

Linking traits to species diversity and community structure in phytoplankton

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Abstract In addition to answering Hutchinson’s question “Why are there so many species?”, we need to understand why certain species are found only under certain environmental conditions and not others. Trait-based approaches are being increasingly used in ecology to do just that: explain and predict species distributions along environmental gradients. These approaches can be successful in understanding the diversity and community structure of phytoplankton. Among major traits shaping phytoplankton distributions are resource utilization traits, morphological traits (with size being probably the most influential), grazer resistance traits, and temperature responses. We review these trait-based approaches and give examples of how trait data can explain species distributions in both freshwater and marine systems. We also outline new directions in trait-based

approaches applied to phytoplankton such as looking simultaneously at trait and phylogenetic structure of phytoplankton communities and using adaptive dynamics models to predict trait evolution.

Keywords Phytoplankton · Community structure · Functional diversity · Traits · Growth · Temperature · Harmful algal blooms · Adaptive dynamics

Introduction

It has been half a century since the publication of G.E. Hutchinson’s “Homage to Santa Rosalia” where he posited the question of why there are so many kinds of animals, and, presumably, other organisms (Hutchinson, 1959). Hutchinson was a visionary who formulated questions that have been influencing ecological thinking for decades. The question of what determines species diversity continues to be at the center stage of ecology to this day. Much progress has been made in identifying the mechanisms leading to and maintaining species diversity. In phytoplankton, several mechanisms are important for maintaining diversity, including spatial and temporal heterogeneity (Sommer, 1984; Litchman & Klausmeier, 2001; Litchman, 2003; Huisman et al., 2006; Yoshiyama et al., 2009), presence of higher trophic levels (Leibold, 1996), internally generated and externally mediated chaotic dynamics (Beninca et al., 2008;

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Dakos et al., 2009), and novel resource dimensions, such as different parts of the light spectrum (Stomp et al., 2004) and different sizes of resource molecules (Yoshiyama & Klausmeier, 2008), all contributing to multiple species coexisting successfully. Coexistence of multiple species inevitably requires trade-offs in species traits that determine their responses to the environment (Tilman, 1982). Therefore, identifying relevant traits and trade-offs in phytoplankton helps explain the mechanisms of species coexistence and diversity.

In addition to answering what determines species diversity, there is a need to understand and ultimately predict what species occur under given environmental conditions. A mechanistic understanding of how communities are organized and what determines the make-up of a community is becoming increasingly important under rapidly changing environmental conditions associated with anthropogenic global change. What will phytoplankton communities look like in the near or more distant future? Are there particular species, taxonomic or functional groups that might increase disproportionately due to global warming and other human-mediated changes? If so, what are the traits that enable their proliferation?

A systematic consideration of phytoplankton traits has the potential to go beyond explaining species diversity by providing a mechanistic understanding of how phytoplankton communities might reorganize in the future. Looking at what traits or trait values may be selected under given environmental conditions and knowing which functional groups are associated with particular traits will allow us to predict community composition and diversity under various environmental scenarios. Trait-based approaches are being increasingly used in ecology, especially in terrestrial plant ecology (Lavorel & Garnier, 2002; McGill et al., 2006; Westoby & Wright, 2006). They consider simultaneously multiple morphological and functional traits in a wide range of species to explain community distributions along various environmental gradients and predict ecosystem functioning (Diaz et al., 2004). Similar approaches have been pioneered in phytoplankton ecology by Margalef, Reynolds, and Sommer (Margalef, 1978; Reynolds, 1984; Sommer, 1984; Reynolds, 1988; Sommer, 1988; Reynolds et al., 2002) and are now being further developed by many researchers (Rojo, 1998; Weithoff, 2003; Litchman et al., 2007; Litchman & Klausmeier, 2008; Kruk et al., 2010).

Among major phytoplankton traits that define fundamental ecological niches are resource acquisition and utilization traits, grazer and parasite resistance traits and various morpho-physiological traits that affect species persistence (e.g., temperature reaction norms, structures counteracting sinking, and shape). We recently extensively reviewed phytoplankton resource utilization traits, and suggested ways to classify traits according to their type and function (Litchman & Klausmeier, 2008). Here we expand on some topics that were not covered in detail previously, such as hydrodynamic consequences of cell size, responses to temperature and a phylogenetic perspective on traits. We further incorporate new topics such as trait frequencies in the environment, traits and harmful algal blooms (HABs), and trait functional diversity. We also link traits to species diversity and community structure. This review thus complements our previous work (Litchman & Klausmeier, 2008) and will hopefully stimulate applications of trait-based approaches to phytoplankton and plankton in general.

