

<div data-bbox="259 193 773 312" data-label="Section-Header"> <h2>The Spring Bloom: Timing &amp; Absence and the Geritol solution to global warming</h2> </div> <div data-bbox="406 321 597 348" data-label="Text"> <p>Class 20, 11/06/08</p> </div> <div data-bbox="656 510 771 537" data-label="Text"> <p>EEOS630</p> </div>	<div data-bbox="818 130 1399 243" data-label="Section-Header"> <h3>Slide 1 The Spring Bloom: Timing &amp; Absence and the Geritol solution to global warming</h3> </div> <div data-bbox="818 327 940 361" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="326 728 699 766" data-label="Section-Header"> <h2>Phytoplankton Readings</h2> </div> <div data-bbox="362 772 660 800" data-label="Section-Header"> <h3>Nutrients and the spring bloom</h3> </div> <div data-bbox="233 798 740 1075" data-label="List-Group"> <ul style="list-style-type: none"> <li>• Nutrient effects on growth, 11/4 (Tu) <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, Today <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="818 693 1271 732" data-label="Section-Header"> <h3>Slide 2 Phytoplankton Readings</h3> </div> <div data-bbox="818 816 940 850" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="339 1218 688 1255" data-label="Section-Header"> <h2>Four major revolutions</h2> </div> <div data-bbox="316 1262 716 1289" data-label="Section-Header"> <h3>In our understanding of nutrient limitation</h3> </div> <div data-bbox="233 1289 753 1549" 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="818 1184 1253 1222" data-label="Section-Header"> <h3>Slide 3 Four major revolutions</h3> </div> <div data-bbox="818 1306 940 1339" data-label="Text"> <p>NOTES:</p> </div>

<div data-bbox="315 168 703 210" data-label="Section-Header"> <h3>Relative growth rate <math>\mu/\mu_{\max}</math></h3> </div> <div data-bbox="311 214 699 243" data-label="Text"> <p>Goldman (1980), replotted by Harris (1986)</p> </div> <div data-bbox="243 245 519 520" data-label="List-Group"> <ul style="list-style-type: none"> <li>Redfield ratios only attained at <math>\mu/\mu'_{\max} = 1</math></li> <li>C:Chl <i>a</i> ratio is a reasonable predictor of relative growth rate                     <ul style="list-style-type: none"> <li>But it is affected by shade adaptation. A shade adapted, slow growing cell may have low relative <math>\mu</math>, and low C:Chl <i>a</i></li> </ul> </li> <li>DiTullio &amp; Laws (1986) developed a <math>^{14}\text{C}</math>-protein labeling procedure to estimate relative growth rate concentration</li> </ul> </div> <div data-bbox="521 241 776 548" data-label="Figure"> </div>	<div data-bbox="815 132 1328 172" data-label="Section-Header"> <h3>Slide 4 Relative growth rate <math>\mu/\mu_{\max}</math></h3> </div> <div data-bbox="815 256 938 291" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="250 651 750 753" data-label="Section-Header"> <h3>Goldman's theory: The relationship between <math>\mu/\mu_{\max}</math> &amp; the Redfield ratio</h3> </div> <div data-bbox="271 758 721 829" data-label="Chemical-Block"> <math display="block">(\text{CH}_2\text{O})_{106} (\text{NH}_3)_{16} \text{H}_3\text{PO}_4 + 138 \text{O}_2 \rightleftharpoons 106 \text{CO}_2 + 16 \text{HNO}_3 + \text{H}_3\text{PO}_4 + 122 \text{H}_2\text{O}.</math> </div> <div data-bbox="235 827 771 1024" data-label="List-Group"> <ul style="list-style-type: none"> <li>The 'Redfield' ratio was first determined approximately by Harvey in the 20s, grinding up seaweeds</li> <li>Only phytoplankton growing near <math>\mu'_{\max}</math> have cellular C:N:P in Redfield proportions</li> <li>The Redfield ratio predicts the rate of regeneration on C:N:P in deep water <span style="float: right;">EEOS630</span></li> </ul> </div>	<div data-bbox="815 621 1310 732" data-label="Section-Header"> <h3>Slide 5 Goldman's theory: The relationship between <math>\mu/\mu_{\max}</math> &amp; the Redfield ratio</h3> </div> <div data-bbox="815 819 938 852" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="326 1218 696 1255" data-label="Section-Header"> <h3>Ecological Stoichiometry</h3> </div> <div data-bbox="279 1264 737 1293" data-label="Text"> <p>Sterner &amp; Elser (2002): Reviews Goldman's theory</p> </div> <div data-bbox="220 1291 771 1589" data-label="Figure"> </div>	<div data-bbox="815 1184 1276 1222" data-label="Section-Header"> <h3>Slide 6 Ecological Stoichiometry</h3> </div> <div data-bbox="815 1306 938 1341" data-label="Text"> <p>NOTES:</p> </div>

## 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 7 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 8 Third Limitation of Ecosystem Production

NOTES:

## Trichodesmium & gyre N<sub>2</sub> fixation

Mat-forming N<sub>2</sub>-fixing cyanobacterium, Capone et al. (1997)

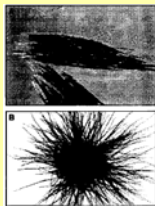
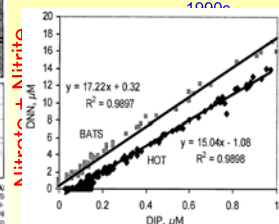


Fig. 1. Examples of Trichodesmium colonies. (A) Filamentous or ball of Trichodesmium colony with 100-150 radial or oval colony of T. thiodiazot. Colonies are typically 2 to 5 mm in length (filamentous) or diameter (ball) and are composed of tens to hundreds of aggregated filaments (trichomes). Each trichome consists of tens to hundreds of cells (typically ~100); cells are generally 5 to 15  $\mu\text{m}$  in diameter and can reach up to 100  $\mu\text{m}$  in length (100 photos by H. Platt).



Wail

More Fe-rich dust & N fixation in Atlantic (Wu et al. 2000)

## Slide 9 Trichodesmium & gyre N<sub>2</sub> fixation

NOTES:

<div data-bbox="311 168 703 207" data-label="Section-Header"> <h3>Banase's three ocean types</h3> </div> <div data-bbox="306 214 709 243" data-label="Text"> <p>1: Oligotrophic gyres, 2: HNLC, 3: Seasonal</p> </div> <div data-bbox="222 252 735 508" data-label="Figure"> </div> <div data-bbox="271 501 565 533" data-label="Text"> <p>Gulf of Maine is Domain 3</p> </div> <div data-bbox="652 512 771 541" data-label="Text"> <p>EEOS630</p> </div>	<div data-bbox="815 132 1302 174" data-label="Section-Header"> <h3>Slide 10 Banase's three ocean types</h3> </div> <div data-bbox="815 256 941 291" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="272 653 764 695" data-label="Section-Header"> <h3>Overview of vernal bloom topics</h3> </div> <div data-bbox="233 726 755 1001" data-label="List-Group"> <ul style="list-style-type: none"> <li>• History of the spring bloom <ul style="list-style-type: none"> <li>• Gran and Braarud (1935)</li> <li>• Riley's near miss</li> <li>• Sverdrup's critical depth concept</li> </ul> </li> <li>• Non-dimensional critical depth &amp; the MA Bay spring bloom <ul style="list-style-type: none"> <li>• Townsend &amp; Spinrad</li> <li>• Nelson's hypothesis for the southern ocean</li> </ul> </li> <li>• Why there are no spring blooms in the tropics, subarctic Pacific, Southern Ocean AND Narragansett Bay in recent years (see today's Boston Globe) <ul style="list-style-type: none"> <li>• Steady-state control of production by grazing, with grazer populations maintained by wintertime production</li> <li>• Lack of rapid spring stratification &amp; macronutrient depletion</li> <li>• Iron limitation</li> <li>• Light limitation (Nelson &amp; Smith, 1991)</li> </ul> </li> </ul> </div> <div data-bbox="613 997 732 1026" data-label="Text"> <p>ECOS630</p> </div>	<div data-bbox="815 621 1399 661" data-label="Section-Header"> <h3>Slide 12 Overview of vernal bloom topics</h3> </div> <div data-bbox="815 741 941 779" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="365 1144 638 1176" data-label="Section-Header"> <h3>The Gulf of Maine bloom</h3> </div> <div data-bbox="263 1188 753 1220" data-label="Text"> <p>Bill Hanlon (UMB M.Sc.): CZCS, pre-bloom and bloom</p> </div> <div data-bbox="233 1251 742 1474" data-label="Figure"> </div> <div data-bbox="652 1486 771 1518" data-label="Text"> <p>EEOS630</p> </div>	<div data-bbox="815 1110 1300 1148" data-label="Section-Header"> <h3>Slide 13 The Gulf of Maine bloom</h3> </div> <div data-bbox="815 1230 941 1266" data-label="Text"> <p>NOTES:</p> </div>

