LETTER

The role of functional traits and trade-offs in structuring phytoplankton communities: scaling from cellular to ecosystem level

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Abstract

Trait-based approaches to community structure are increasingly used in terrestrial ecology. We show that such an approach, augmented by a mechanistic analysis of trade-offs among functional traits, can be successfully used to explain community composition of marine phytoplankton along environmental gradients. Our analysis of literature on major functional traits in phytoplankton, such as parameters of nutrient-dependent growth and uptake, reveals physiological trade-offs in species abilities to acquire and utilize resources. These trade-offs, arising from fundamental relations such as cellular scaling laws and enzyme kinetics, define contrasting ecological strategies of nutrient acquisition. Major groups of marine eukaryotic phytoplankton have adopted distinct strategies with associated traits. These diverse strategies of nutrient utilization can explain the distribution patterns of major functional groups and size classes along nutrient availability gradients.

INTRODUCTION

There has been considerable excitement recently that a trait-based approach may lead to significant advances in community ecology (McGill *et al.* 2006; Westoby & Wright 2006). This approach focuses on four themes and the relationships between them: traits, environmental gradients, the interaction milieu and performance currencies (McGill *et al.* 2006). In this view, functional traits and trade-offs to a large extent define ecological niche of a species, both fundamental and realized, that makes them crucial for determining the distribution of species or functional groups along various environmental gradients.

Despite the enthusiasm for this approach, there are obstacles that have prevented its full application so far. First, it is often difficult to know which traits are most important for defining an organism's niche. Second, the performance currency most relevant to population dynamics is the population growth rate, but this is often difficult to measure and fitness components such as energy intake and seed output are used instead (McGill *et al.* 2006). Third, patterns

of distribution along environmental gradients need to be known.

We suggest that phytoplankton may be an ideal system for implementing a trait-based approach to community ecology. Phytoplankton's niches are largely defined by fundamental physiological processes such as growth and acquisition of a handful of resources (light and macronutrients and micronutrients), along with resistance to grazers and disease (Margalef 1978). These eco-physiological traits are easily measured in the laboratory and can be directly linked to population-level measures of fitness and competitive ability using simple mathematical models (Droop 1973; Tilman 1982; Grover 1991; Klausmeier *et al.* 2004). Furthermore, big patterns in the distribution of phytoplankton exist, where major functional groups are associated with contrasting environmental regimes (Margalef 1978; Reynolds 1984; Li 2002). Finally, understanding phytoplankton distributions and community organization is globally important, as phytoplankton are major primary producers in most aquatic ecosystems responsible for almost half of the total atmospheric carbon fixation (Field *et al.* 1998) and whose

abundance and community structure (e.g. dominance of certain functional groups) have profound effects on higher trophic levels and major biogeochemical cycles (e.g. Falkowski *et al.* 1998).

Phytoplankton are an extremely diverse polyphyletic group of organisms composed of lineages that differ in their origin (e.g. different endosymbiotic events), evolutionary age and modern distribution (Falkowski *et al.* 2004). Moreover, major taxonomic groups of eukaryotic phytoplankton can be classified into distinct functional groups (Iglesias-Rodriguez *et al.* 2002a) with unique biogeochemical signatures. Here, we combine the trait-based approach with the taxonomic/phylogenetic information by broadly sampling relevant traits across major taxonomic groups of marine phytoplankton to gain new insights into the effects of evolutionary history on the physiological trait distributions and community structure.

An important aspect of a trait-based approach to community ecology is the trade-offs between traits (Tilman 1990; Grover 1991; Bohannan *et al.* 2002). When competition for multiple resources is considered, species are thought to have trade-offs in their competitive ability for one vs. another nutrient (Tilman 1982) or for nutrient vs. light (Huisman & Weissing 1994; Leibold 1997; Klausmeier & Litchman 2001). Under non-equilibrium conditions, a trade-off between competitive ability and maximum growth rate may be important (Grover 1991; Litchman & Klausmeier 2001), with fast-growing species dominant under fluctuating conditions. Trade-offs lead to differentiation of ecological strategies and may consequently allow coexistence of multiple species. Trade-offs in the utilization of different resources arise because of limited energy and materials that can be devoted to acquisition and utilization of a particular resource. Phytoplankton are likely to exhibit trade-offs in resource utilization traits (Grover 1991) and thus have different strategies of resource utilization.

Early work on phytoplankton recognized the importance of nutrient utilization traits in defining contrasting ecological strategies (Dugdale & Goering 1967; Hutchinson 1967; Eppley *et al.* 1969). Previous studies related physiological trait values to habitat types (e.g. low nutrient open ocean vs. high nutrient coastal environments) and looked for correlations between traits (e.g. Eppley *et al.* 1969; Shuter 1978; Smayda 1997; Collos *et al.* 2005) but considered only one or two traits or a handful of species at a time. Here, we extend these approaches by analysing laboratory-derived data on multiple physiological traits simultaneously in more than 40 species from four major groups of marine eukaryotic phytoplankton (diatoms, dinoflagellates, coccolithophorids and green algae). We show that these functional traits exhibit trade-offs that can be explained mechanistically at the cellular level, using the surface to volume-scaling

relations and enzyme kinetics. We suggest that these trade-offs define contrasting ecological strategies in major functional groups and thus contribute to the observed phytoplankton diversity. We then suggest that these contrasting strategies of nutrient utilization reflect groups' evolutionary histories and broadly correspond to the distributions of these groups in the modern ocean. Finally, we show that key functional traits scale with cell size (cell volume) as predicted by fundamental scaling relations and thus influence size spectra of phytoplankton communities.

