

# Phytoplankton size scaling with nutrient concentration

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**ABSTRACT:** Phytoplankton, the autotrophic component of the plankton community, is a key factor in oceanic ecosystems and in biogeochemical cycling. Over much of the ocean, phytoplankton growth is limited by nitrogen uptake (as nitrate), which is commonly described in ecosystem modeling by the Michaelis-Menten equation:  $V = V_{\max} S / (K + S)$ . Previous phytoplankton data compilations have shown that the maximum uptake rate,  $V_{\max}$ , and the half-saturation constant,  $K$ , increase with organism size. Independent studies have also reported that  $K$  increases with nitrate concentration,  $S$ . Here, we assume that this  $K$  increase with  $S$  is due to an increase in the dominant organism size in the phytoplankton community with increasing nutrient concentration. Previous studies support this assumption, showing that nitrate abundance is the main factor determining dominant organism size. Based on this assumption and on previously published experimental observations for  $K$ , we show that phytoplankton dominant size,  $r$ , scales approximately with  $S^{0.85}$ . This increase in dominant size can also entail size-related changes in traits (such as the number of porters) that impact  $K$  and  $V_{\max}$ . Furthermore, by combining a trait-based uptake model with the experimental results of  $K$  and  $V_{\max}$ , we derive scaling relations for the number of porters and the handling time in terms of  $r$ . Our results indicate that handling time decreases approximately with  $r^{-0.90}$  while porter number increases approximately with  $r^{1.56}$ . These results may be useful in characterizing size-dependent nutrient uptake in marine ecosystems and biogeochemical cycling models.

**KEY WORDS:** Half-saturation constant · Scaling · Handling time · Porter number · Phytoplankton · Nitrate uptake

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## INTRODUCTION

The Michaelis-Menten (MM) model remains the dominant paradigm for describing uptake rate,  $V$ , as a function of the environmental nutrient concentration,  $S$ , in experiments and modeling (Edwards et al. 2012, Smith et al. 2014). This model is expressed as  $V = V_{\max} S / (K + S)$ , where  $V_{\max}$  is the maximal uptake rate and  $K$  the half-saturation constant, which corresponds to the concentration when the uptake rate is  $V_{\max} / 2$ . The MM model is simple, and measurements of the 2 coefficients are widely available in the literature. However, it is commonly used as a pure empirical description that provides no theoretical predictions on how the kinetic parameters scale with inherent microbial traits (cell size, number of trans-

porters [or 'porters'], handling time and porter size) and environmental variables (temperature and nutrient concentration with its diffusion coefficient). Such relations are commonly required in ecological modeling. Theoretical trait-based models (Aksnes & Egge 1991, Armstrong 2008, Aksnes & Cao 2011, Bonachela et al. 2011) do provide such scaling relations. A challenge to the verification of these theoretical models is that they contain traits that are not commonly measured. These traits include the number of porters, a key property of models where nutrient molecules are assumed to be actively transported through porters at the cell membrane (Aksnes & Egge 1991, Armstrong 2008, Aksnes & Cao 2011), and handling time, which corresponds to the time period during which a porter is occupied because it is handling an

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encountered nutrient molecule. However, a convenient property of these theoretical models is that measured variables like  $V_{\max}$  and  $K$  can be expressed as functions of the unmeasured microbial traits, which facilitates indirect estimation of these parameters. It has been shown experimentally that the maximum uptake rate and half-saturation coefficient increase with phytoplankton size (Litchman et al. 2007, Edwards et al. 2012, Fiksen et al. 2013, Lomas et al. 2014). The half-saturation coefficient has also been shown to increase with the ambient nutrient concentration of nitrate (Harrison et al. 1996, McCarthy et al. 1999, Collos et al. 2005, Smith et al. 2014). In this work, we combine these experimental data from the literature to obtain the scaling relationship of the dominant organism size with nutrient concentration. Additionally, using the theoretical model introduced in Aksnes & Cao (2011), we extract several empirical relationships that determine how microbial traits (such as number of porters and handling time) are expected to vary with organism size and nutrient supply regime. Our results provide simple parameterizations that might be useful in biogeochemical models, but are also likely to encourage future direct measurements of inherent traits, such as the number of nutrient uptake porters and their handling times.

