazers. Phytoplankton can be hard to catch (low c_{ij}), time-consuming to process (high h_{ij}), inedible (low e_{ij}), or nutritionally inadequate (low Q_i). Anti-grazer adaptations include overall size, morphology, extracellular mucilage, and high C:nutrient ratios (Reynolds 2006, Sterner 1989). Some of these adaptations are constitutive, whereas others are inducible (Van Donk & Hessen 1993). Furthermore, many algal species from diverse taxa are capable of producing toxins that are harmful to other organisms such as grazers (Anderson et al. 1998, Huisman et al. 2005).

A complication that arises is that the traits described above are specific to particular pairs of phytoplankton and grazers. This phenomenon leads to an explosion in the number of traits that need to be considered, which nullifies one of the key advantages of the trait-based approach (McGill et al. 2006). We need to replace these interaction-specific terms with a more general formulation. The most obvious ingredients are the sizes of the phytoplankton and of the grazer. Larger grazers can successfully consume larger phytoplankton better than smaller grazers can (Reynolds 2006, Sterner 1989). A function that describes grazing parameters as a function of size differences was suggested by Armstrong (1999) and could be used as a basis for a more general formulation, with additional terms added for general inedibility of phytoplankton and general efficiency of grazers.

Phytoplankton are also susceptible to various parasites and pathogens such as fungi, protozoa, bacteria, and viruses (Reynolds 2006, Van Donk 1989). However much less is known about these interactions; in particular, little is known about the phytoplankton traits that lead to susceptibility or resistance to these pathogens. As with phytoplankton-grazer interactions, one challenge is to reduce the complexity of these interactions (Dieckmann et al. 2002) to a more tractable, general form.

3.4. Morphology

Life in water constrains the whole array of morphological traits in phytoplankton (Vogel 1996). Phytoplankton need to overcome significant diffusion limitation on resources (Pasciak & Gavis 1974, Raven 1980) and to maintain themselves in the water column to have access to light, despite sinking. Therefore, strong selection exists for traits that enable efficient access to resources in a liquid medium.

Cell size is a key trait that impacts growth, metabolism, and access to resources, and in phytoplankton ranges from less than one micron in picocyanobacteria up to several millimeters in oceanic diatoms (Chisholm 1992, Malone 1980, Yoshiyama & Klausmeier 2008). Small cells have several advantages over larger cells: a lower sinking rate, which is proportional to the cell radius squared (Stokes law) (Smayda 1970), and more efficient acquisition of limiting nutrients due to a higher surface to volume ratio and smaller diffusion boundary layer (DBL) that limits nutrient transport, because DBL is proportional to cell radius, at least for spherical cells (Ploug et al. 1999, Sherwood et al. 1975). Small cells also tend to have higher maximum growth rates (Banse 1976) but are more susceptible to grazing (Thingstad et al. 2005). Many other ecophysiological traits, such as nutrient and light utilization and grazer resistance, are significantly correlated with cell size (Banse 1976, Finkel 2001, Litchman et al. 2007, Shuter 1978, Sterner 1989), so cell size is a master trait that shapes ecological niches of phytoplankton.

Other related morphological traits that affect nutrient acquisition, sinking, and grazer susceptibility are cell shape and coloniality (Grover 1989, Ploug et al. 1999, Smayda 1970, Thingstad et al. 2005). Size, shape, and coloniality are extremely plastic traits that depend on many environmental variables, such as light levels, nutrient concentrations, and grazing pressure. (Chisholm 1992, Geider et al. 1986, Litchman et al. 2003). The degree of plasticity differs among taxa and

plays an important role in community composition. Duarte et al. (1990) showed that more plastic genera with respect to cell size and coloniality tend to be more ubiquitous than less plastic genera and occur in a variety of environments.

