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ABSTRACT

This paper presents a compilation of nutrient utilization traits of marine and freshwater phytoplankton. The literature was comprehensively searched for culture experiments using nitrate, ammonium, or phosphate as the limiting nutrient. The following traits were extracted: the response of growth to nutrient supply (maximum growth rate under unlimited nutrient supply and the nutrient concentration at which growth is half-saturated); the response of internal nutrient content to nutrient supply (the minimum subsistence quota at which growth ceases and the maximum nutrient quota under unlimited nutrient supply); and nutrient uptake kinetics for nutrient-limited cells (maximum uptake rate and the nutrient concentration at which uptake is half-saturated). The resulting data set includes 1319 measurements on 129 species from 138 publications. Potential uses of these data include studies of community structure and trait evolution, parameterization of ecosystem models, and biofuel development.

INTRODUCTION

A primary tactic in the study of phytoplankton is the measurement of eco-physiological traits using laboratory cultures. Quantifying how growth and other physiological processes respond to factors such as nutrients, light, and temperature is essential for answering a broad range of questions pertaining to physiology, ecology, and evolutionary biology. For example, comparative analyses of trait variation across species are increasingly used to understand the mechanisms that structure communities (Litchman et al. 2007, Bruggeman 2011, Thomas et al. 2012, Edwards et al. 2013*a*, Marañon et al. 2013, Boyd et al. 2013) and to reconstruct the history of trait evolution (Bruggeman 2011, Quigg et al. 2011). Because trait measurements on cultures are laborious to perform, existing data are scattered across decades of publications. In the past there have been a few compilations of phytoplankton traits (e.g., Shuter 1978, Smayda 1997, Bruggeman 2011), but there are currently no up-to-date compilations that exhaustively cover the available data for how marine and freshwater phytoplankton use nitrogen and phosphorus.

For this data set we have compiled commonly measured traits related to the utilization of nitrogen and phosphorus. The traits compiled quantify the response of growth to nutrient supply (maximum growth rate under unlimited nutrient supply, and the nutrient concentration at which growth is half-saturated); the response of internal nutrient content to nutrient supply (the minimum subsistence quota at which growth ceases, and the maximum nutrient quota under unlimited nutrient supply); and nutrient uptake kinetics for nutrient-limited cells (maximum uptake rate and the nutrient concentration at which uptake is half-saturated). These are the most commonly measured traits that characterize how phytoplankton respond to nutrient limitation, and we have compiled these for the most commonly measured nutrients, nitrate, ammonium, and phosphate. The resulting dataset includes 1319 measurements on 129 species from 138 publications, including marine and freshwater species from 13 major taxonomic groups.

METADATA

CLASS I. DATA SET DESCRIPTORS

A. Data set identity:

Title: Nutrient utilization traits of phytoplankton

B. Data set identification code:

`Table1.csv`

`Table2.csv`

`Table3.csv`

C. Principal Investigators:

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Abstract: Much of the physiology, ecology, and evolution of phytoplankton is defined by their interaction with limiting nutrients. Here we present a comprehensive literature compilation of traits measured on laboratory cultures related to the use of nitrate, ammonium, and phosphate. These traits include maximum growth rate, the half-saturation constant for nutrient-limited growth, the minimum subsistence quota, the maximum nutrient quota, the maximum uptake rate, and the half-saturation constant for uptake. The data set includes 1319 measurements on 129 unique species from 138 publications. We also present a compilation of cell volume measurements covering the species for which nutrient utilization traits have been measured.

D. *Key words*: *affinity; half-saturation; maximum growth rate; Monod curve; nutrient limitation; nutrient storage; phytoplankton; subsistence quota; uptake kinetics*.

CLASS II. RESEARCH ORIGIN DESCRIPTORS

A. Overall project description

Identity: Trait-based approaches to phytoplankton communities

Originators:

Elena Litchman, Christopher A. Klausmeier

Period of Study: 2001–2013

Objectives: To compile existing data on nutrient utilization traits of phytoplankton, which will permit analyses of trait variation and covariation across species, community trait structure, trait-based models, and other topics.