<div data-bbox="240 163 760 541"> <h3>1995 MA Bay Spring Bloom</h3> <p>Craig Taylor (MWRA 1995 water-column report)</p> <p>EEOS630</p> </div>	<div data-bbox="824 134 1333 170"> <h3>Slide 14 1995 MA Bay Spring Bloom</h3> </div> <div data-bbox="824 258 938 289"> <p>NOTES:</p> </div>
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## Sverdrup's (1953) Critical Depth

### His assumptions, with comments

- Thoroughly mixed top-layer of thickness  $D$ 
  - Turbulence strong enough to evenly distribute phytoplankton
  - Within mixed layer, extinction coefficient ( $k$ ) for PAR is constant
    - Wavelength of light (420-560 nm) considered (Too narrow but not a critical violation of assumptions, 400-720 nm -current range for PAR, see Behrenfeld & Falkowski 1997)
- Production not limited by nutrients
- Production by photosynthesis proportional to light
- Energy flux,  $I_c$ , at the compensation depth is known.
  - Riley (1957): 40 langley per day
  - Note that Riley was using full sunlight, not PAR

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## Slide 17 Sverdrup's (1953) Critical Depth

NOTES:

## Units for light intensity

From Parsons et al. (1984), see Table 2 in Chapter 5

$E_{in}$ =mol photon,

so the units of light should be in terms of a flux  
 $\mu E_{in} \text{ cm}^{-2} \text{ s}^{-1}$  in the PAR

PSR<PUR<PAR (Photosynthetically active radiation or Photo, available radiation wavelengths from 400 to 720 nm)

$E_{in}=6.02 \times 10^{23}$  quanta= $2.86 \times 10^9$ /Angstroms g cal  
 where Angstrom= $10^{-10}$  m

1 g cal= $4.185 \times 10^7$  ergs= $4.185$  watt\*sec  
 1 g cal/cm<sup>2</sup>=1 langley

Riley 1957: 0.03 g cal/cm<sup>2</sup>/min = 40 langley/d [Siegel et al. misquote Riley (1957): 0.3 g cal/cm<sup>2</sup>/min cal/cm<sup>2</sup>/min]

For average wavelength of visible light 550 nm,  
 1  $E_{in}$ =( $2.86 \times 10^9/5500$ )g cal= $52 \times 10^3$  g cal  
 note that Harrison and Platt use Watts/m<sup>2</sup>

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## Slide 18 Units for light intensity

NOTES:

Obtained by integrating over time & depth: To find critical depth, need  $k_{PAR}$ ,  $I_o$  &  $I_c$ , the compensation light intensity

$$\frac{D_{cr}}{1 - e^{-k_e D_{cr}}} = \frac{\bar{I}_e}{I_o k_e}$$

where,  $D_{cr}$  = critical depth [m].

$k_e$  = extinction coefficient  $\left[\frac{1}{m}\right]$ .

$\bar{I}_e$  = (avg. energy)/time at sea surface (PAR).

$I_o$  = energy at compensation depth.

$$D_{cr} \approx \frac{I_o}{I_c k_e}$$

$D_{cr}$  = critical depth [meters].

$k_e$  = extinction coefficient.

$I_o$  = Avg. energy passing sea surface.

$I_c$  = energy at compensation depth.

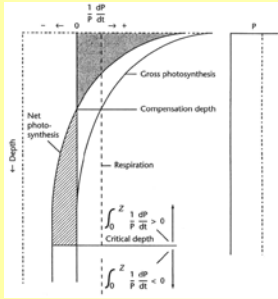
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## Slide 19 Sverdrup's equations

NOTES:

## The classic critical depth diagram

From Parsons et al. (1984) Figure 41; Miller Fig 1.3



Sverdrup, a physical oceanographer, considered loss of phytoplankton to predators as a form of respiration; see Smetacek & Passow's critique and Platt et al. 1991

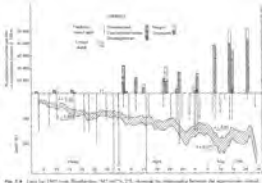
## Slide 20 The classic critical depth diagram

NOTES:

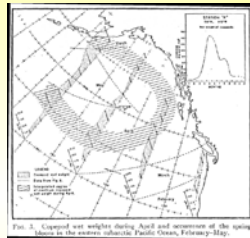
## Two tests of Sverdrup's model

Are either of these valid tests?

N. Atlantic Station M test by Sverdrup (1953)



Parsons et al. (1966) test in subarctic Pacific

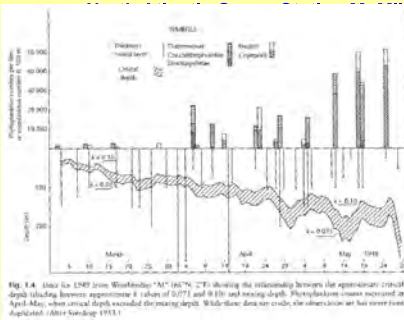


## Slide 21 Two tests of Sverdrup's model

NOTES:

## Sverdrup's Test

Fig 1.4



Phyto- & Zooplankton numbers per liter

Critical depth (2 light attenuation coefficients)

Mixed Layer

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## Slide 22 Sverdrup's Test

NOTES:

<div data-bbox="310 168 711 205" data-label="Section-Header"> <h3>Subarctic Pacific, Station P</h3> </div> <div data-bbox="266 214 755 243" data-label="Text"> <p>Parsons et al. (1966): Macrozooplankton wet weights</p> </div> <div data-bbox="225 254 602 539" data-label="Figure"> <p>Figure 1 shows a map of the Subarctic Pacific with sampling stations marked. To the right, a vertical profile illustrates the distribution of <i>Neocalanus plumchrus</i> and <i>N. cristatus</i> in the water column, with a peak in density around 100-200 meters depth.</p> </div> <div data-bbox="596 436 734 539" data-label="Text"> <p><i>Neocalanus plumchrus</i> &amp; <i>N. cristatus</i> ECOS630</p> </div>	<div data-bbox="816 132 1326 172" data-label="Section-Header"> <h3>Slide 23 Subarctic Pacific, Station P</h3> </div> <div data-bbox="816 256 941 291" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="310 653 711 690" data-label="Section-Header"> <h3>Subarctic Pacific, Station P</h3> </div> <div data-bbox="363 701 639 730" data-label="Text"> <p>Parsons et al. (1966) Figure 2</p> </div> <div data-bbox="237 720 742 1022" data-label="Figure"> <p>Figure 2 displays four panels showing critical depths and depths of mixing for different latitudes: 125°W, 133°W, 142°W, and 155°W. Red arrows indicate 'Mixed depths' and pink arrows indicate 'March Critical depth'. A small map of the Subarctic Pacific is included in the bottom right panel.</p> </div>	<div data-bbox="816 623 1326 661" data-label="Section-Header"> <h3>Slide 24 Subarctic Pacific, Station P</h3> </div> <div data-bbox="816 743 941 779" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="297 1209 734 1291" data-label="Section-Header"> <h3>Predicting Gulf of Maine Spring Blooms</h3> </div> <div data-bbox="266 1297 764 1331" data-label="Text"> <p>Why is the MA Bay bloom delayed until March?</p> </div> <div data-bbox="654 1488 773 1518" data-label="Text"> <p>EEOS630</p> </div>	<div data-bbox="816 1110 1399 1182" data-label="Section-Header"> <h3>Slide 25 Predicting Gulf of Maine Spring Blooms</h3> </div> <div data-bbox="816 1268 941 1304" data-label="Text"> <p>NOTES:</p> </div>



## North Atlantic Critical Depths

Miller (2004) Table 1.2, from Platt *et al.* 1991  
Proc. Royal Soc. London B 246: 205-217.