METHODS

We compiled a database of the nutrient uptake and nutrient-dependent growth parameters measured in the laboratory for major functional/taxonomic groups of phytoplankton in marine environments: diatoms, coccolithophorids, dinoflagellates and green algae. Diatoms are a group of silicified phytoplankton responsible for up to 40% of carbon fixation and are the major exporters of organic carbon to the ocean interior (Smetacek 1999). Coccolithophorids precipitate calcium carbonate cell plates and are well-known producers of the DMSP, a precursor of DMS (dimethylsulphide, gas important in climate regulation; Matrai & Keller 1993; Levasseur *et al.* 1996). Marine dinoflagellates are often mixotrophic, some species are toxic and can produce harmful algal blooms (HABs) that negatively impact water quality (Smayda 1997). Marine green algae, including prasinophytes, represent an older lineage that likely dominated the Proterozoic and early Mesozoic oceans (Falkowski *et al.* 2004) and can be abundant in high nutrient-low chlorophyll (HNLC) areas of the ocean (Boyd & Harrison 1999). In our analysis, we concentrate on parameters for utilization of nitrate, as nitrogen is presumably the most frequently limiting nutrient in marine environments (Dugdale & Goering 1967; Ryther 1969; Hecky & Kilham 1988) and because much more data exist on nitrogen-dependent growth and uptake for marine groups, compared to other nutrients. Here, we do not consider various morphological traits that can also be important in defining phytoplankton ecological strategies (Weithoff 2003).

To characterize nutrient utilization by phytoplankton, we use parameters from the Droop model of phytoplankton growth (Droop 1973) and the Michaelis-Menten equation for nutrient uptake:

$$\text{Netgrowth} = \mu_\infty \left(1 - \frac{Q_{\min}}{Q} \right) - m$$
$$\text{Uptake} = V_{\max} \frac{R}{K + R}, \tag{1}$$

where μ_∞ is the growth rate of species at infinite quota (day^{-1}), Q is the internal nutrient concentration (nutrient

quota; μmol nutrient cell^{-1}), Q_{min} is the minimum quota (when growth rate equals 0), m is mortality (day^{-1}), V_{max} is the maximum nutrient uptake rate (μmol nutrient cell^{-1} day^{-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}). This model (eqn 1) is widely used for both marine and freshwater phytoplankton and is more realistic compared to the Monod model where growth depends on the external nutrient concentration, especially under fluctuating nutrient conditions (Grover 1991). The parameters of this model are frequently measured and constitute important traits that impact fitness, and can thus be defined as functional traits (Violle *et al.* 2007).

According to resource competition theory (Tilman 1982), nutrient competitive ability can be characterized by the breakeven nutrient concentration for a given species in monoculture at equilibrium, R^*. For the model above (eqn 1), R^* can be expressed as:

$$R^* = \frac{K\mu_\infty Q_{min} m}{V_{max}(\mu_\infty - m) - \mu_\infty Q_{min} m}, \tag{2}$$

where symbols are as in (eqn 1; Ducobu *et al.* 1998). At equilibrium, a species with the lowest R^* is predicted to win competition for a given nutrient. Interestingly, when mortality m approaches zero, R^* approaches the following:

$$R^* \rightarrow \frac{K}{V_{max}} Q_{min} m \tag{3}$$

The ratio of V_{max} to K is a commonly used measure of nutrient acquisition capability called nutrient 'uptake affinity' (Healey 1980). A high affinity indicates a superior ability to acquire the nutrient (Healey 1980). Thus, at low mortality, species' competitive ability is largely determined by the ratio of nutrient needs, Q_{min} to nutrient uptake affinity.

Lower R^* values can be achieved in several ways, which are not necessarily mutually exclusive; these include an increase in V_{max} and/or μ_∞, or a decrease in Q_{min}, K and/or m (Sterner & Elser 2002). There is little data on mortality m, which can be highly variable, so we concentrate on V_{max}, K and Q_{min} in our analysis. To determine whether there are constraints and trade-offs on the evolution of lower R^* and, thus, of better competitive abilities, we examined the data for the presence of significant pairwise relationships among major parameters using reduced major axis (RMA) regressions (Legendre & Legendre 1998; Warton *et al.* 2006). We also calculated R^* for individual species where possible and looked for trade-offs involving R^*. Specifically, we looked if there is a positive correlation between the maximum growth rate and R^* indicating a gleaner-opportunist trade-off, shown to be especially important in variable environments (Grover 1991; Litchman & Klausmeier 2001).

Where needed, data were log-transformed to normalize variance. The analysis was performed on pooled data (all taxonomic groups included); in addition, where sufficient data were available, the relationships between traits were examined for individual taxonomic groups. Individual parameters were compared between and among groups using *t*-tests and one-way ANOVA (JMP software, SAS). We did not use multivariate methods (e.g. MANOVA on multiple traits) because we found only very few species with the same multiple traits measured. If multiple studies determining the same parameter for a given species were available, the average value was used in the analysis, so that each species was represented by a single entry, except for coccolithophorids. *Emiliania huxleyi* is the only coccolithophore species for which relevant data are available (except for the maximum growth rate data) and is frequently the most abundant bloom-forming coccolithophore in the contemporary ocean (Iglesias-Rodriguez *et al.* 2002a). Moreover, different strains of *E. huxleyi* used in different studies are genetically and ecologically distinct (Iglesias-Rodriguez *et al.* 2002b). Consequently, we chose different studies of the same species to be represented by separate entries.