Sources of funding: NSF grants DEB 0610531, DEB 0610532, DEB 0845932, DEB 0845825, and OCE 0928819.

B. Specific subproject description

Data acquisition, methodology, and criteria for inclusion. We comprehensively searched the literature for studies that used unialgal cultures to measure how phytoplankton growth, nutrient content, and nutrient uptake rate respond to nutrient supply. We focused on experiments using nitrate, ammonium, or phosphate as the limiting nutrient. We only compiled studies where light was not strongly limiting, and where only a single nutrient was limiting. For one diazotroph (*Trichodesmium*), the experiments compiled here did not include nitrogen in the medium.

Growth as a function of external nutrient concentration. The response of growth to external nutrient supply is typically characterized by the Monod curve (Monod 1949), $\mu(R) = \frac{\mu_{max} R}{K_m + R}$, where μ is the specific growth rate as a function of external nutrient concentration R, μ_{max} is the asymptotic specific growth rate under infinite nutrient concentration, and K_m is the nutrient concentration at which growth equals half of μ_{max}. The Monod curve is usually fit using data from batch cultures, where nutrient supply is varied over a wide range and the corresponding growth rates are measured; or, alternatively, using data from chemostat experiments, where dilution rate is varied and the corresponding steady-state external nutrient concentration is measured. In nearly all cases we report the values of μ_{max} and K_m reported by the authors of the study, although in a few cases where a Monod fit was not reported we extracted data from figures to fit a curve.

A number of studies did not measure Monod-type growth curves but did report the maximum growth rate obtained under saturating nutrient supply, for example in batch culture or in chemostat experiments measuring nutrient content as a function of dilution rate. We have included those measurements as estimates of μ_{max}.

Growth as a function of nutrient content. Phytoplankton growth under limitation by a single nutrient is typically a hyperbolic function of the internal concentration (or quota) of that nutrient. This relationship is most often characterized with the Droop model (Droop 1973), $\mu(Q) = \mu_\infty(1 - \frac{Q}{Q_{min}})$, where μ is specific growth rate as a function of cellular nutrient quota Q, Q_{min} is the minimum quota at which growth ceases, and μ_∞ is the hypothetical asymptotic growth rate at infinite nutrient quota (Klausmeier et al. 2004). For studies that fit the Droop curve or a similar hyperbolic model, we report μ_∞ and Q_{min} as reported by the authors. Nutrient quota can be measured on a per cell or per cellular carbon basis, and we have included studies that use both approaches. It should be noted that μ_∞ does not quantify an attainable growth rate, but is rather a curve-fitting parameter, and will exceed the true μ_{max} to a degree that depends on the magnitude of luxury nutrient consumption (Grover 1991).

Some studies did not measure growth over a range of nutrient quotas, but estimated Q_{min} as the nutrient content when a nutrient-limited batch culture reaches stationary phase and ceases to grow. We have included these estimates of the minimum subsistence quota.

The nutrient quota obtained under saturating nutrient supply (Q_{max}) reflects the ability of a cell to store excess nutrient, and may determine the outcome of competition under variable nutrient supply (Grover 1991). Q_{max} is somewhat tricky to define, because the quota obtained under saturating supply of all nutrients may be less than the quota obtained when growth is slowed because a second nutrient is limiting (Elrifi and Turpin 1985). With this caveat in mind, we have recorded estimates of Q_{max} for a variety of species. In these studies Q_{max} may be estimated as the nutrient content under exponential growth with saturating nutrient supply, or as the nutrient content after 3–24 hours of saturated nutrient uptake.

