OCN621: Biological Oceanography-Microbial Ecology III

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Nutrient limitation of phytoplankton

-growth rate is affected by nutrient concentrations and generally follows a Michaelis-Menten curve

\[ \mu = \frac{\mu_{\text{max}}[N]}{K_N + [N]} \]

\( \mu \) = growth rate
\( \mu_{\text{max}} \) = maximum growth rate
\([N]\) = nutrient concentration
\( K_N \) = half saturation constant

So, if nutrients are less than the \( K_N \), then they are limiting. “High” nutrients are \( >K_N \), “low/limiting” nutrients are \( <K_N \)

This is a simplified expression with assumptions.

More complex equations can be used to describe growth rate as a function of nutrients. Especially for nutrients that require significant “processing” within the cell (ex. nitrate) or co-limitation.

ex. \[ \mu = \frac{\mu_{\text{max}} Q}{A + Q} \]

uptake rate

growth rate of cells

\( Q \)

\( A = \) half saturation constant for intracellular process governing uptake
Nutrient limitation of phytoplankton

Range of maximum growth rates ($\mu_{\text{max}}$)

<table>
<thead>
<tr>
<th>$\mu_{\text{max}}$</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.1-0.7</td>
<td>Oligotrophic, tropical waters</td>
</tr>
<tr>
<td>0.4-1.0</td>
<td>Temperate, eutrophic, coastal waters</td>
</tr>
<tr>
<td>1.0-3.0</td>
<td>Tropical upwelling, and picoplankton under eutrophic conditions at higher temperatures</td>
</tr>
</tbody>
</table>

Half saturation constants ($K_N$) in (\(\mu\text{M}\))

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>$K_N$</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>NO$_3$ or NH$_4$</td>
<td>0.01-0.1</td>
<td>Oligotrophic</td>
</tr>
<tr>
<td></td>
<td>0.05-2.0</td>
<td>Eutrophic oceanic waters</td>
</tr>
<tr>
<td></td>
<td>2.0-10.0</td>
<td>Eutrophic coastal waters</td>
</tr>
<tr>
<td>Silicate</td>
<td>0.5-5.0</td>
<td>General range for diatoms</td>
</tr>
<tr>
<td>Phosphate</td>
<td>0.02-0.5</td>
<td>General range for oligotrophic to eutrophic waters</td>
</tr>
<tr>
<td>Iron</td>
<td>0.0000001</td>
<td>Oligotrophic</td>
</tr>
</tbody>
</table>
Nutrient limitation of phytoplankton

Implications:

3 possible outcomes with coexistence in a simple two member system

Can use this theory, along with measurements of $\mu_{\text{max}}$, $K_N$ to predict:

1. what phytoplankton will dominate (ecology)
2. response of community to nutrient additions / limitations (biogeochemical modeling)
Nutrient limitation of phytoplankton

Implications:

This theory can be used to explain why there are so many plankton:

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THE PARADOX OF THE PLANKTON*

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The problem that I wish to discuss in the present contribution is raised by the very paradoxical situation of the plankton, particularly the phytoplankton, of relatively large bodies of water.

The problem that is presented by the phytoplankton is essentially how it is possible for a number of species to coexist in a relatively isotropic or unstructured environment all competing for the same sorts of materials. The problem is particularly acute because there is adequate evidence from enrichment experiments that natural waters, at least in the summer, present an environment of striking nutrient deficiency, so that competition is likely to be extremely severe.
Nutrient limitation of phytoplankton

Examples:

<table>
<thead>
<tr>
<th>Table 2. Half-saturation constants for uptake (Kₚ) of nitrate and ammonium by cultured marine phytoplankton at 18°C. Kₚ units in μmoles/liter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Organism</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>Oceanic species</td>
</tr>
<tr>
<td>Coccolithus huxleyi BT-6</td>
</tr>
<tr>
<td>C. huxleyi F-5</td>
</tr>
<tr>
<td>Chaetoceros gracilis</td>
</tr>
<tr>
<td>Cyclotella nana 13-1</td>
</tr>
<tr>
<td>Neritic diatoms</td>
</tr>
<tr>
<td>Skeletonema costatum†</td>
</tr>
<tr>
<td>Leptocylindrus danicus</td>
</tr>
<tr>
<td>Rhizosolenia sterletsothii</td>
</tr>
<tr>
<td>R. robusta‡</td>
</tr>
<tr>
<td>Ditylum brightwellii</td>
</tr>
<tr>
<td>Coccosiscus lineatus</td>
</tr>
<tr>
<td>C. weisii</td>
</tr>
<tr>
<td>Asterionella japonica</td>
</tr>
<tr>
<td>Neritic or littoral flagellates</td>
</tr>
<tr>
<td>Gonyaulax polyedra</td>
</tr>
<tr>
<td>Gymnodinium splendens</td>
</tr>
<tr>
<td>Monochrysis lutheri</td>
</tr>
<tr>
<td>Isochrysis galbana</td>
</tr>
<tr>
<td>Dunaliella tertiolecta</td>
</tr>
</tbody>
</table>