Table 1.2 Critical depths as a function of date and latitude, from Platt *et al.* 1991.

Date	Latitude (°N)	Critical depth (m)	
		With (net) phytoplankton respiration	With all losses included
1 February	40	383	131
	50	274	92
1 March	40	447	164
	50	385	141
1 April	40	551	193
	50	521	238
1 May	40	635	272
	50	639	238
1 June	40	691	258
	50	723	270

140 m (all losses) to 450 m in March Does Sverdrup's model apply to a 35 m MA Bay water column?

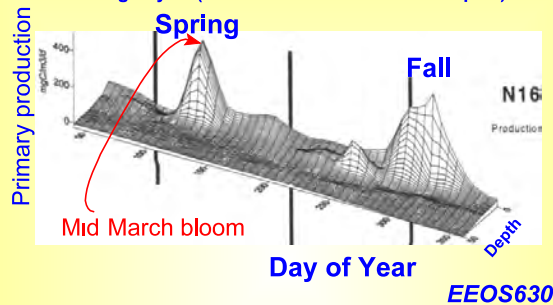
$I_0$  in MA Bay the same,  $k_{PAR}$  higher? **EEOS630**

## Slide 26 North Atlantic Critical Depths

NOTES:

## 1995 Seasonal production

Craig Taylor (MWRA 1995 water-column report)



## Slide 27 1995 Seasonal production

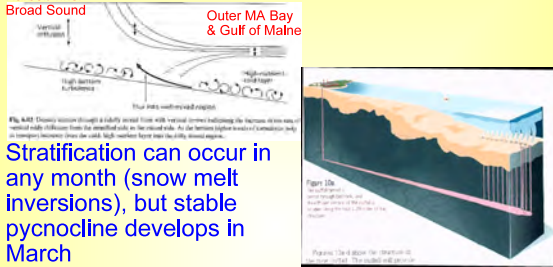
NOTES:

## BH-MA Bay: A tidal front

MWRA State of the Harbor Report & Mann & Lazier

Boston Harbor/Inner Broad Sound

Outer MA Bay & Gulf of Maine

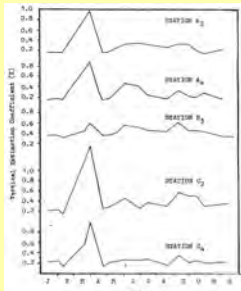
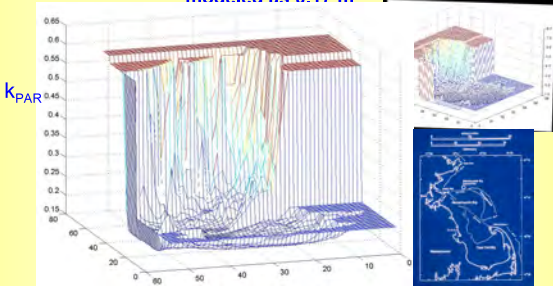
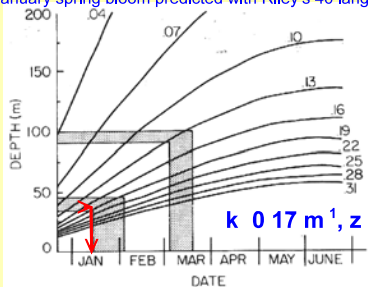


Stratification can occur in any month (snow melt inversions), but stable pycnocline develops in March

## Slide 28 BH-MA Bay: A tidal front

NOTES:

<div data-bbox="321 163 695 201" data-label="Section-Header"> <h3>MA Bay Blooms in March</h3> </div> <div data-bbox="277 212 742 256" data-label="Text"> <p>Parker (1975) documented a March production and biomass bloom in 1973 and 1974</p> </div> <div data-bbox="238 256 771 539" data-label="Figure"> </div>	<div data-bbox="820 130 1310 168" data-label="Section-Header"> <h3>Slide 29 MA Bay Blooms in March</h3> </div> <div data-bbox="820 254 941 287" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="354 653 651 690" data-label="Section-Header"> <h3>2000 MA Bay Bloom</h3> </div> <div data-bbox="306 699 716 726" data-label="Text"> <p>Mid-March spring bloom, massive fall bloom</p> </div> <div data-bbox="224 743 380 1012" data-label="Text"> <p>How much carbon using back-of-the-envelope: assume C:Chl <math>a \approx 30</math> &amp; 10-m euphotic zone. Or, <math>12 \mu\text{g Chl } a / \text{L} * 30 \text{ g C/g Chl } a * 10 \text{ m} * 1000 \text{ L/m}^3 = 3.6 \text{ g C m}^{-2}</math></p> </div> <div data-bbox="397 728 764 1024" data-label="Figure"> </div>	<div data-bbox="820 619 1234 657" data-label="Section-Header"> <h3>Slide 30 2000 MA Bay Bloom</h3> </div> <div data-bbox="820 741 941 774" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="303 1142 709 1180" data-label="Section-Header"> <h3>Townsend &amp; Spinrad (1986)</h3> </div> <div data-bbox="297 1188 719 1218" data-label="Text"> <p>Figure 12: <math>I_0</math> (date) &amp; <math>k_{PAR}</math> needed to predict <math>Z_{cr}</math></p> </div> <div data-bbox="280 1226 732 1516" data-label="Figure"> </div>	<div data-bbox="820 1108 1338 1146" data-label="Section-Header"> <h3>Slide 31 Townsend &amp; Spinrad (1986)</h3> </div> <div data-bbox="820 1230 941 1264" data-label="Text"> <p>NOTES:</p> </div>

<p style="text-align: center;"><b>What is <math>k_{PAR}</math>?</b></p> <p style="text-align: center;">From Parker (1975): <math>\approx 0.2 \text{ m}^{-1}</math> before bloom</p>  <p>Note that <math>k</math>, the light attenuation coefficient, is a function of wavelength, should be expressed as <math>k_{PAR}</math> &amp; is linearly correlated with Chl <math>a</math> concentration</p> <p>Note <math>K</math> is about equal to <math>1.7/\text{Secchi disk depth}</math> (or <math>8.5 \text{ m}</math> for <math>k=0.2 \text{ m}^{-1}</math>)</p> <p style="text-align: right;"><b>EEOS630</b></p>	<p><b>Slide 32 What is <math>k_{PAR}</math>?</b></p> <p>NOTES:</p>
<p style="text-align: center;"><b>Light attenuation, <math>k_{PAR}</math>, for MA Bay</b></p> <p style="text-align: center;">From the MA Bay 3-d Hydroqual model: Bay <math>k_{PAR}</math> modeled as <math>0.17 \text{ m}^{-1}</math></p> 	<p><b>Slide 33 Light attenuation, <math>k_{PAR}</math>, for MA Bay</b></p> <p>NOTES:</p>
<p style="text-align: center;"><b>Townsend &amp; Spinrad (1986)</b></p> <p style="text-align: center;">Figure 12: <math>I_0</math> (date) &amp; <math>k</math> needed to predict <math>Z_{cr}</math> A January spring bloom predicted with Riley's 40 langley's per day <math>I_0</math></p>  <p style="text-align: right;"><b>EEOS630</b></p>	<p><b>Slide 34 Townsend &amp; Spinrad (1986)</b></p> <p>NOTES:</p>