Uptake kinetics. Nutrient uptake rate as a function of nutrient concentration is typically quantified with the hyperbolic Michaelis-Menten curve, where the uptake rate equals $\frac{V_{max}R}{K+R}$, and where V_{max} is the asymptotic maximum rate of uptake at infinite concentration of the nutrient R, and K is the concentration at which uptake rate equals half of V_{max}. It is often the case that V_{max} for a nutrient increases as the cellular content of that nutrient declines (Gotham and Rhee 1981). Therefore, we have recorded estimates of the Michaelis-Menten parameters, using only experiments where the cells were preconditioned to be strongly nutrient-depleted or nutrient-starved. We made this decision so that uptake parameters would be comparable across species in reflecting uptake abilities under nutrient limitation. It is often the case that nitrogen-starved cells will initially exhibit relatively slow uptake when re-supplied with nitrate, and uptake will increase substantially after supplying the cells with a moderate concentration of nitrate for a period of minutes to hours (Eppley et al. 1969). A number of studies in our compilation used such a procedure before measuring nitrate uptake rates. Some studies did not measure uptake rate across a range of nutrient concentrations, but measured V_{max} by supplying cells with a large, saturating pulse of nutrients.

Units. We converted all measurements to a common set of units: specific growth (day^{-1}) for μ_{max} and μ_∞, µmol L^{-1} for K_m and K, µmol $cell^{-1}$ for Q_{min}, and µmol $cell^{-1}$ hr^{-1} for V_{max}. For the small number of cases where a trait was measured multiple times on the same isolate, these values were averaged. Some studies measured V_{max} and/or Q_{min} in carbon-specific units, which we will refer to as $V_{max:C}$ and $Q_{min:C}$. These measurements have been recorded separately, in units of µmol nutrient per µmol C (for Qmin:C), or µmol nutrient per µmol C hr^{-1} (for V_{max}:C). If C per cell was measured in the same study, or if we could find an estimate of C per cell measured on the same isolate, we calculated V_{max} and Q_{min} from $V_{max:C}$ and $Q_{min:C}$. Sources for C:cell data are documented in the data set. In a few cases traits were measured on a dry mass basis, and we converted these to carbon-specific values assuming that carbon is 50% of dry mass.

Nomenclature. We have not exhaustively cross-referenced our data set against recent nomenclatural changes, but for older studies we have updated species names such that all studies in the data set that test the same species are reported with a consistent name. When a name was changed the name used in the original study is recorded in a "synonym" column.

When possible, we have recorded a strain identifier for each experiment, using an identification code from a large culture collection. Culture collection abbreviations include CCMP (National Center for Marine Algae and Protozoa), SAG (Experimental Phycology and Culture Collection of Algae at the University of Goettingen), CCAP (Culture Collection of Algae and Protozoa), UTEX (The Culture Collection of Algae at the University of Texas at Austin), RCC (Roscoff Culture Collection), NEPCC (Canadian Center for the Culture of Microorganisms), and PCC (Pasteur Culture Collection). A few commonly-studied isolates of *Synechococcus*, *Prochlorococcus*, *Trichodesmium*, and *Emiliania* are listed by the strain name given in the source publication.

To facilitate comparison of traits between taxonomic groups, we have coded each species according to the coarse taxonomic groups often used for phytoplankton. These include chlorophyte, chrysophyte, coccolithophore, cryptomonad, cyanobacteria, desmid, diatom, dinoflagellate, euglenoid, haptophyte (other than coccolithophores), pelagophyte, raphidophyte, and xanthophyte. We have also coded whether the species was isolated from a freshwater or marine environment; estuarine species have been coded as marine.

Cell volume. To facilitate the comparison of species that differ vastly in cell size, we have compiled estimates of cell volume for nearly all species in the data set. If volume was measured in the original study, that value was recorded. In a few cases the diameter was reported for

approximately spherical cells, and we converted diameters to volumes assuming a spherical shape. If no studies on a species measured cell volume, we recorded a volume estimate from a different publication when possible. Sources for volume estimates are recorded in the data set.

Use of the data in previous publications. Subsets of the dataset have been used in previous publications by the authors. Litchman et al. (2007) analyzed trait correlations, allometric relationships, and taxonomic differences for nitrate and ammonium traits of marine phytoplankton. Litchman et al. (2009) used allometric relationships of nitrate and phosphate utilization traits to parameterize an eco-evolutionary model. Edwards et al. (2011) analyzed trait correlations for nitrate and phosphate traits of marine and freshwater phytoplankton. Edwards et al. (2012) analyzed allometric relationships for nitrate and phosphate traits of marine and freshwater phytoplankton. Edwards et al. (2013*a*) compared nitrate traits to time series of marine phytoplankton, and Edwards et al. (2013*b*) compared phosphate traits to spatial distributions of freshwater phytoplankton. Edwards et al. (2013*c*) analyzed trait correlations of phosphate traits in freshwater phytoplankton, and used these relationships to parameterize a model of competition. Of these publications, raw trait data was included in Edwards et al. (2013*b*) and Edwards et al. (2013*c*).