Cell size as a master trait

Virtually all studies of phytoplankton traits include some consideration of cell/organism size in phytoplankton. As in most organisms, cell size in phytoplankton affects numerous functional traits and core metabolic rates (Peters, 1983; Chisholm, 1992; Brown et al., 1993; Marba et al., 2007; Naselli-Flores et al., 2007). Phytoplankton size spans several orders of magnitude, from 1 μm to 1 mm or so for individual cells and even more for colonial organisms. Such diversity of sizes suggests that there is not a universal best size but that different sizes are selected for by diverse selective pressures (Litchman et al., 2009). Indeed, natural communities exhibit diverse size spectra that may change spatially and temporally (Platt & Denman, 1978; Gaedke et al., 2004).

Small sizes, e.g., less than 10–20 μm , are advantageous under nutrient-limiting conditions because of the high surface area to volume ratio (Chisholm, 1992). Phytoplankton cells are surrounded by a diffusive boundary layer (Munk & Riley, 1952; Karp-Boss et al., 1996), which poses an additional constraint on cell size. Nutrient molecules are first transported across the boundary layer by molecular diffusion before they are taken up at the cell

membrane. The two steps, transport and uptake, co-limit the nutrient flux (Pasciak & Gavis, 1974; Yoshiyama & Klausmeier, 2008). The transport rate is proportional to cell radius (r) for a spherical cell in stagnant water, while uptake rate is generally proportional to cell surface area ($\sim r^2$) (Aksnes & Egge, 1991; Litchman et al., 2007). This indicates that smaller cell sizes are even more beneficial in competition for nutrients under nutrient-limited conditions than can be predicted based on the larger surface-to-volume ratio. Limitation of transport relative to uptake is more pronounced for larger cells (Pasciak & Gavis, 1974). Hence, hydrodynamic forces influence nutrient uptake capabilities and mediate cell size.

Although larger cells are less efficient at acquiring nutrients relative to smaller cells, several traits can mitigate transport and uptake limitations. When cells swim or sink, the diffusive boundary layer is distorted by the uniform flow around the cell, creating a thinner part at the front. As a result, nutrient transport can be enhanced by more than 50% for swimming and sinking cells that are larger than 10 μm (Karp-Boss et al., 1996). Shear flows created by small-scale turbulence can also increase nutrient transport by more than 50% for large cells (ca. $>60 \mu\text{m}$) suspended in highly turbulent water (Karp-Boss et al., 1996). The benefits of fluid motion for nutrient transport are not appreciable for small cells unless they take up larger molecules (Berg & Purcell, 1977). Nutrient flux can also be enhanced depending on cell shape. In stagnant water, elongated cells can take up more nutrients than spherical cells of equivalent volume due to the larger surface-to-volume ratio (Pahlow et al., 1997). In shear flows, elongated cells rotate intermittently (Jeffery orbits), which can enhance nutrient transport (Pahlow et al., 1997).

Therefore, swimming, sinking, and cell elongation may be traits that can aid nutrient transport for larger cells. Another effective strategy to overcome transport and uptake limitations is being large using non-limiting resources (e.g., carbon), keeping the requirement of the limiting resource low (Thingstad et al., 2005). Large diatoms may adopt this strategy, having huge vacuoles relative to the cell volume (Thingstad et al., 2005; Litchman et al., 2009). Large cell sizes may be advantageous under conditions of fluctuating nutrients because of their increased nutrient storage capacity (Grover, 1991; Stolte & Riegman, 1996;

