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Poor correlation between phytoplankton community growth rates and nutrient concentration in the sea

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Abstract

Nutrient availability is one of the major factors regulating marine productivity and phytoplankton community structure. While the response of phytoplankton species to nutrient variation is relatively well known, that of phytoplankton community remains unclear. We question whether phytoplankton community growth rates respond to nutrient concentration in a similar manner to phytoplankton species composing the community, that is, following Monod's model. Data on in situ marine community growth rates in relation to nutrient concentration and the behaviour of a simple multi-species community model show that community growth rate does not respond to nutrient concentration according to the Monod equation. Through a simulation study we show this can be explained as a consequence of changes in size structure. Marine biogeochemical models involving different phytoplankton functional groups must not parameterize phytoplankton community growth rate response to nutrient concentration following a Monod equation.

1 Introduction

There is little doubt that nutrient availability is one of the major factors regulating marine productivity and phytoplankton community structure. In most areas of the oceans, phytoplankton species compete for available nutrients. We know from laboratory experiments that most of the steady state growth rates of monocultures of phytoplankton species in a gradient of nutrient concentration are well represented by Monod theory (Dugdale, 1967). Small phytoplankton species have low half-saturation constants that allow them to uptake nutrients at a faster rate than larger cells and to dominate in nutrient limited conditions (Eppley et al., 1969; Aksnes and Egge, 1991; Hein et al., 1995). Large phytoplankton species achieve slower growth rates (Grover, 1989) but often dominate when nutrient concentration is high (Tremblay and Legendre, 1994; Li, 2002) (Fig. 1). Indeed, large phytoplankton communities dominate in productive ecosystems thanks to their physical and chemical capacities to escape to zooplankton

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grazing (Irigoien et al., 2004, 2005). Furthermore, it has been observed that large phytoplankton dominate in high turbulence regime (Rodríguez et al., 2001; Li, 2002) and that when nitrogen supply is pulsed, large cells could dominate due to their enhanced storage capacities (Litchman et al., 2009).

This leaves a scenario (Fig. 1) where nutrient-limited ecosystems are dominated by fast-growing, small phytoplankton cells, while high-nutrient environments are dominated by slow-growing, large phytoplankton species. As a result, it is possible to reach the counterintuitive result that the community growth rate (μ_{com}), i.e., the mean growth rate of the phytoplankton cells in a community, can be higher when nutrients are limited (Fig. 1). Franks (2009) contended the common practice in marine ecosystem models to parameterize phytoplankton community growth rates using Michaelis–Menten kinetics. Following our conceptual argumentation, it is indeed quite likely that the response of community growth rate is different to that of individual species.

In this study, we use a database of in situ phytoplankton community growth rate measurements in surface waters of the global ocean covering oligotrophic as well as productive ecosystems and test the hypothesis that the response of phytoplankton community growth rates to nutrient concentration does not follow Monod kinetics. We also develop a simple statistical model summarizing our conceptual framework (Fig. 1). We first parameterize, using in-situ phytoplankton size structure data (Marañón et al., 2012), the steeper phytoplankton size spectra slope when nutrient concentrations are low. We then combine this size structure information with simple allometric equations describing the response of phytoplankton species growth to nutrients (Edwards et al., 2012) and calculate the predicted response of phytoplankton community growth rates to nutrients.

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2 Methods

2.1 In situ community growth data

We used an independent dataset containing phytoplankton in situ growth rate measurements in surface waters of the ocean compiled by Chen and Liu (2010) (see Chen and Liu (2010) Web appendix, Table A1, http://www.aslo.org/lo/toc/vol_55/issue_3/0965a.html). We refer here to community growth rate (μ_{com}) as the specific growth rate measured in a dilution experiment which represents the average biomass-specific growth rates of the cells in a phytoplankton community. The dataset covers open ocean and coastal regions and is restricted to experiments conducted in surface waters to reduce the effects of light limitation. We removed from the original dataset all data for which nitrate concentration was below the detection limit or lower than $0.01 \mu\text{mol L}^{-1}$. The database compiles data from experiments based on the dilution technique (Landry and Hassett, 1982) to estimate in situ phytoplankton community growth rate (μ_{com} , d^{-1}). Two different estimates of phytoplankton community growth rates are obtained in dilution experiments: nutrient amended or maximum growth rate ($\mu_{\text{com_max}}$) and non-amended or growth rate (μ_{com}) under natural conditions.

