SeaWiFS Global Biosphere  September 1997 – August 2000
Three Year Anniversary
A break in the clouds over the Barents Sea on August 1, 2007 revealed a large, dense phytoplankton bloom to the orbiting MODIS aboard the Terra satellite. The bright aquamarine hues suggest that this is likely a coccolithophore bloom. The visible portion of this bloom covers about 150,000 square kilometers (57,000 square miles) or roughly the area of Wisconsin.
Photosynthesis

- The formation of organic matter from inorganic carbon (CO₂) with light as the primary energy source
- 6 carbon dioxide + 6 water = 1 glucose + 6 oxygen

\[ 6 \text{CO}_2 + 6 \text{H}_2\text{O} = \text{C}_6\text{H}_{12}\text{O}_6 + 6 \text{O}_2 \]

- Two reaction steps:
  1. Light reaction: photophosphorylation: production of O₂ and energy from H₂O
  2. Dark reaction: carbon fixation: CO₂ to glucose

- Phytoplankton and algal photosynthesis = primary production
- Organisms that perform photosynthesis = primary producers = autotrophic = phototrophic organisms
- All phototrophic organisms possess chlorophyll a and several accessory pigments (chl. b, c, carotenoids), which serve as antenna pigments to capture light energy and transfer electrons to the photosynthetic reaction center
- Each pigment has a distinct absorption spectrum
- Photosynthesis most efficient in blue and red light, according to absorption maximum of chlorophyll (action spectrum)
Photosynthesis and Light

- P vs. I curves (photosynthesis versus light intensity): shows photosynthetic adaptation
- Gross production = total production; net production = gross prod. – respiration
- Compensation point: photosynthesis = respiration, net production = 0
- $P_{\text{max}}$ = maximum production; depends on dark reaction (unlimited growth) or limiting resources
- Initial slope $a$: photosynthetic efficiency (how well is low light used) also quantum yield $f = \frac{DP}{DI}$; depends on light reaction
- $I_k$: summarizes key characteristics $P_{\text{max}}$ and $a$ in one term; shade-adapted cells have lower $I_k$ than high-light cells

Note: Species (1) and (2) have the same $I_k$ despite different $P_{\text{max}}$ and $a$. The lower $I_k$ of (1) and (2) as compared to (3) reveals them as shade-adapted species.
Sverdrup's Model of Critical Depth

- Photosynthesis decreases exponentially with depth due to decrease in light availability
- Respiration is unaffected by light and remains constant with depth
- Phytoplankton is mixed by turbulence and experiences different light intensities over time, sometimes above and sometimes below compensation point
- **Critical depth** = depth at which photo-synthesis of the total water column phytoplankton population equals their total respiration

A phytoplankton population can only proliferate if mixing is shallower than the critical depth. Only then is the population net production >0.
particulate organic matter = POM
particulate organic carbon = POC
particulate organic nitrogen = PON
Dissolved organic material

Virus

Femto

Pico

Nano

Micro

20000

2000

200

20

2

0.2

0.02

µm

After T. Fenchel
Dissolved organic material

After T. Fenchel
Biogenic Carbon Cycling in the Upper Ocean: Effects of Microbial Respiration
Richard B. Rivkin, et al.
Science 291, 2398 (2001);
DOI: 10.1126/science.291.5512.2398

- CO$_2$ production
- Fraction of consumed DOC that is respired as CO$_2$
Vertical Carbon Flow in the NEW Polynya

(Deming, unpublished)
Vertical Carbon Flow in the NEW Polynya

[\text{mg C m}^{-2} \text{d}^{-1}]^{1}

1992

\begin{itemize}
\item 252 (100\%)
\item 86 (34\%)
\item 156 (62\%)
\end{itemize}

1993

\begin{itemize}
\item 970 (100\%)
\item 499 (51\%)
\item 396 (41\%)
\end{itemize}

(Deming, unpublished)
Fig. 2. Methods of investigations for the DOM-POM continuum.
Sediment-laden sea ice