3.5. Temperature-Related Traits

Temperature is a major environmental axis that governs, to some extent, the distribution of all organisms on Earth. Photosynthesis, respiration, growth, resource acquisition, motility, and sinking all depend on temperature (Eppley 1972, Raven & Geider 1988). This dependence can be characterized by the temperature optimum and Q_{10} value for each process (Eppley 1972, Raven & Geider 1988, Smayda 1970). Temperature optima may not be the same for different processes, even within the same species (Raven & Geider 1988, Rhee & Gotham 1981b). Because major groups of phytoplankton, as well as individual species, have different temperature optima (Eppley 1972, Reynolds 1984b), temperature plays an important role in phytoplankton seasonal succession in both marine and freshwater habitats (Karentz & Smayda 1984, Sommer et al. 1986). Freshwater cyanobacteria have higher temperature optima for growth than other taxonomic groups and tend to dominate in the late summer when water temperatures are higher (Reynolds 1984b, Sommer et al. 1986). However, other factors, such as grazer resistance, contribute to their higher occurrence later in the season (Sterner 1989). Higher temperature optima of cyanobacteria, including toxin-producing species, may lead to the proliferation of harmful algal blooms in the future due to global warming (Huisman et al. 2005). Temperature dependence will be increasingly important under a changing climate (Follows et al. 2007, Strecker et al. 2004).

3.6. Reproductive Traits

3.6.1. Sexual and asexual reproduction. Phytoplankton can reproduce both sexually and asexually (Sandgren 1988). Some taxonomic groups (e.g., diatoms, dinoflagellates, and green algae) are capable of both reproductive modes, depending on environmental conditions (Hiltz et al. 2000, Kremp & Heiskanen 1999), whereas others (e.g., cyanobacteria and most cryptophytes) can only reproduce asexually (Sandgren 1988). Sexual reproduction, as in other organisms, increases genetic variation and thus can be advantageous for species survival under changing selective pressures (Lynch et al. 1991). In diatoms, sexual reproduction is also a means to restore cell size, because asexual reproduction leads to miniaturization (Amato et al. 2005, Mann 1993).

3.6.2. Resting stages. The ability to produce resting stages is widespread in phytoplankton (Sandgren 1988). This trait can confer a competitive advantage in an environment with prolonged periods of unfavorable conditions (resulting in slow growth and/or high mortality) (Lewis et al. 1999, Nehring 1996). The simultaneous emergence of vegetative cells of a given species from resting spores, triggered by temperature or another environmental cue, may have a dramatic and abrupt impact on community composition (McQuoid & Godhe 2004). Many harmful algal blooms (HABs) start with a synchronized germination of resting spores (Anderson & Rengefors 2006, Brunberg & Blomqvist 2003). Global warming may lead to a mismatch between germination of resting stages of different species of phytoplankton and zooplankton, reorganizing communities and disrupting trophic interactions (Edwards & Richardson 2004).

4. KEY TRADE-OFFS AMONG TRAITS

Most traits in organisms are not independent but are instead interrelated. Correlations between and among traits often represent trade-offs and complicate assessment of the selective pressures

on traits. Correlations among traits can also lead to a reduced number of potential strategies characterized by different trait values, where certain combinations of trait values become impossible (Litchman et al. 2007). A trade-off arises when a trait that is advantageous for one function confers a disadvantage for others. Here we outline three categories of trade-offs thought to be important determinants of community structure.

4.1. Maximum Growth Rate-Competitive Ability Trade-Off

The trade-off between maximum growth rate and competitive ability is well known as the *r-K* strategy dichotomy (Kilham & Kilham 1980, MacArthur & Wilson 1967, Sommer 1981) or gleaner-opportunist trade-off (Grover 1997). A high maximum growth rate can be advantageous under fluctuating resource supplies and can lead to either the competitive displacement of slow-growing good competitors or stable coexistence (Grover 1991a,b; Litchman & Klausmeier 2001). Coexistence is usually possible when periods of fluctuations are sufficiently long (Litchman & Klausmeier 2001). The mechanistic basis for such a trade-off is likely the differential investment into growth machinery (P-rich ribosomes) versus resource acquisition machinery (N-rich proteins) (Klausmeier et al. 2004a, Sterner & Elser 2002). Therefore, selection for fast-growing species under high or fluctuating supply of a limiting resource may lower the N:P stoichiometry of phytoplankton (Klausmeier et al. 2004a).

