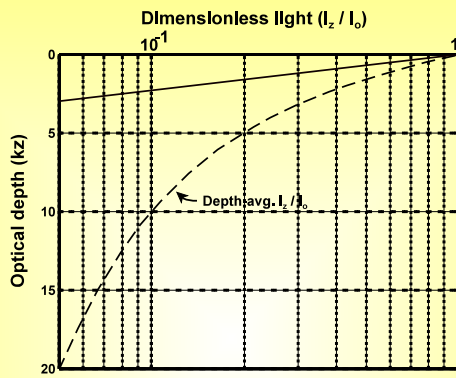


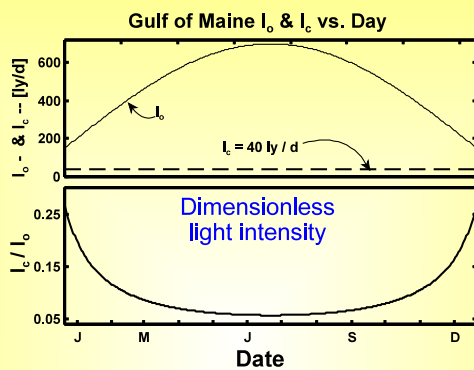
<div data-bbox="243 170 751 485"> <h2>Nutrient Effects on Phytoplankton: Liebig's law, Goldman's relative growth theory (chemostats, internal nutrient pools &amp; Redfield stoichiometry), and the Geritol solution to global warming</h2> </div> <div data-bbox="397 501 769 541"> <p>Class 19, 11/04/08 <i>EEOS630</i></p> </div>	<div data-bbox="818 134 1422 323"> <h3>Slide 1 Nutrient Effects on Phytoplankton: Liebig's law, Goldman's relative growth theory (chemostats, internal nutrient pools &amp; Redfield stoichiometry), and the Geritol solution to global warming</h3> </div> <div data-bbox="818 407 938 441"> <p>NOTES:</p> </div>
<div data-bbox="376 808 634 842"> <h2>Wimba Sessions</h2> </div> <div data-bbox="389 852 617 879"> <p>Tonight, Tuesday, 7 pm</p> </div> <div data-bbox="233 898 751 1129"> <ul style="list-style-type: none"> <li>Quantitative community analysis using Matlab <ul style="list-style-type: none"> <li>I've had to rewrite many of my Matlab m.files.</li> <li>Run the tutorial at the Mathworks site</li> <li>I'll be logged on at 7 pm tonight to demonstrate community analysis using the West Falmouth oilspill data as an example using Matlab</li> <li>I'll also present the solution to the <i>Synechococcus</i> problem</li> </ul> </li> <li>Due date: papers due 4 weeks after projects posted.</li> </ul> </div> <div data-bbox="656 1152 769 1180"> <p><i>EEOS630</i></p> </div>	<div data-bbox="818 772 1156 808"> <h3>Slide 2 Wimba Sessions</h3> </div> <div data-bbox="818 894 938 928"> <p>NOTES:</p> </div>
<div data-bbox="326 1293 699 1331"> <h2>Phytoplankton Readings</h2> </div> <div data-bbox="362 1339 660 1367"> <h3>Nutrients and the spring bloom</h3> </div> <div data-bbox="233 1365 740 1642"> <ul style="list-style-type: none"> <li>Nutrient effects, 11/4 (today) <ul style="list-style-type: none"> <li>Chapter 10: Nitrogen cycle, nutrient limitation &amp; chemostats</li> <li>Howarth, R. W. 1988. Nutrient limitation of net primary production in marine ecosystems. <i>Ann. Rev. Ecol. Syst.</i> 19: 89-110.</li> </ul> </li> <li>Spring bloom, Thursday <ul style="list-style-type: none"> <li>Readings <ul style="list-style-type: none"> <li>Chapter 11: Sverdrup's critical depth concept &amp; the vernal phytoplankton</li> <li>Sverdrup, H. U. 1953. On conditions for the vernal blooming of phytoplankton. <i>J. Conseil perm. int. Explor. Mer.</i> 18: 287-295.</li> <li>Parsons, T. R., M. Takahashi, and B. Hargrave, 1984. <i>Biological Oceanographic Processes</i>, 3rd Edition, Pergamon Press, Oxford &amp; New York, Pages 87-100.</li> <li>Townsend, D. W. and R. W. Spinrad. 1986. Early phytoplankton blooms in the Gulf of Maine. <i>Cont. Shelf Res.</i> 6: 515-529.</li> </ul> </li> <li>Become familiar with the non-dimensional critical depth graphic</li> </ul> </li> </ul> </div>	<div data-bbox="818 1262 1273 1299"> <h3>Slide 3 Phytoplankton Readings</h3> </div> <div data-bbox="818 1383 938 1417"> <p>NOTES:</p> </div>

Slide 4



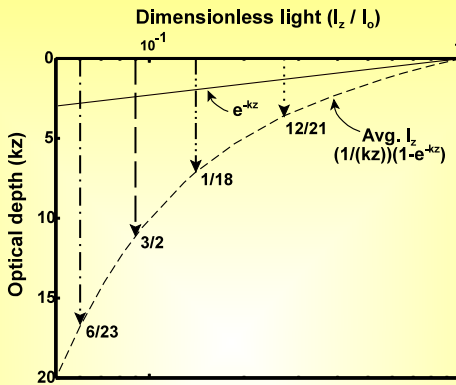
NOTES:

Slide 5



NOTES:

Slide 6



NOTES:

## Four major revolutions

### In our understanding of nutrient limitation

- Brandt (1899) was correct to focus on N limitation, Liebig's law, and the role of denitrification, but he missed the role of vertical mixing providing vertical flux of nutrients
  - The anammox pathway, missed until 2003 provides further insight into the central role of nitrogen removal
- Chemostat work by Droop (1968), Caperon & Meyer (1972), Fuhs & Rhee revealed the central importance of the **Internal nutrient pool** in controlling  $\mu$
- Goldman (Goldman *et al.* 1979, 1980) argued that phytoplankton in nature tend to grow at high relative growth rates, otherwise they would not exhibit Redfield stoichiometry. The internal nutrient pool tends to follow Redfield stoichiometry.
  - Nutrient input controls phytoplankton biomass & species composition
  - One phytoplankton assemblage rapidly replaced by another, each with high relative growth rate.
- Martin's Iron hypothesis: iron is the Liebigian nutrient in major areas of the world's ocean

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## Slide 7 Four major revolutions

NOTES:

## Terms & concepts

### Quick List

- Nitrogen cycle
  - nitrification
  - denitrification (dissimilatory nitrate reduction)
  - Assimilatory nitrate reduction
- Nutrient limitation: What are the different meanings
- Chemostats
  - What are they?
  - Michaelis-Menten Equation
  - Monod Equation
  - Droop Equation
  - Caperon & Meyer's (1972)'s equation
- Four major revolutions in understanding nutrient limitation

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## Slide 8 Terms & concepts

NOTES:

## Hensen's Nets & major cruise

From Mills (1989): 50- $\mu$ m nets, 1889 National cruise



## Slide 9 Hensen's Nets & major cruise

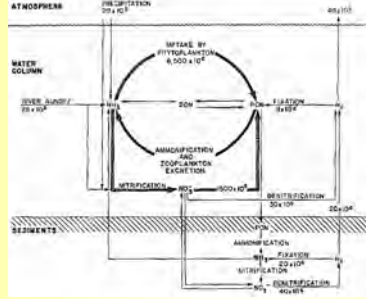
NOTES:

<div data-bbox="280 168 753 205" data-label="Section-Header"> <h2>Hensen's "Blood of the Ocean"</h2> </div> <div data-bbox="339 214 693 241" data-label="Section-Header"> <h3>Uniformly distributed phytoplankton!</h3> </div> <div data-bbox="238 243 748 522" data-label="List-Group"> <ul style="list-style-type: none"> <li>• The German Hensen introduced quantitative Plankton sampling to oceanography (1840s-1880s) <ul style="list-style-type: none"> <li>▸ Hensen introduced quantitative plankton sampling (50-<math>\mu</math>m silk mesh)</li> <li>▸ Phytoplankton are uniformly distributed</li> </ul> </li> <li>• Conclusions from 1889 National Cruise <ul style="list-style-type: none"> <li>▸ Within a biogeographic province, phytoplankton are uniformly distributed in the ocean, like oxygen and other chemical constituents</li> <li>▸ The oceans were in general very poor in plankton standing stocks, especially the tropics.</li> </ul> </li> </ul> </div> <div data-bbox="654 514 771 541" data-label="Text"> <p>EEOS630</p> </div>	<div data-bbox="816 132 1377 170" data-label="Section-Header"> <h2>Slide 10 Hensen's "Blood of the Ocean"</h2> </div> <div data-bbox="816 258 940 291" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="300 655 716 699" data-label="Section-Header"> <h2>SeaWiFS Average Chl a</h2> </div> <div data-bbox="396 703 609 730" data-label="Text"> <p>Oct 1997 -April 2002</p> </div> <div data-bbox="230 726 758 751" data-label="Text"> <p><a href="http://seawifs.gsfc.nasa.gov/SEAWIFS/IMAGES/SEAWIFS_GALLERY.html">http://seawifs.gsfc.nasa.gov/SEAWIFS/IMAGES/SEAWIFS_GALLERY.html</a></p> </div> <div data-bbox="224 753 763 1016" data-label="Figure"> </div>	<div data-bbox="816 623 1289 661" data-label="Section-Header"> <h2>Slide 11 SeaWiFS Average Chl a</h2> </div> <div data-bbox="816 745 940 779" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="261 1144 786 1182" data-label="Section-Header"> <h2>Brandt's denitrification hypothesis</h2> </div> <div data-bbox="310 1188 711 1215" data-label="Section-Header"> <h3>Proposed in 1899, see Mills' (1989) history</h3> </div> <div data-bbox="235 1218 745 1499" data-label="List-Group"> <ul style="list-style-type: none"> <li>• Nitrogen is the Liebigian (1876) limiting nutrient in the ocean, first proposed in 1840 (quoted in Danger et al. 2008) <ul style="list-style-type: none"> <li>▸ 'essential material available in amounts most closely approaching the critical minimum needed will tend to be the limiting one'</li> <li>▸ Liebig proposed 50 agricultural laws, the law of the minimum was #33 (de Baar 1994)</li> <li>▸ The law was proposed for monospecific crops</li> </ul> </li> <li>• Why is N the Liebigian nutrient according to Brandt (1899)? <ul style="list-style-type: none"> <li>▸ Land is the major source of nitrogen to the sea</li> <li>▸ Denitrifying bacteria have higher activities at higher temperatures</li> <li>▸ Nitrogen should be scarcer in warmer waters</li> <li>▸ Phytoplankton production should be less in tropical waters.</li> </ul> </li> </ul> </div>	<div data-bbox="816 1110 1274 1184" data-label="Section-Header"> <h2>Slide 12 Brandt's denitrification hypothesis</h2> </div> <div data-bbox="816 1270 940 1304" data-label="Text"> <p>NOTES:</p> </div>

<div data-bbox="331 168 698 203" data-label="Section-Header"> <h3>The refutation of Brandt</h3> </div> <div data-bbox="345 214 680 241" data-label="Section-Header"> <h4>Mixing &amp; methodological problems</h4> </div> <div data-bbox="238 243 751 525" data-label="List-Group"> <ul style="list-style-type: none"> <li>• Brandt assumed a terrestrial source for N. Terrestrial sources are not the major source of Nitrogen fueling coastal production <ul style="list-style-type: none"> <li>▸ the Norwegians proposed vertical mixing from deep, N-rich water</li> <li>▸ More vertical mixing in coastal waters, less in the tropics</li> </ul> </li> <li>• Methodological problems: <ul style="list-style-type: none"> <li>▸ DIN could not be measured (until the 20s &amp; 30s)</li> <li>▸ Denitrifying activity not measured until the 70s (Seitzinger)</li> <li>▸ Nitrifying bacterial activity not measured accurately until the 80's (Olson, Ward)</li> </ul> </li> </ul> </div> <div data-bbox="656 514 771 541" data-label="Text"> <p>EEOS630</p> </div>	<div data-bbox="816 132 1292 168" data-label="Section-Header"> <h3>Slide 13 The refutation of Brandt</h3> </div> <div data-bbox="816 256 940 291" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="269 655 760 693" data-label="Section-Header"> <h3>Brandt abandons his hypothesis</h3> </div> <div data-bbox="269 701 748 730" data-label="Text"> <p>In 1929, opts for vertical mixing (Mills 1989, p. 161)</p> </div> <div data-bbox="232 730 756 947" data-label="Text"> <p>"The explanation is so evident that my explanation of 1899 that denitrifying bacteria are the cause of plankton deficiency in the tropical oceans is invalidated by it. However, I still maintain the view <b>"that denitrifying bacteria break down an excess of nitrogen compounds and that it is they that maintain the existing equilibrium in nature."</b></p> </div> <div data-bbox="656 1001 771 1029" data-label="Text"> <p>EEOS630</p> </div>	<div data-bbox="816 621 1393 659" data-label="Section-Header"> <h3>Slide 14 Brandt abandons his hypothesis</h3> </div> <div data-bbox="816 743 940 779" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="263 1144 771 1182" data-label="Section-Header"> <h3>Brandt's strengths &amp; weaknesses</h3> </div> <div data-bbox="238 1218 751 1459" data-label="List-Group"> <ul style="list-style-type: none"> <li>• Brandt was correct, but before his time in emphasizing: <ul style="list-style-type: none"> <li>▸ Liebig's law of the minimum. <ul style="list-style-type: none"> <li>■ This has been tested experimentally, and it is usually only 1 nutrient, a rate-limiting nutrient that controls primary production</li> <li>■ Multiple nutrient limitation not a major factor</li> </ul> </li> <li>▸ Denitrification <ul style="list-style-type: none"> <li>■ Largely responsible for low N:P in marine waters</li> <li>■ Phosphorus may be a limiting nutrient over geologic time scales &amp; during glacial periods (Fe &amp; N fixation)</li> </ul> </li> </ul> </li> <li>• Major flaws <ul style="list-style-type: none"> <li>▸ Overestimated terrestrial input of nitrogen</li> <li>▸ Ignorance of vertical mixing</li> <li>▸ Overemphasis of temperature effects</li> </ul> </li> </ul> </div> <div data-bbox="656 1488 771 1516" data-label="Text"> <p>EEOS630</p> </div>	<div data-bbox="816 1110 1408 1148" data-label="Section-Header"> <h3>Slide 15 Brandt's strengths &amp; weaknesses</h3> </div> <div data-bbox="816 1232 940 1268" data-label="Text"> <p>NOTES:</p> </div>

## The Nitrogen cycle

From Mills (1989) Fig. 23 (p. 56)



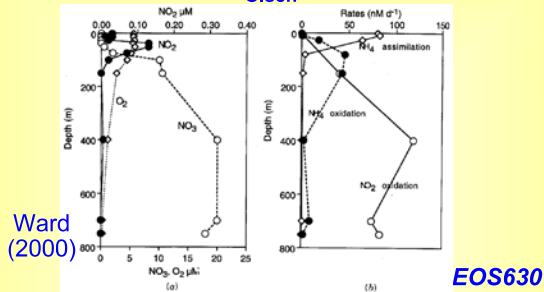
Fluxes in metric tons per year  
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## Slide 16 The Nitrogen cycle

NOTES:

## Subsurface NO<sub>2</sub><sup>-</sup> maximum

Produced by light inhibition of NO<sub>2</sub><sup>-</sup> oxidizers; Ward & Olsen



Ward (2000)

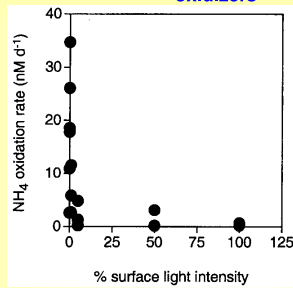
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## Slide 17 Subsurface NO<sub>2</sub><sup>-</sup> maximum

NOTES:

## Light inhibition of NH<sub>4</sub><sup>+</sup> oxidation

Ward (2000), NO<sub>2</sub><sup>-</sup> oxidizers more inhibited than NH<sub>4</sub><sup>+</sup> oxidizers



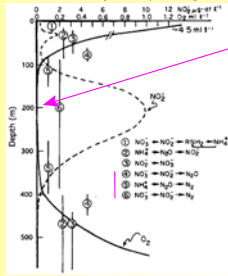
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## Slide 18 Light inhibition of NH<sub>4</sub><sup>+</sup> oxidation

NOTES:

## Eastern tropical Pacific denitrification

Ward (2000): major site of denitrification in the world



**O<sub>2</sub> minimum zone**  
 NO<sub>2</sub><sup>-</sup> and NO<sub>3</sub><sup>-</sup> used as terminal electron acceptors for respiration, under anoxic conditions, by denitrifying bacteria