If the in situ community growth rate (μ_{com}) responds to the nutrient concentration following Monod's equation, we could formulate:

$$\mu_{\text{com}} = \frac{S}{S + K_s} \mu_{\text{com_max}} \quad (1)$$

where S is the nutrient concentration and K_s is the half-saturation constant for that nutrient.

The population maximum growth rate ($\mu_{\text{com_max}}$) is the growth rate measured when the population is not limited by nutrients and depends directly on the same parameters than the growth rate but nutrient concentration.

$$\mu_{\text{com_max}} = f(T, \text{PAR}, \text{s.s.}, \text{d.l.}, \text{s.c.}, \dots), \quad (2)$$

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by the total biomass of each species. This rate is equivalent to the growth rate measured experimentally as the rate of total community in situ growth rate (μ , in the dilution dataset).

2.3 Parameterisation of the size-spectrum dependence on resource levels with in-situ size structure data

Chlorophyll *a* (Chl *a*) data for 3 different size classes (0.2–2, 2–20, and > 20 μm) were collected from Marañon et al. (2012). As Sprules and Munawar (1986), we used the Chl *a* data to calculate the normalized biomass spectrum (NBSS) by regressing the logarithm of the normalized chlorophyll by biovolume. The biovolume was calculated using the volume equation of a sphere (Hillebrand et al., 1999). Nutrient concentration (Σ , $\mu\text{mol}(\text{NO}^3 + \text{NO}^2)\text{L}^{-1}$) for each station of the Chl *a* dataset was estimated from the nitrate climatology in the World Ocean Atlas, 2009 (WOA). We then fitted a model describing the effects of nutrient concentration on NBSS.

2.4 Parameterisation of species size-dependent nutrient resource acquisition and growth rate

The dependence of growth rate (μ) on ambient nutrient concentration is usually modeled using Droop model (Droop, 1973). Aksnes and Egge (1991) developed a theoretical framework that explains how cell size should affect the parameters in Droop model. This theoretical prediction was demonstrated with experimental data by Litchman et al. (2006). Edwards et al. (2012) estimated the allometric parameters for V_{max} (the maximum cell-specific nutrient uptake rate, $\mu\text{mol nutrient cell}^{-1} \text{d}^{-1}$) and K_m that we use here in our model (Fig. 2b):

$$\log_{10}(V_{\text{max}}) = -8.1 + \log_{10}(\text{Vol}) \times 0.82 \quad (4)$$

$$\log_{10}(K_m) = -0.84 + \log_{10}(\text{Vol}) \times 0.33 \quad (5)$$

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where Vol is the cell volume (μm^3) and K_m is the nutrient concentration where $V = V_{\text{max}}/2$ (Litchman et al., 2009).

To reach an estimate of a relationship between μ and S using Droop model requires the solution of a set of differential equations. Because our intention is only to evaluate the possible effects that a nutrient dependence formulation can have on the determination of community growth rates, we have followed a simpler approach by using relative uptake rate as a proxy for growth rate (Aksnes and Egge, 1991). Hence we have formulated the relative uptake rate ($V_{\text{rel}}, \text{d}^{-1}$) as:

$$V_{\text{rel}} = \mu_{\text{sp}} = V_{\text{max}} \frac{S}{Q(K_m + S)} \quad (6)$$

where μ_{sp} the growth rate (d^{-1}), the subscript “sp” is used to differentiate the monospecific growth rate (μ_{sp}) from the multispecific community-average growth rate (μ_{com}) as measured in dilution experiments, Q is the cell nutrient content (μmol of nutrient cell^{-1}) and V_{max} is the maximum uptake rate constrained by diffusion in the boundary layer outside the cell. In Eq. (6), V_{max} and K_m are calculated from cell size using Eqs. (4) and (5). To estimate Q , we follow Aksnes and Egge (1991) in assuming biomass as the average number of atoms of a given element within the cell, estimated from cell carbon content using a carbon-to-volume ratio ($C : V_{\text{ratio}}$) of $0.28 \text{ pg C } \mu\text{m}^3$ based on the empirical equation given in Litchman et al. (2007) and a redfield ratio of 106 C : 16 N. The implications of these assumptions are evaluated in the discussion.