Phytoplankton distributions in nature support, at least to some degree, the importance of this trade-off. In freshwater environments, certain green algae (e.g., *Chlorella* and *Chlamydomonas*), characterized by high maximum growth rates and high nutrient requirements, often dominate high nutrient lakes (Reynolds 1984b). Low nutrient lakes have high proportions of slow-growing chrysophytes with good nutrient competitive abilities (Reynolds 2006). Chemostat studies along a gradient of dilution rates also provide evidence for this trade-off (Sommer 1986). However, some species and taxonomic groups appear to not follow this trade-off: Many marine diatoms have high maximum growth rates and appear to be good competitors for inorganic nutrients such as nitrogen (Banse 1976, Litchman 2007, Litchman et al. 2007, Smayda 1997). Other trait dimensions may define relevant trade-offs in such cases: Marine diatoms, especially large-celled species, appear to be poor competitors for another essential nutrient, iron (Litchman et al. 2006, Sarthou et al. 2005, Timmermans et al. 2004), so a trade-off may exist between maximum growth rate and iron competitive ability.

4.2. Trade-Offs Between Competitive Abilities for Different Resources

Another major trade-off hypothesized to be important in structuring phytoplankton communities is a trade-off between competitive abilities for different resources, either different nutrients or nutrients and light (Leibold 1997, Passarge et al. 2006, Tilman et al. 1982). This trade-off can explain species shifts across supply ratio gradients and the coexistence of as many species as resources (Tilman 1982). The mechanistic basis for such a trade-off is investment constraints on the machinery for acquisition of different resources (Grover 1997, Klausmeier et al. 2004a). Classic studies found a trade-off in the competitive abilities for phosphorus versus silica in freshwater diatoms that could explain the distribution of various species along a silica-phosphorus gradient in Lake Michigan (Tilman 1977) and in laboratory chemostats (Kilham 1986). Strzepek & Harrison (2004) found a trade-off in utilization of iron and fluctuating light in marine diatoms: Open ocean diatoms growing at very low iron have low levels of iron-rich photosystem I (PS I), which lowers their iron requirements but compromises their ability to utilize fluctuating light. Thus, a trade-off exists between iron and light utilization. Coastal diatoms have a contrasting strategy: They have more than

fivefold greater content of PS I than the open ocean diatoms, allowing them to efficiently utilize light fluctuations and iron that is more abundant in coastal waters (Strzepek & Harrison 2004). A higher minimum quota for nitrogen under low irradiance found by Rhee and Gotham (1981a) can also be a manifestation of a trade-off between light and nutrient competitive abilities, because an increase in light-harvesting pigments increases nitrogen requirements. The light-nutrient competitive ability trade-off may control depth distributions and coexistence of phytoplankton, because better light competitors but poorer nutrient competitors occupy greater depths with less light but higher nutrients, and poorer light competitors but better nutrient competitors occupy shallower depths (Klausmeier & Litchman 2001). In contrast, Passarge et al. 2006 found a positive correlation between light and phosphorus competitive ability in five freshwater species.

4.3. Grazer Resistance: Competitive Ability Trade-Off

A trade-off that seems ubiquitous in phytoplankton is the one between competitive abilities and grazer resistance (Grover 1995; Leibold 1989, 1996). This trade-off can explain species replacements along nutrient gradients as well as the coexistence of two species at equilibrium (Leibold 1996), contributing to species diversity (Kneitel & Chase 2004). This trade-off can also drive seasonal succession in phytoplankton (Reynolds 1984b, Sommer et al. 1986). Grazer resistance is often achieved by increasing cell size or by colony formation, which both decrease nutrient competitive abilities due to less efficient surface area to volume ratios, thus creating a trade-off (Reynolds 1988). Indirect evidence for the grazer resistance–competitive ability trade-off comes from patterns of nutrient availability along nutrient gradients (Leibold 1997), whereas a controlled natural selection study provides direct evidence (Yoshida et al. 2004).