## Dimensionless critical depth plots

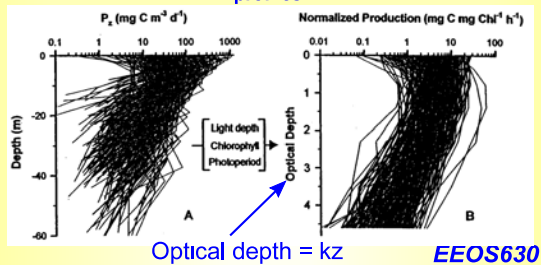
EEOS630

### Slide 35 Dimensionless critical depth plots

NOTES:

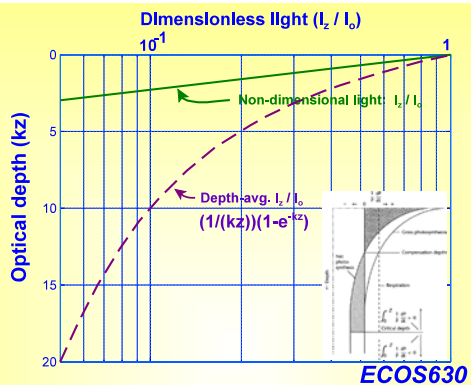
## Behrenfeld-Falkowski remote sensing algorithms

Generalized productivity profiles, 1042 MARMAP profiles



### Slide 36 Behrenfeld-Falkowski remote sensing algorithms

NOTES:

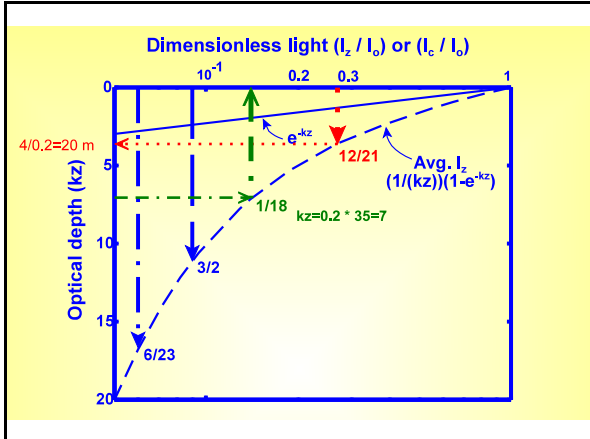


### Slide 37 New England insolation

NOTES:

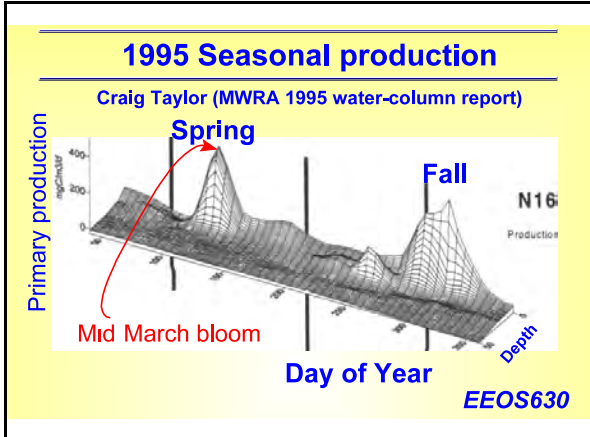


Slide 41



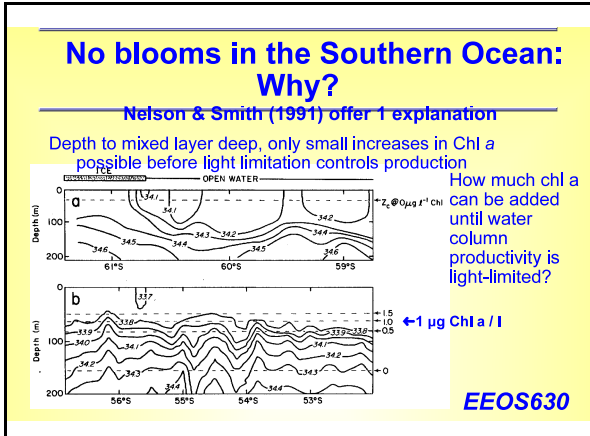
NOTES:

Slide 42 1995 Seasonal production

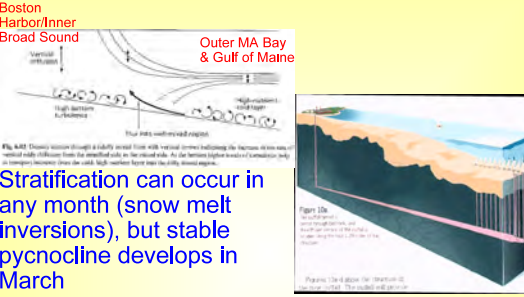
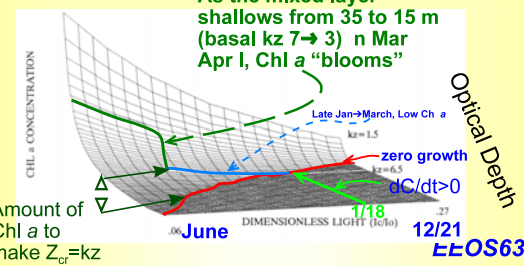


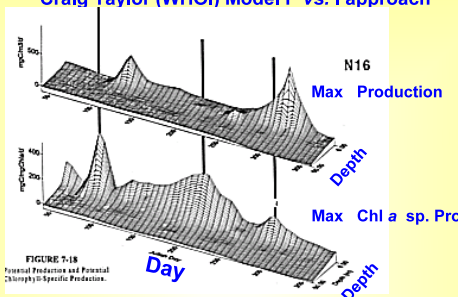
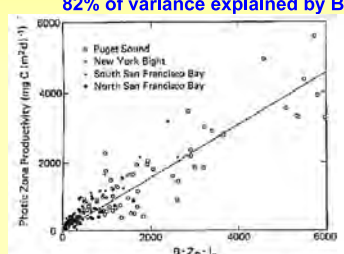
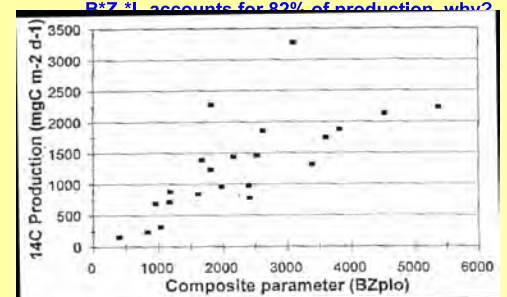
NOTES:

Slide 43 No blooms in the Southern Ocean: Why?



NOTES:

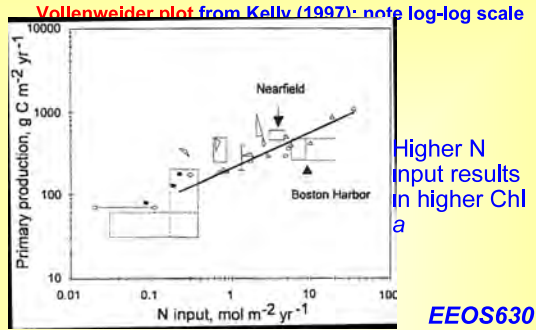
<div data-bbox="235 163 755 541"> <h3>BH-MA Bay: A tidal front</h3> <p>MWRA State of the Harbor Report &amp; Mann &amp; Lazier</p>  </div>	<div data-bbox="824 132 1315 174"> <h3>Slide 44 BH-MA Bay: A tidal front</h3> </div> <div data-bbox="824 258 938 300"> <p>NOTES:</p> </div>
<div data-bbox="235 646 755 1035"> <h3>Why is there a March, not a January bloom?</h3> <p>MA Bay application of Smith &amp; Nelson (1991)</p> <p>As the mixed layer shallows from 35 to 15 m (basal kz 7→3) in Mar Apr I, Chl a "blooms"</p>  </div>	<div data-bbox="824 625 1331 699"> <h3>Slide 45 Why is there a March, not a January bloom?</h3> </div> <div data-bbox="824 783 938 825"> <p>NOTES:</p> </div>
<div data-bbox="235 1234 755 1560"> <h3>Massachusetts Bay Production</h3> <p>Cole-Cloern relationship &amp; Subsurface Chlorophyll maxima</p> <p>EEOS630</p> </div>	<div data-bbox="824 1150 1369 1192"> <h3>Slide 46 Massachusetts Bay Production</h3> </div> <div data-bbox="824 1276 938 1318"> <p>NOTES:</p> </div>