The community-average growth rate (μ_{com}) as measured in dilution experiments can be calculated from knowledge of the monospecific growth rate for each of the species in the community μ_{sp_i} and the biomass of each species in the community which can be calculated from the numerical abundance times the species cell carbon content.

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growth rate does not respond to nutrient concentration either ($R^2 = 0.05$, $p = 0.0578$, Fig. 3b). Even if data are corrected for temperature effects (using Arrhenius–Boltzmann equation with activation energy of -0.33 eV, López-Urrutia et al., 2006), the in situ community growth rate did not follow Monod kinetics (Fig. 4). However, our results show that the in situ $\mu_{\text{com}} : \mu_{\text{com_max}}$ ratios (or $\mu_{\text{com_rel}}$) do indeed follow a Monod model with $K_s = 0.16 \pm 0.02$ and $\mu_{\text{com_rel_max}} = 0.99 \pm 0.02$ (Fig. 3c). For nutrient concentration below $1 \mu\text{mol L}^{-1}$, in situ $\mu_{\text{com_rel}}$ also follows Monod's growth kinetics with $K_s = 0.14 \pm 0.06$ and $\mu_{\text{com_rel_max}} = 0.91 \pm 0.14$ (Fig. 3d).

3.2 Simulation

A linear model of NBSS v.s nutrient concentration explained 43% of the variance with an increasing size spectra slope (i.e., less negative NBSS) with increasing nutrient concentration (Fig. 2a). Each species composing the simulated phytoplankton community was limited by nutrient and respond to the nutrient concentration following Monod's model. However, the predicted community growth rate ($\mu_{\text{com_predicted}}$) for the simulated communities did not follow Monod kinetics (Fig. 5a). On the contrary, and similar to in situ results, the predicted $\mu_{\text{com_rel}}$ was well in accordance with Monod's model (Fig. 5b, $K_s = 0.11 \pm 0.01$ and $\mu_{\text{com_rel_max}} = 0.98 \pm 0.01$).

4 Discussion

In this study, we observed that in situ phytoplankton community growth rate does not respond to nutrient concentration following a Monod kinetic as phytoplankton species composing the community do. However, in relation to its maximum growth rates, the Monod model is a good characterization of community dynamics.

Marine biogeochemical models in use are composed by three or four compartments (i.e. nutrient phytoplankton zooplankton, NPZ or nutrient phytoplankton zooplankton detritus, NPZD) (McCreary et al., 2001; Hood et al., 2003; Kantha, 2004) to 20 or more

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components including different phytoplankton functional groups, various nutrients and so on (Anderson, 2005; Lancelot et al., 2005; Le Quéré et al., 2005). The NPZ and NPZD models describe a simple food web system assuming dissolved nutrients are consumed by the phytoplankton community following Monod kinetics. For these models, the phytoplankton compartment is considered as a whole community and assumed to respond to nutrient concentration as phytoplankton species do. As we observed in this study, in situ and predicted phytoplankton community do not necessarily respond to nutrient concentration like individual phytoplankton. Thus, marine biogeochemical models using different phytoplankton functional groups (Anderson, 2005; Le Quéré, 2005) or based on phytoplankton size structure (Follows et al., 2007; Edwards et al., 2012) should rather be used instead of simpler models as NPZ or NPZD. This is well in line to the findings of Friedrichs et al. (2006, 2007) that observed that complex models with multiple phytoplankton functional groups fit better the available data than the simpler models. The parameterization of planktonic ecosystem models should not use the same variables for a community than for species. Franks (2009) warned about the use of community variables parameterized using data from individual species and suggested that the response to nutrient concentration of an individual or species should not represent necessarily the response of a diverse community. Contrary to our results, Franks (2009) observed a linear relation between the community nutrient uptake rate and nutrient concentration that could be explained by the use of the same half-saturation constant (K_s) for all phytoplankton size classes in his simulations. Several published works reported that K_s is different between species (Sommer, 1991; Chisholm, 1992; Cermeño et al., 2011). In our study, the relationship between the in situ community growth rate and nutrient concentration did not follow a Monod kinetic, neither a linear relationship.