## METHODS

### Use of experimental observations from previous studies

Here, we utilized results and observations reported in Edwards et al. (2012) and Smith et al. (2014). Edwards et al. (2012) compiled trait data from published studies and estimated the scaling relations between the parameters of the MM model and phytoplankton volume measured for nitrate and phosphate in both freshwater and marine species. They used studies in which temperature was at or near 20°C and light was not severely limiting. In order to quantify the scaling relations between the nutrient traits and phytoplankton volume, they applied standardized major axis (SMA) regression. The results for marine species with nitrate as the limiting nutrient (Edwards et al. 2012, their Table 1) are:

$$K (\log_{10} \mu\text{mol l}^{-1}) = 0.33 (0.24, 0.45) \\ \times \text{Vol} (\log_{10} \mu\text{m}^3) - 0.84 (0.44, 1.20) \quad (1)$$

and

$$V_{\max} (\log_{10} \mu\text{mol d}^{-1}) = 0.82 (0.65, 1.00) \\ \times \text{Vol} (\log_{10} \mu\text{m}^3) - 8.1 (7.3, 8.8) \quad (2)$$

where  $K$  and  $V_{\max}$  are, respectively, the half-saturation constant and the maximal uptake rate at which the dominant organism's volume is Vol. The values in parentheses represent the 95 % confidence intervals of each parameter. The above scalings are also compatible with the data of Lomas et al. (2014, their Fig. 2); our SMA fit to their data gives slopes of 0.34 (0.18, 0.51) and 1.09 (0.56, 1.61) for  $K$  and  $V_{\max}$ , respectively. Litchman et al (2007) also reported compatible slope values of 0.27 (0.20, 0.36) and 0.67 (0.53, 0.84) for  $K$  and  $V_{\max}$ , respectively. Written as power laws in terms of the dominant organism radius,  $r$ , in the units we use, Eqs. (1) & (2) become:

$$K (\text{molecules } \mu\text{m}^{-3}) = 140 r^{0.99} (\mu\text{m}) \quad (3)$$

$$V_{\max} (\text{molecules s}^{-1}) = 1.79 \times 10^5 r^{2.46} (\mu\text{m}) \quad (4)$$

where the conversion factors  $\text{Vol} = 4\pi r^3/3$ ,  $1 \mu\text{mol l}^{-1} = 602 \text{ molecules } \mu\text{m}^{-3}$  and  $1 \mu\text{mol d}^{-1} = 6.97 \times 10^{12} \text{ molecules s}^{-1}$  were used.

Smith et al. (2014) collected  $K$  values that were measured for natural communities in various ship-board incubation studies from a wide variety of ocean regions (Harrison et al. 1996, McCarthy et al. 1999, Collos et al. 2005). They showed that incorporation of a physiological trade-off between maximum uptake rate and affinity (Pahlow 2005, Smith et al. 2009) into the model of Aksnes & Cao (2011) might explain the increasing trend of the half-saturation constant with ambient nitrate concentration and its range of variation for typical phytoplankton sizes in the ocean. Fitting the collected data (Smith et al. 2014, their Fig. 2B) with SMA regression, the following scaling relation is obtained (Fig. 1):

$$K (\log_{10} \mu\text{mol l}^{-1}) = 0.84 S (\log_{10} \mu\text{mol l}^{-1}) + 0.27 \quad (5)$$

Written as power law in the units applied in our study, it becomes:

$$K (\text{molecules } \mu\text{m}^{-3}) = 5.18 S^{0.84} (\text{molecules } \mu\text{m}^{-3}) \quad (6)$$

Small phytoplankton species tend to dominate in low-nutrient regions of the ocean, whereas large species tend to thrive in nutrient-rich waters (Chisholm 1992, Marañoń et al. 2001, Li 2002, Kostadinov et al. 2010, Smith et al. 2014, Marañoń 2015). In addition, Acevedo-Trejos et al. (2013) showed that nutrient concentration is the main factor determining phytoplankton community size structure. The relationship in Eq. (6) is then expected to be affected by this correlation between dominant organism size and nutrient supply regime. In the present study, we have assumed that the observed increase of  $K$  with nutrient concentration is due to the larger sizes of phyto-

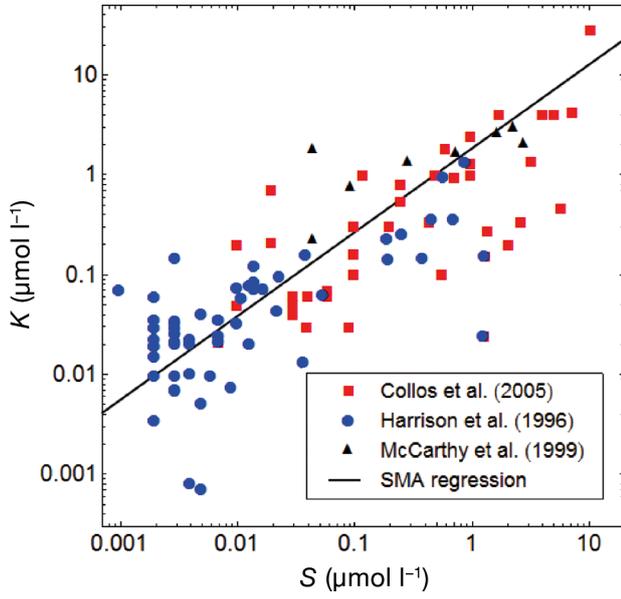


Fig. 1. Compilation of half-saturation values,  $K$ , as a function of nutrient concentration,  $S$  (adapted from Fig. 2B in Smith et al. 2014) observed for natural communities from a wide variety of marine environments (Collos et al. 2005, Harrison et al. 1996, McCarthy et al. 1999) and our fit using standardized major axis (SMA) regression

plankton present at higher nutrient concentrations (this larger phytoplankton size may also entail the change of other traits that affect  $K$  and  $V_{\max}$ .) Thus, we combined the empirical relations for the half-saturation as a function of size and nutrient concentration (Eqs. 3 & 6) in order to express phytoplankton dominant size as a function of the ambient nitrate concentration in the ocean.

### Trait model of an individual organism

The trait-based model proposed by Aksnes & Cao (2011) gives the nutrient uptake rate of an idealized spherical and non-swimming organism as:

$$V = \frac{b}{2a} \left( 1 - \sqrt{1 - \frac{4a}{b^2}} \right) \quad (7)$$

with

$$a = \frac{h}{4\pi DrSn} \left( 1 - \frac{\pi rp}{ns} \right), \quad b = \frac{1}{\alpha S} + \frac{h}{n}, \quad \alpha = 4\pi Dr \frac{ns}{ns + \pi r(1-p)}$$

and  $p = \frac{ns^2}{4r^2}$ , and where the handling time,  $h$ , is the time interval required to process 1 nutrient by 1 porter; during this time interval the porter is blocked and unable to absorb additional nutrients.  $D$  is the diffusivity of nutrient particles in the extracellular medium,  $S$  is the bulk nutrient particle concentration,  $r$  is the radius of the individual organism,  $s$  is the

effective porter radius,  $n$  is the number of uptake porters in the surface,  $\alpha$  is the uptake affinity (i.e.  $\alpha = \lim_{S \rightarrow 0} V/S$ ) and  $p$  is the porter density (i.e. the fraction of the sphere's surface covered by porters). This model is not of MM type but it can be written as an approximated MM functional form (see also Armstrong 2008), with:

$$V_{\max} = V_{S \rightarrow \infty} = \frac{n}{h}, \quad K = \frac{\pi r(2-p) + ns}{8h\pi Drs} \quad (8)$$

The error of this MM approximation diminishes for low porter densities, i.e. when  $ns^2 \ll 4r^2$ , and particularly when the stronger condition  $ns \ll \pi r$  holds (Aksnes & Cao 2011). This individual trait-based model gives  $V_{\max}$  and  $K$  for an organism of radius  $r$ , with  $n$  porters and handling time  $h$ . Organisms may, in principle, present any combination of these 3 traits. However, the fitness of an organism in a given nutrient concentration determines its optimal size, together with the optimal number of porters and optimal handling time for this size. Thus, the dominant organism at a given nutrient concentration would be expected to present optimal trait values for that nutrient concentration. The optimal radius at a given nutrient concentration defines the dominant organism radius,  $r$ , at this concentration. Hereafter nutrient concentration,  $S$ , is specifically nitrate concentration.

## RESULTS

### Relationship between cell size and ambient nutrient concentration

Previous phytoplankton data compilations have shown that  $K$  increases with both dominant radius,  $r$ , and nitrate concentration,  $S$ . Previous studies (Acevedo-Trejos et al. 2013, Marañón 2015) have shown that the distribution of phytoplankton community size structure is mainly influenced by  $S$ , especially in eutrophic regimes (in oligotrophic conditions the temperature has also a structuring impact). Consequently, we here assume that the increase in  $K$  with  $S$  is mainly due to an increase in  $r$  (of the phytoplankton community) with increasing nutrient concentration. This allows us to combine the empirical Eqs. (3) & (6), obtaining that  $r$  scales approximately with  $S$ , as:

$$r (\mu\text{m}) = 8.20S^{0.85} (\mu\text{mol l}^{-1}) \quad (9)$$

or, equivalently,  $r (\mu\text{m}) = 0.036S^{0.85}$  (molecules  $\mu\text{m}^{-3}$ ). This equation gives the expected dominant phyto-

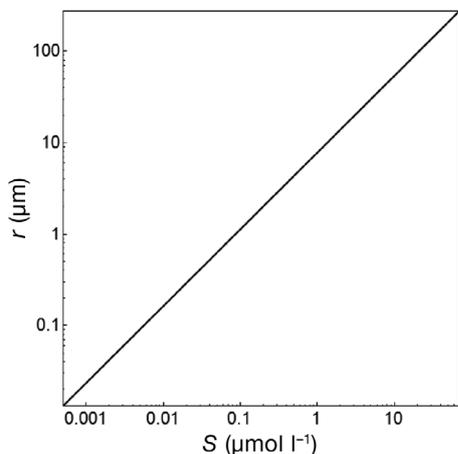


Fig. 2. Dominant phytoplankton size,  $r$ , as a function of nutrient concentration,  $S$  (see Eq. 9)

plankton size for a given  $S$  (Fig. 2). This increase in the dominant size entails size-related changes in other traits (such as  $n$  and  $h$ ) that impact  $K$  and  $V_{\max}$ .

If we invert Eq. (9), we obtain the nutrient concentration  $S$ , at which the dominant size is  $r$ :

$$S (\mu\text{mol l}^{-1}) = 0.082r^{1.18} (\mu\text{m}) \quad (10)$$

or, equivalently,  $S (\text{molecules } \mu\text{m}^{-3}) = 50r^{1.18} (\mu\text{m})$ .

### Estimates of scaling relationships of handling time and porter number as a function of dominant size

Eq. (8) relates  $h$  and  $n$  (inherent traits) on the one hand with  $V_{\max}$  and, on the other hand, with  $K$  (apparent traits). The observed scaling of  $V_{\max}(r)$  and  $K(r)$ , with the dominant size  $r$ , is given by Eqs. (3) & (4). Therefore, by inverting Eq. (8) we can estimate the relationship between handling time  $h$  (or porter number  $n$ ) and  $r$  by:

$$h = \frac{8\pi r^2}{s(32\pi D r^2 K - 4rV_{\max} + \pi s V_{\max})} \quad (11)$$

and

$$n = V_{\max} h \quad (12)$$

From these equations, we get  $h(r)$  and  $n(r)$  by insertion of the empirical relations from Edwards et al. (2012) for  $K(r)$  and  $V_{\max}(r)$ , Eqs. (3) & (4), a nutrient diffusion coefficient of  $D = 1000 \mu\text{m}^2 \text{s}^{-1}$  (Tambi et al. 2009) and  $s = 0.01 \mu\text{m}$  (Berg & Purcell 1977). For these values we see that the denominator of Eq. (11) can be approximated by  $32\pi s D r^2 K$ , and then:

$$h \approx \frac{1}{4sDK}, \quad n \approx \frac{V_{\max}}{4sDK} \quad (13)$$

These formulas lead to the approximate scalings:

$$h (\text{s}^{-1}) \approx 1.78 \times 10^{-3} r^{-0.99} (\mu\text{m}) \quad (14)$$

and

$$n \approx 320 r^{1.47} (\mu\text{m}) \quad (15)$$

Alternatively, we can fit power laws to the exact formulas (Eqs. 11 & 12), obtaining:

$$h (\text{s}^{-1}) = 1.90 \times 10^{-3} r^{-0.90} (\mu\text{m}) \quad (16)$$

and

$$n = 338 r^{1.56} (\mu\text{m}) \quad (17)$$

These relations indicate that  $h$  decreases while  $n$  increases with  $r$  (Fig. 3). Replacing in Eq. (17) the scaling behavior  $r(S)$  given by Eq. (9) provides an estimate of the average porter number for different ambient nitrate concentrations as:

$$n = 1.89 S^{1.32} (\text{molecules } \mu\text{m}^{-3}) \quad (18)$$

Eq. (17) implies  $p = ns^2/4r^2 \sim r^{-0.44}$ . This result, obtained from the Edwards et al. (2012) and Smith et al (2014) experimental data compilation, is consistent with Lindemann et al. (2016), who report a downward trend in  $p$  with  $r$  when all data points in their analysis were included (Lindemann et al. 2016, their Fig. 3).

## DISCUSSION

The experimental datasets from different oceanic regions measured by Collos et al. (2005), Harrison et al. (1996) and McCarthy et al. (1999), and collected by Smith et al. (2009, 2014), show an increase in  $K$  with an increase in ambient  $S$ . Additionally, as pointed out by Smith et al. (2014), previous studies have indicated that natural assemblages tend to have larger (smaller) cell sizes at higher (lower) ambient  $S$  (Chisholm 1992, Marañón et al. 2001, Li 2002, Kostadinov et al. 2010, Acevedo-Trejos et al. 2013, Marañón 2015). They also indicate that larger cells tend to have greater  $K$  (Litchman et al. 2007, Edwards et al. 2012, Smith et al. 2014). Acevedo-Trejos et al. (2013) showed that  $S$  is the main factor determining the size structure of phytoplankton community in the ocean while temperature only has an impact under low-nutrient conditions (within the range of conditions present in the ocean) (Marañón 2015). Based on these observations, it might be assumed that the observed relationship between  $K$  and  $S$  would emerge from the scaling between phytoplankton size and nutrient supply regime. Under this assumption, using the scaling relation of  $K$  versus  $r$  we obtained a relationship that predicts  $r$  as a function of  $S$  (Eq. 9). It is important to note that this does not mean that size is the only rele-

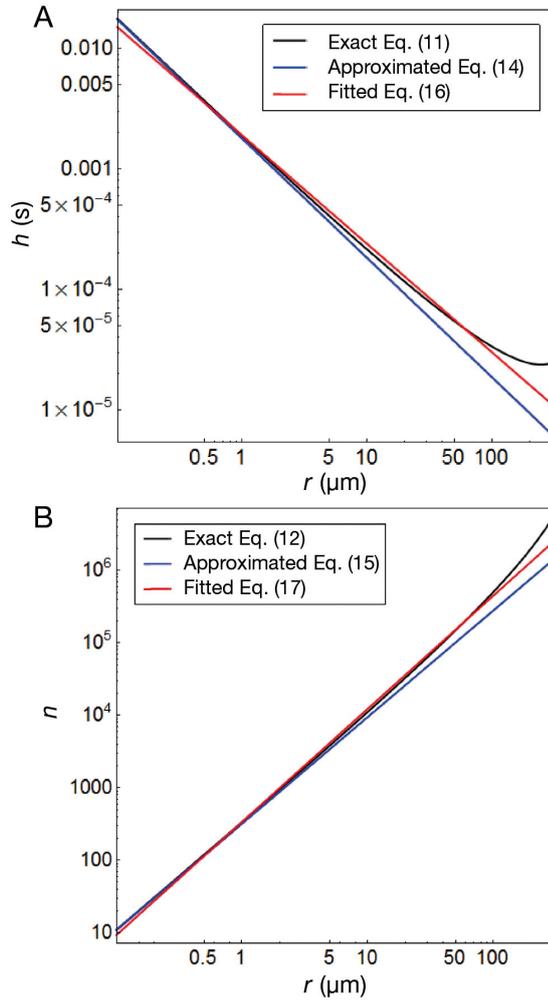


Fig. 3. (A) Handling time,  $h$ , and (B) porter number,  $n$ , as a function of dominant phytoplankton size,  $r$ , obtained by combining the empirical scaling of the half-saturation constant,  $K$  (Eq. 3) and the maximal uptake rate,  $V_{\max}$  (Eq. 4) with the trait-based model proposed by Aksnes & Cao (2011) (Eq. 7). Black lines: exact results from Eqs. (11) & (12), respectively for  $h$  and  $n$ ; blue lines: approximated results from Eq. (13) giving, respectively for  $h$  and  $n$ , the Eqs. (14) & (15); red: approximated power law fits of Eqs. (16) & (17), respectively for  $h$  and  $n$

vant trait, as other traits (such as  $p$ ) may change with size. The  $r$  predicted by Eq. (9) as a function of  $S$  is in agreement with experimental observations (Brewin et al. 2010, Acevedo-Trejos et al. 2013). For example,  $S$  at around  $0.1 \mu\text{mol l}^{-1}$ , as in low-nutrient regions of the ocean, indicate smaller phytoplankton with  $r$  of the order of  $1 \mu\text{m}$ .  $S$  ranging from 1 to  $10 \mu\text{mol l}^{-1}$ , as in the medium and nutrient-rich regions in the ocean, suggest  $r$  of the range 8 to  $60 \mu\text{m}$ . Future experimental observations of  $r$  versus  $S$  in the ocean would be useful to further tests of the predicted relationship between  $r$  and  $S$ .

We also derived the dominant size dependence of 2 traits ( $p$  and  $h$  for the dominant organisms) in the Aksnes & Cao (2011) model. We estimated the scaling of  $h$  with  $r$  from the experimental data of Edwards et al. (2012) and Smith et al. (2014).  $h$  is predicted to decrease with size according to  $h \sim r^{-0.90}$ , implying that larger organisms have shorter  $h$ . This result is approximately consistent with the size dependency of the  $h$ , i.e.  $h \sim r^{-1}$ , assumed by Smith et al. (2014) to give a good fit to experimental data. Smith et al. (2014) showed that incorporation of a physiological trade-off between  $V_{\max}$  and affinity (Pahlow 2005, Smith et al. 2009) into the model of Aksnes & Cao (2011) might explain the increasing trend of  $K$  for nitrate uptake with ambient  $S$  and its range of variation as measured by shipboard experiments in the ocean. Smith et al. (2014) also assumed that  $n$  increased with the square of the phytoplankton dominant size,  $n \sim r^2$ , which implies a constant  $p$  with increasing  $r$ . As shown above, our results imply a decreasing  $p$ , i.e.  $p = ns^2/4r^2 \sim r^{-0.44}$ , which is consistent with Lindemann et al. (2016). It should be noted that our results for  $n(r)$  and  $h(r)$  are not assumptions. They are derived from observed  $V_{\max}$  and  $K$  scaling with  $r$  from the observations reported in Edwards et al. (2012) and Smith et al. (2014).

It should be noted that the dependences of  $K$  and  $V_{\max}$  on  $r$  are led by indirect contributions through dependences of  $n$  and  $h$  on  $r$ . From Eq. (8), we see that organism size modifies  $V_{\max}$  only indirectly, through the changes it implies in  $n$  and  $h$ . In Eq. (8), we see that size changes both directly and indirectly the value of  $K$ . In addition, using in Eq. (8) the size scaling of  $n$  obtained in Eq. (17), it can be shown that, for medium and large phytoplankton sizes, the contribution of the size dependence on  $n$  in the numerator is of the same order or greater than the direct contribution of  $r$ . This is consistent with the hypothesis, suggested by Collos et al. (2005), that increasing  $n$  could be a mechanism to increase  $K$  in high ambient  $S$ .

It is intriguing that, according to our analysis, phytoplankton  $h$  decreases approximately proportional to the inverse of the organism radius, i.e.  $h \propto r^{-1}$ . It might be hypothesized that the arrival of an enzyme is the rate-limiting process of the reset of the porter after capture of a nutrient. In that case,  $h$  is inversely proportional to the enzyme collision rate, and it seems reasonable to assume that the collision rate of the enzymes with the porter is proportional to the enzyme density. Thus, enzyme density,  $\rho_e$ , will be proportional to the inverse of the handling time,  $\rho_e \sim 1/h \sim r$  (i.e. enzyme density will grow proportionally to phytoplankton size  $\tilde{r}$ ). If the enzyme and porter

encounter is mainly a surface process, the relevant enzyme density would be a surface density  $\rho_e = N_e/r^2$ , implying a growth of the number of enzymes  $N_e \sim r^3$  (i.e. proportional to the organism volume). Whereas if enzyme and porter encounter is a volume rather than a surface process, the relevant enzyme density would be a volume density  $\rho_e = N_e/r^3$ , implying an increase in the number of enzymes proportional to  $r^4$  (i.e. faster than the organism volume increase).

By using nutrient uptake theory in combination with MM experimental results, our study aimed at increasing understanding of how empirical scaling relations in phytoplankton nutrient uptake connect with inherent phytoplankton traits. Although classical MM uptake experiments are useful, further insight into the role of porter dynamics in phytoplankton nutrient uptake and growth will require actual experimental measurements of the  $p$ , their  $h$ , and processes involved in  $h$ . The results presented here and the experimental measurements proposed could be used to improve current biogeochemical models, which specifically account for atmospheric carbon dioxide abundance and fixation.

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