Key parameters of nutrient uptake often depend on growth conditions, e.g. the maximum uptake rate may be orders of magnitude greater under nutrient-limited conditions (Harrison *et al.* 1989), possibly due to activation of the high affinity uptake system (Rexach *et al.* 2002). For consistency, we included only studies where nutrient uptake and growth parameters were determined for cultures grown under limitation by that nutrient. We, however, allowed other experimental conditions, such as temperature, light levels and culturing regime (batch or chemostat) to vary across studies, as stricter study selection criteria would greatly reduce the number of applicable studies. Nevertheless, the patterns appear sufficiently robust (see Results), despite the variation in experimental conditions among studies. Most experiments were performed at 18 or 20 °C, some at 15 or 25 °C, in the presence of light.

Although there are numerous data on the maximum growth rates of different algae, the reports of the μ_∞ of the Droop model are much rarer. For species with data on Q_{min}, V_{max} and/or K but not μ_∞, we substituted the maximum reported growth rate (μ_{max}). Maximum growth rate (μ_{max}) approaches the growth rate at infinite quota (μ_∞) if the minimum quota is much smaller than the maximum quota (Turpin 1988).

Cell volumes were recorded to explore possible relationships between cell size and various parameters. If cell

volumes were not given in a study, we used average volumes from other studies or calculated them from the dimensions given in taxonomic keys (Thomas 1997) using formulas from Hillebrand *et al.* (1999). The mass-dependent parameters such as Q_{min} and V_{max} were expressed on both the 'per cell' and 'per carbon' basis. Carbon-normalized values diminish the effect of cell size on a given parameter. Where cell carbon data were absent, we used previously derived relationships between cell size and carbon content for appropriate taxonomic groups (Strathmann 1967; Montagnes *et al.* 1994; Menden-Deuer & Lessard 2000). The relationships between major parameters and cell size (cell volume) were examined by fitting the RMA regressions to $\log_{10}$-transformed data (Warton *et al.* 2006). The scaling exponents were compared with the theoretically predicted exponents derived based on the cell surface to volume-scaling relationships (Aksnes & Egge 1991).

RESULTS

Correlations and trade-offs between physiological parameters across taxonomic groups

Our data analysis reveals significant correlations and trade-offs between the parameters of nutrient (nitrate) uptake and growth across taxonomic groups. There is a significant positive relationship between the cell-specific maximum uptake rate for nitrate and half-saturation constant for nitrate uptake (Fig. 1a and Table 1). Major functional groups of marine eukaryotic phytoplankton tend to cluster along this trade-off curve, except for green algae (Fig. 1a), which suggests functional group differences in strategies of nutrient (nitrate) utilization. High cellular maximum nitrate uptake rates in diatoms and especially in dinoflagellates are associated with higher half-saturation constants for nitrate uptake. Coccolithophores exhibit a contrasting
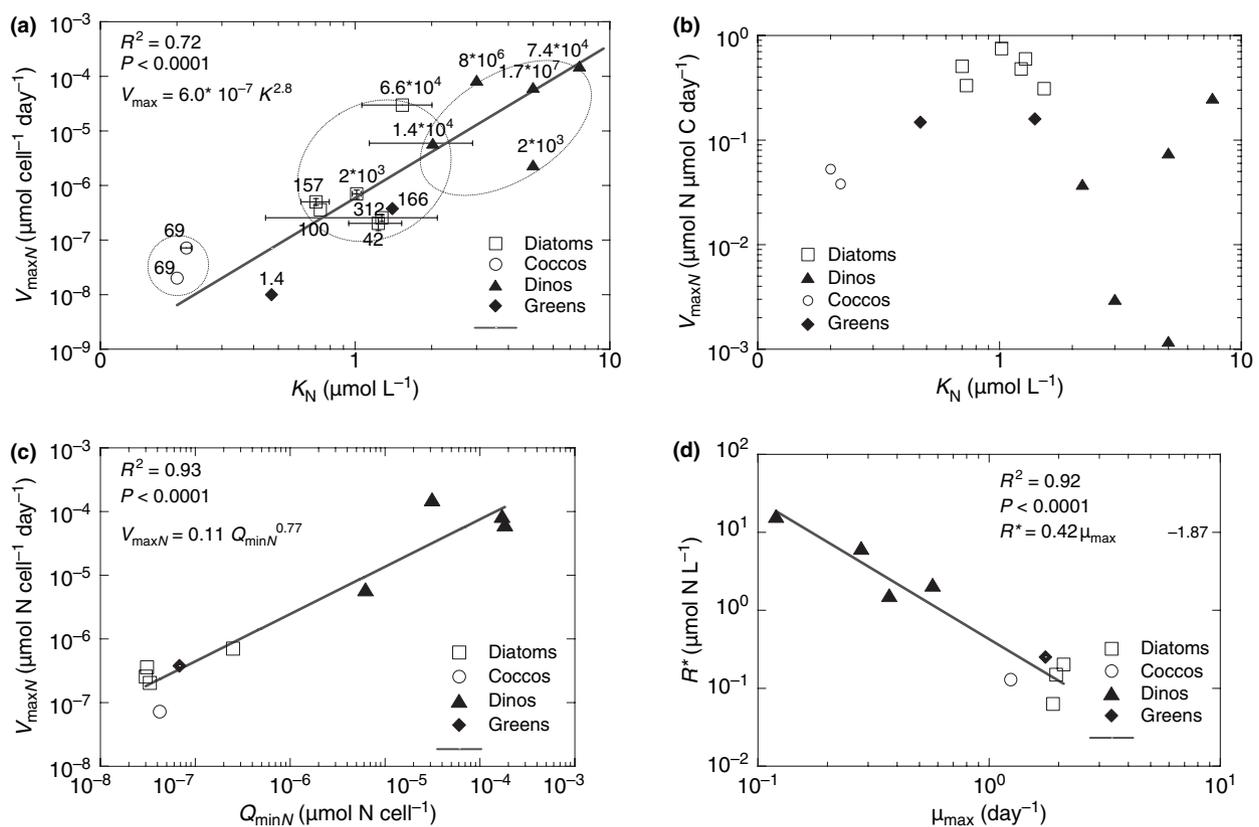
Figure 1 Correlations between major nutrient-dependent growth and uptake parameters. The R^2, P-value and the equation are for the reduced major axis regression of the $\log_{10}$-transformed data for all taxonomic groups. Source references for the data are listed in Appendix S1. (a) Cell-specific maximum uptake rate of nitrate vs. half-saturation constant for nitrate uptake. Error bars are standard errors of all studies for a given species, numbers by each data point are cell volumes (μm^3); oval contours outline species from same taxonomic group, (b) carbon-normalized maximum uptake rate of nitrate vs. half-saturation constant for nitrate uptake; (c) carbon-specific maximum uptake rates of nitrate vs. carbon-specific minimum nitrogen quota, (d) $R*$ (measure of competitive ability at equilibrium), calculated as in eqn 3, assuming low constant mortality of 0.01 day^{-1}, vs. maximum growth rate.