Several studies have shown that the high surface area to volume ($S : V$) ratio of small phytoplankton species result in high nutrient uptake rates and low K_s and may explain why small phytoplankton species dominate in natural nutrient-limited ecosystems (Eppley et al., 1969; Aksnes and Egge, 1991; Hein et al., 1995). Conversely,

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large phytoplankton species seem to dominate in productive and well-mixed ecosystems (Irwin et al., 2006) due to their physical and chemical capacities to escape to zooplankton grazing (Irigoien et al., 2004, 2005) and due to upward motion increasing their residence time in upper layer against their tendency to sink (Li, 2002; Rodríguez et al., 2001). Furthermore, allometric equations explain that small phytoplankton species achieves higher growth rate than a large phytoplankton species at a same nutrient concentration (Edwards et al., 2012). Considering the allometric equations and the low nutrient-small phytoplankton and high nutrient-large phytoplankton relations, the community growth rate can be higher at low than at high nutrient concentration. We observed in this study that most of the community growth rates tended to decrease from 5 to 30 mmol NO³ + NO² m⁻³ (Fig. 3a) for the in situ data ($R^2 = 0.15$, $p < 0.001$) and from 2.5 to 25 mmol NO³ + NO² m⁻³ (Fig. 5a) for the predicted data ($R^2 = 0.17$, $p < 0.001$). Therefore, our results support our hypothesis of higher community growth rates at intermediate than at the highest nutrient concentrations.

In our simulation, we assumed that the intrinsic nutrient storage is related to the growth rate and ignored, for the sake of simplicity in the simulations the cell storage capacity. Indeed, Litchman et al. (2009) observed that when nitrogen supply is pulsed, large cells could dominate due to their enhanced storage capacities. By this observation, we should expect to observe higher growth rates for large phytoplankton species at high nutrient concentration than for small phytoplankton species, but if so a better relationship between community growth rate and nutrient concentration would be expected. The relationship between μ_{sp_max} and cell volume might influence the kinetic of the community growth rate response to nutrient concentration. Although there is consensus on the fact that smaller cells have lower half-saturation constants, the relationship between μ_{sp_max} and cell size is still under debate (Chen and Liu, 2011; Sal and López-Urrutia, 2011). Two different relations have been observed between μ_{sp_max} and cell volume: unimodal (Bec et al., 2008; Chen and Liu, 2011; Marañón et al., 2013) and declined lineal (Edwards et al., 2012). In addition, the parameterizations of some models argue for an increased lineal relationship (Follows et al., 2007). To understand the

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consequences of different relationships between μ_{sp_max} and cell size, we repeated our simulations but using unimodal (Fig. 6a) and positive (Fig. 6b) relationships between μ_{sp_max} and cell size. We observed that when the relation between μ_{sp_max} and cell volume is unimodal, the predicted community growth rates did not follow Monod's kinetic either (Fig. 6a). When the relation between μ_{sp_max} and cell volume is positive (i.e., larger cells have higher μ_{sp_max}), the model output suggests a possible relation between the predicted community growth rates and nutrient concentration (Fig. 6b). Hence, the observed lack of relationship in the in situ data (Fig. 3a) could be reproduced with the unimodal but not with the positive relationship.

Although community growth rates did not respond to nutrient concentration following Monod kinetics, the in situ and simulated μ_{com_rel} did (Figs. 3b and 5b). The μ_{com_rel} is exempted from the effects of temperature, light and size structure. The size structure of a phytoplankton community depends on nutrient concentration (Fig. 5a). Hence, by removing the size structure effect, the μ_{com_rel} is removing the effects that change in size structure have on the way that different communities uptake nutrients. The K_s and $\mu_{com_rel_max}$ were quite similar between the in situ ($K_s = 0.16 \pm 0.02$ and $\mu_{com_rel_max} = 0.99 \pm 0.02$) and predicted ($K_s = 0.11 \pm 0.01$ and $\mu_{com_rel_max} = 0.98 \pm 0.01$) μ_{com_rel} . So when the community growth rate depends only on nutrient concentration, the response of the community growth rate to nutrient variation follows the predicted Monod kinetic.

In summary, our study demonstrates that the lack of relationship between community growth rates and nutrients can be explained even if we disregard the effects of temperature, light or community composition. We could expect that such factors might further distort the observed relationship between the community growth rate and nutrient concentration.

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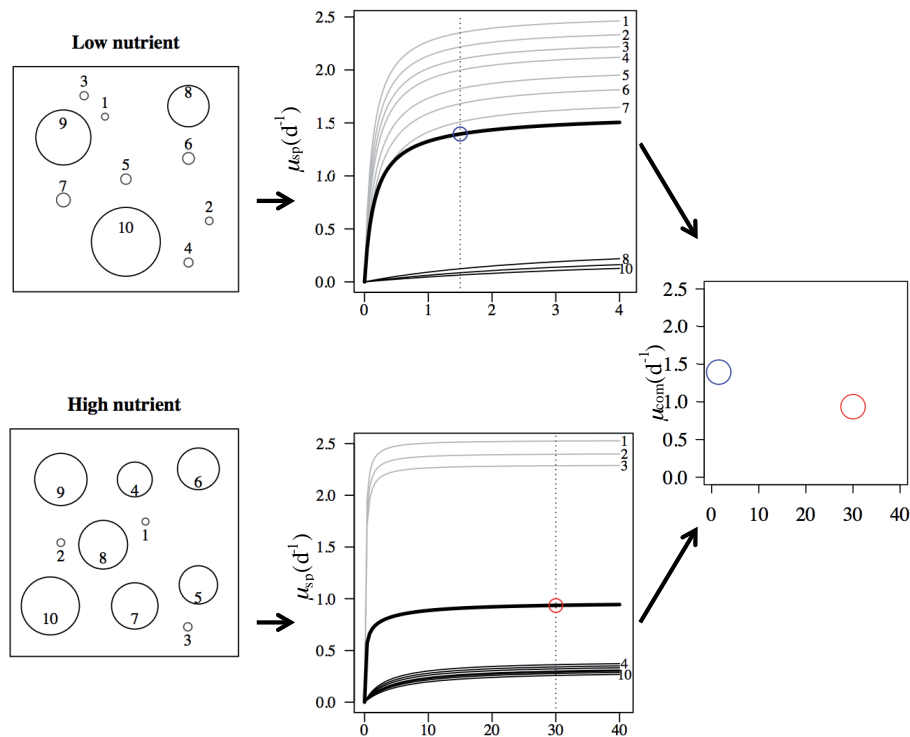


Figure 1. Conceptual diagram representing phytoplankton communities composed by small and large phytoplankton species (small grey and large black circles, respectively) in nutrient-limited and productive ecosystems. Each phytoplankton species composing their respective communities had its own growth rate response to nutrient concentration following a Monod kinetic. The growth rates for the whole community in both ecosystems have been evaluated by the mean of the cell-specific growth rates of each phytoplankton species composing their respective communities. At the bottom of the diagram, community growth rates for both ecosystems are represented at specific nutrient concentrations.

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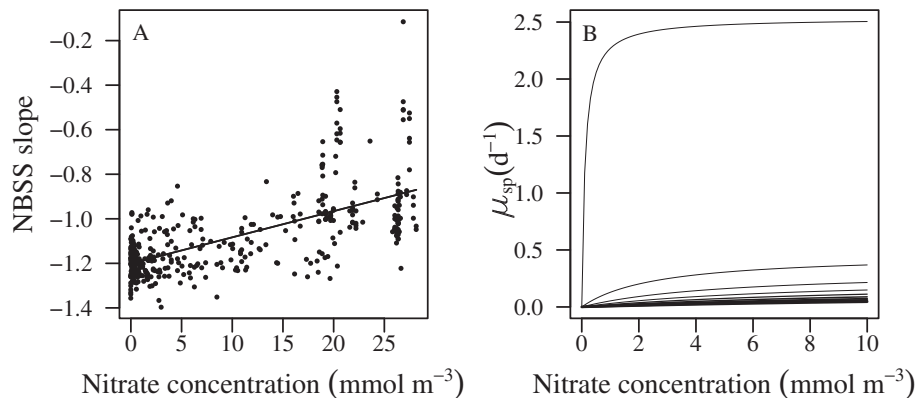


Figure 2. Functional forms of **(a)** normalized biomass spectrum (NBSS) and **(b)** phytoplankton species growth rate to nutrient concentration. **(b)** Simple allometric trade-offs are indicated by the size range from small (thinnest lines) to large (thickest lines) size species. **(a)** The solid line represents the linear regression.

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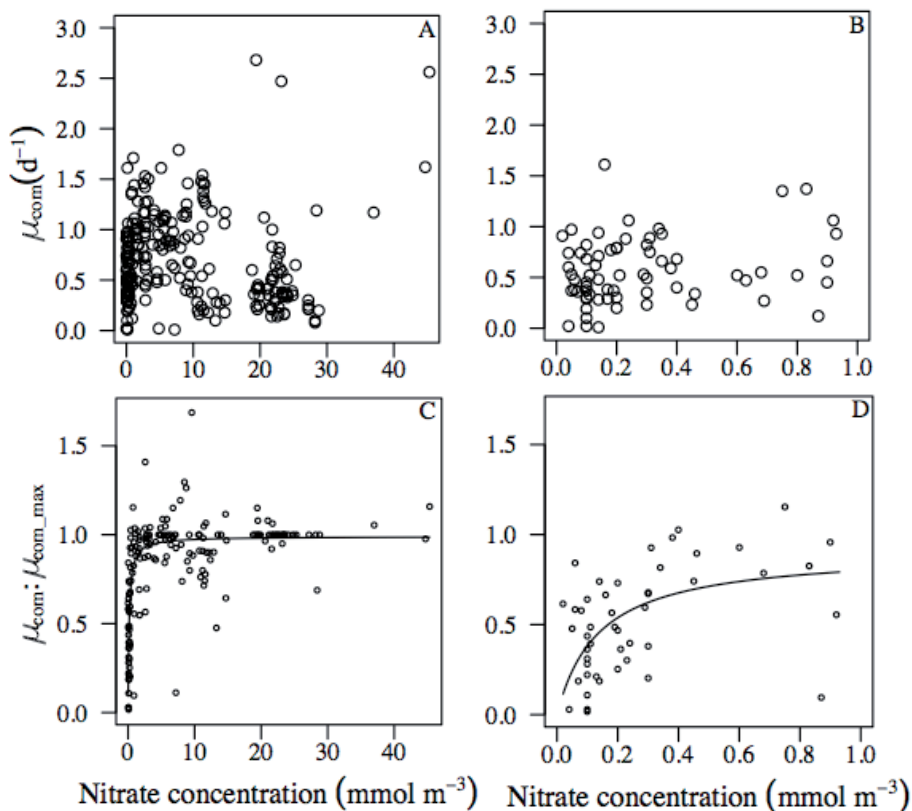


Figure 3. Relationships between in situ community growth rate (μ_{com} , d⁻¹) and nutrient concentration **(a)** from 0 to 40 mmol m⁻³ and **(b)** from 0 to 1 mmol m⁻³. Relationships between in situ $\mu_{com} : \mu_{com_max}$ ratio and nutrient concentration **(c)** from 0 to 40 mmol m⁻³ and **(d)** from 0 to 1 mmol m⁻³. **(c, d)** The solid lines represent the nonlinear least square fits.