<p><b>1995 MA Bay Production</b></p> <p>Craig Taylor (WHOI) Model P vs. I approach</p>  <p>FIGURE 7-18 Potential Production and Potential Chlorophyll Specific Production.</p>	<p><b>Slide 47 1995 MA Bay Production</b></p> <p>NOTES:</p>
<p><b>Cole-Cloern relationship: No N!</b></p> <p>82% of variance explained by <math>BZ_p I_o</math></p>  <p>Fig. 2. Regression of photoc zone productivity against the composite parameter <math>BZ_p I_o</math> for 211 incubation experiments.  <math>P = 1.50 + 0.73 (BZ_p I_o)</math>; <math>r^2 = 0.82</math>; <math>S_{est}</math> (standard error of the estimate) = 410</p> <p>EEOS630</p>	<p><b>Slide 48 Cole-Cloern relationship: No N!</b></p> <p>NOTES:</p>
<p><b>Cole-Cloern works in MA Bay</b></p> <p><math>BZ_p I_o</math> accounts for 82% of production, why?</p>  <p>Figure Kelly/Doering MA Bay data</p> <p>EEOS630</p>	<p><b>Slide 49 Cole-Cloern works in MA Bay</b></p> <p>NOTES:</p>



## MA Bay production $\propto$ N Loading

Vollenweider plot from Kelly (1997) - note log-log scale

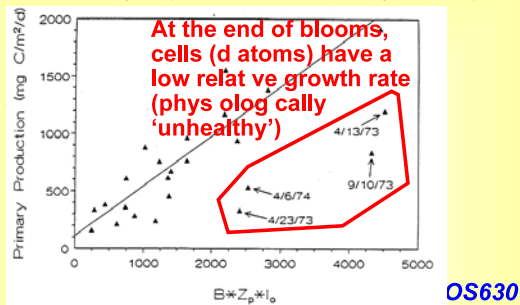


## Slide 50 MA Bay production $\propto$ N Loading

NOTES:

## Bz<sub>p</sub>I<sub>0</sub> model fails after blooms

Jim Shine (1992) UMASS Ph.D., Parker (1975 data)



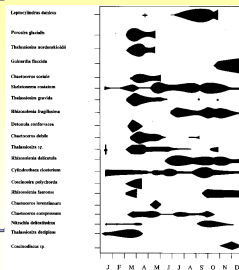
## Slide 51 Bz<sub>p</sub>I<sub>0</sub> model fails after blooms

NOTES:

## Phytoplankton succession in bay

Diatom species composition from Parker (1975)

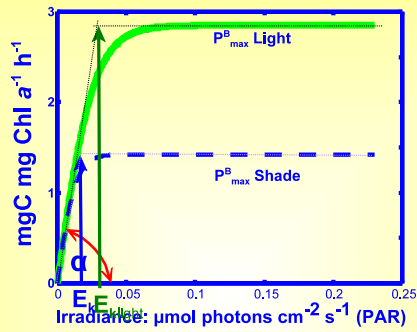
- Rapid reduction of dissolved inorganic nitrogen to < 1  $\mu$ M at end of bloom
- Rapid succession of diatom species at the termination of the spring bloom
  - Bloom species settle out to the bottom
  - Very high fluorescent yield
  - Low relative growth rates;
    - High C:Chl a ratios
    - Low assimilation numbers



## Slide 52 Phytoplankton succession in bay

NOTES:

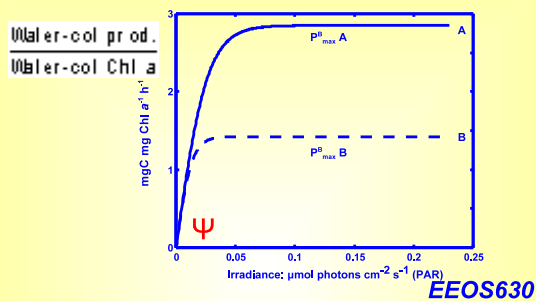
### Chl a-specific gross productivity



### Slide 53 Platt's (1986) Explanation

NOTES:

### Platt's biooptical model

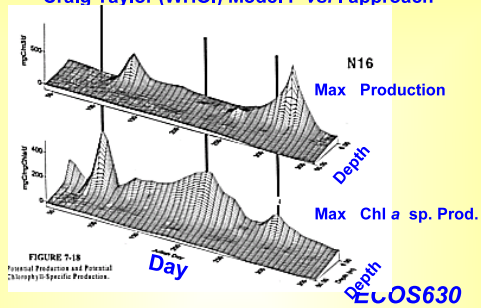


### Slide 54 Platt's biooptical model

NOTES:

### 1995 MA Bay Production

Craig Taylor (WHOI) Model P vs. I approach



### Slide 55 1995 MA Bay Production

NOTES:

## Cole-Cloern relationship

82% of variance explained by  $BZ_p I_0$

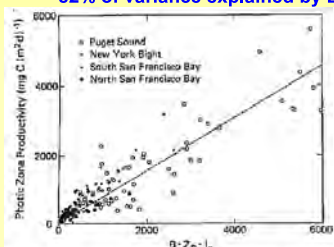


Fig. 2. Regression of photic zone productivity against the composite parameter  $BZ_p I_0$  for 211 incubation experiments.  $P = 150 \pm 0.73 (BZ_p I_0)$ ;  $r^2 = 0.82$ ;  $S_p$  (standard error of the estimate) = 410

## Slide 56 Cole-Cloern relationship

NOTES:

## Why does the Cole-Cloern model work?

Wofsy is wrong, Platt (1986) appears correct

- Wofsy (1983)
  - Nutrient-rich lakes, bays and estuaries:
    - Phytoplankton grow until the mixed layer is equivalent to five optical depths.
    - Production is light-controlled, and nutrients are usually in excess {Wofsy incorrect: Nutrients still limit yield as noted in Howarth's (1988) 2nd sense of nutrient limitation}
- Platt (1986)
  - Succession among phytoplankton groups leads to phytoplankton acclimated to current nutrient input regime
  - Their P vs. I parameters are close to temperature-controlled optima

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## Slide 57 Why does the Cole-Cloern model work?

NOTES:

## Why does the model work?

Wofsy is wrong, Platt (1986) appears correct

- Bio-optical models &  $\Psi$  (psi)
  - Platt (1986) Initial slope of the generalized P vs. I relationship,  $\Psi$  (pronounced psi), relatively constant at  $0.4 \text{ g C g}^{-1} \text{ Chl a m}^{-2} \text{ mol}^{-1} \text{ photons}$
  - Raven & Falkowski (1997) Figure 9.9
    - $\Psi$  not a constant
      - Higher at low light intensities
      - Lower in nutrient-stressed cells
- A high relative specific growth rate produces the Cole-Cloern or Malone-Platt relationship
  - If relative growth rate is high (coupled mainly to temperature), then
  - There must be a close coupling between nutrient loading and Chl a concentration

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## Slide 58 Why does the model work?

NOTES:

## Why no phytoplankton bloom in the Subarctic Pacific?

Parsons et al. (1966): the Major Grazer hypothesis  
 Evans & Parslow's Micrograzer Hypothesis  
 Martin's Iron Hypothesis  
 Ecumenical Iron hypothesis

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### Slide 59 Why does the model work?