4.4. Evidence for Trade-Offs

Species distributions along natural and experimental gradients provide empirical support for interspecific trade-offs between traits as outlined above. However, the expected trade-offs between two traits may not always be apparent in comparative studies. Two possible issues arise. The first is the difficulty in accurately measuring traits in the lab (Sommer 1986). The second is that trade-offs should be identified ceteris paribus. Two traits with a negative partial correlation (a trade-off) may appear positively correlated if there are other traits that vary between species (Stearns 1989). For example, the species studied by Passarge et al. (2006) varied in growth rates as well as in light and nutrient affinities. Controlling for other traits, either statistically or experimentally through choice of species, may reveal a trade-off that would otherwise be obscured. Controlled natural selection experiments can also demonstrate trade-offs. The search for trade-offs should concentrate on species that co-occur to isolate the mechanisms of their coexistence.

4.5. Role of Phylogeny

Despite the potential power of trait-based approaches, taxonomic perspectives can provide complementary insights and synergy with trait-based approaches. Many phytoplankton traits, such as general shape, pigment composition, requirements for certain nutrients or vitamins, motility, and others, are conserved within broad evolutionary lineages (Alverson et al. 2006, Hackett et al. 2007, Raven & Richardson 1984). Conserved traits often determine the fundamental niche of a given lineage (Webb et al. 2002), whereas divergent traits of closely related groups may define local adaptation strategies (Rocap et al. 2003). Recent advances in molecular genetics allow the construction of much better-resolved and accurate phylogenies of diverse groups of phytoplankton

than previously possible. A simultaneous consideration of phylogenetic relationships, trait value distributions, and environmental gradients yields fascinating insights into phytoplankton community assembly and evolution. Studies of the distributions and ecophysiological traits of closely related ecotypes of the marine picocyanobacterium *Prochlorococcus* from the oligotrophic ocean showed that, despite a high degree of relatedness (less than 3% divergence of rDNA sequence), ecotypes from different depths differed markedly in their light utilization traits: Ecotypes isolated from greater depths were significantly lower-light adapted than those that dwell in the surface waters (Johnson et al. 2006, Moore et al. 1998, Rocap et al. 2003). Interestingly, *Prochlorococcus* ecotypes that occur in the shallower depths have lost the ability (genes) to utilize NO_3^- and NO_2^-, because concentrations of these forms of nitrogen are vanishingly small near the surface; they rely on NH_4^+ instead (Moore et al. 2002). In contrast, ecotypes from greater depths, where the concentrations of NO_2^- (and NO_3^-) are greater, can utilize NO_2^- as well (Moore et al. 2002).

5. MARINE-FRESHWATER COMPARISONS

Marine and freshwater environments differ in a number of fundamental ways that likely affect trait selection in phytoplankton. The density and osmolarity of seawater are higher than of freshwater (Stumm & Morgan 1981); consequently, organisms are more buoyant in seawater and do not have to cope with osmotic stress to the same degree as in freshwater (Raven 1982). A comparison of traits in related groups from marine versus freshwater environments could provide new insights on the role of environment and phylogenetic relationships on trait distributions. Differences in buoyancy may in part be responsible for the differences in size distributions between marine and freshwater diatoms: Much larger forms occur in marine but not in freshwater systems (E. Litchman, C. Klausmeier, and K. Yoshiyama, unpublished data). A general view of nutrient limitation is that marine ecosystems are more frequently nitrogen limited and freshwater ecosystems are often phosphorus limited (Elser et al. 2007, Hecky & Kilham 1988, Kilham & Hecky 1988). This difference in limitation would exert different selective pressures on nutrient utilization traits.

