

Light and Nutrient Availability Affect Size-scaling of Phytoplankton Growth

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Motivation

The size-structure of phytoplankton communities influences the biological pump and the structure of the food web (Figure 1). There is evidence of changes in phytoplankton size-structure in response to environmental conditions on ecological and evolutionary time scales (ZV Finkel, Poster 610).

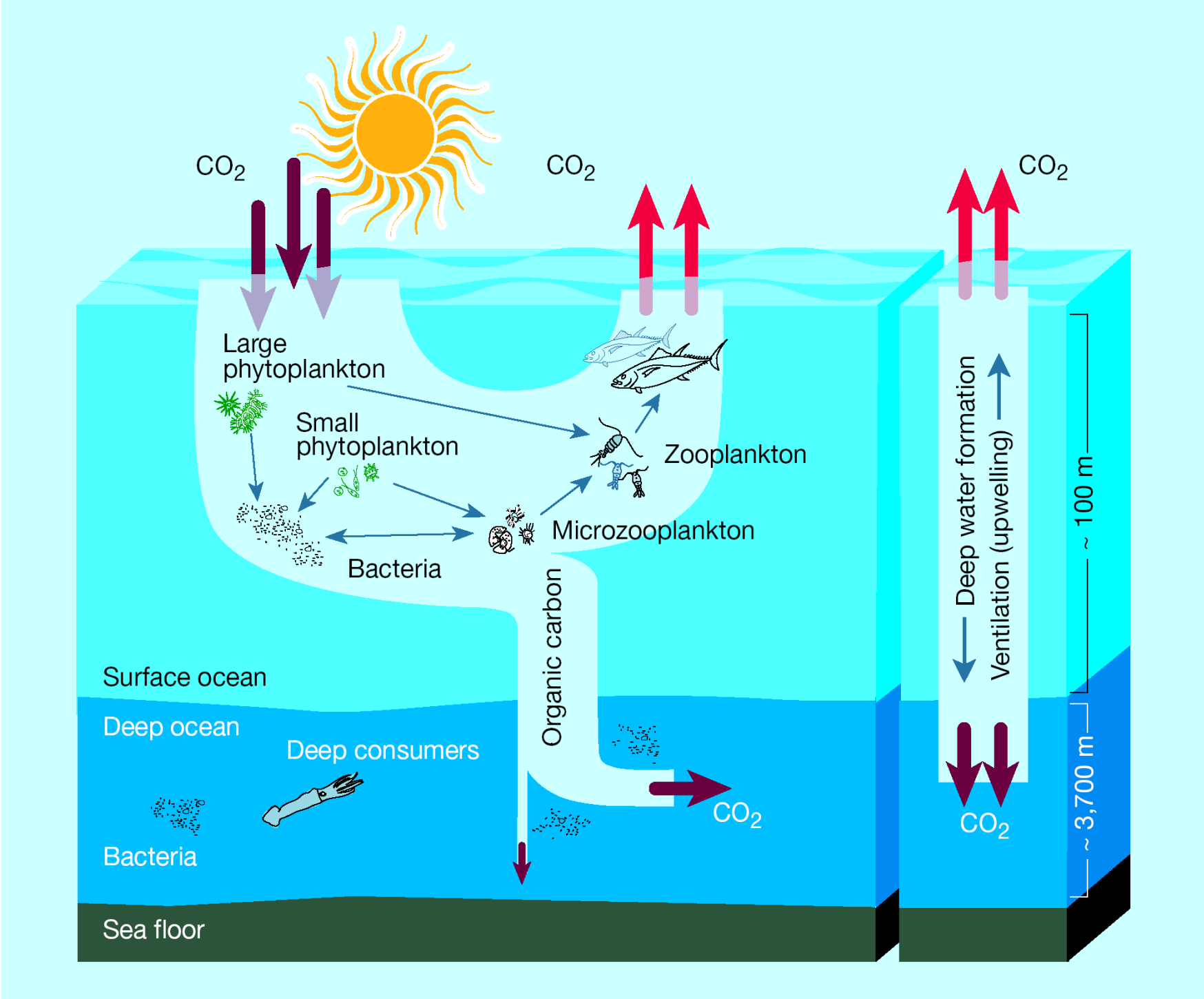


Figure 1. Phytoplankton size-structure influences trophic transfer and the biological pump. (Chisholm 2000).

What determines phytoplankton community size structure?

The size structure of phytoplankton communities is a function of a variety of source and loss terms, many of which are size-dependent. We focus on the growth terms here. Phytoplankton growth rate is most frequently expressed as a function of nutrient concentration, irradiance, and temperature. Resource acquisition rates are size-dependent (Figure 2).

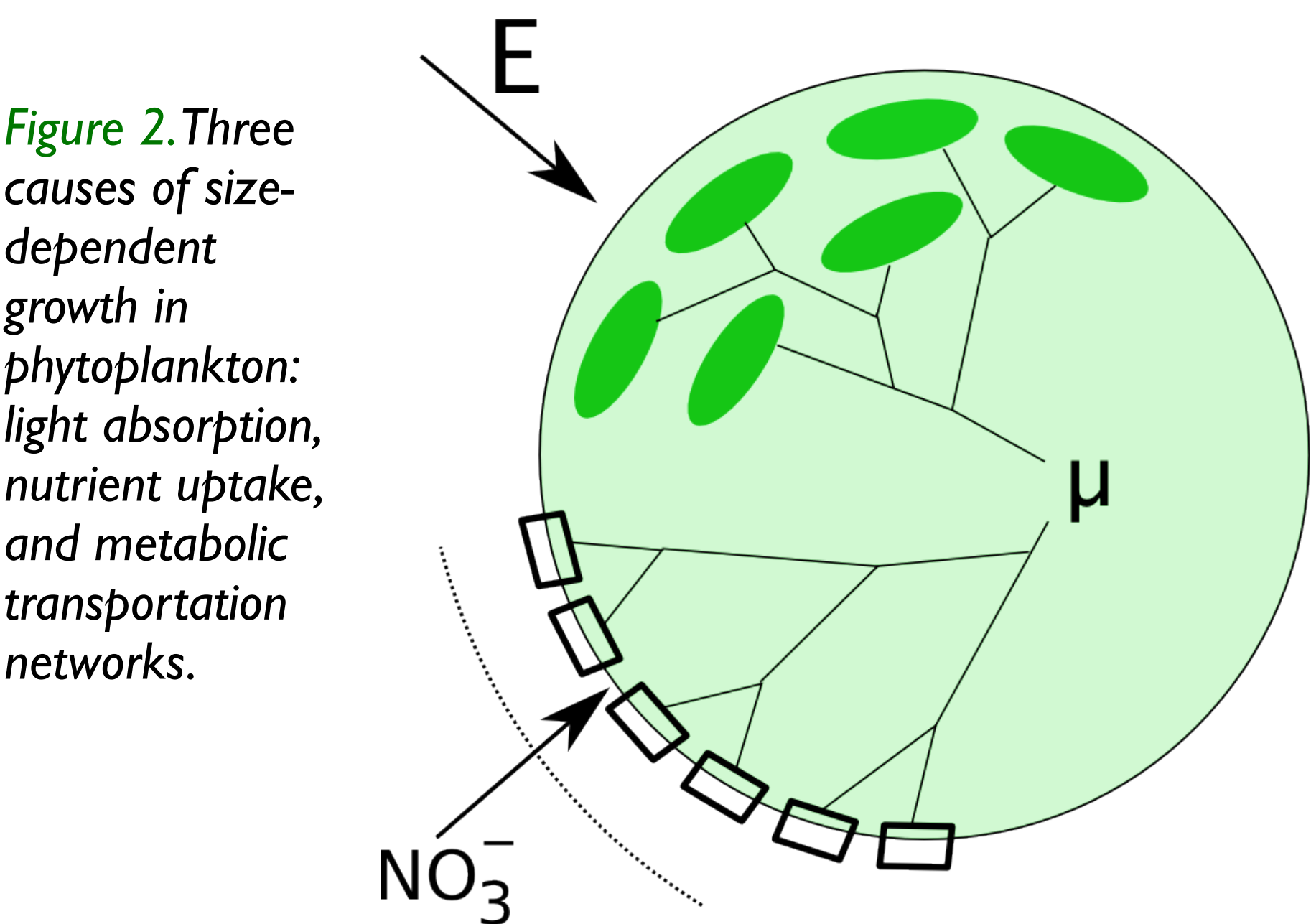
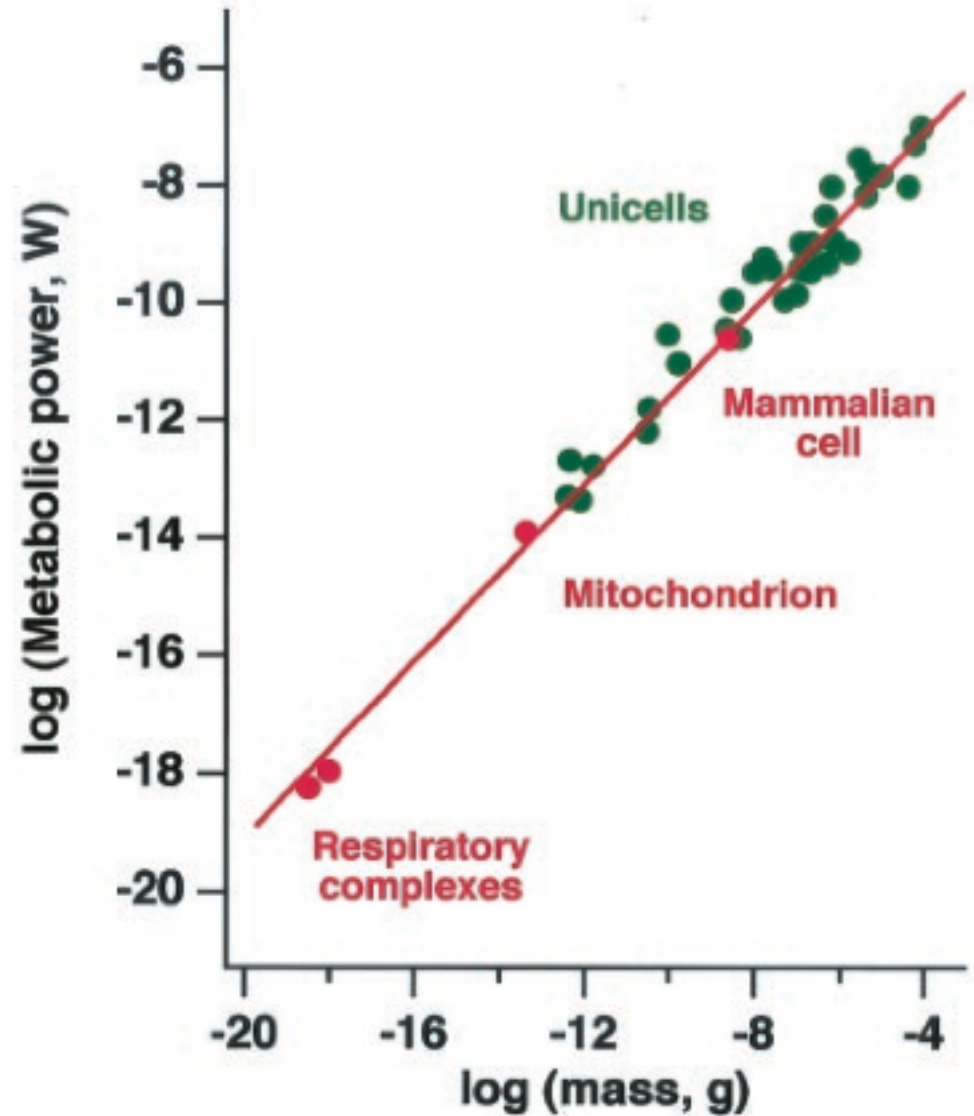


Figure 2. Three causes of size-dependent growth in phytoplankton: light absorption, nutrient uptake, and metabolic transportation networks.