NOTES:

## Why does the model work?

Wofsy is wrong, Platt (1986) appears correct

- Bio-optical models &  $\Psi$  (psi)
  - Platt (1986) Initial slope of the generalized P vs. I relationship,  $\Psi$  (pronounced *psi*), relatively constant at  $0.4 \text{ g C g}^{-1} \text{ Chl a m}^{-2} \text{ mol}^{-1}$  photons
  - Raven & Falkowski (1997) Figure 9.9
    - $\Psi$  not a constant
      - Higher at low light intensities
      - Lower in nutrient-stressed cells
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  - If relative growth rate is high (coupled mainly to temperature), then
  - There must be a close coupling between nutrient loading and Chl a concentration

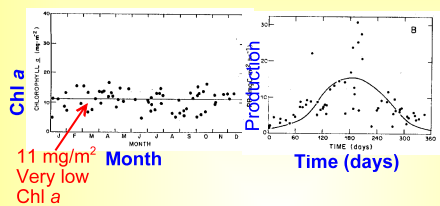
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### Slide 60 Why no phytoplankton bloom in the Subarctic Pacific?

NOTES:

## No bloom at Station P in the Subarctic Pacific

Chl a and production from Frost (1987)



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### Slide 61 No bloom at Station P in the Subarctic Pacific

NOTES:

<div data-bbox="292 163 732 201" data-label="Section-Header"> <h2>The 'Major Grazer' hypothesis</h2> </div> <div data-bbox="285 212 737 237" data-label="Text"> <p>Macrozooplankton grazing keeps bloom in check</p> </div> <div data-bbox="245 243 474 268" data-label="Section-Header"> <h3>Major grazer Hypothesis</h3> </div> <div data-bbox="256 266 422 352" data-label="List-Group"> <ul style="list-style-type: none"> <li>Heinrich (1957)</li> <li>Beklemishev (1957)</li> <li>McAllister (1960)</li> <li>Parsons et al. (1966)</li> <li>Fulton (1973)</li> </ul> </div> <div data-bbox="570 243 670 352" data-label="Image"> </div> <div data-bbox="245 352 505 394" data-label="Section-Header"> <h3>Neocalanus plumchrus &amp; N. cristatus:</h3> </div> <div data-bbox="256 392 477 445" data-label="List-Group"> <ul style="list-style-type: none"> <li>Horsefly-sized calanoids</li> <li>Keep blooms in check due to unique life history</li> </ul> </div> <div data-bbox="532 363 691 506" data-label="Figure"> </div> <div data-bbox="701 378 782 409" data-label="Text"> <p>→ Zooplankton biomass</p> </div> <div data-bbox="656 508 773 537" data-label="Text"> <p>EEOS630</p> </div>	<div data-bbox="820 130 1378 168" data-label="Section-Header"> <h2>Slide 62 The 'Major Grazer' hypothesis</h2> </div> <div data-bbox="820 254 941 287" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="266 648 776 741" data-label="Section-Header"> <h2>Neocalanus life history, different from Calanus finmarchicus, Calanus pacificus &amp; Pseudocalanus</h2> </div> <div data-bbox="259 749 779 779" data-label="Text"> <p>Reproduce at depth, CIII stages feeding on bloom</p> </div> <div data-bbox="233 787 427 909" data-label="Figure"> </div> <div data-bbox="287 919 378 1018" data-label="Image"> </div> <div data-bbox="441 787 719 1001" data-label="Figure"> </div> <div data-bbox="656 999 773 1026" data-label="Text"> <p>EEOS630</p> </div>	<div data-bbox="820 619 1399 732" data-label="Section-Header"> <h2>Slide 63 Neocalanus life history, different from Calanus finmarchicus, Calanus pacificus &amp; Pseudocalanus</h2> </div> <div data-bbox="820 816 941 850" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="292 1215 737 1253" data-label="Section-Header"> <h2>N. Atlantic Calanus life history</h2> </div> <div data-bbox="297 1264 732 1289" data-label="Text"> <p>Calanus finmarchicus: the N. Atlantic dominant</p> </div> <div data-bbox="250 1289 639 1545" data-label="Figure"> </div> <div data-bbox="276 1541 625 1591" data-label="Text"> <p>Females must feed to produce eggs: 20-30 d lag</p> </div> <div data-bbox="656 1562 773 1589" data-label="Text"> <p>EEOS630</p> </div>	<div data-bbox="820 1182 1375 1220" data-label="Section-Header"> <h2>Slide 64 N. Atlantic Calanus life history</h2> </div> <div data-bbox="820 1304 941 1339" data-label="Text"> <p>NOTES:</p> </div>

## The micrograzer hypothesis: ciliates

Evans & Parslow's (1985) model

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### Slide 65 The micrograzer hypothesis: ciliates

NOTES:

## Blooms with constant mixed layers

Evans & Parslow (1985), Figures 2 & 3

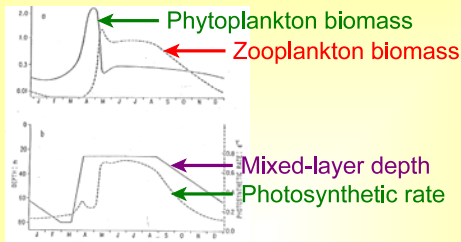


FIGURE 1. (a) The annual cycle of Model 1 phytoplankton (—) and zooplankton (---) expressed in millimoles of nitrogen per cubic meter, for the parameters of Table 1. (b) The annual cycle of mixed layer depth (—) and photosynthetic rate (---) in  $10^3$   $g C m^{-2} d^{-1}$ .

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### Slide 66 Blooms with constant mixed layers

NOTES:

## Protozoan grazing & winter standing stocks the key!

Evans & Parslow's (1985)

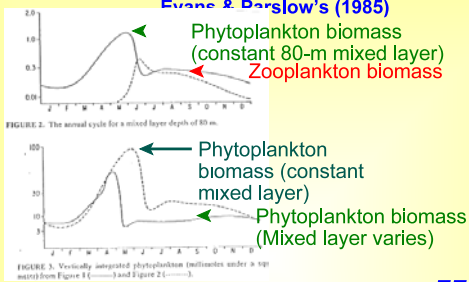


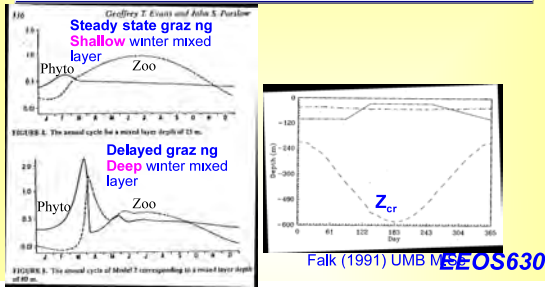
FIGURE 2. Vertically integrated phytoplankton (millimoles under a 100 m) from Figure 1 (—) and Figure 2 (---).

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### Slide 67 Protozoan grazing & winter standing stocks the key!

NOTES:

### Permanent halocline is one key to the lack of spring bloom in the N. Pacific



Slide 68 Permanent halocline is one key to the lack of spring bloom in the N. Pacific

NOTES:

### Evans & Parslow's micrograzer hypothesis

- North Pacific blooms are kept in check by protozoan grazing
- The permanent halocline in the North Pacific (relatively high rainfall relative to evaporation) results in a permanent surface mixed layer and higher winter-time production than the N. Atlantic
- Protozoan grazer standing stocks remain high during the winter and can keep phytoplankton in check

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Slide 69 Evans & Parslow's micrograzer hypothesis

NOTES:

### Problems with the "naive" micrograzer hypothesis

- Why are there spring and fall blooms in areas like MA Bay, where the critical depth usually always exceeds the bottom depth?
- What controls diatom production, a group that owes much of its evolutionary success to its resistance to microzooplankton grazing?