Natural marine communities (from MacIsaac and Dugdale 1969)

<table>
<thead>
<tr>
<th>Condition</th>
<th>Nitrate</th>
<th>Ammonium</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oligotrophic</td>
<td>≤0.2 (6 expts)</td>
<td>0.1–0.6 (3 expts)</td>
</tr>
<tr>
<td>Eutrophic</td>
<td>≥1.0 (3 expts)</td>
<td>1.3 (1 expt)</td>
</tr>
</tbody>
</table>

* Geometric mean diameter rounded off to the nearest micron.
† This notation means that -0.2 < Kₚ < 0.4. Negative Kₚ values have no physical interpretations.
‡ At 28°C, Kₚ for nitrate uptake was 1.0 ± 0.5; at 3°C, it was 0.8 ± 0.5.
§ As an oceanic species according to Cupp (1943).
Nutrient limitation of phytoplankton

Examples:

So, since the $K_N$ for iron in this environment is 0.12 nM and the measured concentrations are <0.10 nM in the euphotic zone, these populations are iron-limited

Coale et al. 1996
Nutrient limitation of phytoplankton
Growth rate is affected by light limitation much like nutrients
- light can be considered a “nutrient”

\[ P = P_m \left(1 - \exp\left(-\frac{E}{E_k}\right)\right) \]

\[ E_k = \frac{P_m}{\alpha} \]

P-E curves can be constructed by exposing phytoplankton to different light levels and measuring primary production. Tell about how light is affecting cells/populations.

As with nutrients, there are many different models to describe relationship. No clear “winner.”

Compensation irradiance \((E_c)\) is where net photosynthesis is greater than respiration. (Can only be measured using oxygen techniques)
Light limitation: P-E curves examples

Platt et al. 1980

Johnson and Barber 2003
Light limitation

Light decreases exponentially with depth:

\[ E_z = E_o \exp(-k_d z) \]

- \( E_z \): light at depth \( z \) (\( \mu \text{mol quanta m}^{-2} \text{ sec}^{-1} \))
- \( E_o \): light at surface (\( \mu \text{mol quanta m}^{-2} \text{ sec}^{-1} \))
- \( k_d \): diffuse attenuation coefficient (1/m)
- \( z \): depth (m)

Since light can be considered a nutrient, light strongly regulates primary production.

Most of the ocean is light limited (> ~150m, <1% \( E_o \)).
Light limitation: critical depth

Mixed-layer is the vertical portion of the water from the surface down that is homogeneous with respect to a given parameter (temperature, salts, nutrients, phytoplankton, etc.)

If we assume the mixed layer to contain uniform phytoplankton concentration and light to be regulating primary production, at some depth the integrated primary production (areal production) will be equivalent to the integrated (area) respiration (assumed to be constant with depth), i.e. water column $P=R$. This is called the critical depth. This is different from the compensation depth/light, where $P=R$ at that particular depth.
Spatial Distributions: Z

(Bottom up) regulated by the interplay between:
- nutrients
- light
- temperature

Depth distribution of biomass:
1. Chlorophyll (a) – extracted values in stratified waters have subsurface maximum
2. Subsurface maximum in chl biomass is trade off between light (top) and nutrients (bottom)
   - growth rate driven
   - photoacclimation driven
   - depth depends on light penetration, nutricline depth

Cullen 1982
Spatial Distributions: Z

(2) Carbon (POC) biomass also has a subsurface maximum

Prochlorococcus ($\mu$g C $\Gamma^{-1}$)

Synechococcus ($\mu$g C $\Gamma^{-1}$)

Eukaryotic Phytoplankton ($\mu$g C $\Gamma^{-1}$)

Coccolithophore ($\mu$g C $\Gamma^{-1}$)

Karl 2002

Durand et al. 2001
Spatial Distributions: Z

(3) Cell Number

Durand et al. 2001
Spatial Distributions: Z

(4) Fluorescence
- subsurface max.
- microvariability
- affected by physiology

(5) Inter-comparison
- all subsurface max.
- max not at same depth
- both photoacclimation & growth rate
- know what you’re trying to measure: “biomass” measurements may not be influenced only by biomass

Falkowski and Raven 1997
Spatial Distributions: Z

Depth Distribution of Production:
1. Carbon uptake (photosynthesis)
   -(near) surface maximum
   -sometimes slight decrease at surface, likely due to photoinhibition / photodamage
   -decreases ~exponentially with depth
   -consistent with P-E curves

2. Other estimates
   -ditto
   -fairly close agreement, with the resolution of the techniques

Falkowski and Kolber 1998