The trait data presented here includes all of the trait data used in these publications, with the following exceptions: Edwards et al. (2012) and Edwards et al. (2013*a*) include data on maximum growth rate from thermal response curves compiled in Thomas et al. (2012); Edwards et al. (2013*a*, 2013*b*, 2013*c*) use light utilization trait data, which have been compiled in Schwaderer et al. (2011) and Edwards et al. (2015); a few measurements of uptake kinetics used in previous analyses were not included in the present data set because the cultures were not conditioned to be strongly nutrient-depleted before measuring uptake, which is a criterion used in the present compilation to ensure comparability across species. The data set presented here also includes a few entries appropriate for the previous analyses but not previously used, either because they are from literature published subsequently, or because they are from publications newly discovered by the authors during preparation of the data set.

CLASS III. DATA SET STATUS AND ACCESSIBILITY

A. Status

Latest update: December 2013

Latest Archive date: December 2013

Metadata status: Metadata is current and up to date.

Data verification: All data has been at minimum double-checked.

B. Accessibility

Storage location and medium: The Ecological Society of America's *Ecological Archives*.

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Copyright restrictions: None.

Proprietary restrictions: None.

Costs: None.

CLASS IV. DATA STRUCTURAL DESCRIPTORS

A. Data Set File

The data set is downloadable as a single archive, NutrientTraits.zip (29 KB), which contains the following *.csv files:

Table 1: Nutrient utilization traits. Each row presents a single species/strain from one publication. If multiple traits were measured on that strain in that publication, they are all listed in the same row. If the same strain was tested at multiple temperatures, the measurements from each temperature are recorded in different rows. Temperature of the experiment, irradiance, daylength, taxon, system (freshwater/marine), isolate ID, cell volume, C per cell, and citation source are all included as well.

Table 2: Citation information for nutrient utilization traits, with a corresponding integer code that matches with the citation column in Table 1.

Table 3: Cell volume measurements for nearly all species in the nutrient trait data set. These measurements supplement those in Table 1, which only includes measurements reported in the nutrient trait publications. The volume measurements in Table 1 are presented again, along with measurements from the literature for species not measured in the nutrient trait publications.

Size:

Table 1: 66 KB, 385 rows and 42 columns.

Table 2: 28 KB, 138 rows and 2 columns.

Table 3: 30 KB, 135 rows and 4 columns.

Format and Storage mode: CSV text, comma delimited. Special characters/fields: All missing values are denoted as "NA".

Authentication procedures: SHA checksum for Table 1: eea495550b172644396fe7dc2be3b011f4f7b8c6, for Table 2: 34e9a636a8d573290300ed3cf85ff55e440a51b2, for Table 3: 56a00f999c9c98ad72074c1bb8df8bbe2bafbfd2.

B. Variable definitions:

Table 1

Column name	Variable definition	Units	Storage type
species	Species name	text	string

isolate	Isolate ID	text	string
taxon	Taxon name	text	string
system	Freshwater/marine	text	string
temperature	Culture temperature	°C	floating point
irradiance	Culture irradiance	µmol photons m^{-2} s^{-1}	floating point
light_hours	Culture daylength	hr	integer
synonym	Former species name	text	string
volume	Cell volume	μm^3	floating point
c_per_cell	Carbon per cell	µmol $cell^{-1}$	floating point
c_citation	C per cell citation	integer	integer
mu_inf_amm	μ_∞ for ammonium-limited growth	day^{-1}	floating point
mu_amm	μ_{max} for ammonium-limited growth	day^{-1}	floating point
k_amm_m	K_m for ammonium-limited growth	µmol L^{-1}	floating point
k_amm	K for ammonium uptake	µmol L^{-1}	floating point
vmax_amm	V_{max} for ammonium uptake	µmol N $cell^{-1}$ day^{-1}	floating point
vmax_amm_c	V_{max}:C for ammonium uptake	µmol N µmol C^{-1} day^{-1}	floating point
qmin_amm	Q_{min} for ammonium-limited growth	µmol N $cell^{-1}$	floating point