Relationship	Predicted exponent	Observed exponent	CI	R^2	P-value
V_{maxN} vs. V_{cell}	0.67	0.67	0.53–0.84	0.83	< 0.0001
K vs. V_{cell}	0.33	0.27	0.20–0.36	0.56	< 0.0001
Q_{minN} vs. V_{cell}	0.67–1	0.77	0.66–0.91	0.94	< 0.0001
V_{maxN} vs. K	2	2.81	2.10–3.84	0.72	< 0.0001
V_{maxN} vs. Q_{minN}	0.67–1	0.77	0.62–0.96	0.93	0.003
K vs. Q_{minN}	0.33–0.5	0.31	0.20–0.49	0.63	< 0.0001

Table 1 Predicted and observed slopes (exponents), 95% confidence intervals (CI) and P-values of the reduced major axis regressions of the $\log_{10}$-transformed parameters

Predicted values are derived from cellular scaling relationships (Aksnes & Egge 1991). See text for explanations.

association of parameters and, hence, a different nutrient uptake strategy, with the relatively low maximum uptake rates and low half-saturation constants of uptake (Fig. 1a). There is also an association of smaller cell sizes with low V_{max} and low K (Figs 1a and 3a,b). To factor out cell size influence, V_{max} was also normalized to cellular carbon content (Fig. 1b). Diatoms have the highest carbon-normalized V_{max} and intermediate K values, while coccolithophores have low V_{max} and low K. Dinoflagellates have a widespread of V_{max} and high K values (Fig. 1b).

Maximum uptake rate for nitrate is also positively correlated with minimum cell quota for nitrogen (Fig. 1c and Table 1). Significant positive relationships between V_{max} and K or Q_{min} represent potential constraints on the evolution of competitive ability (measured as R^*), as high V_{max}, low Q_{min} and K simultaneously would lead to the lowest R^*, if other parameters of eqn 2 are held constant. The maximum growth rate is negatively correlated with the half-saturation constant for nitrate uptake (data not shown). This relationship, however, does not constitute a trade-off, as both high maximum growth rate, μ_∞, and low K would lead to lower R^*. Interestingly, there is a significant negative correlation between maximum growth rate and R^*, suggesting the absence of the gleaner-opportunist trade-off, at least in this data set when all groups are considered together (Fig. 1d). Diatoms by themselves, however, show a positive relationship between R^* and maximum growth rate (relationship not shown). We did not find significant relationships between the maximum growth rate and minimum nitrogen quota or between the maximum growth rate and the maximum uptake rate for nitrate.

Taxonomic group differences among traits

Diatoms have significantly higher carbon-specific nitrate uptake rates compared to coccolithophorids (*E. huxleyi*), dinoflagellates or chlorophytes (Fig. 2a). At the same time, they have higher minimum quota for nitrogen compared to coccolithophorids (Fig. 2b). Coccolithophorids have the lowest half-saturation constants for nitrate uptake (Fig. 2c). Dinoflagellates have relatively low maximum uptake rates

and high half-saturation constants for nitrate uptake. Green algae exhibit intermediate values of parameters of nitrate-dependent growth and uptake (Fig. 2). The affinity (V_{max}/K) for nitrate is high in diatoms and coccolithophores and low in dinoflagellates and green algae (Table 2). In contrast, the affinity for ammonium uptake is high in green algae and coccolithophores and lower in diatoms and dinoflagellates. The relative affinity for ammonium over nitrate is markedly higher in green algae compared to other taxonomic groups (Table 2). Maximum growth rates of dinoflagellates are significantly lower than the growth rates of diatoms (Fig. 2d).

Allometric scaling relationships

Major parameters of nutrient uptake and growth scale with cell size (Table 1). The general relationship is a power function of cell volume. Maximum uptake rate for nitrate on a per cell basis increases with cell size (Fig. 3a) and the exponent (Table 1) is not significantly different from that predicted by Aksnes & Egge (1991), based on cell surface area considerations (see Discussion). K also increases with cell volume across taxonomic groups, with the exponent consistent with the predicted one (Fig. 3b and Table 1). Within groups, there is a highly significant relationship between K and cell size in diatoms ($K = 0.17\ V_{cell}^{0.25}$, $P = 0.019$), but not in dinoflagellates (Fig. 3b). Minimum cellular quota for nitrogen is also positively correlated with cell volume (Fig. 3c and Table 1).

