Announcements

• Quiz and discussion of microbe reading Tuesday November 22
• Next problem set due Nov. 27 (Bellingham Bay nutrient budget)

Spring bloom Bering Sea

Paradox of the plankton
Competitive exclusion principle

• Gause’s (1934) experiments with *Paramecium* species.
• When species share the same resources, the competitive dominant species can exclude other species.

Paradox of the plankton (G. E. Hutchinson)

• More than 5,000 species identified.
• Phytoplankton presumably compete for the same light and nutrients.
• Why doesn’t one superior competitor exclude the other species? What allows such high species diversity?

Learning goals

• Understand how to quantify phytoplankton biomass and productivity
• Learn how to measure primary production
• Understand the processes that lead to the spring bloom
• Consider why there are so many species of phytoplankton in the ocean
Primary production: Synthesis of organic materials from inorganic substances by photosynthesis (or chemosynthesis)

Biomass vs. production: mass/volume or mass/area vs. rate of change in mass/volume

Units: mass carbon per area per time, e.g., gC/m²/y
Or gC/m²/y (carbon per unit volume per time)
gC / gChl-a / time = assimilation number

Who does it: autotrophs
Who consumes it? Autotrophs and heterotrophs via respiration

Photosynthesis:
6CO₂ + 6H₂O (+ nutrients, light) → 6O₂ + C₆H₁₂O₆ (+ proteins, Chl, etc.)

Respiration:
6O₂ + C₆H₁₂O₆ (+ proteins, Chl, etc.) → 6CO₂ + 6H₂O (+ nutrients)

Chemosynthesis:
6CO₂ + 6H₂S + 6O₂ → 6H₂O + C₆H₁₂O₆ + 12H⁺ + SO₄⁻

Measuring primary production:

What can you measure?
Change in oxygen, carbon, N, P, Chl-a, light

Oxygen method:
Collect water sample, incubate, re-measure [O₂]
Use dark and light bottles

O₂ change (ΔO₂) in dark bottle: respiration
ΔO₂, Light bottle: net production (gross production + respiration)
ΔO₂, Light bottle - ΔO₂, dark bottle: gross production
Advantage: measure both gross and net production
Disadvantages: 1: not as sensitive as other techniques
2: need to know O₂:C ratio
(Photosynthetic quotient ~ 1.2 – 1.8)
(depending on N source)

More sensitive method: ¹⁴C incubation (also ¹³C)

Method:
Collect water sample
Add ¹⁴C labeled HCO₃⁻
Incubate (~1 hour - gross photosynthesis, ~1 day - net photosynthesis)
Measure ¹⁴C in particles (phytoplankton and possibly “other” particles)

Calculate:
¹⁰ production = 1.05 \( \frac{¹⁴C(\text{particles}) \times \text{DIC concentration (gC/l)}}{¹⁴C(\text{added}) \times \text{incubation time}} \)

Measure ¹⁴C uptake in dark bottle to determine if other particles have taken up labeled HCO₃⁻. Subtract dark bottle uptake from light bottle uptake

In situ measurement of PP

Respiration (-)  Primary productivity (mg/d)
Simulated *in situ* incubations:
- Collect samples from several depths
- Measure Chl-α and irradiance at each depth
- Incubate samples on board a ship
- Simulate the light field and temperature
- Determine the $P$ vs. $I$ (irradiance) relationship
- Calculate PP at each depth

$$P_l = P_{\text{max}} \tanh \left( \frac{\alpha \cdot I}{P_{\text{max}}} \right)$$

$P_{\text{max}}$ = asymptote
$\alpha$ = initial slope

What nutrients are limiting in the ocean?

- N, P, Fe, and other nutrients or trace elements (Si, Cu, Zn, Co, etc.)
- PP limitation in general: P = freshwater, N = coastal, Fe = open ocean

How can we determine what nutrients are limiting?

1: Bottle incubation experiments
2: Biochemical investigations

Primary production can be limited by light or nutrients, depending upon the season and geographic location

Primary production and nitrogen cycling

“New” vs. “Regenerated” production

N input (N-fixation, rivers, dust)
Temperature effects on phytoplankton

- Different species have different optimal temperatures
- Although temperature does not strongly influence productivity, it can affect population growth rate and species composition.

Seasonality in primary production and phytoplankton biomass:

THE SPRING BLOOM

In coastal waters in Spring, phytoplankton numbers explode! Waters turn deep green. Zooplankton begin feeding and reproducing. Sometimes a fall bloom occurs as well.

What is going on?

Changes in light?
Changes in nutrients?

Mar 22
May 8
Jun 14
Aug 31
Spring bloom in the North Atlantic: Ocean-basin-wide effect

Pre bloom  
Spring Bloom

Spring Bloom in Puget Sound

From Nakata and Newton 2001

What determines the timing and intensity of the Spring Bloom?

Spring Bloom in Puget Sound

From Rynearson et al. 2006  
Limnology and Oceanography

Stratification and mixing

Density  
Depth

Winter profile  
Deep mixing

Summer profile  
Shallow mixing

After a storm  
mixed-layer deepens
Changes in phytoplankton numbers in the North Atlantic (Sverdrup, 1953)

What limits primary productivity in Puget Sound?

What causes the Spring bloom to crash? Fall bloom?
Dissolved inorganic nitrogen

PP in Puget Sound generally limited by light and mixing. Nitrogen limitation apparent in summer.

Nutrient addition experiments

From Nakata and Newton 2001

PP and light

$y = 6.9x - 72.5$

$R^2 = 0.78$

MODIS
(Mod Res Imagery spectroradiometer)
August 2002

Note the “squirts” off the WA coast
Paradox of the plankton: Is the ocean more complex than it seems?

From Stocker (2012) *Science*

Atomic force microscopy of *Synechococcus* and heterotrophic bacteria (Malfatti and Azam 2009)

Species associations within thin layers:

*Pseudo-nitzschia fraudulenta* and *Chaetoceros socialis*

*Trichodesmium* - a nitrogen-fixing cyanobacterium from the Sargasso sea. Photo by Sonya Dyhrman, WHOI.

Rines et al. 2002