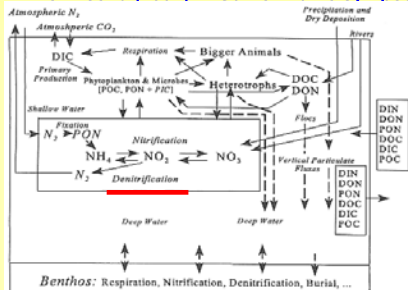
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## Slide 19 Eastern tropical Pacific denitrification

NOTES:

## N cycle in the Gulf of Maine

Townsend (1997) in Gulf of Maine symposium



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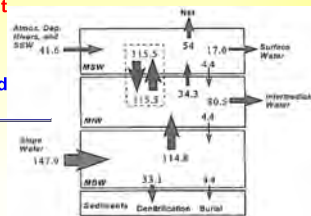
## Slide 20 N cycle in the Gulf of Maine

NOTES:

## Gulf of Me Nitrogen budget

Townsend (1997): denitrification very important

- Total Production = 290 g C m<sup>-2</sup> y<sup>-1</sup>
- Slope water major N Input
  - Slope 147.9
  - River & Atmosphere 42
- Denitrification Important, nearly balancing river and atmospheric input



## Slide 21 Gulf of Me Nitrogen budget

NOTES:

## Denitrification in the coastal zone

Seitzinger (1988): about 40-50% of N loading to coastal zones lost as  $N_2$ .

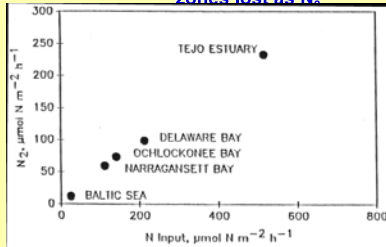


Fig. 2. Denitrification rates vs. external N inputs rates in estuaries. Data explained in Table 7.

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## Slide 22 Denitrification in the coastal zone

NOTES:

## About 40-50% of N load lost as $N_2$

Seitzinger (1988); Giblin & Howes: similar rates for BH

Table 7. The importance of denitrification as a sink for external nitrogen inputs to various aquatic systems. Only systems in which denitrification rates were measured at near-ambient conditions are included. N input,  $\mu\text{mol N m}^{-2} \text{h}^{-1}$ .

Location	N input	N input removed by denitrification (%)	N loss*	Time interval
<b>Lakes</b>				
ELA 227†	3,200	1.4	1	Annual
Kvidet sø†	1,227	7	2	Annual
Byrrup Langel†	690	28	2	Annual
Arresø	81	14	3	Annual
Oksebohoe	46	9-23	4	Annual
Meadow†	45	36	5	Annual
<b>Rivers</b>				
Potomac	632	35	6	Fall
Delaware	1,452	20	7	Summer
<b>Estuaries</b>				
Tejo estuary	316	43	8	Fall
Delaware Bay	213	46	9	Jul-Sep
Ochlockonee Bay	174	43	10	Annual
Narragansett Bay	112	50	11	Annual
Baltic Sea	25	40	12	Annual
Baltic Sea	25	25	13	Annual
Four Lagoon Bay†	25	20	14	Annual

## Slide 23 About 40-50% of N load lost as $N_2$

NOTES:

## Denitrification in Boston Harbor sediments: *Ampelisca* mats

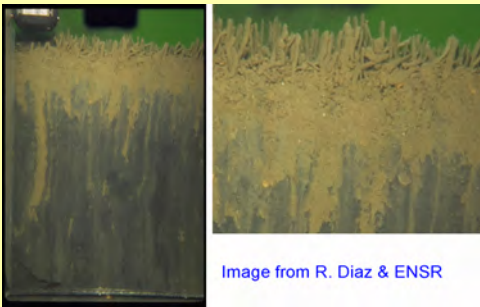


Image from R. Diaz & ENSR

S630

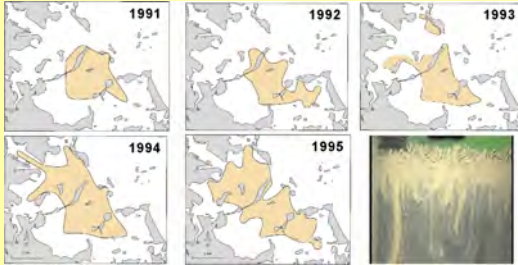
## Slide 24 Denitrification in Boston Harbor sediments: *Ampelisca* mats

NOTES:



## Ampelisca mats in Boston Harbor

Oligochaete-spionid-Capitella → *Ampelisca*



Data from MWRA & ENSR

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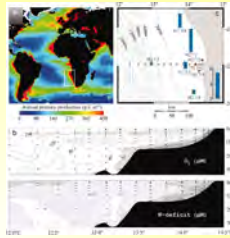
## Slide 25 Ampelisca mats in Boston Harbor

NOTES:

## Anammox

Anaerobic ammonia oxidation

- Process discovered in the 1990s
- $\text{NH}_4^+ + \text{NO}_2^- = \text{N}_2 + 2\text{H}_2\text{O}$
- Kuypers *et al.* (2005) studied anammox in the Benguela Current upwelling (see right)
  - Low dissolved oxygen ( $<10 \mu\text{M}$ ) on broad portions of the shelf near the bottom
  - In Namibian coastal waters, there is an N-deficit, relative to Redfield stoichiometry, which had been attributed to denitrification



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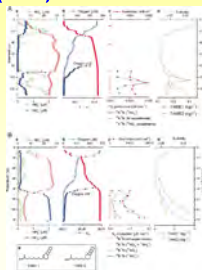
## Slide 26 Anammox

NOTES:

## Anammox in the Benguela current

Kuypers *et al.* (2005)

- Isotopic labeling indicates little  $\text{N}_2$  production through denitrification
- Anammox activity and  $\text{N}_2$  production peaked at about 100-120 m
- Specific molecular markers used to identify the anammox bacteria



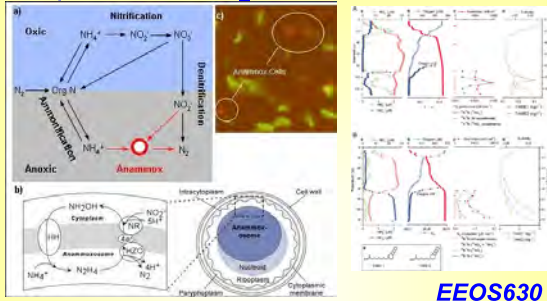
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## Slide 27 Anammox in the Benguela current

NOTES:

## Anammox

[http://www.nioz.nl/nioz\\_nl/fb7bc8c70b02a22a459dee41c](http://www.nioz.nl/nioz_nl/fb7bc8c70b02a22a459dee41c)



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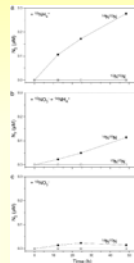
## Slide 28 Anammox

NOTES:

## $^{15}\text{N-NH}_4^+$ labeling reveals anammox

Kuypers et al. (2005)

- **Anammox**
  - $\text{NH}_4^+ + \text{NO}_2^- = \text{N}_2 + 2\text{H}_2\text{O}$
- **Denitrification**
  - $106(\text{CH}_2\text{O})16(\text{NH}_3) + \text{H}_3\text{PO}_4 + 94\text{HNO}_3 \rightarrow 106\text{CO}_2 + \text{H}_3\text{PO}_4 + 177\text{H}_2\text{O} + 55\text{N}_2$
  - See also Gallagher Chapter 4 for a slightly different equation using Redfield stoichiometry
  - **Methods**
    - Measure  $\text{N}_2$  gas production after adding  $^{15}\text{N-NO}_3^-$
    - Measure  $\text{N}_2\text{O}$  gas production, an intermediate compound, after blocking final steps of denitrification with an acetylene inhibitor
- **Only a few samples showed any  $^{15}\text{N-N}_2$  production using  $^{15}\text{N-NO}_3^-$**



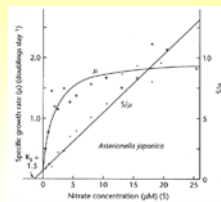
## Slide 29 $^{15}\text{N-NH}_4^+$ labeling reveals anammox

NOTES:

## The Monod relationship

Miller (2004) Fig. 3.11 is misleading/wrong

- Fig. 3.11 is **NOT** the pattern observed with phytoplankton in chemostat culture
- The pattern in Eppley & Thomas (1969) is not correct!
- Caperon & Meyer (1972), also at Scripps, showed the true relationship, described earlier by Droop (1968) for Vit B<sub>12</sub>
- It is the internal cell pool of limiting N that is associated with  $\mu$



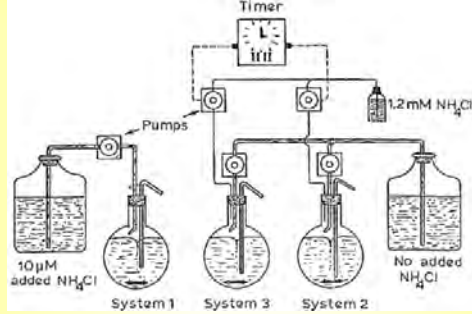
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## Slide 30 The Monod relationship

NOTES:

## Principles of a chemostat

Turbin & Harrison's (1979) pulsed N experiment



## Slide 31 Principles of a chemostat

NOTES:

## The Michaelis-Menten Equation

1905: Used to model the rate of enzyme reactions

$$V = \frac{V_{max} S}{K_M + S}$$

where,  $K_M$  = Half-saturation constant.  
 =  $S$  at which  $V = \frac{1}{2} V_{max}$ .  
 $S$  = Substrate concentration.  
 $V$  = Reaction velocity.  
 =  $\frac{-dS}{dt} = \frac{d \text{Product}}{dt}$   
 $V_{max}$  = Maximum  $V$ .