Litchman et al., 2009) in vacuoles. A recent model analysis showed that different regimes of fluctuations may select for different diatom sizes, with either fast and/or extremely slow fluctuations selecting for small sizes and intermediate frequency fluctuations selecting for large sizes (Litchman et al., 2009). Interestingly, intermediate fluctuation regimes may also lead to a stable coexistence of small and large sizes with small cells growing fast after a nutrient pulse and large but slower growing cells persisting on stored nutrients (Litchman et al., 2009). Which size would be beneficial under certain nutrient supply regimes depends on how nutrient utilization traits scale with cell size (Litchman et al., 2009). Large sizes are more likely to evolve if nutrient storage capacity, i.e., maximum nutrient quota, increases faster than the minimum possible nutrient concentration in the cell, i.e., the minimum quota (Litchman et al., 2009). Nitrate fluctuations can select for large sizes because this nutrient is stored in vacuoles that increase disproportionately fast with increasing cell size. On the other hand, phosphate fluctuations may not have such a strong selection for large sizes because P is mostly stored in the cytoplasm, so that P storage capacity does not increase as fast, at least in diatoms (Litchman et al., 2009). If we assume that nitrate is more frequently limiting in fresh water (Elser et al., 2007), then differences in allometric scaling of nutrient utilization parameters with cell size may explain different size distributions in marine and freshwater diatoms (Litchman et al., 2009) and potentially in phytoplankton in general. It is possible that nutrient fluctuation regimes of varying frequency and alternating nitrogen versus phosphorus limitation may lead to coexistence, and hence diversity, of a wide range of cell/species sizes. Small cells may also be more efficient at utilizing low light because of the smaller packaging effect, self-shading of light-capturing pigments (Kirk, 1994). Our meta-analysis of light utilization traits (Schwaderer et al., submitted) revealed a negative relationship between the initial slope of the growth–irradiance curve (α) and cell size, supporting the size effect on light preferences based on first principles. Consequently, low light conditions may preferentially select for small sizes. However, a frequent association of low light conditions with high nutrients that often favor large cells may counteract this trend.

Large cell sizes or colonial morphology are thought to increase grazer resistance and thus reduce

overall mortality (Reynolds, 1984; Smetacek, 2001). In a typical seasonal succession of phytoplankton, grazer-resistant forms appear later in the season following increased grazing pressure (Sommer et al., 1986). Over the course of the season, alternating selective pressures such as nutrient limitation, grazers, light availability or fluctuating nutrient supply can select for different sizes, thus creating diversity in size distributions in natural communities. It may also be possible to infer a dominant selective pressure on phytoplankton communities by analyzing cell size distributions. If the range of optimal sizes selected for by temporally varying drivers is greater than the intraspecific size variation, different optimal sizes would be represented by different species, and therefore trait diversity would lead to species diversity.

Temperature-related traits

Because of anthropogenic increases in temperature, phytoplankton responses to temperature would be among the most important traits for predicting phytoplankton community reorganizations in the future. In temperate lakes, the growing season commonly begins with a spring diatom bloom, followed by periods of dominance by green algae and then cyanobacteria in summer before returning to a predominantly diatom and/or dinoflagellate-dominated community in late fall (Lewis, 1978). Temperature is a major driver of this successional pattern (Karentz & Smayda, 1984), both through its direct effects on phytoplankton population growth and its indirect effects through changes in water column stability and predator population growth. Though changes in temperature are correlated with changes in day length and light intensity, multivariate studies of lake community succession have shown that temperature is an important factor behind the changes in community composition (Grover & Chrzanowski, 2006). A better understanding of phytoplankton responses to temperature could improve our ability to predict species turnover and productivity, which could be particularly important given predictions of near-term lake warming (De Stasio et al., 1996; Magnuson et al., 1997).

An abundance of laboratory studies show that temperature exerts a strong effect on the growth rate

and physiology of phytoplankton (Eppley, 1972, Karentz & Smayda, 1984, Butterwick et al., 2005). Species exhibit strong physiological responses to temperature, some of which include changes in mean cell size (Atkinson et al., 2003), organism size (Komárek & Ruzicka, 1969), cell carbon and nitrogen content (Montagnes & Franklin, 2001), phosphate uptake rate (Senft et al., 1981), nitrogen metabolism, C:N ratio, and chlorophyll content (Berges et al., 2002). Gaining a mechanistic understanding of how temperature affects the organism through each of these pathways is extremely challenging, but its overall effect on fitness is easily characterized by the population growth rate at different temperatures.