qmin_amm_c	$Q_{min:C}$ for ammonium-limited growth	µmol N µmol C^{-1}	floating point
qmax_amm	Q_{max} for ammonium-limited growth	µmol N $cell^{-1}$	floating point
qmax_amm_c	$Q_{max:C}$ for ammonium-limited growth	µmol N µmol C^{-1}	floating point
mu_inf_nit	μ_∞ for nitrate-limited growth	day^{-1}	floating point
mu_nit	μ_{max} for nitrate-limited growth	day^{-1}	floating point
k_nit_m	K_m for nitrate-limited growth	µmol L^{-1}	floating point
k_nit	K for nitrate uptake	µmol L^{-1}	floating point
vmax_nit	V_{max} for nitrate uptake	µmol N $cell^{-1}$ day^{-1}	floating point
vmax_nit_c	V_{max}:C for nitrate uptake	µmol N µmol C^{-1} day^{-1}	floating point
qmin_nit	Q_{min} for nitrate-limited growth	µmol N $cell^{-1}$	floating point
qmin_nit_c	$Q_{min:C}$ for nitrate-limited growth	µmol N µmol C^{-1}	floating point
qmax_nit	Q_{max} for nitrate-limited growth	µmol N $cell^{-1}$	floating point
qmax_nit_c	$Q_{max:C}$ for nitrate-limited growth	µmol N µmol C^{-1}	floating point
mu_inf_p	μ_∞ for phosphate-limited growth	day^{-1}	floating point
mu_p	μ_{max} for phosphate-limited growth	day^{-1}	floating point
k_p_m	K_m for phosphate-limited growth	µmol L^{-1}	floating point
k_p	K for phosphate uptake	µmol L^{-1}	floating point

vmax_p	V_{max} for phosphate uptake	µmol P cell^{-1} day^{-1}	floating point
vmax_p_c	V_{max}:C for phosphate uptake	µmol P µmol C^{-1} day^{-1}	floating point
qmin_p	Q_{min} for phosphate-limited growth	µmol P cell^{-1}	floating point
qmin_p_c	$Q_{min:C}$ for phosphate-limited growth	µmol P µmol C^{-1}	floating point
qmax_p	Q_{max} for phosphate-limited growth	µmol P cell^{-1}	floating point
qmax_p_c	$Q_{max:C}$ for phosphate-limited growth	µmol P µmol C^{-1}	floating point
citation	Publication code	integer	integer

If the entry for c_citation is 0, this indicates that the citation for this measurement is the same as the citation for the nutrient traits. The other c_citation sources (1–4) are:

1. Davidson, K., and G. Wood. 1999. An investigation of non-steady-state algal growth. I. An experimental model ecosystem. Journal of Plankton Research 21:811–837.

2. Lomas, M., and P. Glibert. 2000. Comparisons of nitrate uptake, storage, and reduction in marine diatoms and flagellates. Journal of Phycology 913:903–913.

3. Marchetti, J., G. Bougaran, and T. Jauffrais. 2013. Effects of blue light and the biochemical composition and photosynthetic activity of *Isochrysis* sp. (T-iso). Journal of Applied Phycology 25:109–119.

4. Riegman, R., and W. Stolte. 2000. Nutrient uptake and alkaline phosphatase (EC 3:1:3:1) activity of *Emiliania huxleyi* (Prymnesiophyceae) during growth under N and P limitation in continuous cultures. Journal of Phycology 36:87–96.

Table 2

Column name	**Variable definition**	**Units**	**Storage type**
citation_number	Publication code	integer	integer
full_citation	Citation for the original publication	string	string

Table 3

Column name	Variable definition	Units	Storage type
species	Species name	text	string
isolate	Isolate ID	text	string
volume	Cell volume	μm^3	floating point
volume_citation	Citation for volume measurement	text	string

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