6. USING FUNCTIONAL TRAITS TO DETERMINE COMMUNITY STRUCTURE

6.1. Statistical Techniques

Species are characterized by a large number of quantitative and qualitative traits. Therefore, the appropriate statistical techniques come from the field of multivariate statistics (Legendre & Legendre 1998, Manly 2004). Multivariate statistics have been used to relate phytoplankton species to each other and environmental variables on the basis of their densities and growth rates (Anneville et al. 2002, Lehman et al. 2004, Mieleitner et al. 2007). However, there has been much less multivariate analysis of phytoplankton trait data, possibly because of the relatively incomplete collection of traits that have been measured on a wide range of phytoplankton species; there are many holes in our knowledge. Below we suggest a more systematic program of trait measurement (section 7.3). Meanwhile, statistical techniques to deal with missing data such as multiple imputation (Schafer 1997) might be applied. Below we outline three possible types of multivariate trait analyses that have been used in other branches of ecology that could also be applied to phytoplankton.

6.1.1. Combining species into functional groups based on traits. Here species are grouped into clusters of species with similar trait values. Plant ecologists have made use of this technique

(e.g., Lavorel et al. 1997), but to our knowledge, phytoplankton ecologists have not (see Barnett et al. 2007 for such an approach in zooplankton). Details on clustering algorithms can be found in Legendre & Legendre (1998). Depending on what traits are included in the cluster analysis, dendrograms can differ significantly, so the task is to identify the most important traits (Barnett et al. 2007, Petchey & Gaston 2006).

6.1.2. Relating traits to environmental factors. Relating traits to environmental factors is one of the main objectives of the trait-based research program (McGill et al. 2006). Perhaps the best-studied environmental factor affecting phytoplankton is trophic status of the water body. Unfortunately, although the relationships between trophic status and many aspects of phytoplankton community structure and dynamics are well known, the relationship between functional traits and trophic status remains poorly characterized (Rojo 1998). Trait-environment linkages are even less explored for other gradients.

One exception is the study of Seip & Reynolds (1995), who characterized fifteen genera according to the typical season and trophic status of lakes where they are found. These researchers then performed a multiple quadratic regression of many traits against these two environmental parameters and found significant regressions for cell volume, maximum growth rate, optimum N:P ratio, P affinity, and optimal light level. The only trait with no significant relation to season or trophic status was sinking rate.

More quantitative analyses are possible, such as the fourth-corner technique (Legendre et al. 1997) and RLQ analysis (Dolédec et al. 1996). These techniques allow researchers to infer the linkages between traits and environmental factors by combining data on the relationships between (*a*) species and samples, (*b*) samples and environmental factors, and (*c*) species and traits. Although these and other similar approaches have been used in other branches of ecology (e.g., Nygaard & Ejrnaes 2004), they have not been used to study phytoplankton.

6.1.3. Relating traits to each other. The standard approach to this type of problem is regression. Examples involving phytoplankton traits include relating minimum nutrient quotas (Shuter 1978) and maximum growth rates (Banse 1976) to cell size. Litchman and colleagues (2007) extended this approach to include trade-offs between nutrient uptake rates and half saturation constants or minimum nutrient quotas. Three statistical issues need to be considered for future studies of this kind: (*a*) Because both variables are measured with error, a regression model such as reduced major axis regression is more appropriate than ordinary least squares (McArdle 2003, Warton et al. 2006). (*b*) Multiple correlation analysis would help tease apart multi-way trade-offs among traits. (*c*) The need to correct for shared evolutionary history (Felsenstein 1985) is debated (one exchange was summarized in Ricklefs 1996), but can provide added insight into the historical dynamics of trait evolution (e.g., Moles et al. 2005).