Nutrients. A Michaelis-Menten function is commonly used to combine the size-dependence of resource uptake under saturating concentrations, proportional to the surface area ($V^{2/3}$), and diffusion-limited uptake rates, proportional to cell radius ($V^{1/3}$).
Irradiance. Light-acquisition varies with the geometric cross-section of the cell ($V^{2/3}$), the pigment concentration (chlorophyll per cell proportional to $V^{2/3}$), and the effect of pigment packaging (see Model).
Metabolic networks. After resources have been acquired by a cell, fundamental constraints imposed by internal transportation networks further regulate the growth rate of cells with rates proportional to $V^{3/4}$ (Figure 3).

Figure 3. Temperature corrected metabolic rates (in watts) for unicells, mammalian cells grown in vitro, and intracellular components of respiration mechanisms obey a 3/4 size-scaling rule. (West et al. 2002)



Our goal is to create a model to predict the size-scaling of phytoplankton growth rate under different environmental conditions incorporating these three size-dependent physiological rates.

Metabolic Transportation Network Model

We separate the allometry arising from transportation networks and the allometry due to resource acquisition.

Growth rate is the minimum of transportation limited metabolic rate, M , photosynthetic rate, P , and nutrient uptake rate, ρ :

$$\mu = \min(M, P, \rho).$$

The metabolic allometry imposes a 3/4 size-scaling exponent on resource-saturated growth:

$$M \propto V^{3/4}.$$

Potential photosynthetic rate P is defined as the rate of photon absorption times the quantum yield, and is size-dependent because of the consequences of cell size on σ :

$$P = E\sigma\phi$$

The absorption cross-section is size dependent because of both the geometric cross-section (cell radius r) and the size-dependent package effect (the saturating function Q):

$$\sigma = 4\pi r^2 Q(2\sigma_{sol}^* c_i r)$$

The package effect is affected by the size-dependent intracellular chlorophyll concentration $c_i \propto V^b$, with $-1/3 \leq b \leq 0$ (Figure 6).

Potential nutrient uptake rate ρ is defined as the maximum uptake rate possible: the rate of diffusive flux of nutrients into a perfectly absorbing sphere,

$$\rho = 4\pi D(C_{\infty} - C_0)r$$

This rate has a volume-scaling exponent of 1/3, and will strongly limit growth of large cells, depending on nutrient concentration. The size-scaling relationships of M , P , and ρ are compared in Figure 4.

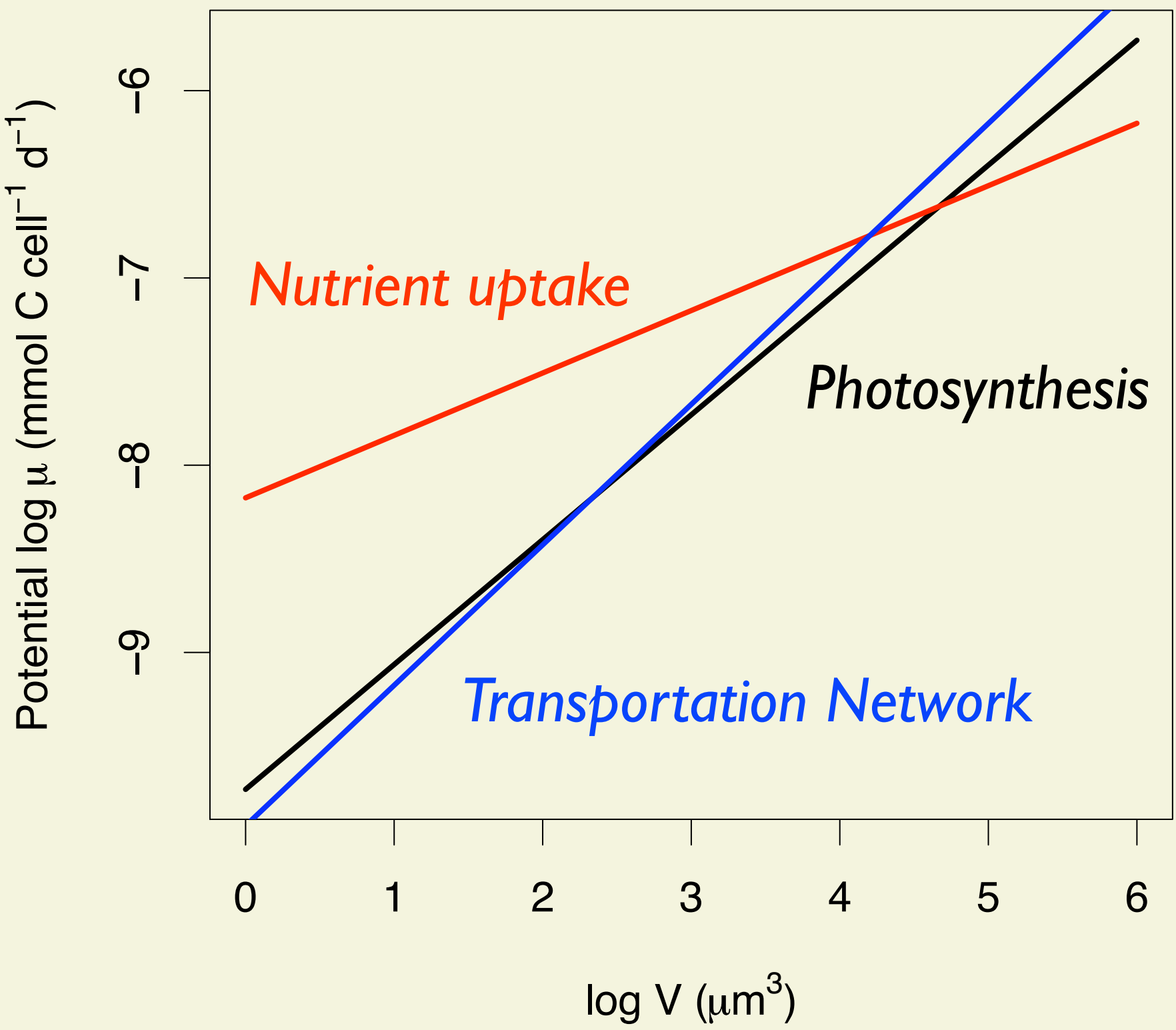


Figure 4. Allometry of potential growth rates, with transportation networks, photosynthesis, or nutrient uptake limiting growth depending on cell size at moderate irradiance and nutrient concentrations.

Results & Discussion

Under conditions of growth-saturated resource supply, phytoplankton growth rate ($\text{mol C cell}^{-1} \text{d}^{-1}$) scales with cell volume with size-scaling exponent 3/4; light-limitation reduces the size-scaling exponent to approximately 2/3, and nutrient limitation decreases the exponent to 1/3 as a consequence of the size-scaling of resource acquisition (Figure 5). Exponents between 1/3 and 3/4 occur under intermediate resource conditions.

The size-dependence of intracellular chlorophyll concentration affects the size-dependence of P , and thus sometimes growth. Figure 6 shows the volume-scaling exponent of growth under low irradiance ($E = 25 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) as the pigment concentration in large cells increases (b_{chl} increasing from 2/3 to 1). The effect is modest, but we know relatively little about b_{chl} .

Different groups of phytoplankton (pico, nanno, diatoms) exhibit allometric size-scaling, but have different maximum growth rates due to group-specific adaptations; this can easily be incorporated by changing intercepts for M .

Figure 5. Allometry of realized growth rates for the Metabolic Transportation Network model. (a) Light-limited growth results in a volume-scaling exponent of 2/3. As irradiance increases, the exponent changes to match the nutrient exponent (1/3 or larger, depending on nitrate concentration), or the 3/4 exponent of metabolic allometry. (b) The same data, viewed as a function of nitrate concentration.

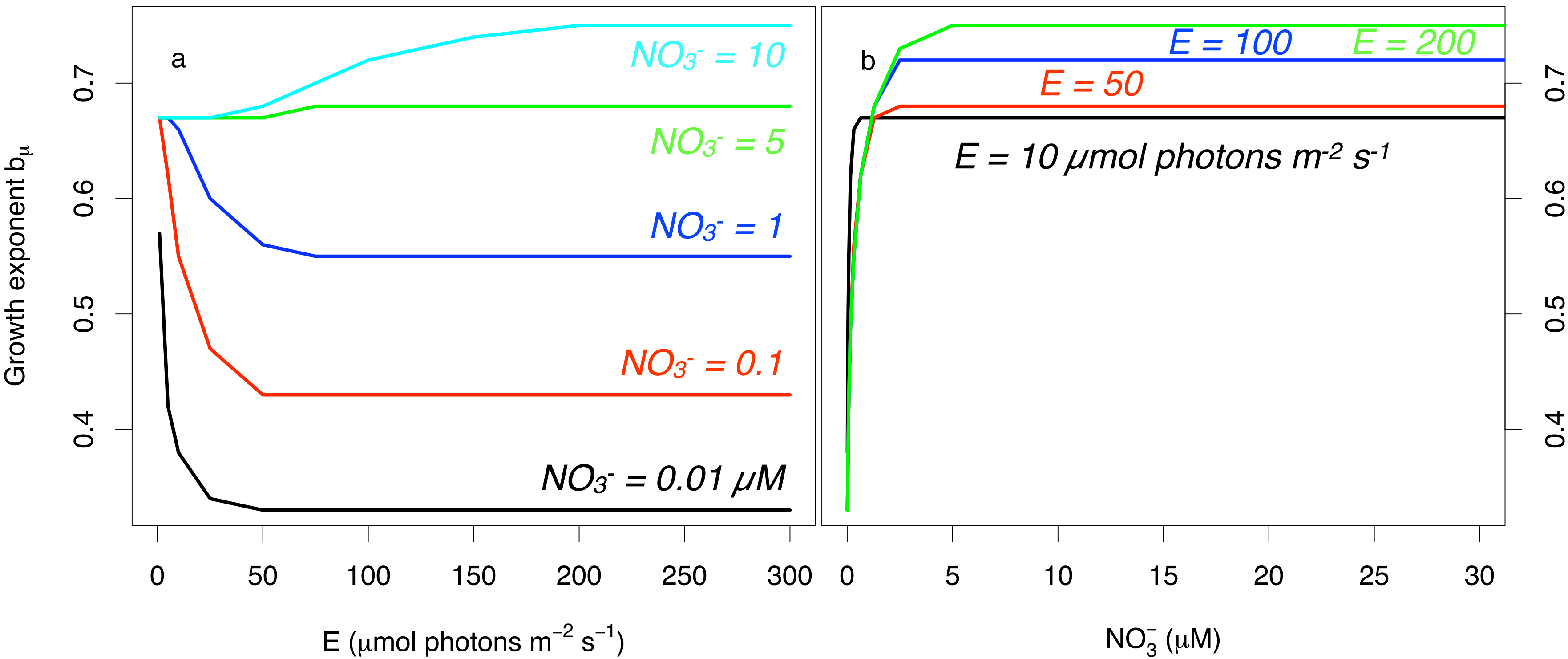
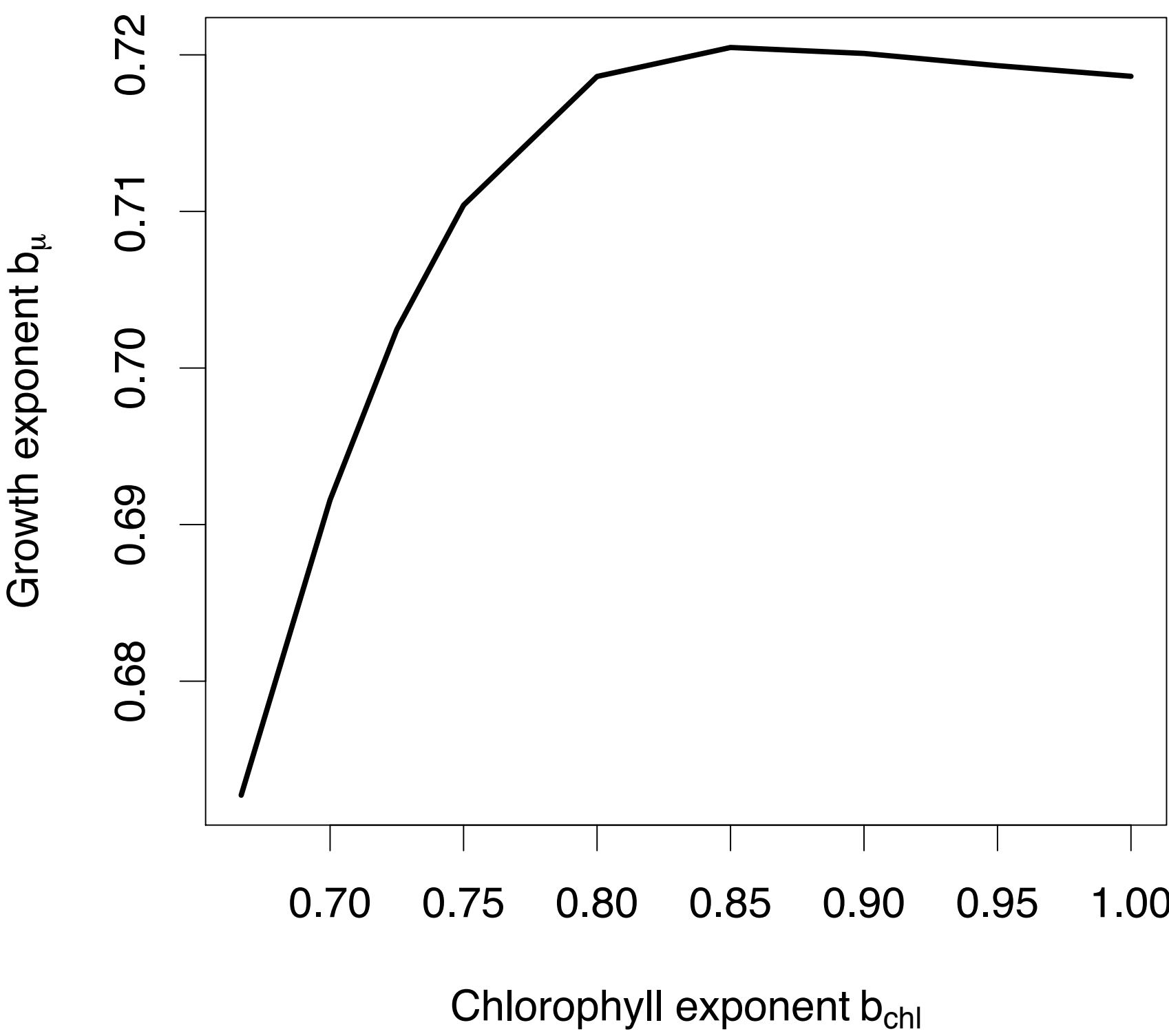


Figure 6. Allometry of maximum growth rates at low $E = 25 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, from the Metabolic Transportation Network model as a function of the volume scaling exponent of cellular chlorophyll content. At high E , the growth exponent is always 3/4.



An extension of this work permits dynamic carbon and nitrogen content (quotas), creating a complex interaction between quota and growth allometry and adds size-dependent losses in a 3D GCM (ZP Mei, Friday 12:15 in the Clio room).