The shape of the relationship between temperature and growth rate in phytoplankton is most commonly a slow (frequently nonlinear) increase in growth rate up to the optimum temperature, followed by a fast decrease in growth at temperatures above this optimum. Different models have been used to describe this relationship (Ahlgren, 1987, Briand et al., 2004, Jöhnk et al., 2008, Montagnes et al., 2008), but more data are needed to test their generality. The main parameters describing these curves—maximum growth rate, optimum temperature for growth and temperature range—are species- and strain-specific traits that determine their ability to respond to changes in temperature. Optimum temperatures for growth and temperature range have been shown to correlate with the environmental temperature at the time of strain isolation and annual temperature range in diatoms isolated from a variety of environments (Suzuki & Takahashi, 1995). In addition, many diatoms appear to have relatively low optimum temperatures for growth (15–25°C), as one would predict if temperature played an important role in determining succession. These include *Aulacoseira* (Foy & Gibson, 1993), *Asterionella* (Butterwick et al., 2005), and *Rhizosolenia* (Ignatiades & Smayda, 1970). Cyanobacteria tend to have higher optimum temperatures for growth, with a majority of measured species exhibiting optima between 25 and 35°C (Robarts & Zohary, 1987), though some species possess optima below 15°C, such as a Lake Baikal phytoplankton, *Synechocystis limnetica* (Richardson et al., 2000). Many green algae have also been shown to have optima in the 25–35°C range, including *Chlorella* (Cho et al., 2007), *Scenedesmus* (Zargar et al., 2006), *Coelastrum*, *Cosmarium* (Boutefas

et al., 2002), and *Dunaliella* (Sosik & Mitchell, 1994). Consequently, other traits, such as differences in response to nutrient load and predation pressure between green algae and cyanobacteria, are likely to be better explanations for the summer dominance of cyanobacteria. This suggests that many diatoms would be excluded in warm lakes because the high temperatures fall outside their fundamental niches, while the dominance of cyanobacteria over green algae might be better explained by differences in their realized niches. These temperature-related traits suggest a possible decrease of phytoplankton diversity in a warmer future.

In order to make stronger predictions about species turnover, however, we need a clearer understanding of the interactive effects of temperature with other environmental parameters on phytoplankton. Many studies have demonstrated interactive effects of temperature with light and nutrient concentration on maximum growth rate, but some have also shown that interactions with light (Novak & Brune, 1985), salinity (Cho et al., 2007) and nutrient concentrations (Maddux & Jones, 1964) can shift the optimum temperature for growth. More studies are needed to determine whether these and other factors shift the optimum and maximum growth rate in a predictable manner. Given that interactions with nutrients take place, estimates of these temperature response traits in a relatively low-nutrient growth medium resembling natural concentrations could prove to be more accurate predictors of performance in the wild.

We also need more data on individual species responses and interactive effects in order to incorporate these temperature response traits into predictive models of species distributions and turnover, both now and in the future. In particular, more fine-grained measurements in the 20–30°C range are needed, as these could help us predict community structure under different climate change scenarios, some of which predict temperate lake warming in the range of 1–7°C (De Stasio et al., 1996, Magnuson et al., 1997).

Trait values, trait frequency, and ecosystem functioning

Often, average trait values or trait frequency in a community reflect a particular physiological status of the community integrating the environmental signal.