DISCUSSION

Trade-offs as determinants of contrasting ecological strategies

Significant positive correlations between V_{max} and Q_{min} and V_{max} and K found in our data analysis imply inherent physiological trade-offs between these physiological traits. These correlations may constrain competitive evolution of R^* that would result in a 'super species' with the lowest R^* within the planktonic community and lead to a competitive
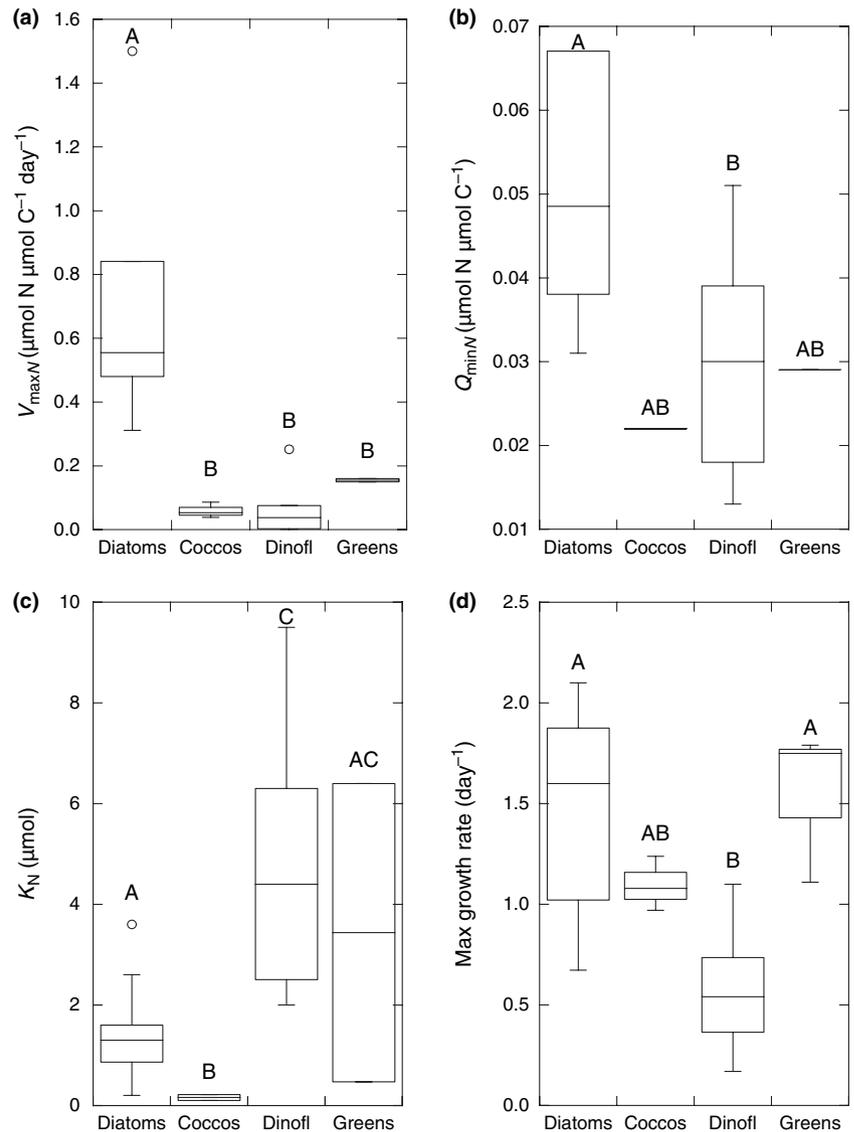
Figure 2 Parameter distribution in major groups of eukaryotic marine phytoplankton. Data were obtained from references listed in Appendix S1. n is number of species. (a) Maximum uptake rates (carbon-normalized) for nitrate in diatoms ($n = 7$), coccolithophorids ($n = 3$), dinoflagellates ($n = 5$) and green algae ($n = 2$); (b) minimum quota for nitrogen (carbon-normalized) in diatoms ($n = 7$), coccolithophorids ($n = 1$), dinoflagellates ($n = 6$) and green algae ($n = 1$); (c) half-saturation constant for uptake of nitrate for diatoms ($n = 12$), coccolithophorids ($n = 2$), dinoflagellates ($n = 8$) and green algae ($n = 2$); (d) maximum growth rates for diatoms ($n = 8$), coccolithophores ($n = 3$), dinoflagellates ($n = 7$) and green algae ($n = 3$). t-Tests were used to compare each pair, distributions with non-overlapping letter combinations are significantly different ($P < 0.05$).

exclusion of other species. The existence of these physiological trade-offs (correlations) in the nutrient uptake and growth parameter space also suggests the evolution of contrasting ecological strategies of nutrient utilization. Remarkably, major functional groups cluster along the trade-off curves, thus adopting different strategies of nutrient utilization. For example, high maximum uptake rates found in diatoms may be advantageous under high or fluctuating nutrients, while the low half-saturation constants for uptake characteristic for coccolithophores may optimize nutrient acquisition under low nutrient conditions (Doyle 1975; Turpin 1988; Grover 1991).