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## Slide 32 The Michaelis-Menten Equation

NOTES:

## Monod (1948): $\mu = f(S_{\text{external}})$

Adapted the Michaelis-Menten equation

$$\mu = \frac{\mu_{max} S}{K_M + S}$$

where,  $K_M$  = Half-saturation constant.  
 =  $S$  at  $\mu = \frac{1}{2} \mu_{max}$ .  
 $S$  = Substrate concentration.  
 $\mu$  = Specific growth rate.

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## Slide 33 Monod (1948): $\mu = f(S_{\text{external}})$

NOTES:

## Early history of chemostats

### Discovery of the internal cell quotient, $Q$

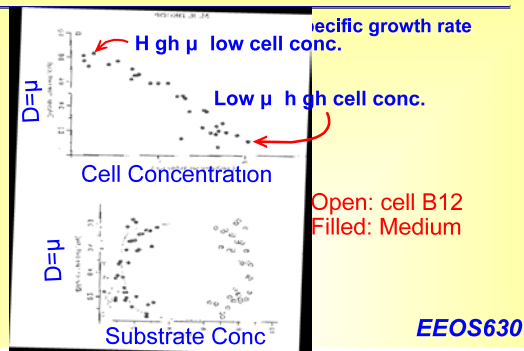
- Droop (1968) determined relationship between  $\mu$ ,  $Q$ , and  $k_q$ 
  - He was studying Vitamin B-12 limitation
  - Monod's relationship did not work
    - External nutrient concentration could not be used to predict  $\mu$
    - The internal nutrient pool, or cell quotient  $Q$ , could be used to predict  $\mu$
- Fuhs (1969) showed the clear relationship between  $q$  and  $\mu$  and introduced  $Q_0$  for P limitation

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## Slide 34 Early history of chemostats

NOTES:

## Droop's (1968) Landmark paper

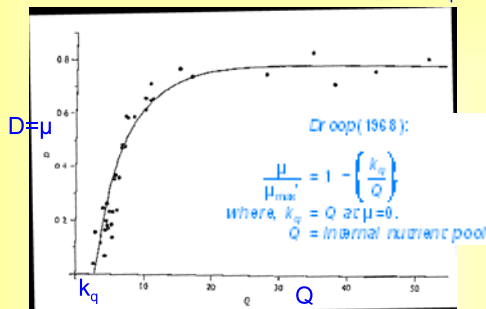


## Slide 35 Droop's (1968) Landmark paper

NOTES:

## Droop's Internal nutrient pool

A 2-parameter equation:  $\mu'_{max}$  and  $k_q$



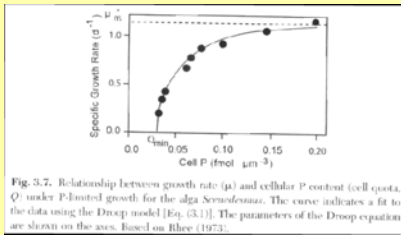
## Slide 36 Droop's Internal nutrient pool

NOTES:

Slide 37 P-limited  $\mu=f(\text{Cell P})$

P-limited  $\mu=f(\text{Cell P})$

Rhee (1973): Droop's internal pool model applies



Sterner & Elser (2002) Fig. 3.7

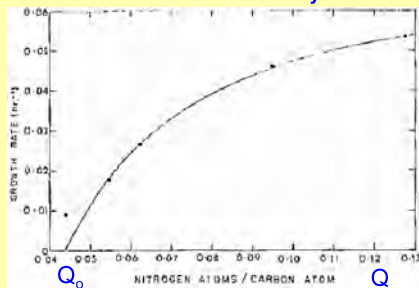
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NOTES:

Slide 38 N-limited  $\mu=f(\text{N:C})$

N-limited  $\mu=f(\text{N:C})$

Caperon & Meyer (1972a): 1st valid marine N-limitation chemostat study

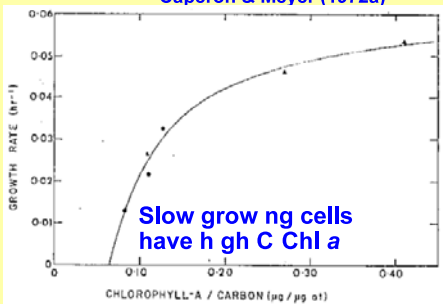


NOTES:

Slide 39  $\mu=f(\text{Chl a:C})$

$\mu=f(\text{Chl a:C})$

Caperon & Meyer (1972a)



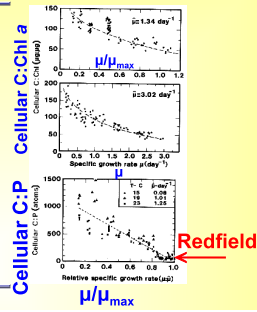
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NOTES:

## Relative growth rate $\mu/\mu_{\max}$

Goldman (1980), replotted by Harris (1986)

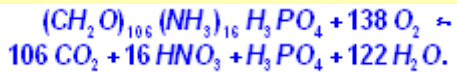
- Redfield ratios only attained at  $\mu/\mu_{\max} = 1$
- C:Chl *a* ratio is a reasonable predictor of relative growth rate
  - But it is affected by shade adaptation. A shade adapted, slow growing cell may have low relative  $\mu$ , and low C:Chl *a*
- DiTullio & Laws (1986) developed a  $^{14}\text{C}$ -protein labeling procedure to estimate relative growth rate concentration



## Slide 40 Relative growth rate $\mu/\mu_{\max}$

NOTES:

## Goldman's theory: The relationship between $\mu/\mu_{\max}$ & the Redfield ratio



- The 'Redfield' ratio was first determined approximately by Harvey in the 20s, grinding up seaweeds
- Only phytoplankton growing near  $\mu_{\max}$  have cellular C:N:P in Redfield proportions
- The Redfield ratio predicts the rate of regeneration on C:N:P in deep water

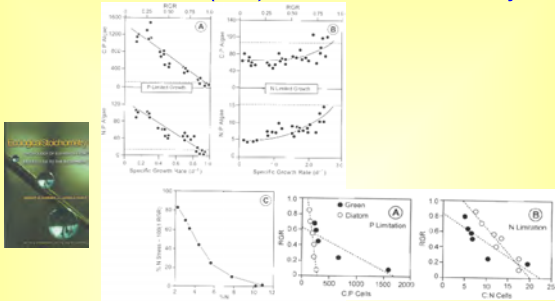
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## Slide 41 Goldman's theory: The relationship between $\mu/\mu_{\max}$ & the Redfield ratio

NOTES:

## Ecological Stoichiometry

Sterner & Elser (2002): Reviews Goldman's theory



## Slide 42 Ecological Stoichiometry

NOTES:

## The 3 meanings of N limitation

From Howarth (1988)

- **First**, Limitation of the specific growth rate of cells that are there
  - The cells that often dominate production are growing at high relative growth rates ( $\mu/\mu_{\max} \approx 1$ )
  - In blooms terminated by nutrient depletion, cells exhibit low relative growth rates
- **Second**, limitation of potential production or yield
  - Nitrogen-spike experiments increase phytoplankton standing stock and production
  - The cells that increase disproportionately in abundance & growth rate may have been rare in the original community

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## Slide 43 The 3 meanings of N limitation

NOTES:

## Third Limitation of Ecosystem Production

See Howarth (1988)

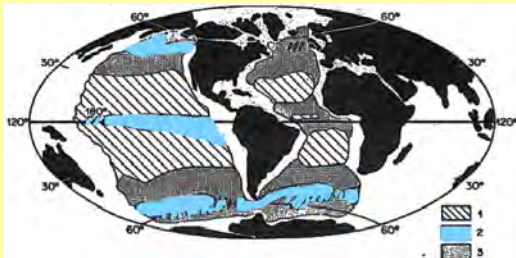
- Eutrophication: increased loading of a nutrient that is in short supply
  - If the MA Bay outfall had an effect on dissolved oxygen, would tertiary treatment reducing DIN input be the solution?
  - Or, does tertiary sewage treatment merely reduce rates of coastal denitrification? Smith & Hollibaugh
- Fe limitation
  - May produce only short-term increases in areal production
  - May not translate to long-term increases in oceanic production
- Phosphorus limitation on geologic time scales
  - There is a better correlation between phosphorus and production than nitrogen and production over geologic time scales
  - Nitrogen fixation can perhaps make up deficits in N, if iron is present for nitrogen fixation

## Slide 44 Third Limitation of Ecosystem Production

NOTES:

## Banase's three ocean types

1: Oligotrophic gyres, 2: HNLC, 3: Seasonal



Gulf of Maine is Domain 3

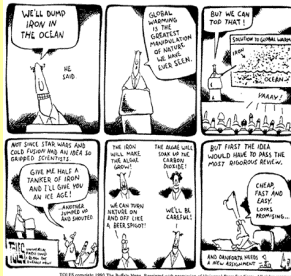
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## Slide 45 Banase's three ocean types

NOTES:

## Martin's Geritol solution

The late John Martin's hypothesis created a frenzy of activity in 1989; based on a talk at WHOI



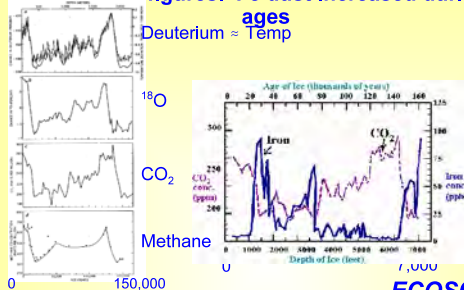
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### Slide 46 Martin's Geritol solution

NOTES:

## The Greenhouse effect & Fe

Woodwell figures. Fe dust increased during ice ages  
Deuterium  $\approx$  Temp



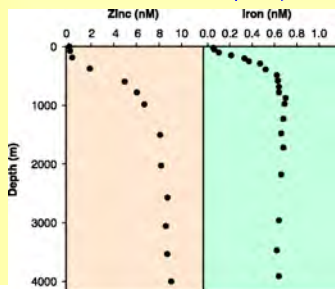
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### Slide 47 The Greenhouse effect & Fe

NOTES:

## Iron & Zn depletion in surface water

Morel & Price (2003) Subarctic Pacific



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### Slide 48 Iron & Zn depletion in surface water

NOTES:



## Roles of Fe in plant metabolism

Geider & LaRoche (1994)

- Cytochrome oxidase
- Fe-superoxidize dismutase
- Catalase
- Peroxidase
- Ferredoxin (needed for  $N_2$  fixation)
- Nitrate reductase, nitrite reductase
- Glutamate synthetase
- Others

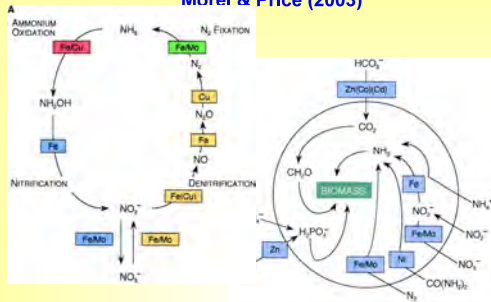
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## Slide 49 Roles of Fe in plant metabolism

NOTES:

## Key uses of Fe & Zn by microbes

Morel & Price (2003)



## Slide 50 Key uses of Fe & Zn by microbes

NOTES:

## C:N:P:Fe Redfield ratios

C:N:P:Fe ≈ 106:16:1:(0.003 to 0.0003)

### • Lab cultures

- Geider & LaRoche (1994)
  - Dinoflagellate (*Gymnodinium*) N:Fe ≈ 2000
  - Diatom N:Fe ≈ 10,000
  - *Synechococcus* (blue green) N:Fe ≈ 3000
- Sunda *et al.* (1995), quoted in Fung *et al.* (2000)
  - Measured range N:Fe 13,000 - 116,000
    - Low productivity N:Fe ≈ 60,000 C:Fe 400,000
    - High productivity N:Fe ≈ 34,000 C:Fe 220,000
- Boyd *et al.* (2004) Gulf of Alaska bloom
  - N:Fe 5800
  - C:Fe 38,000

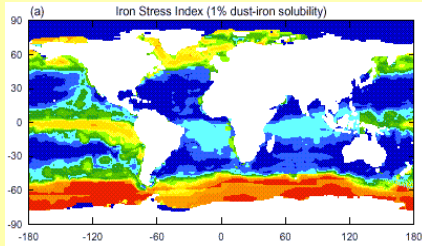
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## Slide 51 C:N:P:Fe Redfield ratios

NOTES:

## Iron stress in the oceans

Zones where Fe:N uptake > Fe:N supply (from dust & upwelling), Fung *et al.* (2000)



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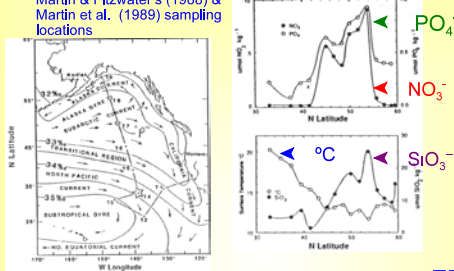
### Slide 52 Iron stress in the oceans

NOTES:

## Martin & Fitzwater's Fe hypothesis

They argue that iron, not grazing, limit standing stocks

Martin & Fitzwater's (1988) & Martin *et al.* (1989) sampling locations



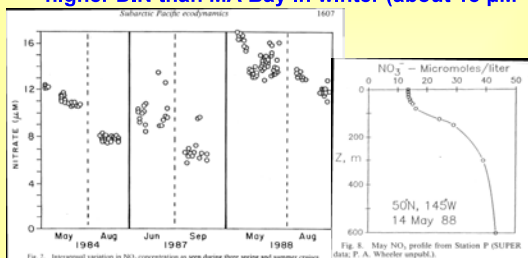
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### Slide 53 Martin & Fitzwater's Fe hypothesis

NOTES:

## High nitrate all year at Station P

Data from Frost (1991): 5-17  $\mu\text{M}$   $\text{NO}_3^-$ , which is higher DIN than MA Bay in winter (about 15  $\mu\text{M}$ )



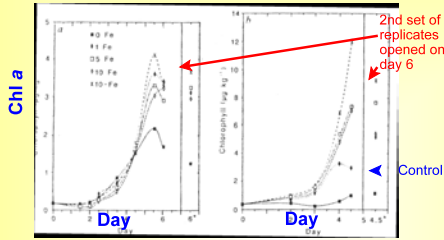
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### Slide 54 High nitrate all year at Station P

NOTES:

## Martin & Fitzwater (1988), Martin et al. (1999)

Increase in Chl a at Station P, T7



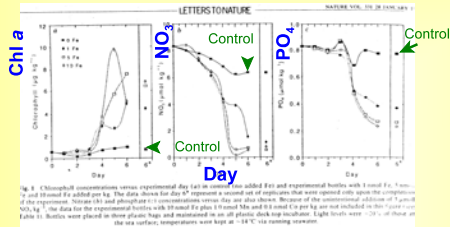
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## Slide 55 Martin & Fitzwater (1988), Martin et al. (1999)

NOTES:

## Station P: Effects of Fe on Chl a, N & P

No replicates, Banse (1990) noted the statistical problems



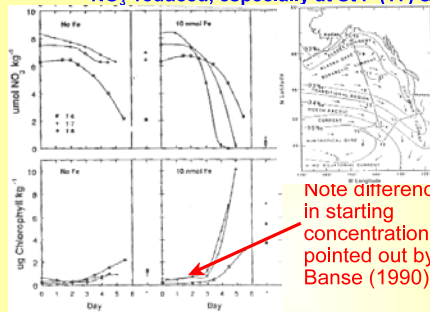
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## Slide 56 Station P: Effects of Fe on Chl a, N & P

NOTES:

## Fe effect dependent on lat & long

NO<sub>3</sub><sup>-</sup> reduced, especially at St P (T7) & T8



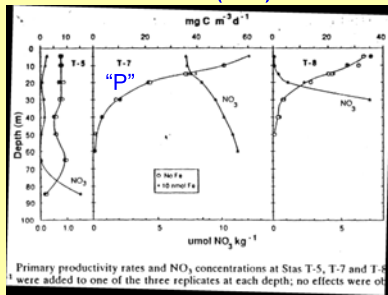
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## Slide 57 Fe effect dependent on lat & long

NOTES:

## No Fe effect on production!

Martin *et al.* (1989): *in situ* incubations



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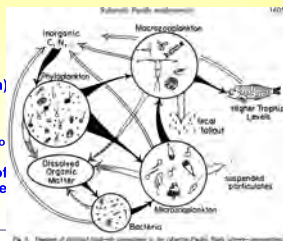
## Slide 58 No Fe effect on production!