Average trait value or frequency may, in turn, affect ecosystem function. For example, a community dominated by species with efficient utilization of low-nutrient concentrations (e.g., low half-saturation constants for nutrient uptake) most likely assembles under low-nutrient conditions and, consequently, such a community would efficiently draw down nutrients (Arrigo et al., 1999; Litchman et al., 2007). Another example is the N fixation trait: in heterocystous nitrogen-fixing cyanobacteria, the development of heterocysts, the specialized cells where fixation occurs, indicates low nitrogen availability. The rate of fixation per heterocyst can be fairly constant (de Tezanos Pinto & Litchman, 2010a) and hence heterocyst density can be used as a proxy for assessing biological N fixation in the ecosystem. High heterocyst density indicates an active influx of new nitrogen into the ecosystem. Akinetes are resting cells in heterocystous nitrogen-fixing cyanobacteria; they develop only in response to certain environmental triggers, which may differ among species. A high akinete density indicates strong ecological constraints on a given population, may mark the end of the population's growing season and may result in nutrient recycling from decaying filaments. Gas vesicles are synthesized in several cyanobacteria (e.g., *Microcystis*, *Anabaena*, and *Planktothrix*) and allow buoyancy control. Gas vesicles collapse with increased photosynthesis because of turgor pressure. Thus, a high proportion of cyanobacteria expressing gas vesicles reflect low light environments and low productivity (Reynolds, 2006). In cyanobacteria, these morphological traits (motility, nitrogen fixation, and resting cells) and other physiological traits (toxicity and pigmentation) are strongly plastic. Plasticity arises from different gene expression within a species, probably in response to the environment, and increases the diversity of trait values. Plastic responses reflected in morphological traits occur on the scale of days (O'Farrell et al., 2007; de Tezanos Pinto & Litchman, 2010a), quickly integrating the prevailing environmental situation.

At the community level, a high percentage of mixotrophic organisms may indicate low nutrient and/or low light availability. Also, the prevalence of non-palatable taxa (GALD > 35 µm; greatest axial lineal dimension) may reflect high predation pressure on smaller fractions (GALD < 35 µm). A high occurrence of grazer avoidance traits (spines, toxins,

mucilage) may decrease grazer-mediated recycling of nutrients. This results in higher nutrient immobilization by phytoplankton biomass, as frequently happens during HABs (Sunda et al., 2006). Hence trait frequency, at the population or community level, may reflect the dominant ecological drivers, and can ultimately affect ecosystem function.

Integrating community ecology and phylogeny

Santa Rosalia, the patroness of evolutionary studies, would most certainly appreciate the elegance of trait-based approaches, as they can be used to integrate community ecology and phylogeny. Phytoplankton traits differ significantly in their conservatism. Some traits, such as grazer susceptibility and maximum growth rates, appear quite labile, exhibiting significant variation at the genus or even species level (Bruggeman, in press; Schwaderer et al., submitted), while others, such as cell size and the initial slope of the growth–irradiance curve, are conserved at the highest taxonomic levels (domain, kingdom) (Bruggeman, in press; Schwaderer et al., submitted).

The simultaneous study of multiple trait associations allows the determination of whether and how functional traits of species correspond to their spatial distribution, abiotic features of the environment and community affiliation (Cavender-Bares et al., 2004). Such approaches make it necessary to (1) quantify distributions of species, (2) classify the species with respect to traits, (3) analyze trait distributions in relation to critical environmental factors, and (4) map phylogenetic affiliations. This allows the examination of interspecific variation in species traits with respect to both community affiliation and phylogenetic lineage, to determine whether traits tend to show similarity within communities, within lineages or both (Cavender-Bares et al., 2004). Alternatively, multiple trait associations can be used to calculate community phylogenetic diversity and then infer the process leading to that pattern (see below).

Traits and diversity: functional and phylogenetic approaches

Standard measures of diversity (α , β , and γ diversity) treat taxa equivalently, without considering neither

functional nor phylogenetic affiliations (Martin, 2002). For example, two phytoplankton communities with completely different taxa can have low α and β diversity, but possess high functional and phylogenetic diversity. Traits can be used for assessing both functional and/or phylogenetic diversity. Functional diversity is calculated by measuring the total branch lengths connecting all species to each other in a dendrogram (Petchey & Gaston, 2007); the dendrogram is produced from a matrix of species and traits. Similarly, phylogenetic diversity is assessed by measuring the total branch lengths connecting all species to each other in a phylogeny (Martin, 2002); the tree can be produced from a molecular matrix or from a molecular and traits matrix. Alternatively, molecular phylodiversity focuses on the diversity of particular taxa within a tree, by adding all branch lengths that support the group of interest (Lewis & Lewis, 2005). For assessing diversity between two communities with different number of taxa, the genetic diversity of each community is calculated on a tree containing the combined communities and then compared (Martin, 2002). In all approaches, an excess of divergent lineages renders high diversity, whereas an excess of closely related lineages renders low diversity. It is hypothesized that low phylogenetic diversity resulting from closely related species occurring together in a community indicates strong environmental filtering, presumably because the environment selects certain traits that are shared by phylogenetically related species (Webb et al., 2002). Conversely, it is hypothesized that high phylogenetic diversity indicates that communities contain distantly related species, probably reflecting current or past competition between closely related species (Cavender-Bares & Wilczek, 2003). However, competition can also lead to convergent strategies and, hence, similar traits (Abrams, 1990; Fox & Vasseur, 2008), so caution should be exercised when deducing major driving forces of community structure from phylogenetic information.