What are the mechanistic bases for the observed physiological trade-offs? The positive correlation of $V_{\max}$ and K for nitrate uptake observed in this and other studies (see Collos *et al.* 2005) can be explained mechanistically,

based on such fundamental relationships as cell surface to cell volume scaling and enzyme kinetics. According to Aksnes & Egge (1991), the maximum uptake rate of a nutrient

$$V_{\max} = \frac{n}{h}, \tag{4}$$

where n is the number of uptake sites and h is the ion handling time. The half-saturation constant can be expressed as follows:

$$K = \frac{1}{Avh}, \tag{5}$$

where A is the area of one uptake site and v is the mass transfer coefficient. n, The number of uptake sites increases with cell surface and, thus, $V_{\max}$ should increase linearly
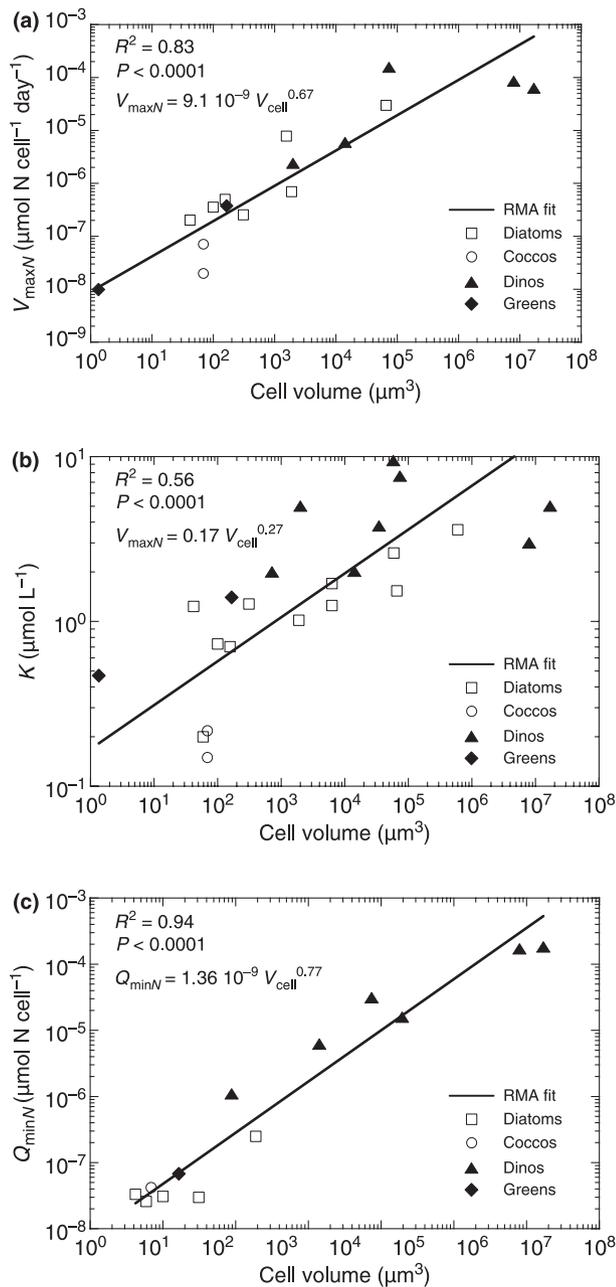
Figure 3 Cell volume dependence of major uptake parameters (log–log scale). Data were obtained from references listed in Appendix S1. The R^2, *P*-value, slope (cell volume exponent) and intercept are for the reduced major axis regression of the $\log_{10}$-transformed data for all taxonomic groups. (a) Maximum cell-specific uptake rate for nitrate, (b) half-saturation constant for nitrate uptake vs. cell volume, (c) minimum cell-specific nitrogen quota vs. cell volume.

with cell surface (cell radius squared) or with a 2/3 exponent of cell volume (Aksnes & Egge 1991). The observed exponent agreed with the predicted relationship (Fig. 3a and

Table 1). Because the mass transfer coefficient scales linearly with radius, so K is predicted to increase linearly with cell radius. Therefore, V_{max} should be proportional to K^2. Interestingly, the exponent of the V_{max} vs. K relationship (Fig. 1a and Table 1) is close to 2, thus supporting Aksnes and Egge's scaling argument.

According to Aksnes and Egge's calculations following Raven (1980), the total uptake area for a nutrient can comprise *c*. 10% of the cell surface. Given the fact that algae need to take up at least five macronutrients and up to 54 micronutrients (nitrate, ammonium, phosphate, iron, molybdenum, etc.) and carbon, it is possible that there may be a limited surface area available for an uptake of a particular ion, as only a part of cell surface is occupied by active uptake sites (Button 1998) and those sites are ion-specific (Gouaux & MacKinnon 2005). This limited surface area can be divided into uptake sites in at least two different ways: high number of uptake sites (high *n*; i.e. greater density of transporters, Raven 1980) packed in; that results in a relatively small active area per each (small A) leading to high V_{max} and high K (eqns 4 and 5) or few uptake sites (small *n*) spread out with a large uptake area of each site (large A) leading to low K and low V_{max} (eqns 4 and 5). If each uptake site is associated with a fixed number of uptake proteins (transporters; Button 1998), then under chronic nitrogen limitation the optimal strategy could be to reduce the number of uptake sites and thus, the investment in uptake proteins, and to increase the active uptake area per site, instead. This would produce a relatively low maximum uptake rate and low half-saturation constant for uptake, as observed in coccolithophorids, and corresponds to the association of this group with oligotrophic conditions. Under high and/or fluctuating nutrient conditions, investment of nitrogen into uptake proteins is not constrained. Having more uptake sites would alleviate uptake limitation by the handling time and allow more ions taken up per unit time. Therefore, the optimal strategy under high nutrients may be a high number of uptake sites leading to high V_{max} (and high K).

A positive correlation between V_{max} and Q_{min} for nitrogen (Fig. 1c) may occur if the nutrient uptake- and transport-related proteins comprise a significant fraction of Q_{min} for nitrogen. A high V_{max} associated with high concentration of uptake proteins will then cause high Q_{min} for nitrogen. Conversely, having high nitrogen needs could select for higher uptake capabilities (Klausmeier *et al.* 2007).

A limited cell surface area available for uptake of individual nutrients (ions) may also lead to trade-offs between the uptake parameters (V_{max} or K) for different nutrients (e.g. nitrate vs. phosphate). Such trade-offs may be present if the uptake sites (i.e. protein transporters) are ion-specific, which may be true for many ion transporters (Gouaux & MacKinnon 2005). More data on the uptake

parameters of different nutrients are needed to address the possibility of such trade-offs. Grover (1991) suggested that other physiological trade-offs may be important in defining species competitive abilities under equilibrium vs. non-equilibrium nutrient supplies, such as the trade-off between V_{max} and maximum nutrient quota, Q_{max}. We did not find enough Q_{max} measurements to detect the hypothesized trade-off.

Our data analysis shows that diverse species of marine phytoplankton spanning several orders of magnitude in cell volume and belonging to biogeochemically distinct functional groups obey the same fundamental relationships between key functional traits, yet adopt different ecological strategies of nutrient utilization defined by those relationships and nutrient availability. Marine diatoms, with their high maximum nutrient uptake rates and high growth rates, exhibit the 'velocity' strategy according to a classification proposed by Sommer (1984) for phytoplankton. Large diatoms, with their lower growth rates (due to negative correlation of growth rate with cell size, Banse 1976) and high maximum nutrient uptake rates may be more 'storage-adapted' (Sommer 1984). Large diatoms have disproportionately large storage vacuoles compared to smaller diatoms (Sicko-Goad et al. 1984) and since nitrate (but not ammonium) is stored in vacuoles (Raven 1987), large diatom size can lead to a 'storage-adapted' strategy. In contrast, coccolithophores having the intermediate maximum nitrate uptake rates but low half-saturation constants for uptake are more the 'affinity' strategists (Sommer 1984, 1989). Marine dinoflagellates have significantly lower maximum carbon-specific nutrient uptake rates than diatoms, and significantly higher half-saturation constants for nitrate uptake and relatively low maximum growth rates [although some dinoflagellates are capable of rapid growth (Smayda 1997)], thus being poor competitors for nitrate. It is likely that such 'dirty tricks' (Thingstad 1998) as the ability to feed heterotrophically and migrate in the water column allows dinoflagellates to persist, despite the relatively non-competitive parameters for nitrogen uptake and growth (Eppley et al. 1969; Smayda 1997). Green algae appear to have intermediate values for nitrate uptake parameters (Fig. 2) and exhibit the 'velocity-adapted' strategy as they have high maximum growth rates and second highest nitrate uptake rates. They have an extremely high affinity for ammonium uptake and thus may be superior competitors for ammonium (Table 2). Therefore, trade-offs in competitive abilities for different forms of inorganic nitrogen and trade-offs in utilizing inorganic vs. organic forms of nitrogen may also contribute to diversity of marine eukaryotic phytoplankton.

Besides being adapted to contrasting nutrient regimes, major groups of phytoplankton appear to be adapted to the whole suite of physico-chemical conditions, such as light and turbulence, associated with those nutrient regimes.

Table 2 Uptake affinity {ratio of V_{max} [μmol N (μmol C)$^{-1}$ day^{-1}] to K (μmol)} for nitrate and ammonium and relative affinity for ammonium over nitrate in major groups of marine eukaryotic phytoplankton

	Ammonium	Nitrate	Ammonium/ nitrate
Diatoms	0.586 (7/10)	0.446 (7/12)	1.31
Dinoflagellates	0.003 (3/7)	0.009 (5/8)	0.31
Coccolithophores	1.588 (1/2)	0.265 (2/1)	5.99
Chlorophytes	1.715 (3/4)	0.045 (2/2)	37.76

Median values of V_{max} and K for each group were used to calculate affinity. Number of species used to calculate affinity is given in parentheses (number of species with known V_{max} over number of species with known K).

Coccolithophores are well adapted not only to oligotrophic (low nutrient) conditions, but also to high irradiance levels often associated with such conditions (Iglesias-Rodriguez et al. 2002a). In contrast, diatoms have low half-saturation constants for irradiance-dependent growth (Richardson et al. 1983) and are generally more adapted to low light characteristic of high nutrient, intense mixing conditions (Falkowski 1980). Thus, phytoplankton nutrient utilization strategies, in conjunction with their responses to physical environment, such as turbulence and light, to a large extent define ecological niches of the two groups. The idea of phytoplankton functional groups associated with different nutrient and turbulence regimes was pioneered by Margalef and elegantly expressed in his nutrient-turbulence 'mandala' (Margalef 1978).

These ecological niches correspond remarkably well to the distributions of the two groups in the ocean. Diatom relative abundance is positively correlated with nitrogen (and phosphorus) concentrations (e.g. Schiebel et al. 2004) and negatively correlated with the stability of the water column (Li 2002). In contrast, coccolithophorid abundance is greater at low nitrate and phosphate and high water column stability and irradiance (Cavender-Bares et al. 2001; Haidar & Thierstein 2001; Iglesias-Rodriguez et al. 2002a; Schiebel et al. 2004). Consequently, the abundances of the two groups are significantly negatively correlated (Schiebel et al. 2004).