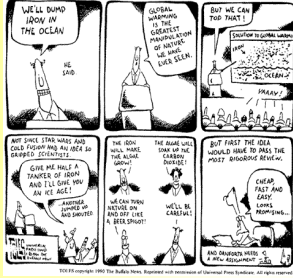
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Slide 70 Problems with the "naive" micrograzer hypothesis

NOTES:

## Martin's Geritol solution

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



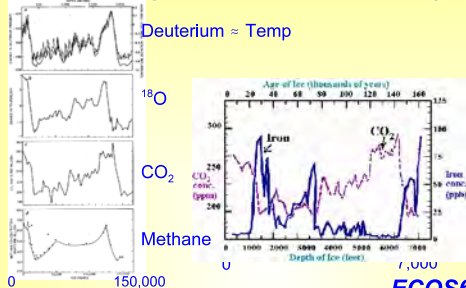
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## Slide 71 Martin's Geritol solution

NOTES:

## The Greenhouse effect & Fe

Woodwell figures. Fe dust increased during ice ages



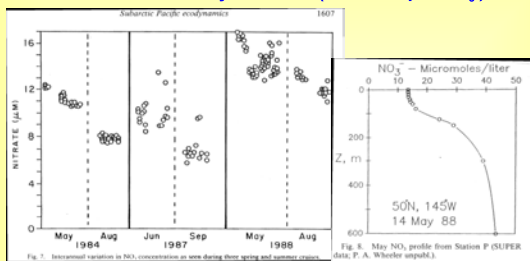
ECOS630

## Slide 72 The Greenhouse effect & Fe

NOTES:

## High nitrate all year at Station P

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



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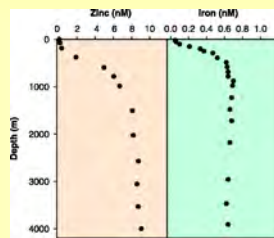
## Slide 73 High nitrate all year at Station P

NOTES:



## Iron & Zn depletion in surface water

Morel & Price (2003) Subarctic Pacific



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## Slide 74 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

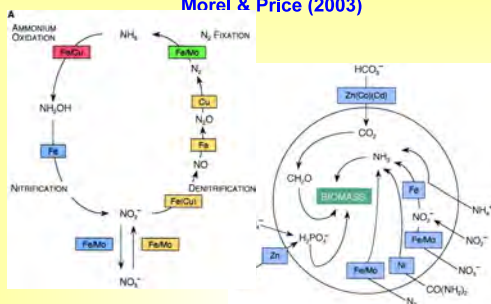
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## Slide 75 Roles of Fe in plant metabolism

NOTES:

## Key uses of Fe & Zn by microbes

Morel & Price (2003)



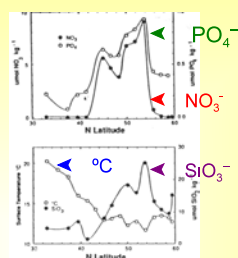
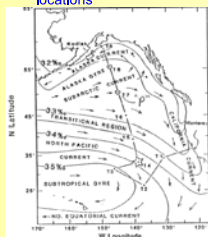
## Slide 76 Key uses of Fe & Zn by microbes

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



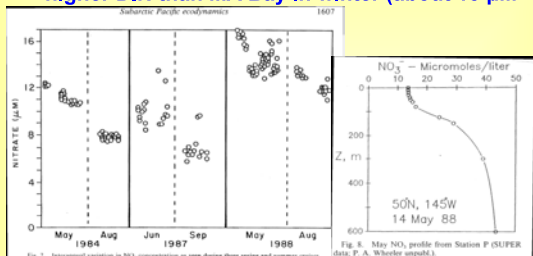
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## Slide 77 Martin & Fitzwater's Fe hypothesis

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  $\mu\text{M}$ )



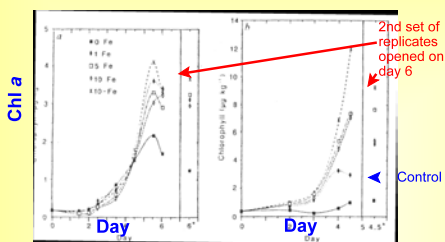
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## Slide 78 High nitrate all year at Station P

NOTES:

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

Increase in Chl a at Station P, T7



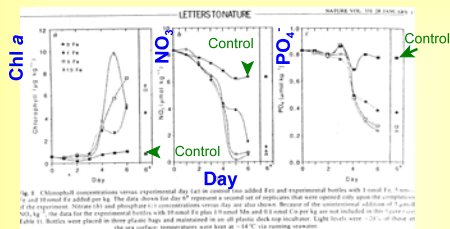
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## Slide 79 Martin & Fitzwater (1988), Martin et al. (1999)

NOTES:

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

No replicates, Banse (1990) noted the statistical problems



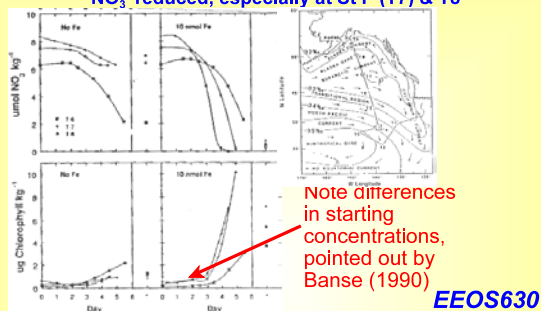
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## Slide 80 Station P: Effects of Fe on Chl a, N & P

NOTES:

## Fe effect dependent on lat & long

$\text{NO}_3^-$  reduced, especially at St P (T7) & T8



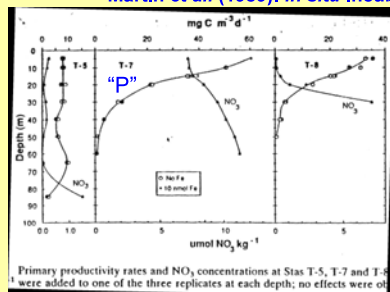
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## Slide 81 Fe effect dependent on lat & long

NOTES:

## No Fe effect on production!

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



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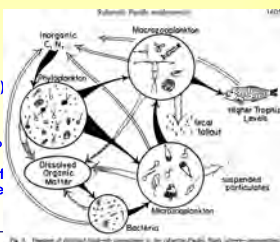
## Slide 82 No Fe effect on production!

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  $\text{NO}_3^-$



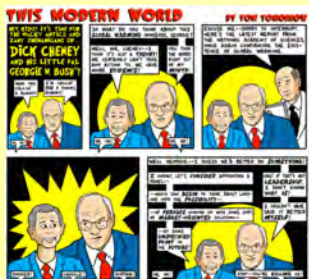
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## Slide 83 The ecumenical Fe hypothesis

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.

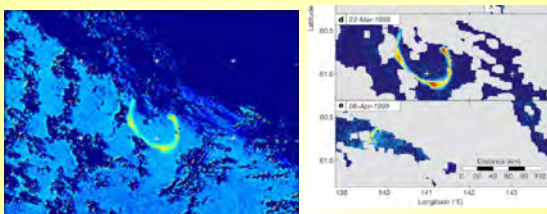
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## Slide 84 Market-oriented CO<sub>2</sub> solution

NOTES:

## SOIREE (Southern Ocean iron release experiment)

SeaWiFS Image of 100 km bloom, 30 d after Fe-II spike



Abraham *et al.* 2000

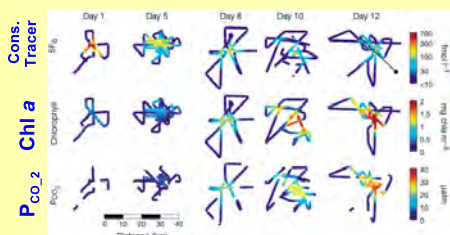
## Slide 85 SOIREE

(Southern Ocean iron release experiment)

NOTES:

## IRONEX III, SOIREE

Boyd et al. (2000) Figure 2



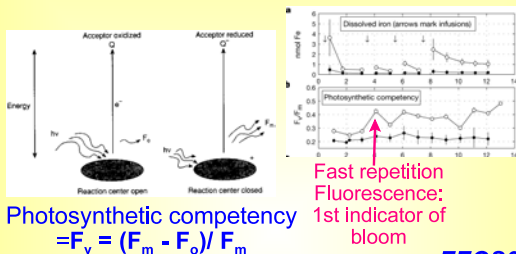
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## Slide 86 IRONEX III, SOIREE

NOTES:

## Variable fluorescence & Fe limitation

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



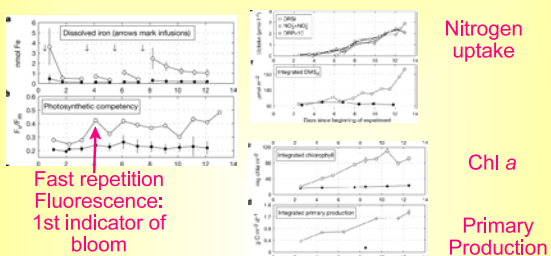
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## Slide 87 Variable fluorescence & Fe limitation

NOTES:

## IRONEX III: bloom by 30-50 μm diatoms

Boyd et al. (2000) Fig. 3



## Slide 88 IRONEX III: bloom by 30-50 μm diatoms

NOTES:

<div data-bbox="315 163 699 201" data-label="Section-Header"> <h2>Fe increases CO<sub>2</sub> gradient</h2> </div> <div data-bbox="362 212 636 237" data-label="Text"> <p>Watson <i>et al.</i> (2000): SOIREE</p> </div> <div data-bbox="220 228 498 531" data-label="Figure"> </div> <div data-bbox="490 256 587 304" data-label="Text"> <p>Warming, 0.3° C</p> </div> <div data-bbox="524 348 703 378" data-label="Text"> <p>But, little export!</p> </div> <div data-bbox="519 373 742 533" data-label="Figure"> </div> <div data-bbox="737 512 769 537" data-label="Text"> <p>30</p> </div>	<div data-bbox="818 130 1312 168" data-label="Section-Header"> <h2>Slide 89 Fe increases CO2 gradient</h2> </div> <div data-bbox="818 254 940 287" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="337 653 680 690" data-label="Section-Header"> <h2>SOIREE: major results</h2> </div> <div data-bbox="315 697 719 724" data-label="Text"> <p>Confirms the 'ecumenical' iron hypothesis</p> </div> <div data-bbox="235 722 755 1014" data-label="List-Group"> <ul style="list-style-type: none"> <li>• Increase in photosynthetic parameters by day II, measured by variable fluorescence</li> <li>• Increase in large chain-forming diatoms by day 5: 30-50 µm cell size</li> <li>• Microzooplankton abundance quadrupled             <ul style="list-style-type: none"> <li>➢ Grazing only on small phytoplankton cells (&lt; 20 µm cells)</li> </ul> </li> <li>• <b>No evidence of macrozooplankton response</b> <ul style="list-style-type: none"> <li>➢ <b>No increased carbon export to sediment traps</b></li> </ul> </li> <li>• Partial pressure of CO<sub>2</sub> decreased in surface ocean; this gradient would increase the atmosphere to ocean flux of CO<sub>2</sub></li> </ul> </div>	<div data-bbox="818 619 1271 657" data-label="Section-Header"> <h2>Slide 90 SOIREE: major results</h2> </div> <div data-bbox="818 741 940 774" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="430 1142 553 1176" data-label="Section-Header"> <h2>SOIREE</h2> </div> <div data-bbox="308 1188 706 1215" data-label="Text"> <p>Abraham <i>et al.</i> 2000. Importance of stirring</p> </div> <div data-bbox="238 1236 529 1432" data-label="List-Group"> <ul style="list-style-type: none"> <li>• 150-km long bloom 6 weeks after the Fe fertilization experiment</li> <li>• 23 March 1999             <ul style="list-style-type: none"> <li>➢ 3 mg Chl <i>a</i> m<sup>-3</sup></li> <li>➢ In an area where SeaWiFS indicates the mean Chl <i>a</i> was 0.2 ± 0.06 mg Chl <i>a</i> m<sup>-3</sup> (15X increase)</li> </ul> </li> <li>• Stirring plays a key role             <ul style="list-style-type: none"> <li>➢ Fit growth rates of µ=0.19 d<sup>-1</sup></li> <li>➢ Loss due to horizontal diffusion=0.07 d<sup>-1</sup></li> <li>➢ Loss due to grazing = 0.01 d<sup>-1</sup></li> <li>➢ Loss due to sinking = 0.02 d<sup>-1</sup></li> </ul> </li> <li>• Accumulation of 600-3000 t of algal C</li> </ul> </div> <div data-bbox="550 1211 732 1520" data-label="Figure"> </div>	<div data-bbox="818 1108 1071 1144" data-label="Section-Header"> <h2>Slide 91 SOIREE</h2> </div> <div data-bbox="818 1230 940 1264" data-label="Text"> <p>NOTES:</p> </div>

### 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

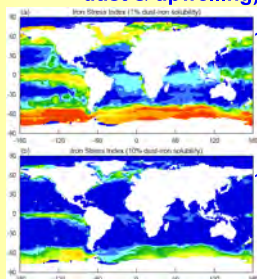
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### Slide 92 C:N:P:Fe Redfield ratios

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 93 Iron stress in the oceans

NOTES:

### Controls on tropical Pacific Ocean productivity revealed through nutrient stress diagnostics

Michael J. Behrenfeld<sup>1</sup>, Kirby Wirtzberg<sup>1,2</sup>, Robert M. Sherrell<sup>3</sup>, Francisco P. Chavez<sup>4</sup>, Peter Strickland<sup>5</sup>, Michael A. Brzezinski<sup>6</sup>, & Francisco A. J. Armbrust<sup>1</sup>

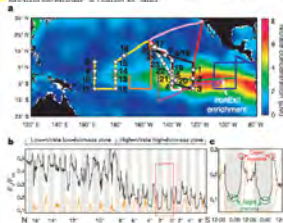
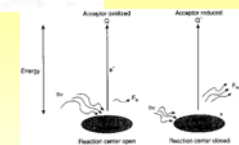


Figure 1 | The tropical Pacific study area. a, Ship tracks (lines) and



Photosynthetic competency  
 $= F_v = (F_m - F_0) / F_m$

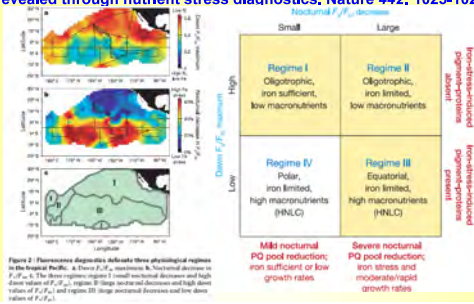
Nature 442: 1025-1028. August 2006 EEOS630

### Slide 94 The ecumenical Fe hypothesis

NOTES:

## Iron-limitation zones

Behrenfeld, M. J. et al. 2006. Controls on tropical ocean productivity revealed through nutrient stress diagnostics. *Nature* **442**: 1025-1028.



## Slide 95 Iron-limitation zones

NOTES:

## Does Fe limit production in the Southern California Bight?

Bruland et al. (2001) *Limnol. Oceanogr*

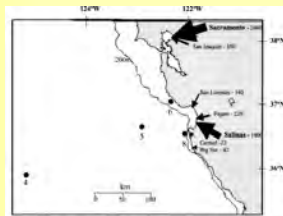


Fig. 1. Map of the Southern California Bight showing the location of the study area. The size of the basin depicts the relative amount of annual average suspended sediment discharge by the major rivers as reported by Gregory and Banta (1980). The average specific value of suspended sediment discharge (in thousand metric tons per year) is reported next to the river name. Size of dots and labels indicates (a) 1, 2, 3, 4, and 5 of the study area profile area outlined in Fig. 1(b).

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## Slide 96 Does Fe limit production in the Southern California Bight?

NOTES: