Phytoplankton size and porter scaling: optimal net nutrient uptake

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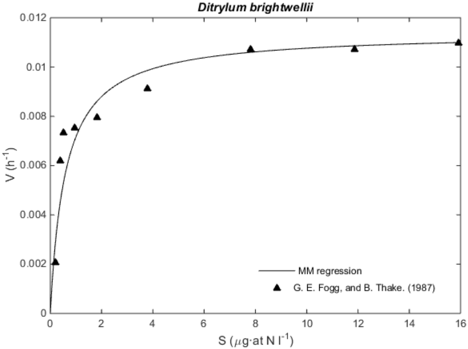
Michaelis-Menten model (I)

Phytoplankton nutrient uptake has most commonly been described by the Michaelis- Menten (MM) equation

$$V = V_{\text{max}} \frac{S}{S + K}.$$



V_{max}: maximal uptake rate.

S: ambient nutrient concentration.

K: half-saturation constant, which corresponds to the concentration when uptake rate is $V_{\text{max}}/2$.

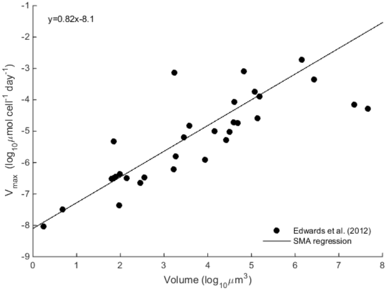
Michaelis-Menten model (II)

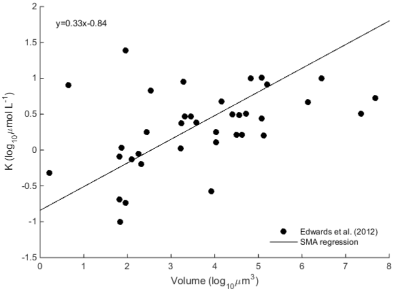
✓ MM model is simple, and measurements of kinetic parameters (V_{max} and K) are available in the literature.

✗ However, MM-model provides no theoretical predictions on how the kinetic parameters scale with:

1. **inherent microbial traits** (cell size, number of porters, handling time and porter size).
2. **environmental variables** (temperature,nutrients concentration and their diffusion coefficients).

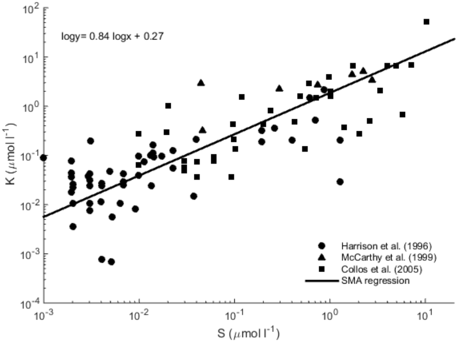
Experimental scaling of V_{max} and K with size





$$V_{max}(\mu\text{mol d}^{-1}) = 1.79\times10^5\, r^{2.46}(\mu\text{m}) \qquad K(\text{molecules } \mu\text{m}^{-3}) = 140\, r^{0.99}(\mu\text{m})$$

Experimental scaling of K with nutrient concentration

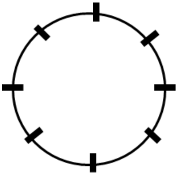


$$K(\text{molecules } \mu\text{m}^{-3}) = 5.27\, S^{0.84}(\text{molecules } \mu\text{m}^{-3})$$

Trait model

In 2011, Aksnes and Cao derived a non-MM trait-based model where the nutrient uptake rate $V(S)$ depends on inherent microbial traits

- r: cell radius.
- s: porter radius.
- n: porter number.
- h: handling time, time to process one nutrient.



and environmental properties

- D: diffusion coefficient.
- S: ambient nutrient concentration.

For small porter density, $p = \dfrac{ns^2}{4r^2} \ll 10^{-3}$ there is a MM approximation with

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

Proposed cost model

We propose here that:

- Porters not only increase the intracellular concentration of nutrients, but also imply a certain effective **cost of porters** $\Rightarrow$ **optimal number of porters** in the cell, n_{opt}.
- For the porter cost we assume $V_{\mathsf{cost}} = d\, n^f$.
- Thus, the net uptake is:

$$V_{\mathsf{net}} = V - V_{\mathsf{cost}} = V - d\, n^f.$$

Optimal number of porters

- Higher V_{net} imply faster growth rates and shorter division times.
- We assume that organisms with traits giving the maximum V_{net} at a given S have a natural selection advantage.
- Through a maximization of V_{net} we can determine the values d and f that reproduce the observations.
- Given an organism with the typical size for the given nutrient concentration S we find n_{opt} as

$$\left.\frac{\partial V_{\text{net}}}{\partial n}\right|_{n=n_{\text{opt}}} = 0.$$

Results (I): Size and inherent traits

- **Size scaling with nutrient concentration**:
  The dominant size of phytoplankton is found to grow with regional nutrient concentration in the ocean.
  Thus, we assume here that the relation $K(S)$ is dominanted by differences in phytoplankton size with nutrient concentration.
  From $K(S)$ and $K(r)$ we obtain

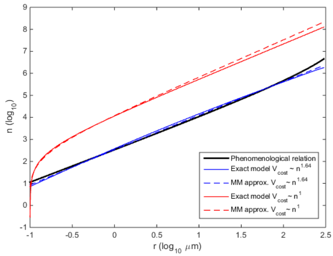
$$r(\mu\text{m}) = 0.036 S^{0.84} (\text{molecules } \mu\text{m}^{-3}).$$

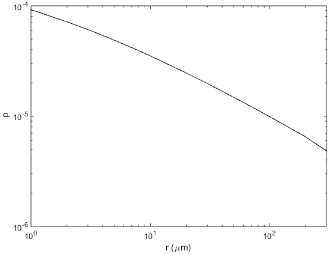
- **Inherent traits scaling with size**:
  Replacing the observed scaling relations $V_{\text{max}}(r)$ and $K(r)$ into the trait model it is obtained

$$h(\text{s}) = 1.90\, r^{-0.90} (\mu\text{m}), \quad n = 338\, r^{1.56} (\mu\text{m}).$$

Results (II): Nutrient cost

- **Optimization with free f**:
  Given $h(r)$ and $r(S)$, we maximize V_{net} and determine the values of d and f that best fits the relation $n(r)$ obtaining $V_{\text{cost}} = d\, n^f = 1.81\,(\text{molecules s}^{-1})\, n^{1.64}$, reproducing the observations quite accurately for $n(r)$.
- **Optimization with $f = 1$**:
  $V_{\text{cost}} = d\, n = 10.67\,(\text{molecules s}^{-1})\, n$ and it does not give a good fit for $n(r)$
  $\Rightarrow V_{\text{cost}}$ is not proportional to n, but follows a power law with an exponent of 1.64.





Conclusions

1. Number of porters scales with size as $n \sim r^{1.56}$ implying for the porter density $p \sim r^{-0.44}$.
2. Handling time scales with size as $h \sim r^{-0.90}$.
3. Size scales with nutrient concentration as $r \sim S^{0.84}$.
4. Porter cost is found to be $V_{\text{cost}} \sim n^{1.64} \sim p \times \text{Volume}$.
5. With this porter cost, the maximization of the net nutrient uptake rate $V_{\text{net}} = V - V_{\text{cost}}$ leads to the observed scaling relation $n(r)$.