Size-scaling of phytoplankton metabolism and growth

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Things are different, so we need science; things are similar, so science is possible

Levins & Lewontin, 1980
Macroecological pattern: body size and metabolic rate

\[ y = 0.76x + 25.22 \]
\[ r^2 = 0.99, n = 747 \]

slope = \( \frac{3}{4} \)
Kleiber’s rule

Brown et al. 2004 Ecology
Phytoplankton: basis of most aquatic ecosystems
Phytoplankton: basis of most aquatic ecosystems
Global primary productivity
Outline

• Do phytoplankton follow Kleiber’s rule?
• Mechanisms underlying the size-scaling of growth
• Links with phytoplankton size structure
The importance of phytoplankton cell size

Many key phytoplankton processes are affected by cell size:

- Growth and metabolic rates
- Resource acquisition and use
- Susceptibility to predation and sinking
The importance of phytoplankton cell size

<table>
<thead>
<tr>
<th>Property</th>
<th>Small cells</th>
<th>Large cells</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant trophic pathway</td>
<td>Microbial food web</td>
<td>Herbivorous food chain</td>
</tr>
<tr>
<td>Main fate of primary production</td>
<td>Recycling in the upper layer</td>
<td>Export toward deep waters</td>
</tr>
</tbody>
</table>

% picophytoplankton chl a
(small cells)

% microphytoplankton chl a
(large cells)

Hirata et al 2011 Biogeosci.
The importance of phytoplankton cell size

Phytoplankton size largely determines food-web structure and the fate of primary production.

Size-scaling of phytoplankton properties (meta-analysis of literature data)

Maximum growth rate ($\mu$)

Finkel et al. 2010 J Plankton Res

Negative slope implies that small cells are controlled by top-down processes

Maximum nutrient uptake rate

Litchman et al. 2006 Ecol Lett

Exponent of 2/3 implies that larger cells are limited by nutrient supply
Large phytoplankton sustain high C-specific production in nutrient-rich waters

Cermeño et al. 2005 MEPS
Early estimates suggested a slope value higher than $\frac{3}{4}$...

Size-fractionated production and biomass data from many locations

Data from the literature

Marañón et al. 2006 L&O

Marañón 2008 J Plankton Res
...and more accurate measurements confirm that the slope is approximately 1 (isometric size-scaling)

Trynitrop 2007

Chl a map from MODIS Aqua (NASA)


mean slope = 1.16 (±0.09)
Linking the size-scaling of abundance and metabolic rate

Assuming populations grow until resources are limiting, in steady-state we will have (Enquist et al 1998) that $N_{\text{max}} = R/Q$, where $N$ is abundance, $R$ is resource supply rate and $Q$ is the individual rate of resource use (e.g. metabolic rate).

Let $S$ be body size. If $R \propto S^0$ and $Q \propto S^b$ then $N_{\text{max}} \propto S^{-b}$ \rightarrow reciprocal size-scaling of abundance and metabolic rate.

Phytoplankton cultures grown under identical conditions show near-isometric size-scaling of metabolic rates.

\[ \text{slope} = 0.90 \]

\[ \text{slope} = 0.91 \]

→ phytoplankton metabolism does not follow the \( \frac{3}{4} \)-power rule
A closer look reveals that in fact the size-scaling of phytoplankton growth and production is unimodal.
Droop’s model of phytoplankton growth

\[ \mu = \mu_\infty \left( 1 - \frac{Q_{\text{min}}}{Q} \right) \]

\[ \frac{dQ}{dt} = V - N_{\text{assim}} \]

\[ N_{\text{assim}} = Q \times \mu \]
Unexpected size-scaling of nutrient maximum uptake rate ($V_{\text{max}N}$)

Theoretically, $V_{\text{max}} \propto (\text{cell size})^{2/3}$, and volume-specific $V_{\text{max}} \propto (\text{cell size})^{-1/3}$. 
In contrast, our data suggest that volume-specific $V_{\text{max}}$ is size-independent.

As cell size increases, the ability to take up nutrients increases faster than requirements.

Marañón et al. 2013 Ecol Lett
An illustration of the importance of using different size-scaling exponents for nutrient uptake

<table>
<thead>
<tr>
<th>Cell volume (µm³)</th>
<th>Uptake rate (fgN cell⁻¹ h⁻¹)</th>
<th>Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( V_{\text{max}} \propto V^1 )</td>
<td>( V_{\text{max}} \propto V^{0.66} )</td>
</tr>
<tr>
<td>1</td>
<td>0.1</td>
<td>1</td>
</tr>
<tr>
<td>10</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>100</td>
<td>10</td>
<td>22</td>
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<td>2089</td>
</tr>
<tr>
<td>1000000</td>
<td>100000</td>
<td>9549</td>
</tr>
</tbody>
</table>

Overestimation

Underestimation
Size-scaling of $Q_{\text{max}}:Q_{\text{min}}$ and C:N ratios

Marañón et al. 2013 Ecol Lett
Potential mechanisms underlying the size-scaling of phytoplankton metabolism and growth

Increasing space for catalysts
Increasing $V_{\text{maxN}:Q_{\text{minN}}}$

Increasing intracellular distances
Reduced light absorption

Nitrogen-rich cells
Non scalable components
Low $V_{\text{maxN}}:Q_{\text{minN}}$

High $V_{\text{maxN}}:Q_{\text{minN}}$
High $Q_{\text{maxN}}:Q_{\text{minN}}$
Limited by assimilation

Mañón E. 2015.
Links with natural patterns of size structure

70 bloom samples, species ranked according to their contribution to total biomass

Links with natural patterns of size structure

![Graph showing proportion of total biomass by size class (ESD, μm).](image)

- **Low biomass**
- **Intermediate biomass**
- **High biomass**

Links with natural patterns of size structure

![Graph showing biomass in size class vs. total phytoplankton biomass](image)

- Picophytoplankton
- Nanphytoplankton
- Microphytoplankton

Main points

• Size-scaling of phytoplankton metabolism and growth is unimodal

• Unimodality results from trade-off processes between nutrient requirement, uptake and assimilation

• Intermediate-size species dominate natural blooms and biogeochemical cycling in the ocean
References