Traits arise as innovations along the tree of life and tend to be shared by species that have common ancestry (Cavender-Bares et al., 2009), hence often displaying similarity in values among more closely related species. Most phylogenies are based only on molecular information, but the combined use of molecules and traits in phylogenetic matrices may allow for better tree resolution (review in Assiss,

2009). Including traits into matrices (e.g., growth rate, resource acquisition traits, and morphological traits) can be extremely useful for resolving algal phylogenies. For example, for some HAB cyanobacteria, 16S rRNA approaches cannot differentiate between very similar genera that may display morphological and physiological differences (e.g., *Anabaena* and *Aphanizomenon*).

A promising new approach of inferring the unknown trait values of species, based on phylogenetic relationships and the knowledge of trait values of related species, may allow a much better characterization of the trait space for ecological studies (Bruggeman, in press).

Traits and harmful algal blooms

Harmful algal blooms (HAB) have a pronounced impact not only on water quality, but on species diversity, community structure and ecosystem functioning. Most HABs lead to a significantly decreased diversity and an impairment of many ecosystem functions and are predicted to increase in the changing climate (Paerl & Huisman, 2009). Therefore, it would be useful to develop trait-based approaches to explain and predict the occurrence of HABs in diverse ecosystems. All algae that produce HABs share a striking common characteristic: they possess a wide suite of plastic traits, with some traits being major innovations (e.g., N fixation and mixotrophy), and can express toxicity (Table 1). Such eco-physiological flexibility in HAB species favors their success in different environments. Possessing a suite of flexible traits may help maintain high fitness in a wide range of environmental conditions. For example, de Tezanos Pinto & Litchman (2010a) showed that heterocystous nitrogen fixers grown in low N and high light gained dominance because of nitrogen fixation. However, when grown in low light, the traits providing higher fitness were related to light acquisition (low I_k and high relative growth rates at low light) and behavior (gas vesicles that enable positioning in better illuminated zones). Analyzing trait–environment and trait–trait relationships in HABs may provide tools for preventing or mitigating their occurrences. Are HAB species traits correlated? Several trait–trait relationships seem uncorrelated, such as akinete, heterocyst, and gas vesicle synthesis.

Other traits, however, such as growth and N fixation, show trade-offs (e.g., Kenesi et al., 2009). A trade-off between N fixation and toxin synthesis may also occur: Sunda et al. (2006) showed that *Nodularia spumigena* grown in low TN:TP ratios (where fixation occurs) synthesized significantly less toxin than at increased TN:TP ratios, where P was limiting but N sufficient. Finally, akinetes seem dependent on light availability, as their viability is lost under persistent darkness (de Tezanos Pinto & Litchman, 2010b).

In scenarios of global climate change, widespread expansion of cyanobacteria HABs is predicted (Paerl & Huisman, 2009), as many cyanobacterial traits allow a successful exploitation of most of the predicted scenarios: (a) high temperature optima for growth will increase fitness in a warmer world, (b) the ability to control buoyancy allowing upward movement for light and CO₂, and downwards for nutrients (Paerl & Huisman, 2009) will be advantageous under highly stratified conditions, (c) N fixation capabilities would allow dominance under decreased N:P ratios (Weyhenmeyer et al., 2007; Noges et al., 2008), and (d) resting stages (akinetes) and desiccation tolerance would allow enhanced population viability in prolonged droughts.