NOTES:

## The ecumenical Fe hypothesis

Morel (1991), Miller *et al.* (1991)

- Small phytoplankton (<10  $\mu\text{m}$ ) less affected by low Fe
  - Use  $\text{NH}_4^+$  as primary N source
  - Outcompete diatoms for  $\text{NH}_4^+$  and Fe
  - Are Grazer-limited
  - Grow with high relative growth rates
- Large phytoplankton cells (>10  $\mu\text{m}$ ) Fe-limited
  - More likely to use  $\text{NO}_3^-$ ; Nitrate reductase requires Fe;
  - Outcompeted for Fe due to low surface:volume ratios
- Fe additions leads to stimulation of large cells which synthesize nitrate reductase and remove  $\text{NO}_3^-$



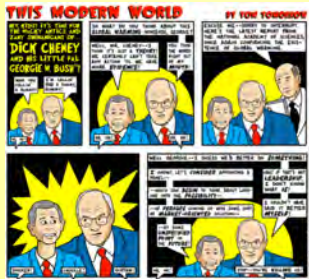
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## Slide 59 The ecumenical Fe hypothesis

NOTES:

## Market-oriented CO<sub>2</sub> solution

Carbon credits for the geritol solution



What is the geritol solution & could it work?

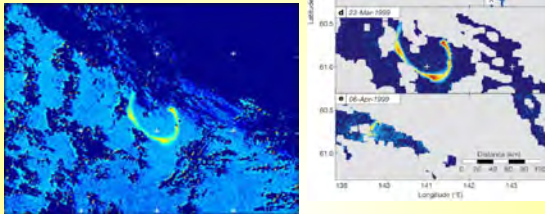
Chisholm, S. W., P. G. Falkowski and J. J. Cullen. 2001. Dis-crediting ocean fertilization. *Science* 294: 309-310.

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## Slide 60 Market-oriented CO<sub>2</sub> solution

NOTES:

# SOIREE (Southern Ocean iron release experiment) SeaWiFS Image of 100 km bloom, 30 d after Fe-II spike



Abraham *et al.* 2000

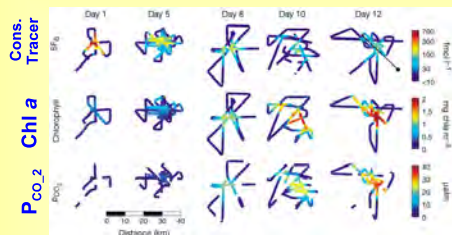
## Slide 61 SOIREE

(Southern Ocean iron release experiment)

NOTES:

# IRONEX III, SOIREE

Boyd *et al.* (2000) Figure 2



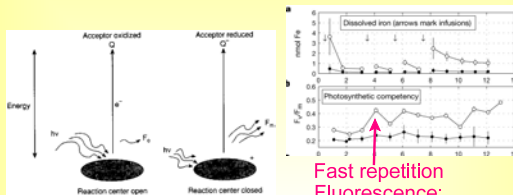
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## Slide 62 IRONEX III, SOIREE

NOTES:

# Variable fluorescence & Fe limitation

$$\text{Photosynthetic competency} = F_v = (F_m - F_o) / F_m$$



Fast repetition  
Fluorescence:  
1st indicator of  
bloom

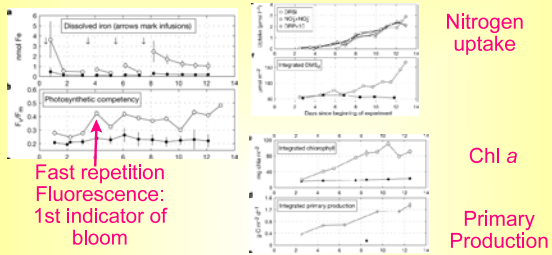
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## Slide 63 Variable fluorescence & Fe limitation

NOTES:

## IRONEX III: bloom by 30-50 $\mu\text{m}$ diatoms

Boyd *et al.* (2000) Fig. 3

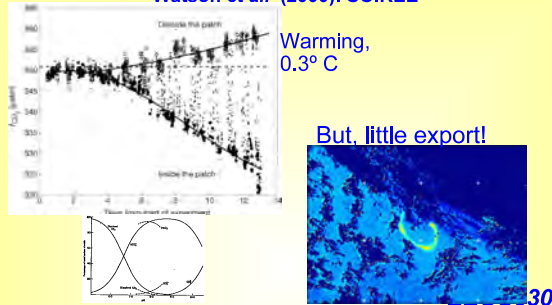


## Slide 64 IRONEX III: bloom by 30-50 $\mu\text{m}$ diatoms

NOTES:

## Fe increases $\text{CO}_2$ gradient

Watson *et al.* (2000): SOIREE



## Slide 65 Fe increases $\text{CO}_2$ gradient

NOTES:

## SOIREE: major results

Confirms the 'ecumenical' iron hypothesis

- Increase in photosynthetic parameters by day II, measured by variable fluorescence
- Increase in large chain-forming diatoms by day 5: 30-50  $\mu\text{m}$  cell size
- Microzooplankton abundance quadrupled
  - Grazing only on small phytoplankton cells (< 20  $\mu\text{m}$  cells)
- **No evidence of macrozooplankton response**
  - **No increased carbon export to sediment traps**
- Partial pressure of  $\text{CO}_2$  decreased in surface ocean; this gradient would increase the atmosphere to ocean flux of  $\text{CO}_2$

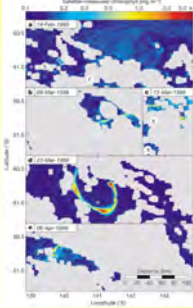
## Slide 66 SOIREE: major results

NOTES:

## SOIREE

Abraham *et al.* 2000. Importance of stirring

- 150-km long bloom 6 weeks after the Fe fertilization experiment
- 23 March 1999
  - 3 mg Chl  $a\ m^{-3}$
  - In an area where SeaWiFS indicates the mean Chl  $a$  was  $0.2 \pm 0.06\ mg\ Chl\ a\ m^{-3}$  (15X increase)
- Stirring plays a key role
  - Fit growth rates of  $\mu = 0.19\ d^{-1}$
  - Loss due to horizontal diffusion =  $0.07\ d^{-1}$
  - Loss due to grazing =  $0.01\ d^{-1}$
  - Loss due to sinking =  $0.02\ d^{-1}$
- Accumulation of 600-3000 t of algal C

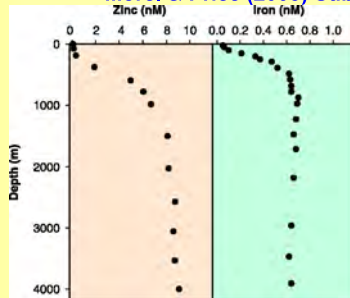


## Slide 67 SOIREE

NOTES:

## Iron & Zn depletion

Morel & Price (2003) Subarctic Pacific



Leblanc *et al.*  
(Deep-Sea Res.  
2005)  
documented Zn  
limitation in the  
sub Antarctic

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## Slide 68 Iron & Zn depletion

NOTES:

## Problems with the Geritol solution

Not a solution for reducing atmospheric  $CO_2$

- Fe may be the Liebigian nutrient now, but would be replaced by another, *e.g.*, Zn or Si (Leblanc *et al.* 2005)
- Increased production may not reduce the partial pressure of  $CO_2$  sufficiently: no change in  $CO_2$  in IronEx I or IronEx II (only in SOIREE)
  - No transport of carbon to deep waters in SOIREE
- Sarmiento: bottom waters, especially in the Southern Ocean, might go anoxic
- David Archer's calcite buffering effect: increased organic matter degradation in deep ocean sediments may dissolve calcite, increasing  $CO_2$  concentrations: Fe only sequesters DIC on the century time scale