Trait correlations with cell size

Major parameters of nutrient uptake scale with cell size consistent with general cell surface area relationships and enzyme kinetics (Aksnes & Egge 1991; Table 1). As predicted (Aksnes & Egge 1991), maximum uptake rate for nitrate V_{maxN} should scale linearly with cell surface area (cell volume exponent of 0.67), due to uptake sites located

on cell surface. Based on the diffusion limitation considerations, the predicted power relationship between K and cell volume should have the exponent of $1/3$ (linear scaling with cell radius; Aksnes & Egge 1991). The observed scaling exponents for these two functional traits are not significantly different from the predicted values (Table 1). In general, the relationships hold across different functional groups. There are also group-specific differences as well: K is significantly correlated with cell volume in diatoms but not in dinoflagellates. A lack of correlation of K with cell size in dinoflagellates suggests minimal diffusion limitation effects and could perhaps be explained by non-spherical cell shapes and motility, reducing diffusion limitation (Pahlow *et al.* 1997) or by heterotrophy, decreasing selection on K. An increase of Q_{min} (expressed on a per cell basis) with cell volume was reported and discussed previously by Shuter (1978). We may hypothesize that Q_{min} is proportional to cytoplasm volume and thus should be proportional to cell volume (exponent of 1) in small cells and to cell surface in large cells (exponent of 0.67) because vacuoles increase faster with cell size than cytoplasm, especially in diatoms (Sicko-Goad *et al.* 1984), causing cytoplasm to be distributed more peripherally along the cell surface. As our data covered a wide range of sizes, the observed exponent of 0.77 falls predictably within these two bounds.

Based on these volume-scaling relationships for individual physiological traits, we can also derive exponents for power relationships between these traits (Table 1). Interestingly, the observed exponents of such pairwise relationships are remarkably close to the predicted ones (Table 1).

The correlations of nutrient uptake parameters with cell size may explain general patterns of phytoplankton size distributions in the ocean, where small cells [often coccolithophores and green algae (prasinophytes)] dominate low nutrient environments and large cells (often diatoms) increase in abundance with increasing nutrients (Cavender-Bares *et al.* 2001; Li 2002). As discussed above, high V_{max}, correlated with high K, may be advantageous under high/fluctuating nutrients, while low V_{max} and low K may be advantageous under low nutrient conditions. Given that V_{max} and K are positively correlated with cell size (Fig. 3), it follows that low nutrient environments should have small-celled species and high nutrient environments should have large-celled species.

Effects of evolutionary history on traits

We hypothesize that major characteristics of nutrient uptake and growth of phytoplankton reflect both adaptations to particular environments and their evolutionary history. Coccolithophorid diversification occurred in the oligotrophic ocean of late Jurassic and Cretaceous in the Mesozoic (Vargas *et al.* 2007). Modern coccolithophores remain associated with stratified oligotrophic conditions (Cavender-Bares *et al.* 2001; Haidar & Thierstein 2001; Schiebel *et al.* 2004). In contrast, diatoms diversified under highly mixed, more nutrient-rich conditions in late Mesozoic to early Cenozoic (Falkowski *et al.* 2004) and their association with such conditions appears to be preserved in the modern ocean as well.

All algal groups appear to preferentially take up ammonium over nitrate, likely because nitrate but not ammonium has to be reduced before assimilation and thus may require more energy to be assimilated (Syrett 1981). However, as our analysis indicates (Table 2), the relative preference for ammonium over nitrate (measured as the affinity [V_{max}/K, Healey 1980) for ammonium over nitrate affinity] is greater in green algae, compared to diatoms and other taxonomic groups of marine eukaryotic phytoplankton. This may reflect the effect of the oceanic redox conditions at the time of origin of respective groups: green algae appeared around 1.5 billion years ago (Hedges *et al.* 2004; Yoon *et al.* 2004) in mid-Proterozoic, when suboxic conditions (Anbar & Knoll 2002) could have caused the reduced form of N (i.e. ammonium) to be prevalent (Stumm & Morgan 1981). In agreement with this reasoning, cyanobacteria, the earliest photoautotrophs, evolved under anoxic conditions (Anbar & Knoll 2002; Hedges *et al.* 2004), also have a strong preference for ammonium over nitrate (Herrero *et al.* 2001). Diatoms appeared much later, *c.* 150 Ma (Medlin *et al.* 1996), when the oceans were highly oxidized and consequently are better adapted at utilizing nitrate. Therefore, modern strategies of nutrient utilization by major taxonomic groups appear to be consistent with the conditions at the time of their origin and/or diversification and suggest conservatism in trait values over groups' evolutionary histories. A theoretical study by Kraft *et al.* (2007) showed that conserved traits led to a better agreement between trait- and phylogeny-based characterizations of community structure compared to highly evolving traits. Physiological trait conservatism in phytoplankton, at least at the level of major taxonomic groups, may then explain group clustering in the physiological trait space (Fig. 1) and their association with contrasting environmental conditions in the modern ocean.

A trait-based approach that includes information on key physiological traits and trade-offs such as presented here is a very promising tool for successfully explaining global phytoplankton distributions. Follows *et al.* (2007), using a model with multiple phytoplankton types defined by simple trade-offs in physiological traits, showed that different biogeochemical groups 'emerged' under different environmental conditions. Trait-based approach to phytoplankton communities may be useful not only in explaining existing distribution patterns, but also in predicting future community structure (Litchman *et al.* 2006).

Here, we concentrated on the physiological relationships in nutrient utilization traits and showed that mechanistic trade-offs between traits, arising from fundamental relationships, provide basis for diverse ecological strategies of major phytoplankton groups and can explain global patterns of their distribution in the ocean. Trade-offs between other ecophysiological or morphological traits, such as trade-offs between light and nutrient competitive abilities, resource competitive ability – maximum growth rate trade-off (Grover 1991; Litchman & Klausmeier 2001), nutrient competitive ability – grazer resistance trade-off (e.g. Leibold 1997) are also crucial in defining ecological strategies of phytoplankton and likely influence phytoplankton distributions along environmental gradients. A consideration of functional traits and trade-offs in an ecological context that defines major selective pressures should improve our understanding of the mechanisms structuring past, present and future ecological communities.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Source references for Table 1, 2 and Figs 1-3.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2007.01117.x.

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