Traits within food webs

As phytoplankton are an integral part of many aquatic food webs, we also need to focus on traits that define interactions of phytoplankton with the rest of aquatic food webs (Fig. 1). Grazer resistance traits and interactions with bacteria (e.g., DOC excretion) are examples of such traits. While trait-based approaches are being actively developed within single trophic levels, traits relevant to interactions across different trophic levels, for example primary producer–herbivore interactions, are still poorly defined. The challenge is to find ways to reduce complexity in characterizing such interactions. Clearly, having different traits that characterize every pairwise interaction, for example for every phytoplankton species and every grazer, would not significantly reduce complexity. One approach would be to determine the allometric scaling of phytoplankton grazer resistance to different grazers. Then grazer resistance for any pair of phytoplankton and grazer can be estimated

Table 1 Suite of traits in freshwater and marine HAB and non-HAB species, including: toxicity, nitrogen fixation, shape (GALD, greatest axial lineal dimension), gas vesicles, flagella, accessory pigments, mixotrophy, and resting stages

Species	HAB Form	Habitat	Morphology	Toxicity	N fixation	GALD	Gas vesicles	Flagella	Acc. pigments	Mixotrophy	Resting stage	No. of Traits
N fixers	HAB	Planktonic	Freshwater/marine	1*	1*	1	1*	0	1*	0	1*	6
<i>Microcystis aeruginosa</i>	HAB	Planktonic	Freshwater	1*	0	1	1*	0	1*	0	0?	4
<i>Planktothrix</i> sp.	HAB	Planktonic	Freshwater	1*	0	1	1*	0	1*	0	0	4
<i>Lyngbya</i> sp.	HAB	Benthic	Freshwater/marine	1*	0	1	0	0	1*	0	0	3
<i>Synechococcus elongatus</i>	HAB	Planktonic	Marine	1*	0	0	0	0	1*	0	0	2
<i>Nannochloris atomus</i>	HAB	Planktonic	Marine	1*	0	0	0	1*	0	0?	0	2
<i>Nannochloropsis gaditana</i>	HAB	Planktonic	Marine	1*	0	0	0	1*	0	0?	0	2
<i>Aureococcus anophagefferens</i>	HAB	Planktonic	Marine	1*	0	0	0	0	1*	0?	?	2
<i>Aureocembra lagunensis</i>	HAB	Planktonic	Marine	1*	0	0	0	0?	1*	0	?	2
<i>Chrysochromulina polylepsis</i>	HAB	Planktonic	Marine	1*	0	0	0	1*	0?	1*	1*	5
<i>Prymnesium parvum</i>	HAB	Planktonic	Marine	1*	0	0	0	1*	0?	1*	?	3
<i>Chlamydomonas</i> spp.	No	Planktonic	Freshwater	0	0	0	0	1*	0	0	0	1
<i>Chlorella</i> spp.	No	Planktonic	Freshwater	0	0	0	0	0	0	0	0	0

All traits are binary coded where 0 = absence and 1 = presence, except for GALD where 0 = GALD < 35 µm (edible phytoplankton) and 1 = GALD > 35 µm (non-edible). * indicates plastic traits and ? indicates lack of or inconclusive data. Marine HAB species were selected from Sunda et al. (2006), and freshwater HAB species from Paerl & Huisman (2009)

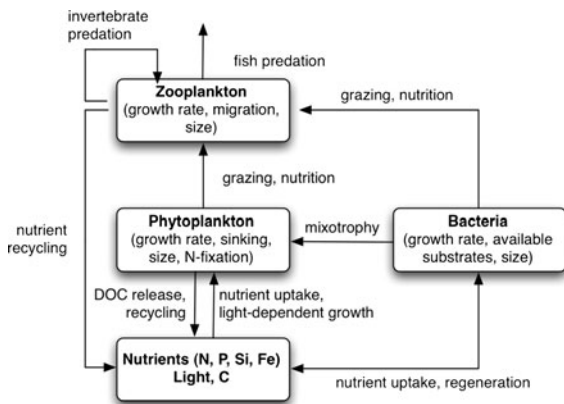


Fig. 1 Plankton traits in a food web perspective. Some examples of specific traits are given for each group and interaction between groups

from the size of the phytoplankton species. It is possible that allometric relationships may be different for different taxonomic/functional groups of phytoplankton (e.g., cyanobacteria vs. green algae).