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## Slide 69 Problems with the Geritol solution

NOTES:

<div data-bbox="339 170 688 207" data-label="Section-Header"> <h3>Four major revolutions</h3> </div> <div data-bbox="318 216 716 241" data-label="Section-Header"> <h4>In our understanding of nutrient limitation</h4> </div> <div data-bbox="235 243 768 548" data-label="List-Group"> <ul style="list-style-type: none"> <li>• Brandt (1899) was correct to focus on N limitation, Liebig's law, and the role of denitrification, but he missed the role of vertical mixing providing vertical flux of nutrients <ul style="list-style-type: none"> <li>▸ The anammox pathway, missed until 2003 provides further insight into the central role of nitrogen removal</li> </ul> </li> <li>• Chemostat work by Droop (1968), Caperon &amp; Meyer (1972), Fuhs &amp; Rhee revealed the central importance of the <b>Internal nutrient pool</b> in controlling <math>\mu</math></li> <li>• Goldman (Goldman <i>et al.</i> 1979, 1980) argued that phytoplankton in nature tend to grow at high relative growth rates, otherwise they would not exhibit Redfield stoichiometry. The internal nutrient pool tends to follow Redfield stoichiometry. <ul style="list-style-type: none"> <li>▸ Nutrient input controls phytoplankton biomass &amp; species composition</li> <li>▸ One phytoplankton assemblage rapidly replaced by another, each with high relative growth rate.</li> </ul> </li> <li>• Martin's Iron hypothesis: iron is the Liebigian nutrient in major areas of the world's ocean</li> </ul> </div>	<div data-bbox="816 134 1271 172" data-label="Section-Header"> <h3>Slide 70 Four major revolutions</h3> </div> <div data-bbox="816 258 938 291" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="332 653 691 724" data-label="Section-Header"> <h3>Applications to MA Bay production</h3> </div> <div data-bbox="227 726 747 951" data-label="List-Group"> <ul style="list-style-type: none"> <li>• Studies funded by the MWRA since 1992 <ul style="list-style-type: none"> <li>▸ Estimating production <ul style="list-style-type: none"> <li>■ <math>O_2</math> used for the 1992-1993 MA Bay monitoring by Kelly &amp; Doering</li> <li>■ Model P vs. I approach introduced by Craig Taylor</li> <li>■ Current methods involve incubations with a photosynthetron (tungsten light source) at U. Rhode Island</li> </ul> </li> <li>▸ Problems with the model approach <ul style="list-style-type: none"> <li>■ Assimilation numbers too high, especially at the start of the spring bloom <ul style="list-style-type: none"> <li>○ May indicate non-steady-state conditions at the onset of the spring bloom</li> </ul> </li> <li>■ Subsurface chlorophyll maximum can be a productivity maximum in MA Bay <ul style="list-style-type: none"> <li>○ Which P vs. I parameters should be used to estimate water-column production?</li> </ul> </li> </ul> </li> <li>▸ Cole-Cloern model used recently, but it is not accurate after blooms (will be covered during Remote Sensing)</li> </ul> </li> </ul> </div> <div data-bbox="654 1001 769 1029" data-label="Text"> <p>EEOS630</p> </div>	<div data-bbox="816 623 1281 697" data-label="Section-Header"> <h3>Slide 71 Applications to MA Bay production</h3> </div> <div data-bbox="816 783 938 816" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="328 1180 690 1218" data-label="Section-Header"> <h3>BH-MA Bay: A tidal front</h3> </div> <div data-bbox="276 1228 740 1253" data-label="Section-Header"> <h4>MWRA State of the Harbor Report &amp; Mann &amp; Lazier</h4> </div> <div data-bbox="248 1255 396 1379" data-label="Image"> </div> <div data-bbox="248 1383 457 1547" data-label="Figure"> </div> <div data-bbox="464 1251 768 1419" data-label="Figure"> </div> <div data-bbox="482 1425 748 1543" data-label="Text"> <p>Stratification can occur in any month (Winter snow melt inversions), but stable pycnocline develops in March</p> </div>	<div data-bbox="816 1148 1313 1184" data-label="Section-Header"> <h3>Slide 72 BH-MA Bay: A tidal front</h3> </div> <div data-bbox="816 1270 938 1304" data-label="Text"> <p>NOTES:</p> </div>



### Realistic P vs. I parameters

Many published assimilation numbers and  $\alpha$ 's are too high

- There **are** theoretical limits for  $\alpha$  and A.N.
  - Maximum  $\alpha$  set by the quantum efficiency of photosynthesis
  - A.N. is set by the maximum specific growth rate (assuming balanced growth)
  - Falkowski published a theoretical maximum of about 20-25
  - Harris in Phytoplankton Ecology, maximum assimilation numbers in the gyres should be: 6-8 mg C mg Chl a h<sup>-1</sup>

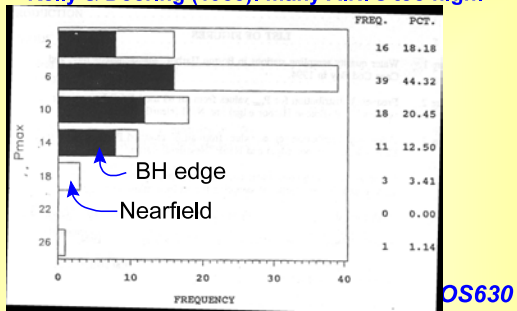
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### Slide 73 Realistic P vs. I parameters

NOTES:

### MA Bay P vs. I parameters

Kelly & Doering (1985): many A.N.'s too high!



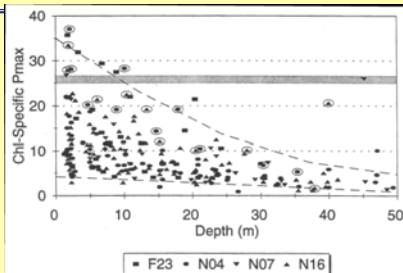
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### Slide 74 MA Bay P vs. I parameters

NOTES:

### MA Bay assimilation numbers

Including Falkowski's theoretical maximum= 25



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### Slide 75 MA Bay assimilation numbers

NOTES:

## Why might assimilation numbers be too high?

- Theoretical maximum assimilation numbers are often exceeded, due to:
  - Improper methods
    - Filters not retaining phytoplankton
    - Improper estimate of Chl *a*
  - Unbalanced growth = non-steady state conditions
  - Failure to subtract controls

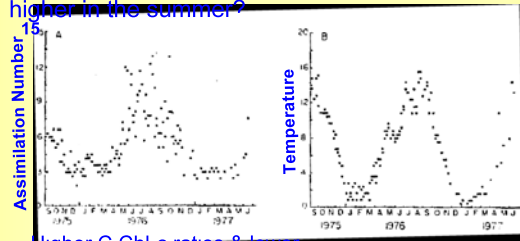
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## Slide 76 Why might assimilation numbers be too high?

NOTES:

## Seasonal variation in A.N.

Harrison & Platt (1980), max. AN < 15  
Does this mean that production is higher in the summer?



Higher C:Chl *a* ratios & lower biomass in summer

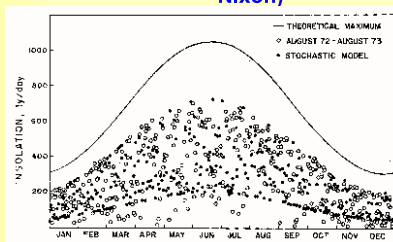
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## Slide 77 Seasonal variation in A.N.