(photos provided by Hajo Eicken)
**Bacterial abundance\(^a\) in ice**

<table>
<thead>
<tr>
<th>Ice type</th>
<th>Sampling location</th>
<th>Sample T (°C)</th>
<th>Particle-poor ice</th>
<th>Particle-rich ice</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snow</td>
<td>South Pole</td>
<td>–15</td>
<td>0.2–5 x 10³</td>
<td></td>
</tr>
<tr>
<td>Ice sheet</td>
<td>Over Lake Vostok (2–4 km)</td>
<td>–3</td>
<td>0.2–8 x 10³</td>
<td>6 x 10⁷</td>
</tr>
<tr>
<td></td>
<td>Greenland (bottom of sheet)</td>
<td>–9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lake ice</td>
<td>Lake Bonney, Antarctica</td>
<td>&lt;–5?</td>
<td>5 x 10³</td>
<td>0.1–4 x 10⁵</td>
</tr>
<tr>
<td></td>
<td>Imikpuk Lake, Alaska</td>
<td>–5</td>
<td>7 x 10⁴</td>
<td>7 x 10⁵</td>
</tr>
<tr>
<td>Sea ice</td>
<td>Southern Ocean, summer</td>
<td>–2</td>
<td>0.01–3 x 10⁶</td>
<td>0.2–2 x 10⁶</td>
</tr>
<tr>
<td></td>
<td>Southern Ocean, winter</td>
<td>–2</td>
<td>0.02–2 x 10⁶</td>
<td>1 x 10⁷</td>
</tr>
<tr>
<td></td>
<td>Arctic Ocean, summer</td>
<td>–2</td>
<td>0.4–2 x 10⁶</td>
<td>0.05–1 x 10⁷</td>
</tr>
<tr>
<td></td>
<td>Arctic Ocean, winter</td>
<td>–2 to –20</td>
<td>0.2–1 x 10⁵</td>
<td>0.5–3 x 10⁶</td>
</tr>
<tr>
<td>Permafrost</td>
<td>Northeast Siberia</td>
<td>–10</td>
<td></td>
<td>&gt; 1 x 10⁸</td>
</tr>
</tbody>
</table>

\(^a\) Number ml\(^{-1}\) melted ice or g\(^{-1}\) soil for permafrost; data compiled from Carpenter et al. (2000), Delille et al. (1995), Gradinger and Zhang (1997); Grossman and Dieckmann (1994); Helmke and Weyland (1995); Junge et al. (2001, 2003a, 2004), Karl et al. (1999), Priscu and Christner (2004), Rivkina et al. (2000), and Sheridan et al. (2003).

*(Deming and Eicken, 2007)*
Sediment-laden sea ice
Lake ice vs. sea ice and the role of microstructure

Arctic lake ice: $k_{\text{eff}} \leq 0.01$, $n_l \leq 0.05 \, \%\%$, $\alpha \leq 0.15$

Arctic sea ice: $k_{\text{eff}} \geq 0.28$, $n_l \geq 50 \, \%\%$, $\alpha \geq 0.40$

(from Eicken, 2003)
Lake ice vs. sea ice: Impurity content and pore microstructure

- Effective segregation coefficient $k_{\text{eff}} = S_i / S_w$
- $k_{\text{eff}}$ dependent on impurity concentration, hydrodynamics, growth rate
- Lake ice: $k_{\text{eff}} \leq 0.01$; Sea ice: $k_{\text{eff}} \geq 0.12$

(from Eicken, 2003)
Frozen habitats: Thermal evolution and constraints

Assur (1960)
(also shown in Eicken, 2003)
Frozen habitats: Thermal evolution and constraints

Seawater, model by Marion & Grant (1997)

Eutectic ($V_l/V = 0$) at about $-55 \, ^\circ C$

$V_l/V, \%$

$\alpha(H_2O)$

$\phi$

Temperature, K

H$_2$O(s)

MgCl$_2$•12H$_2$O

KCl

NaCl•2H$_2$O

NaSO$_4$•10H$_2$O
Microstructural evolution as a function of temperature: Thin section studies

-30 °C, p=0.03
A=0.015 mm²
Pₐ = 0.80 mm⁻¹

-2.7 °C, p=0.08
A=0.041 mm²
Pₐ = 1.50 mm⁻¹

-1.3 °C, p=0.11
A=0.108 mm²
Pₐ = 1.83 mm⁻¹

-30 °C, p=0.02
A=0.012 mm²
Pₐ = 0.58 mm⁻¹

-2.4 °C, p=0.17
A=0.127 mm²
Pₐ = 3.02 mm⁻¹

-1.5 °C, p=0.21
A=0.199 mm²
Pₐ = 2.54 mm⁻¹

Cold ice → Warm ice

(see Eicken, 2003)
Microstructural evolution as a function of temperature: Magnetic resonance imaging

(from Eicken, 2003)
Hydrodynamic control of pore microstructure
Artificial sea ice, no current

Artificial sea ice, 0.16 m/s current

(see Eicken, 2003)
Impact of microstructure on transport properties: Permeability

Darcy:
\[ Q = K_f A \frac{\Delta h}{l} \quad [\text{m}^3 \text{s}^{-1}] \]

Hydraulic conductivity
\[ K_f \quad [\text{m} \text{s}^{-1}] \]

(Intrinsic) Permeability
\[ k = \frac{\mu}{\rho g} K_f \quad [\text{m}^2] \]

Freitag (1999), Eicken (unpubl.)

Level ice
\[ \square \]
Pressure ridge ice
\[ \triangle \]
Data fit to \[ \square \] and \[ \triangle \]
New ice
\[ \cdots \]
Summer FY/MY ice
(SHEBA)

Effective Porosity \( n_{\text{eff}} \) [\%]

(From Eicken, 2003)
March 2001
Sea ice north of Barrow, Alaska
Air temperature of \(-40^\circ C\)

vertical ice gradient of \(-20^\circ C\)
(2 m thick)
Arctic sea-ice core (cm scale)

-20°C
~2% brine vol
~20% salt

-5°C
Sea-ice microbial community

-2°C

10 cm
Image obtained by epifluorescence microscopy after staining with a DNA-specific stain (called SYBER Green I). The larger fluorescing objects are the bacteria; arrows point to viruses.
Typical sea-ice algae (diatoms) and bacteria (DAPI-stained)
Typical chlorophyll profile in “clean” sea ice

Fig. 5. Chlorophyll a profile in sea ice, 17 June

(Rysgaard et al., 2001)
Distribution of ice biota: “Dirty” Elson Lagoon ice

Bacterial abundance:
- $2.2 \pm 0.7 \times 10^5$ cells ml$^{-1}$ (ice, med. sed. conc.)
- $8.8 \pm 8.0 \times 10^5$ cells ml$^{-1}$ (ice, high sed. conc.)

(Eicken, Junge, Deming, unpublished)
Subzero examination of ice thin sections (µm scale)

cold room at –5 to –20°C

(see Junge et al., 2001)
Thermal evolution and precipitation of salts

(see Eicken, 2003)
Thermal evolution and precipitation of salts: Mirabilite (T < −8.2 °C)
Pore connectivity and fluid transport (transmitted light)

(photos by Krembs; in Deming, 2007)
Transmitted light

brine pores

-20°C

(photos by Krembs; in Deming, 2007)
Transmitted light
(no stain)

Epifluorescent light
(DNA stain)

(Junge et al., 2001)

-15°C
Transmitted light with Alcian Blue stain for EPS

EPS = extracellular polysaccharide substances (exopolymers, gelatinous material, or mucous)

(Krembs et al., 2002)
(Krembs et al., submitted)
EPS alters the structure of sea-ice pores

(Krembs & Deming, 2008; Krembs et al., submitted)
The habitat is altered in both artificial and natural sea ice

2-D relationship: pore diameter to circumference

Artificial ice, no EPS

Artificial ice, with EPS

Barrow ice, 2001

Barrow ice, 2002

(Euclidean)

(Fractal)

(Krembs et al., submitted)
EPS alteration of ice structure, anchoring of algae

(Krembs and Deming, 2008)
Biomass, production and horizontal patchiness of sea ice algae in a high-Arctic fjord (Young Sound, NE Greenland)

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Fig. 2. *In situ* equipment for measuring sea ice algal fluorescence and oxygen profiles
Fig. 3. (a) Mean diurnal irradiance in air ($E_a$) and below sea ice ($E_b$), (b) irradiance below sea ice in relation to irradiance in air, (c) mean diurnal temperature in air and in bottom ice, (d) sea ice and snow thickness, the freshwater layer overlying the ice (under the snow), and (e) salinity immediately below sea ice (V) and in brine (O) and nutrients (V, $NO_3^-$; O, $NH_4^+$; □, $PO_4^{3-}; \bigtriangleup$, Si) in bottom ice brine during the investigation period.

(Rysgaard et al., 2001)
Fig. 5. Chlorophyll a profile in sea ice, 17 June

Fig. 6. Oxygen concentration profile at the sea ice-water interface, 25 June

(Rysgaard et al., 2001)
Fig. 7. Primary production (O) and relative electron transport rate (ETR, ●) versus irradiance. Error bars represent standard error (n = 5).

Fig. 10. Relative electron transport rate (ETR) versus irradiance for 3 different dates.

(Rysgaard et al., 2001)
Fig. 11. Spatial heterogeneity in algal biomass ($F_0$) at Stns A, B and C obtained on 23 June. The lower right panel shows the distance between stations, and A, B and C show the 2-dimensional variation in $F_0$ (chl a).

(Rysgaard et al., 2001)
Transmitted light
(no stain)

Epifluorescent light
(DNA stain)

-15°C

(Junge et al., 2001)
DAPI-stained bacteria

Triple-point juncture

Brine pore

(Junge et al., 2001)
Particle aggregates

Bacteria

(Junge et al., 2001)
Transmitted light

-15°C

dividing bacterium

10 μm

(Junge et al., 2001)
At the coldest temperatures, virtually all active bacteria were associated with surfaces.

(Junge et al., 2004)
Sea-ice bacteria are also embedded in EPS

(Meiners, 2002)
CASES Overwinterring Leg 5
February 23, 2004
CCG Amundsen

Noel Green, wildlife observer
Ice temperature contours through the winter

(Collins et al., 2008)
Cells were lost from coldest horizons

(Collins et al. 2008)
EPS was produced in the coldest horizons 
(also known to be produced copiously in warm bottom ice)

(Collins et al. 2008) 
(Riedel et al. 2006)
The colder the ice, the greater the EPS production per cell

Fig. 7.5. Wintertime increases in EPS concentration per bacterium in Arctic sea ice as a function of ice temperature in situ. Increases are relative to concentration at the warmest temperature, highlighted by the dotted line at unity. Data are from upper ice depths of 40–70 cm over a 3-month period from January to March 2004 (Collins et al., 2008), best fit to an exponential curve where $r^2 = 0.46$.
Fig. 7.4. Idealized depth profiles of seasonal changes in bacterial abundance in sea ice: autumn cell entrainment and enrichment (relative to seawater) into new ice (orange line); winter losses (blue line); spring gains, greatest where algae bloom (green line); and continued summer gains prior to ice melt, with osmotic losses in surface melt ponds and releases from bottom ice during ice melt (from data and concepts in Grossmann & Dieckmann, 1994; Gradinger & Zhang, 1997; Delille et al., 2002; Brinkmeyer et al., 2004; Meiners et al., 2004, 2008; and Collins et al., 2008).
Food web components, and physical and chemical properties of Baltic Sea ice

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Fig. 2. Air temperature (2 m height) and ice temperature (15 cm from ice surface) approximately 200 m away from sampling site used from 25 January 2000 onward. Continuous ice temperature records were available from 22 February onward (modified from Granskog et al. 2003)
Bacteriophage, viruses that attack bacteria
(virus = poison in Latin; phage = to eat)
Fig. 7.3. Transmission electron micrograph of the Siphoviridae phage 9A that infects two species of the γ-Proteobacterial genus Colwellia at subzero temperatures, including the sea ice bacterium C. demingiae (from Wells & Deming, 2006b, with permission).
Fig. 7.6 (a) Springtime increases in concentrations of chlorophyll $a$, bacteria and viruses in melted sea ice samples. Data are best fit to linear regressions where $r^2 = 0.74$, 0.71 and 0.53, respectively. (b) Springtime relationship between ratio of viruses to bacteria (the dotted line highlights the typical ratio of 10 in seawater) and cell-specific bacterial growth (measured by thymidine incorporation). Data are best fit to a logarithmic curve where $r^2 = 0.53$. (All data re-plotted from Maranger et al., 1994, with permission).

(Deming, in press)
Bacterial and viral numbers in sea-ice brine were not static.

Viral densities were high, approaching $10^8$ ml$^{-1}$ brine.

Contact rates between viruses and bacteria were very high, almost 600 times that in seawater.

(Wells and Deming, 2006)
Cold-active viral enzymes must have been at work

(from Hughes et al., 1998)
Fig. 7.9. Schematic (not drawn to scale) of a recently opened lead in winter with newly formed sea ice and its surficial frost flowers containing brine (and bacteria and viruses) wicked from the sea ice. Upper left photo shows a field of frost flowers in the Amundsen Gulf of the Canadian Arctic during December 2007 (provided by R.E. Collins); right photo, individual frost flowers (bar = 2 cm) in the same region during the dark month of January 2008 (provided by M. Lin).