6.2. Translating Traits into Fitness

It is usually straightforward to determine which traits are advantageous and which are not. Comparing the benefits accrued from different advantageous traits, measured in different units, is not so simple: Mathematics is required. Therefore, a key step in the trait-based research agenda is translating traits into fitness (McGill et al. 2006). We begin with two cases that are particularly easy to analyze: exponential growth and competitive equilibrium (r- and K-selection; MacArthur & Wilson 1967).

In a constant environment, fitness is given as the exponential growth rate when rare, once a stable age-/stage-/physiological-structure has been reached (Metz et al. 1992). For example, a

phytoplankton species growing on one nutrient with variable internal stores can be described by
the Michaelis-Menten/Droop model

$$\frac{dQ}{dt} = v(R) - \mu(Q)Q$$
$$\frac{dP}{dt} = \mu(Q)P - mP,$$ 3.

where Q is the internal nutrient quota, R is available nutrient, P is phytoplankton biomass, $v(R)$
and $\mu(Q)$ are given by Equation 1, and m is phytoplankton mortality rate. Once the quota reaches
a quasi-steady state (balanced growth), fitness can be computed to be

$$\frac{1}{P} \cdot \frac{dP}{dt} = \frac{\mu_\infty v_{\max} R}{\mu_\infty Q_{\min}(K + R) + v_{\max} R} - m$$ 4.

(Klausmeier et al. 2004b). This expression integrates the traits of maximum theoretical growth
rate, minimum nutrient quota, maximum nutrient uptake rate, and mortality rate along with the
environmental parameter of available nutrient into a composite measure of evolutionary fitness.
Under nutrient-replete conditions, a species which maximizes its fitness according to Equation 4
can be considered optimal.

However, if interspecific competition for a shared nutrient runs to completion, then a resident
species controls the level of available nutrient, reducing it to its break-even concentration, termed
R^* (Tilman 1982). For this model,

$$R^* = \frac{Q_{\min} m \mu_\infty K}{v(\mu_\infty - m) - Q_{\min} m \mu_\infty}$$ 5.

(Ducobu et al. 1998, Grover 1997, Klausmeier et al. 2004b). Substituting the resident's R^* given
by Equation 5 into the fitness of an invader given by Equation 4 leads to an expression that
combines the traits of both species into a measure of fitness for the focal species. The expression is
fairly complicated, but in this case of pure resource competition, a shortcut is available. Here the
species with the lowest R^* outcompetes all others (Tilman 1982). A similar result holds for light
competition in well-mixed water columns, with the difference that the outcome of competition
depends on light supply (Huisman & Weissing 1994).

Thus, we've identified two ecological scenarios (exponential growth and competitive exclusion)
for which trait values can be combined into single numbers (maximum growth rate and R^*) that
summarize ecological aptitude. These expressions can be used to calculate an optimal strategy
given trade-offs between the traits that contribute to them. Such an approach has been used to
determine the optimal balance between resource uptake and growth machinery (Klausmeier et al.
2004a) and how the optimal cell size depends on the size of resource molecules (Yoshiyama &
Klausmeier 2008). This is a powerful approach to understanding how ecology selects for certain
combinations of traits.

Can this approach be extended to more complex ecological scenarios? Yes, but in general, there
is no single number composed of different ecological traits that summarizes ecological aptitude.
Complications arise from the fact that an organism's fitness depends on environmental parameters
as well as the densities and traits of the other species in the community (McGill et al. 2006), making
fitness frequency dependent. However, recent work in evolutionary ecology (Geritz et al. 1998,
McGill & Brown 2007, Metz et al. 1992) provides a theoretical framework for integrating traits,
environments, and the interaction milieu into fitness. In a constant environment, fitness is defined
as the invasion rate when rare (Metz et al. 1992). Although the frequency dependence of fitness
complicates the mathematical analysis, it allows for the evolutionarily stable coexistence of more
than one species (Brown & Vincent 1987, Geritz et al. 1998). Thus, the frequency dependence

of fitness lays the foundation for a trait-based theory of communities, not only of single species. Different frameworks such as quantitative genetics (Taper & Case 1992), adaptive dynamics (Geritz et al. 1998), and complex adaptive systems (Norberg et al. 2001, Savage et al. 2007) use the same trait-based definition of fitness, but differ in the source of new phenotypes (reviewed in Abrams 2001).

The three more complicated scenarios we discuss below are food webs, spatial heterogeneity, and temporal heterogeneity.

6.2.1. Grazing. Grazing can be incorporated by modifying Equation 3 using Equation 2 to

$$\frac{dQ}{dt} = v(R) - \mu(Q)Q$$

$$\frac{dP}{dt} = \mu(Q)P - mP - f(P)Z$$

$$\frac{dZ}{dt} = g(P)Z - m_z Z, \qquad\qquad 6.$$

where Z represents grazer density. Because the nutrient level R and grazer density Z are determined by the traits of a resident species, the fitness of an invader depends on all its traits, those of the resident species, as well as environmental parameters such as nutrient supply (Leibold 1996). Models such as these can show how phytoplankton traits vary with nutrient loading (Loeuille & Loreau 2004) and how food web structure can emerge (Loeuille & Loreau 2005).

6.2.2. Spatial heterogeneity. The most pronounced aspect of spatial heterogeneity in phytoplankton communities is in the vertical dimension. Phytoplankton traits that can be incorporated in a vertically resolved model include light-dependent growth traits and sinking/floating/swimming speed, along with environmental parameters such as light supply and turbulence (Huisman et al. 2002, Klausmeier & Litchman 2001). In this spatially explicit situation, fitness is the dominant eigenvalue of a linear operator, computed using an appropriate discretization of the continous model (Troost et al. 2005a). Only one study to date has examined the evolution of traits in a spatially explicit phytoplankton model (Troost et al. 2005a), which leaves many possible trade-offs to be explored.

6.2.3. Nonequilibrium dynamics. Phytoplankton experience nonequilibrium dynamics from many causes on a range of timescales from minutes (e.g., light fluctuations and nutrient pulses) to decades (e.g., changes in nutrient loading), the most pronounced of which are the daily light-dark cycle and the annual cycle. These fluctuations must be averaged to determine fitness. In a periodic environment, the proper measure of fitness is a Floquet exponent (Kooi & Troost 2006, Klausmeier 2008); in an aperiodic environment, the proper measure of fitness is a Lyapunov exponent (Ferrière & Gatto 1995, Metz et al. 1992). Traits that can been considered in a fluctuating environment include those related to nutrient uptake and storage (Grover 1991b, Kooi & Troost 2006, Litchman et al. 2004) and growth rate versus competitive ability (Litchman & Klausmeier 2001), but only one study has looked at evolutionary outcomes (Kooi & Troost 2006).

7. CHALLENGES AND FUTURE DIRECTIONS

7.1. Trait Evolution

A fascinating question is how traits evolve in response to different selective pressures. This question is particularly relevant for phytoplankton, because traits may evolve rapidly owing to short

generation times and large population numbers, making microevolutionary processes likely to affect community dynamics (Hairston et al. 2005, Lynch et al. 1991, Yoshida et al. 2003). Genetic shifts in trait values of a given species can easily occur over relatively short timescales (within a single growing season), often because of clonal selection (Kardinaal et al. 2007, Yoshida et al. 2003). Predation, competition, or changing environmental conditions can exert sufficient selective pressures to cause such shifts (Chonudomkul et al. 2004, Kardinaal et al. 2007, Yoshida et al. 2003). Kardinaal et al. (2007) observed a rapid decrease (within 30 days) in toxicity of the cyanobacterium *Microcystis* due to a competitive displacement of toxic strains by nontoxic strains with better competitive abilities for light.

7.2. Using Trait-Based Approaches to Predict Community Reorganizations Under Global Change

One of the great potential applications of trait-based approaches is to increase our ability to predict community composition and dynamics under rapidly changing conditions. Researchers have started using trait-based models of phytoplankton functional groups forced with different global change scenarios to predict community reorganization in marine and freshwater environments (Elliott et al. 2005, Litchman et al. 2006). Models that allow novel functional types to arise under different environmental scenarios could be especially promising (Follows et al. 2007).

7.3. Global Database of Relevant Traits

A global database of phytoplankton traits would be an invaluable resource for predicting phytoplankton distributions along diverse environmental gradients and for parameterizing models of phytoplankton community structure to predict community reorganizations under global change (Follows et al. 2007, Le Quéré et al. 2005, Litchman et al. 2007). Numerous studies measure various traits in diverse species, but usually in one or a handful of species at a time. The challenge is to put these data together, so that information is readily available to a wide community of researchers. We have started assembling a database of nutrient acquisition traits in marine and freshwater phytoplankton (Litchman et al. 2006, 2007). Such a global database of phytoplankton traits would also inform researchers of gaps in the coverage of species and traits. Researchers working with marine phytoplankton clearly emphasize nitrogen and more recently iron acquisition traits over those for phosphorus, probably because of the dominant paradigm that nitrogen and iron are more commonly the limiting nutrients in the contemporary ocean (Dugdale 1967, Hecky & Kilham 1988, Martin et al. 1991; but see Elser et al. 2007). The reverse is true for freshwater phytoplankton, for which phosphorus acquisition parameters are much more readily available from the literature (Litchman et al. 2007).

Another issue evident from reviewing the experimental literature on trait measurements is the bias toward a handful of species. Both marine and freshwater researchers repeatedly measure the same traits in several species that are easily grown in the lab and became model systems (e.g., *Thalassiosira pseudonana*, *Cyclotella meneghiniana*, *Emiliania huxleyi*, *Trichodesmium* sp., *Scenedesmus* sp.). This is justified for species that are globally important and widely distributed (*E. huxleyi* is a cosmopolitan coccolithophore blooming in the world ocean, *C. meneghiniana* is one of the most commonly occurring freshwater diatoms, and *Trichodesmium* sp. is a major player in marine N fixation). Measuring traits of different strains of the same species also provides information on intraspecific variability of traits. However, phytoplankton researchers should now expand their focus to include more species. For example, in marine environments little is known about ecophysiological traits of many open ocean species, such as large diatoms or coccolithophores other than

E. huxleyi. In freshwater environments, more information is needed on species from oligotrophic environments that are harder to culture, possibly because of mixotrophy (chrysophytes and freshwater dinoflagellates). The methods for measuring these traits also need to be standardized.

SUMMARY POINTS

1. Trait-based approaches are increasingly used in community ecology. Phytoplankton are well-suited for these approaches because phytoplankton possess a manageable number of well-defined traits.

2. Phytoplankton traits can be classified by ecological function (reproduction, resource acquisition, and predator avoidance) and trait type (morphological, physiological, behavioral, and life history). These traits are often used to define major phytoplankton functional groups.

3. Phytoplankton traits vary predictably over major environmental gradients, but more work is needed to determine relationships between multidimensional trait surfaces and environmental axes.

4. Several mechanistic pairwise trade-offs are thought to shape phytoplankton community structure, diversity, and seasonal succession.

5. Mechanistic models provide a theoretical basis for distilling traits and environmental parameters into ecological growth rates and evolutionary fitness.

FUTURE ISSUES

1. There is a need for a global database of phytoplankton traits, both marine and freshwater, with guidelines for standardized measurements of various traits.

2. Trade-offs need to be characterized, including the shapes and interaction of multiple traits.

3. New approaches need to be devised to parameterize interspecific interactions such as predator-prey interactions in terms of a small number of traits (instead of idiosyncratic pairwise interaction coefficients).

4. More attention should be paid to the potential evolution of traits and its effect on community dynamics.

5. Novel mathematical and statistical approaches should be pursued to derive community composition based on functional traits and trade-offs.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

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