NOTES:

## Model P vs. I approach: can account for differences in irradiance (due to clouds)

Rhode Island solar irradiance (from Kremer & Nixon)



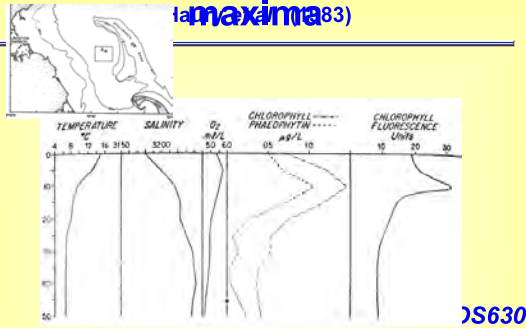
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## Slide 78 Model P vs. I approach: can account for differences in irradiance (due to clouds)

NOTES:

<div data-bbox="292 168 725 212" data-label="Section-Header"> <h2>1995 MA Bay Production</h2> </div> <div data-bbox="280 214 732 243" data-label="Text"> <p>Craig Taylor (WHOI) Model P vs. I approach</p> </div> <div data-bbox="280 245 747 531" data-label="Figure"> <p>FIGURE 5-18 Potential Production and Potential Chlorophyll Specific Production.</p> </div>	<div data-bbox="815 132 1299 172" data-label="Section-Header"> <h2>Slide 79 1995 MA Bay Production</h2> </div> <div data-bbox="815 256 940 291" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="267 651 763 690" data-label="Section-Header"> <h2>2 different production estimates</h2> </div> <div data-bbox="285 695 712 749" data-label="Text"> <p>Using deep vs. surface P vs. I paramter estimates (Kelly &amp; Doering MWRA 95-19)</p> </div> <div data-bbox="263 743 769 1033" data-label="Figure"> <p>Production (mg C m-2 d-1)</p> <p>Calculated from deep sample</p> <p>Calculated from surface sample</p> <p>4 X difference</p> <p>DS630</p> </div>	<div data-bbox="815 621 1391 659" data-label="Section-Header"> <h2>Slide 80 2 different production estimates</h2> </div> <div data-bbox="815 743 940 779" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="267 1209 766 1291" data-label="Section-Header"> <h2>Excursis on the Subsurface Chlorophyll maxima</h2> </div> <div data-bbox="246 1297 751 1421" data-label="Text"> <p>Prevalent in Gulf of Maine (and MA Bay) from April through early September, many coastal zones (including the Washington-Oregon-California shelf) &amp; oligotrophic gyres (called the Typical Tropical Structure)</p> </div> <div data-bbox="652 1486 771 1518" data-label="Text"> <p>EEOS630</p> </div>	<div data-bbox="815 1110 1325 1184" data-label="Section-Header"> <h2>Slide 81 Excursis on the Subsurface Chlorophyll maxima</h2> </div> <div data-bbox="815 1268 940 1304" data-label="Text"> <p>NOTES:</p> </div>

## MA Bay subsurface Chl a maxima

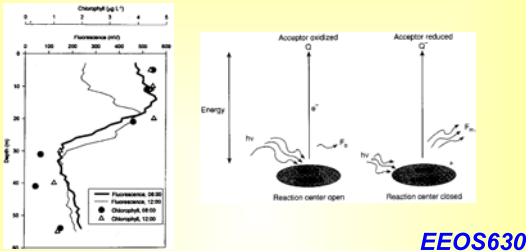


### Slide 82 MA Bay subsurface Chl a maxima

NOTES:

As noted by Cullen, SSFluorescence not necessarily a SSChl max nor SSCarbon max

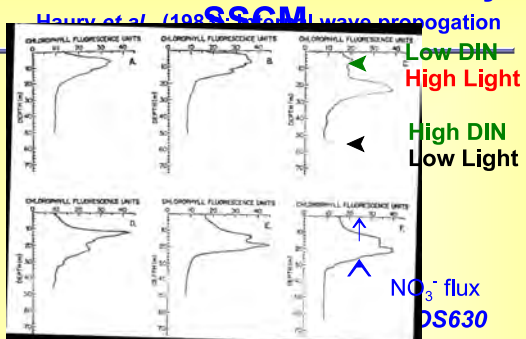
Falkowski & Raven Figure 9.6



### Slide 83 As noted by Cullen, SSFluorescence not necessarily a SSChl max nor SSCarbon max

NOTES:

## Internal waves and MA Bay SSCM

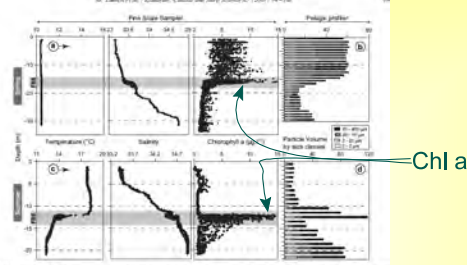


### Slide 84 Internal waves and MA Bay SSCM

NOTES:

## Fine structure of the SSCM

Lunven et al. (2005)



Chl a

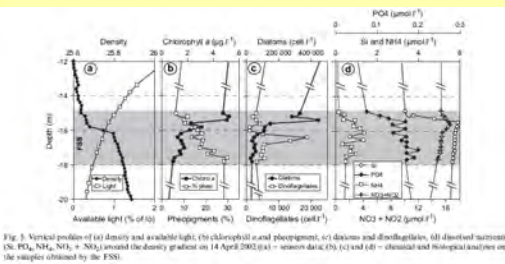
EEOS630

### Slide 85 Fine structure of the SSCM

NOTES:

## Fine structure of the SSCM

Lunven et al. (2005)



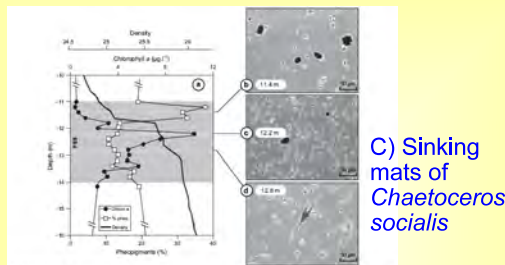
EEOS630

### Slide 86 Fine structure of the SSCM

NOTES:

## Fine structure of the SSCM

Lunven et al. (2005)



C) Sinking mats of *Chaetoceros socialis*

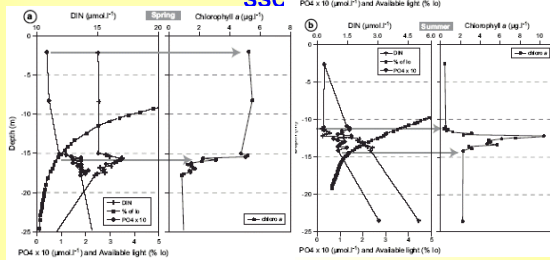
EEOS630

### Slide 87 Fine structure of the SSCM

NOTES:

## Fine structure of the SSCM

Lunven et al. (2005): 0.5% light level at base of SSC



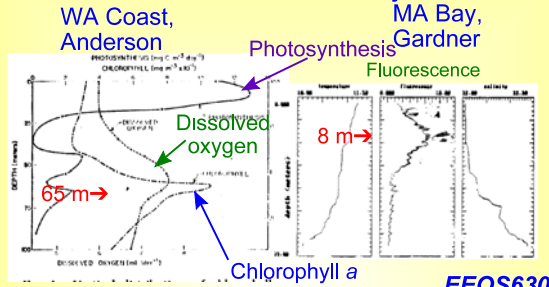
EEOS630

## Slide 88 Fine structure of the SSCM

NOTES:

## SSCM off the Washington-Oregon Coast, also off California

West coast vs. MA Bay



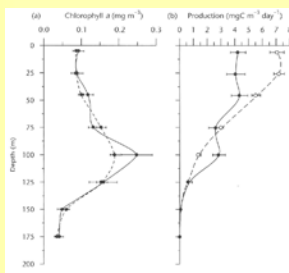
EEOS630

## Slide 89 SSCM off the Washington-Oregon Coast, also off California

NOTES:

## Central N. Pacific gyre: Typical tropical structure

SSCM at 100 meters; Miller (2004) Fig. 10.6

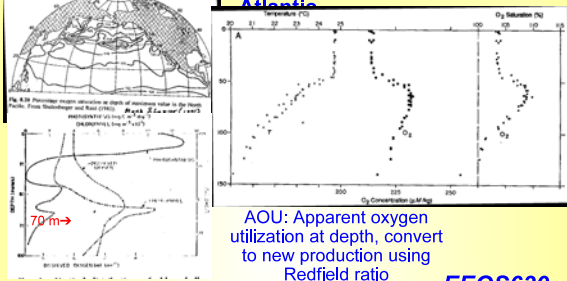


In Lundven's European coastal zone & in MA Bay, the SSCM can be a major component of total water-column production

EEOS630

## Slide 90 Central N. Pacific gyre: Typical tropical structure

NOTES:

<h2 style="text-align: center;">SSCM O<sub>2</sub>: 120% saturation</h2> <p style="text-align: center;">Neukirchner, Reid (1981), Jenkins (1982) In Atlantic</p>  <p style="text-align: center;">             AOU: Apparent oxygen utilization at depth, convert to new production using Redfield ratio  <b>EEOS630</b> </p>	<h3 style="text-align: center;">Slide 91 SSCM O<sub>2</sub>: 120% saturation</h3> <hr/> <p>NOTES:</p> <hr/> <hr/> <hr/> <hr/> <hr/> <hr/>
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