Developing trait-based mathematical models

Traditional models in community ecology typically involve the interaction between only a few species, as few as one per trophic level in marine NPZ (nitrogen–phytoplankton–zooplankton) models (Franks, 2002). While these models have often been successful, it is increasingly realized that diversity at each trophic level can modify the dynamics and patterns of ecosystem function across environmental gradients. Recent models have begun to incorporate the effect of diversity by including functional groups within trophic levels (e.g., Le Quééré et al., 2005; Litchman et al., 2006). Still, much diversity remains unaccounted for within these functional groups, and trait variation may be more continuous than discrete. New analytical and simulation techniques (adaptive dynamics: Geritz et al. (1998); complex adaptive systems: Norberg et al. (2001), Savage et al. (2007), Merico et al. (2009); Monte Carlo sampling: Follows et al. (2007)) allow for the self-organization of community structure from a continuum or a large number of possible phenotypes (determined by the trade-offs between ecologically relevant traits). Specifically, these approaches add equations describing

the trait spectrum (at least mean trait value, sometimes variance) of each guild to the traditional equations describing population dynamics. Mean traits change in the direction of increasing fitness (defined as invasion rate when rare, which captures the frequency-dependence of ecological interactions) (Litchman & Klausmeier, 2008). At equilibrium, no phenotype not present in the community can invade. This may require more than one species within a guild. These approaches account for the direct effects of environmental factors such as nutrient loading on ecosystem function (such as primary production and nutrient cycling) as well as the indirect effects mediated by altered community structure.

Electronic trait database

We advocate for an electronic trait database that would include diverse phytoplankton traits and be available to a wide range of researchers. Making trait information available to the scientific community will: (a) allow enhancement of the use of trait-based approaches in answering fundamental questions in phytoplankton ecology and phylogeny, (b) allow development of a deeper understanding of the physiology of HABs as well as other ecologically relevant algal groups, (c) allow prediction of community reorganization under scenarios of global climate change, (d) aid in phylogenetic reconstructions, (e) ease functional diversity calculations, (f) better parameterize mathematical models with empirical parameters, and (g) combine traits into single numbers (see below), among others.

The compilation of morphological, behavioral, and ecological traits can be easily obtained, even for the less well-known species. The opposite is true for physiological traits, as they are scattered in the literature, determined only for select species, and measured with different methodologies and units. Standardized protocols for methodologies and unit expression of resource acquisition and other physiological traits should be encouraged. Standardization of trait categorization is also suggested. Taxonomic/phylogenetic relationships could be used to infer the missing trait values (Bruggeman, in press).

The following traits could be included: algal size, shape, phagotrophy, silica demand, motility, and nitrogen fixation, as proposed by Weithoff (2003);

growth rates, toxicity, resting stages, multicellular morphology, nutrient and light acquisition, and type of reproduction, as proposed by Litchman & Klausmeier (2008). We propose several other relevant traits: ultrastructure (thylakoid structure, chromosome number, genome size), cell wall type, mucilage, aerotopes, symmetry (symmetric, asymmetric), polarity (isopolar, heteropolar), coiling (straight, coiled), life stages (zoospores), types of toxins (neurotoxins, hepatotoxins, dermal toxins), toxic molecule (e.g. anatoxin-a, saxitoxins), filament type (filament, pseudofilament), filament branching (true, false, not branching), type of filament branching (T, Y), habitat preference (marine, freshwater, terrestrial), and community type (pelagic, benthic). We also propose using composite traits, such as the organism's degree of elongation (GALD*S/V, Reynolds, 2006, Naselli-Flores & Barone, 2007) and the breakeven concentration of resources where growth equals mortality (R^*_{LIGHT} , R^*_N , and R^*_P , Tilman, 1982; Litchman et al., 2007). It would be interesting to develop a composite grazing resistance trait, combining palatability (e.g., as a function of internal quotas and toxins) and handling time (as a function of shape, GALD, and spines number).

Conclusions

We propose that trait-based approaches for phytoplankton, plankton in general and other aquatic organisms are an effective way to integrate and synthesize molecular, physiological and ecological knowledge of individual species, taxonomic and functional groups. Trait-based approaches can be used to link species diversity and community structure in phytoplankton and would allow us to increase the generality and predictive power of aquatic ecology by providing mechanistic explanations of why certain species are found under given environmental conditions. These approaches should be especially useful in our attempts to predict aquatic community re-organizations under anthropogenically driven global environmental change.

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