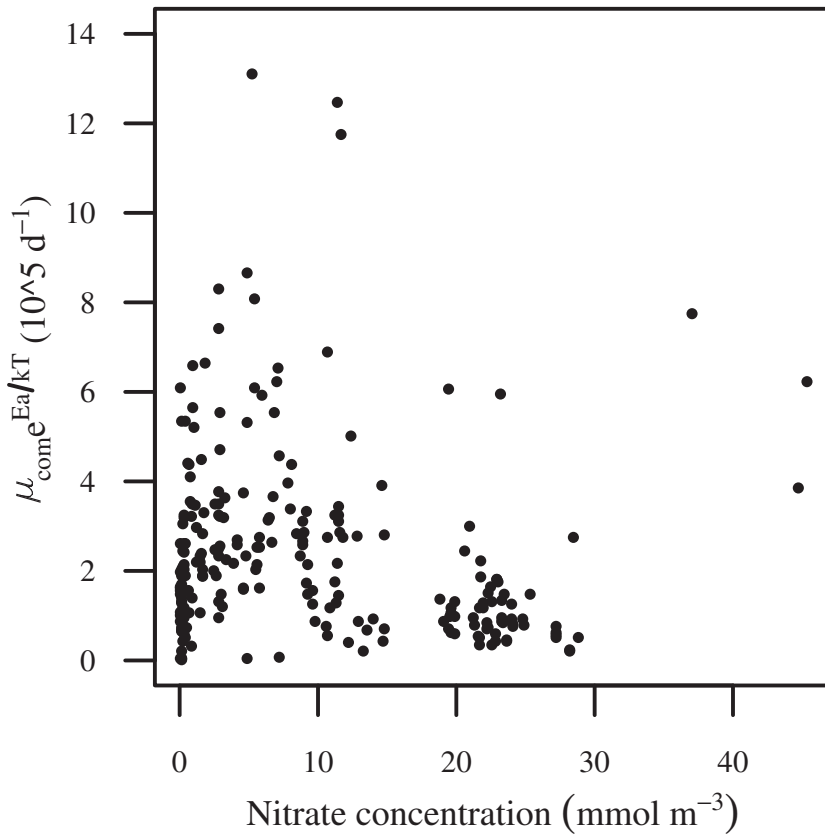


Figure 4. Relationship between in situ community growth rates ($\mu_{\text{com}} e^{E_a/kT}$, d^{-1}) corrected by temperature using the average activation energy for autotrophic respiration ($E_a = -0.33 \text{ eV}$, López-Urrutia et al., 2006) and nitrate concentration (mmol m^{-3}) from 0 to 40 mmol m^{-3} .

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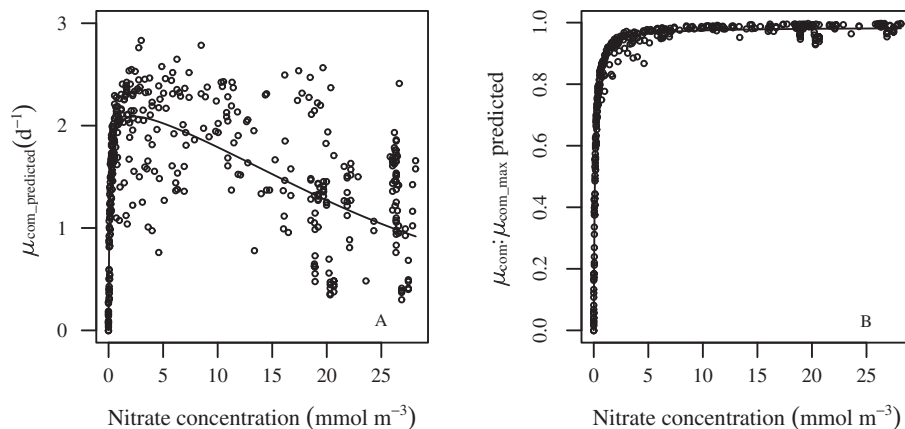


Figure 5. Relationships between **(a)** predicted community growth rate ($\mu_{\text{com_predicted}}$, d^{-1}) and **(b)** predicted $\mu_{\text{com}} : \mu_{\text{com_max}}$ ratio, and nutrient concentration (mmol m^{-3}). The solid lines represent the nonlinear least square fits.

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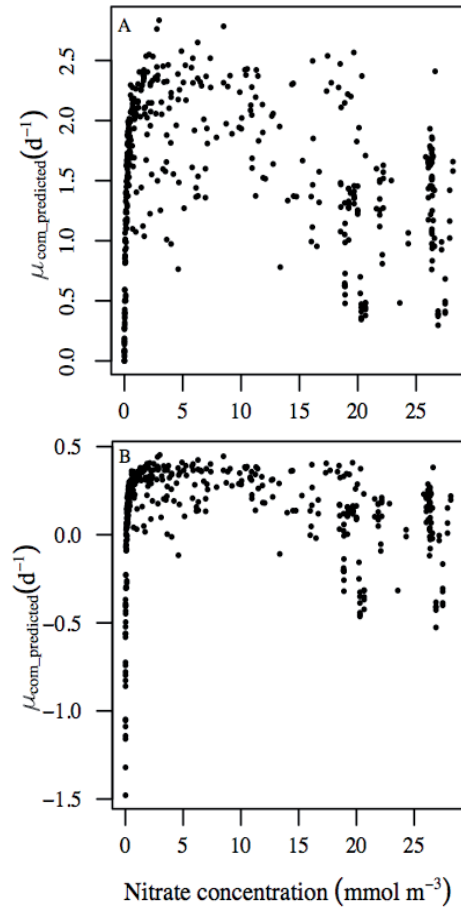


Figure 6. Relationships between the predicted community growth rates ($\mu_{\text{com_predicted}}$, d^{-1}) and nitrate concentration (mmol m^{-3}) with **(a)** unimodal and **(b)** positive relationships between $\mu_{\text{com_max}}$ and cell size.