Light effects on photosynthesis, Model P vs. I approach for estimating production & Subsurface Chlorophyll maxima

Class 18, 10/30/08

EEOS630

Slide 1 Light effects on photosynthesis, Model P vs. I approach for estimating production & Subsurface Chlorophyll maxima

NOTES:

Wimba Sessions

Tonight, Thursday 10/30, 7 pm – only if I can get files posted - Will know by 3 pm.

- Quantitative community analysis using Matlab
  - I've had to do rewriting of my Matlab m.files.
  - Run the tutorial at the Mathworks site
  - I'll be logged on at 7 pm tonight to demonstrate community analysis using the West Falmouth oilspill data as an example using Matlab
  - I'll also present the solution to the *Synnechococcus* problem
- Due date: papers due 4 weeks after projects posted.

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Slide 2 Wimba Sessions

NOTES:

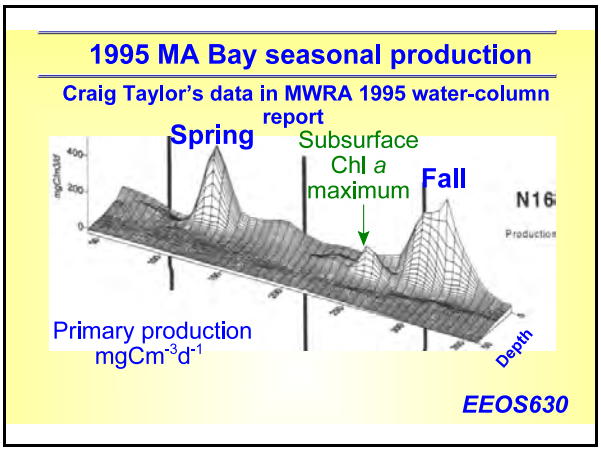
Phytoplankton Readings

Nutrients and the spring bloom

- Nutrient effects, Tuesday
  - Chapter 10: Nitrogen cycle, nutrient limitation & chemostats
  - Howarth, R. W. 1988. Nutrient limitation of net primary production in marine ecosystems. Ann. Rev. Ecol. Syst. *19*: 89-110.
- Spring bloom, Thursday
  - Chapter 11: Sverdrup's critical depth concept & the vernal phytoplalnkton
  - Sverdrup, H. U. 1953. On conditions for the vernal blooming of phytoplankton. J. Conseil perm. int. Explor. Mer. *18*: 287-295.
  - Parsons, T. R., M. Takahashi, and B. Hargrave. 1984. Biological Oceanographic Processes. 3rd Edition. Pergamon Press, Oxford & New York. Pages 87-100.
  - Townsend, D. W. and R. W. Spinrad. 1986. Early phytoplankton blooms in the Gulf of Maine. Cont. Shelf Res. *6*: 515-529.

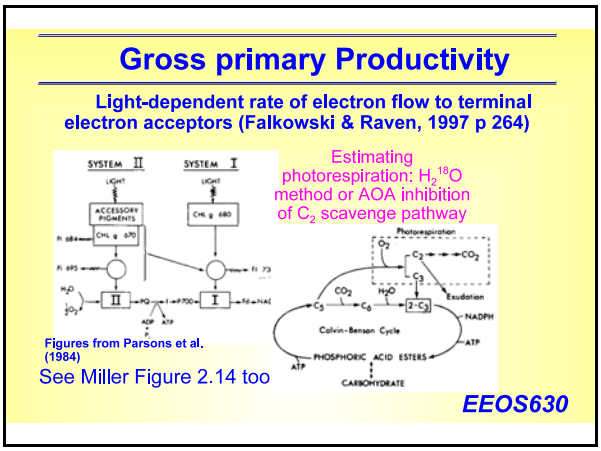
Slide 3 Phytoplankton Readings

NOTES:



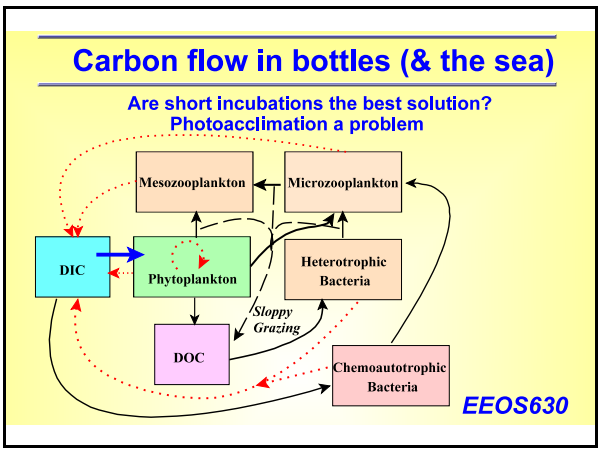
Slide 4 1995 MA Bay seasonal production

NOTES:



Slide 5 Gross primary Productivity

NOTES:



Slide 6 Carbon flow in bottles (& the sea)

NOTES:

The oxygen method

Separating Gross vs. Net production.

- Use light and dark bottles
- Dark bottle measures respiration (but not photorespiration)
  - Photorespiration may not be too important
  - In the absence of grazers, light bottle measures net production.
  - In the absence of grazers, light-Dark measures gross production.
- Photorespiration and heterotrophs create large problems

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Slide 7 The oxygen method

NOTES:

O_2 *vs.* ^{14}C

$$n\,CO_2 \xrightarrow{light} \underset{1}{\text{Particulate organic C}} + \underset{2}{\text{Dissolved organic C}} + n\,\underset{3}{O_2}$$

O_2 method measures O_2 production, = measuring 1 + 2.
^{14}C method measures only 1 if only filtered POC is counted.

- In theory, the O_2 method can estimate gross and net production
  - Increase in light bottle is net
  - Dark bottle decrease is respiration
  - Light-dark = gross production
- The ^{14}C activity of dissolved organic matter should be determined

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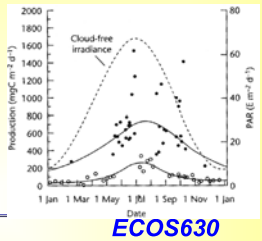
Slide 8 O2 vs. 14C

NOTES:

Primary production underestimated

Miller (2004) Fig. 3.4, Welschmeyer *et al.* 1993

- **Open circles: data collected before 1980**
- **Filled circles 1980-1984, Trace-metal clean conditions**
- **2-fold difference**
- **There may have also been interannual variability: the Pacific interdecadal oscillation (first discovered after Welschmeyer's 1993 paper)**



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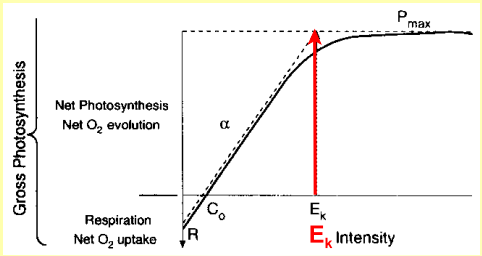
Slide 9 Primary production underestimated

NOTES:

Falkowski & Raven P vs. E curves

Falkowski & Raven (1997, p. 196, Fig 7.2)



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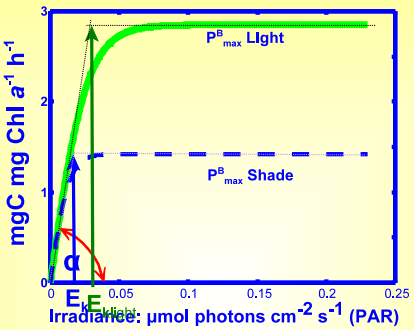
Slide 10 Falkowski & Raven P vs. E curves

NOTES:

Chl *a*-specific gross productivity



Slide 11

NOTES:

PAR & units of light intensity

- Parsons, Takahashi & Hargrave (1984)
  - Parsons_1984.pdf on ereserve
    - the direct link the ECOS630 reserves is: http://docutek.lib.umb.edu/eres/coursepass.aspx?cid=65
    - Password: deep
- Photosynthetically available radiation [PAR] The quantity of light in those wavelengths that can be utilized for photosynthesis (400 to 700 nm Behrenfeld & Falkowski (1997), some earlier papers listed PAR from 300 to 720 nm);
  - Falkowski & Raven (2007, 341), PAR was defined as 350 to 720, but it is difficult to construct detectors to measure photon flux at 340-400 nm, so now it is 400 to 700)
- To convert to energy, 550nm light assumed

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Slide 12 PAR & units of light intensity

NOTES:

Converting units of light intensity

Flux of photons or energy

- Flux of photons
  - Ein=mol photon of PAR (μEin $cm^{-2}s^{-1}$)
    - PSR<PUR<PAR (Photosynthetically active radiation or Photo. available radiation: wavelengths from 400 to 700 nm
    - Ein=6.02 * 10^{23} quanta = 2.86 x 10^{8}/Angstroms g cal where Angstrom= 10^{-10} m
- Energy
  - 1 g cal =4.185 x 10^{7} ergs=4.185 watt*sec
  - 1 g cal/cm^{2} =1 langley
  - 1 Joule [mks unit of work] = 10^{3} g 10^{4}cm s^{-2} =10^{7} erg
- Conversion, assuming 550 nm light
  - 1 Ein=(2.86 x 10^{8}/5500)g cal=52 x 10^{3} g cal
    - note that Harrison and Platt use watts/m^{2}
    - Gieskes & Kraay (1975) use J $m^{-2}s^{-1}$

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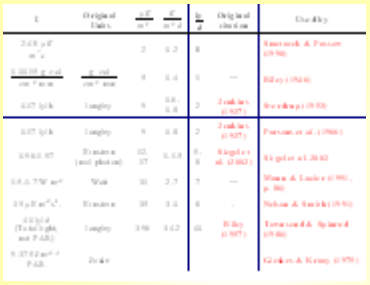
Slide 13 Converting units of light intensity

NOTES:

I_c, Compensation light intensity

40X range, full citations in Table 2 in Chapter 11, p. 15



Phytoplankton respiration only

With other loss terms

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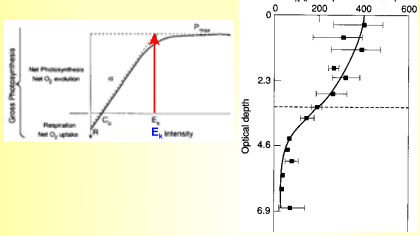
Slide 14 Ic, Compensation light intensity

NOTES:

Photoacclimation: to light intensity & light quality

Falkowski & Raven Fig. 9.8;
Light intensity: $I_z=I_o$ *exp(- K_d *z); ξ=K_dz=optical depth



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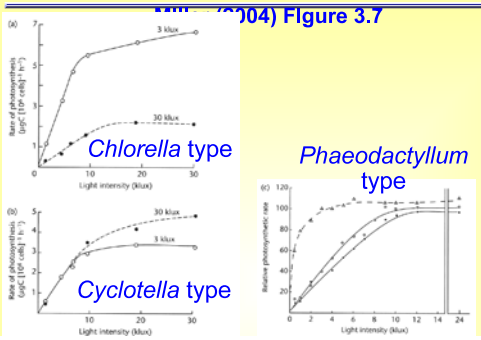
Slide 15 Photoacclimation: to light intensity & light quality

NOTES:

Types of shade acclimation

004) Figure 3.7



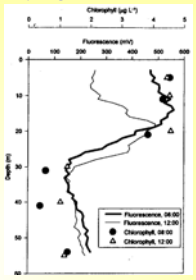
Slide 16 Types of shade acclimation

NOTES:

Measuring the Chl *a* profile

Falkowski & Raven (1997) Figure 9.6

- **Fluorescence yield reduced by:**
  - Photochemical quenching: can occur with a diel cycle
  - Shade acclimation & increase in PSII activity
  - Increase in the physiological status of the cells
- **Fluorescence yield Increased by:**
  - Reduction in PSII activity
  - Toxic effects (used to estimate Cu contamination)
  - Nutrient stress
  - Senescence



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Slide 17 Measuring the Chl a profile

NOTES:

Shade acclimation (adaptation)

Phytoplankton can adapt to both the intensity and quality of light by:

- Changes in the ratios of photosynthetic pigments
- Changes in the size and number of photosynthetic units (measured by the Chl *a*:P700 size, Perry *et al.* 1981)
- Changes in chloroplast size & orientation
- Changes in the enzyme activities of both the light and dark reactions

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Slide 18 Shade acclimation (adaptation)

NOTES:

Quenching

Refers to both scintillation counting and fluorescence yield; Falkowski & Raven (2007)

Quenching and quantum yield for fluorescence

$$\Phi_{f'} = \frac{k_{f'}}{(k_{f'}+k_d+k_p)}, \text{ where}$$

$\Phi_{f'}$ = ratio of light emitted as fluorescence to light absorbed.
$k_{f'}$ = de-excitation of singlet to fluorescence
k_d = heat.
k_p = photochemistry.

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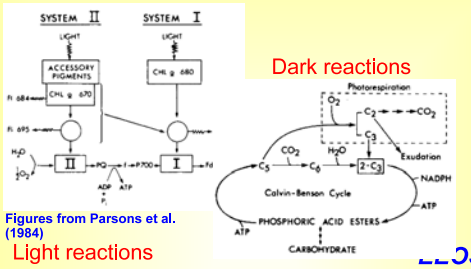
Slide 19 Quenching

NOTES:

Gross primary productivity

Light-dependent rate of electron flow to terminal electron acceptors (Falkowski & Raven, 1997 p 264)



Figures from Parsons et al. (1984)

Light reactions

Dark reactions

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Slide 20 Gross primary productivity

NOTES:

Jassby & Platt's (1976) Equation

Without photoninhibition

$$P^{B} = P^{B}_{m} \tanh\left(\frac{\alpha^{B} I}{P^{B}_{m}}\right)$$

where, P^{B} = Chla-specific production $\left[\frac{mgC}{mgChla\ h}\right]$.

P^{B}_{m} = Max. rate at light saturation.
= Assimilation number
= the maximum photosynthetic rate at light saturation.

α^{B} = initial slope of the P vs. I curve.

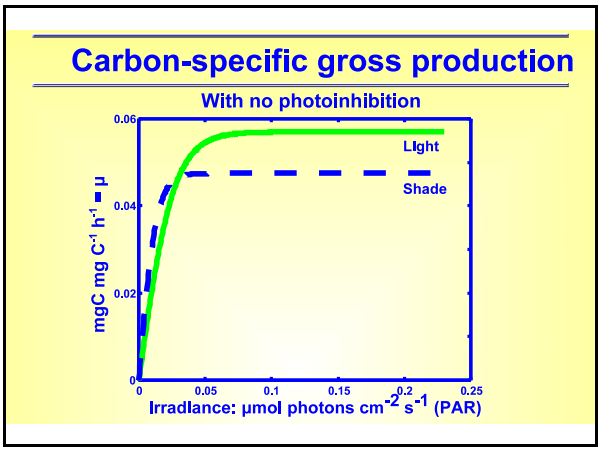
$$= \left[\frac{mgC}{mgChla\ h\ (W\ m^{-2})}\right] \text{ or}$$

$$= \left[\frac{mgC}{mgChla\ h\ (E\ m^{-2}\ h^{-1})}\right]$$

I = the light intensity of PAR. [Watts m^{-2}], or [Einsteins $m^{-2}\ h^{-1}$].

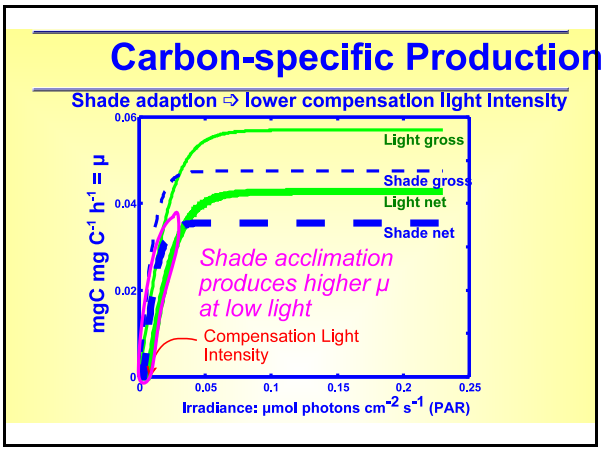
Slide 21 Jassby & Platt's (1976) Equation

NOTES:



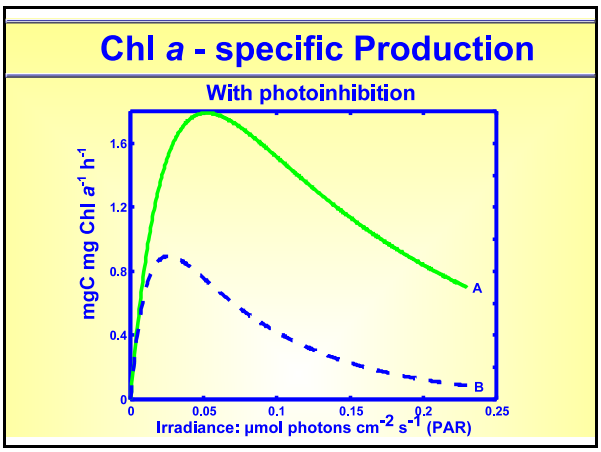
Slide 22 Carbon-specific gross production

NOTES:



Slide 23 Carbon-specific Production

NOTES:



Slide 24 Chl a - specific Production

NOTES:

Photoinhibition Equation

Jassby & Platt (1976)

$$P^B = P_s^B \left(1 - e^{\left(\frac{-\alpha I}{P_s^B}\right)}\right) e^{\frac{-\beta I}{P_s^B}}$$

α = Initial slope of P vs. I curve.
β = Photoinhibition parameter.
= Negative slope at high light intensity.
P_s^B = Max. photo. rate without photoinhibition.

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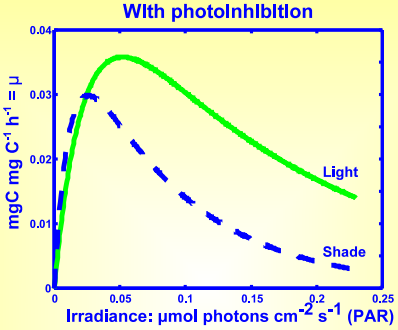
Slide 25 Photoinhibition Equation

NOTES:

Carbon-specific gross production

With photoinhibition



Slide 26 Carbon-specific gross production

NOTES:

Vertical profiles of photosynthesis

Miller (2004) Fig. 3.9, May (●) & Sept (○)

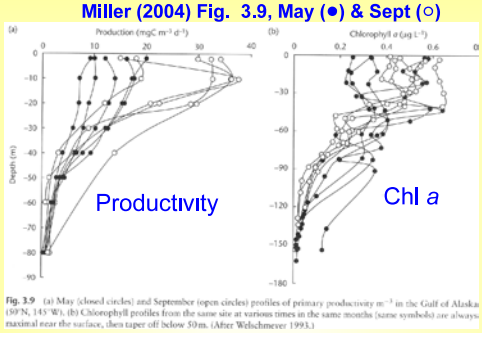
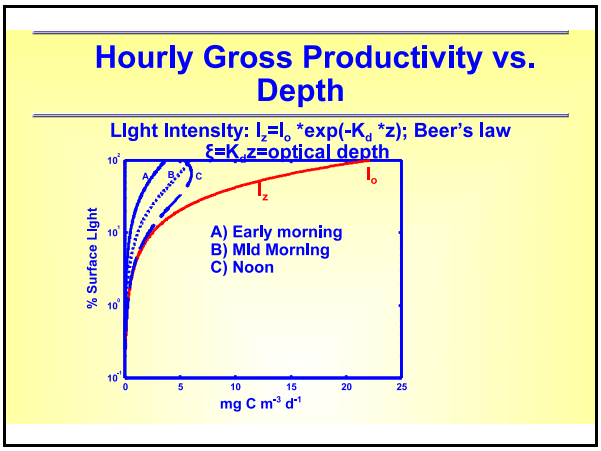


Fig. 3.9 (a) May (closed circles) and September (open circles) profiles of primary productivity m⁻³ in the Gulf of Alaska (50°N, 145°W). (b) Chlorophyll profiles from the same site at various times in the same months (same symbols) are always maximal near the surface, then taper off below 50 m. (After Welschmeyer 1993.)

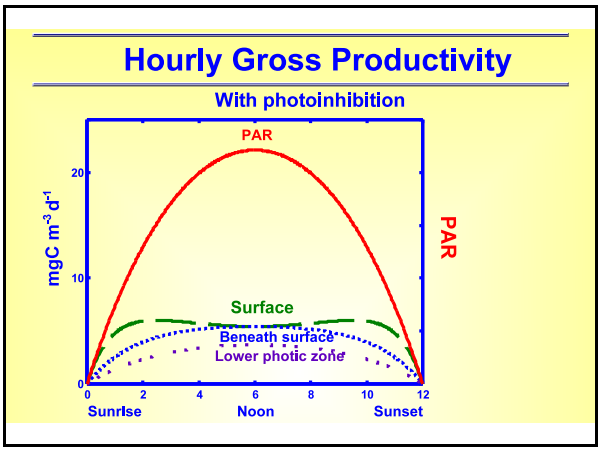
Slide 27 Vertical profiles of photosynthesis

NOTES:



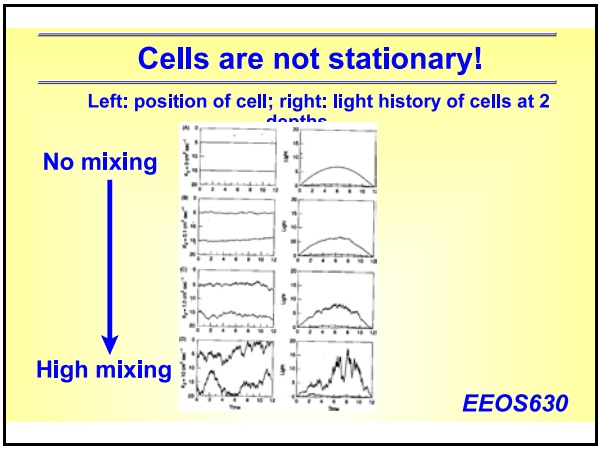
Slide 28 Hourly Gross Productivity vs. Depth

NOTES:



Slide 29 Hourly Gross Productivity

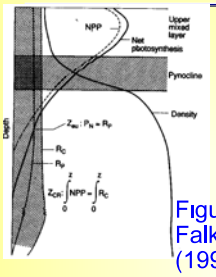
NOTES:



Slide 30 Cells are not stationary!

NOTES:

Euphotic zone (≈1% light depth), mixed layer depth, and critical depth



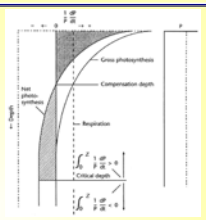


Figure from Falkowski & Raven (1997, 2007)

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Slide 31 Euphotic zone (≈1% light depth), mixed layer depth, and critical depth

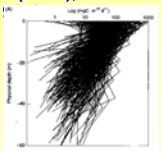
NOTES:

Non-dimensional production

Behrenfeld & Falkowski (1997), Falkowski & Raven (1

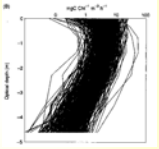
Production vs. Depth

Meters



Chl-specific P vs. Depth

Optical depth



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Slide 32 Non-dimensional production

NOTES:

The model P vs I approach vs. SIS

Harrison et al. (1985)

- Light & Chl a profiles determined
- SIS
  - 30-L Niskin bottles from 100, 50, 25, 10, and 1% light depths
  - **24 h** 200-ml incubations on board deck
  - natural sunlight & neutral density filters
  - Trapezoidal integration over depth interval
- Model P vs. I approach
  - Water collected at 50% and 1% Light depths
  - 30-50 100-ml incubations
  - Artificial light
  - Time-zero or dark-bottle blanks

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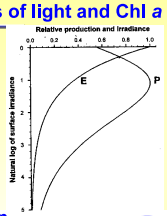
Slide 33 The model P vs I approach vs. SIS

NOTES:

Model estimates of production

Requires profiles of light and Chl *a*

- Profile light over a 24-h day and chl a
- Estimate α and AN at the 1% and 50% light depth only using 30-50 P vs. I incubations
- Calculate hourly production using Chl *a*, I, P^B and α
- Sum 24-h est mates to obta n daily product on
- Compare with SIS prof les



$$P(t) = P^B(I(t)) \cdot B.$$

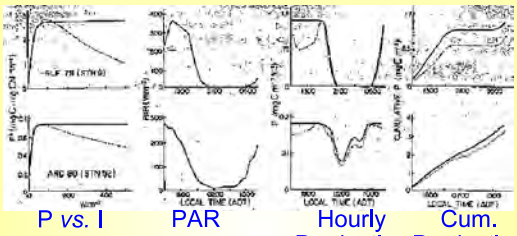
$$P_* = \sum_{t=1}^{24} P(t).$$

Slide 34 Model estimates of production

NOTES:

Model P vs. I approach

Fig 1 (dotted=photoinhibition) Harrison *et al.* (1985)



P *vs.* I | PAR | Hourly Production | Cum. Production

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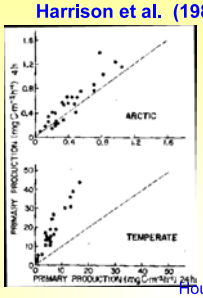
Slide 35 Model P vs. I approach

NOTES:

4- *vs.* 24-h incubations

Harrison et al. (1985) Figure 2



Hourly production (4-h)

Nighttime productivity, midnight sun

Hourly production (24-h)

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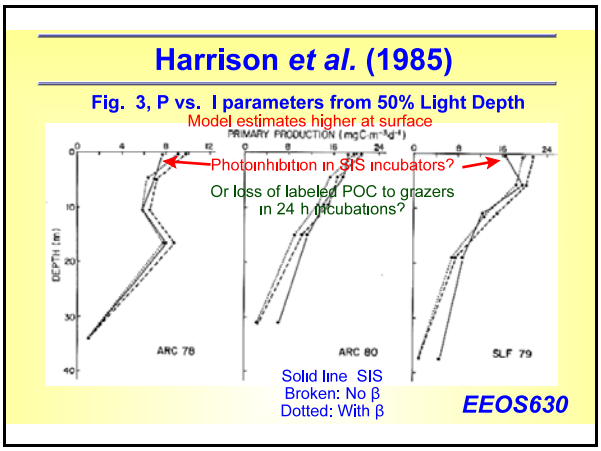
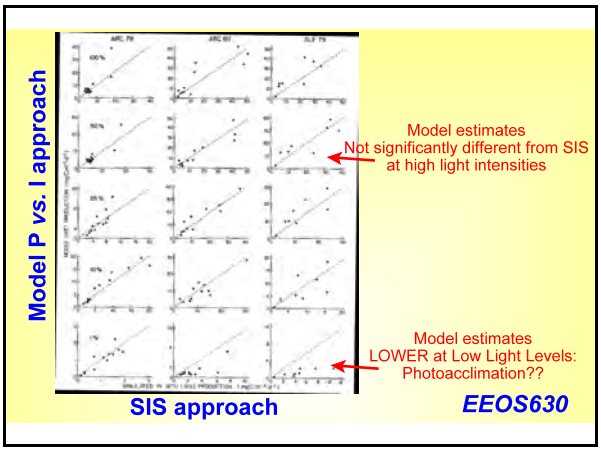
Slide 36 4- vs. 24-h incubations

NOTES:



Slide 37 Harrison et al. (1985)

NOTES:



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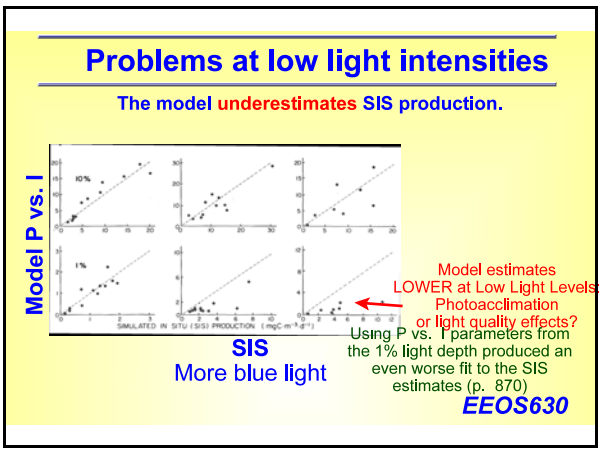
NOTES:



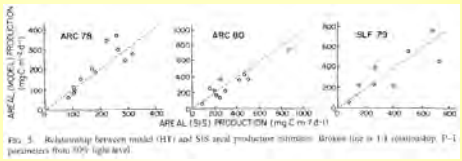
Slide 39 Problems at low light intensities

NOTES:

Areal production accurate

Harrison et al. (1985) Fig. 5

Model P vs. I



SIS

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Slide 40 Areal production accurate

NOTES:

P vs. I parameters indicate shade adaptation/stratification

50% Light depth chosen for P *vs.* I parameters

TABLE 3. Depth differences in P–I model parameters (units given in text). *Depth difference significant at the 95% confidence level; **significant at the 99% confidence level.

Cruise	No. of observations	Light depth (%)	P–I parameters: $\bar{x}$ (±SE) P_s	P_m	α	β
ARC 78	12	50	1.50 (0.16)	1.42 (0.15)**	0.052 (0.003)**	0.0005 (0.0001)**
	12	1	1.34 (0.18)	0.84 (0.12)	0.039 (0.005)	0.0056 (0.0010)
ARC 80	8	50	1.20 (0.28)	1.07 (0.24)*	0.054 (0.010)*	0.0012 (0.0004)
	8	1	0.88 (0.11)	0.76 (0.10)	0.047 (0.008)	0.0046 (0.0004)
SLF 79	8	50	3.46 (0.49)	2.80 (0.31)**	0.056 (0.008)	0.0035 (0.0014)*
	8	1	3.25 (0.56)	1.91 (0.34)	0.044 (0.007)	0.0063 (0.0023)

Shade acclimation

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Slide 41 P vs. I parameters indicate shade adaptation/stratification

NOTES:

Applications

- Application to MA Bay monitoring
  - Measuring Chl *a*
  - Measuring production
    - O_2
    - Model approach introduced by Craig Taylor
    - Incubation method
  - Problems with the model approach
    - Assimilation numbers too high
    - Subsurface chlorophyll maximum can be a productivity maximum in MA Bay
      - Which P vs. I parameters should be used?

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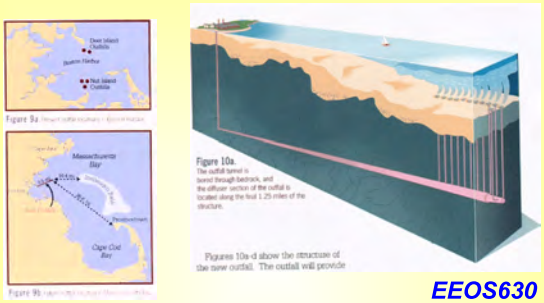
Slide 42 Applications

NOTES:

The MA Bay Outfall

From MWRA State of the Harbor Report



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Slide 43 The MA Bay Outfall

NOTES:

Realistic P vs. I parameters

Many published assimilation numbers and α's are too high

- There **are** theoretical limits for α and A.N.
  - Maximum α 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^{-1}

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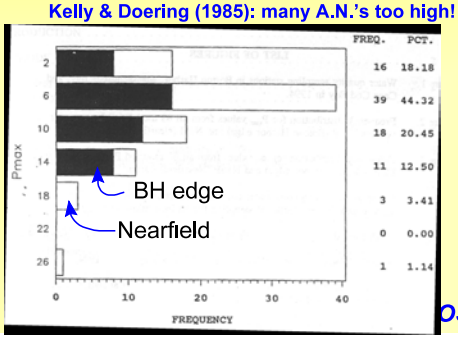
Slide 44 Realistic P vs. I parameters

NOTES:

MA Bay P vs. I parameters

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



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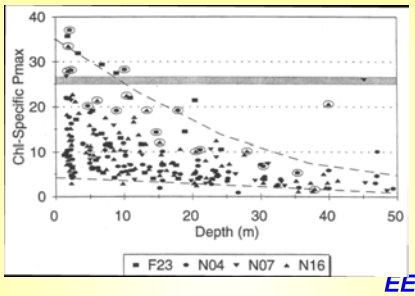
Slide 45 MA Bay P vs. I parameters

NOTES:

MA Bay assimilation numbers

Including Falkowski's theoretical maximum= 25



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Slide 46 MA Bay assimilation numbers

NOTES:

Why might assimilation numbers be too high?

- Theoretical maximum assimilation numbers are 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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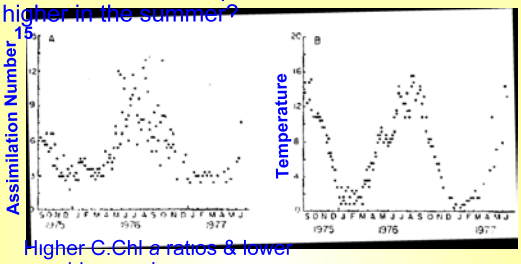
Slide 47 Why might assimilation numbers be too high?

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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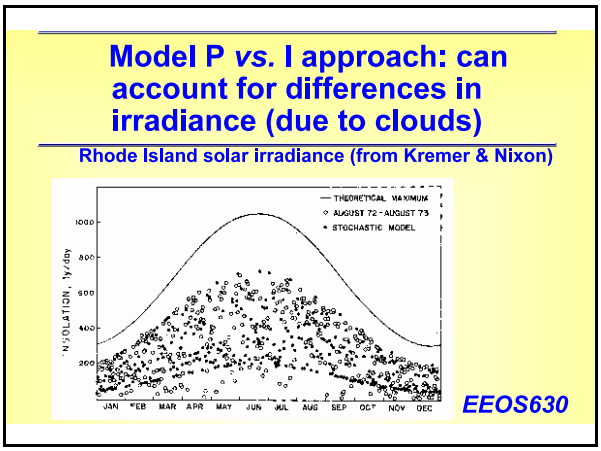
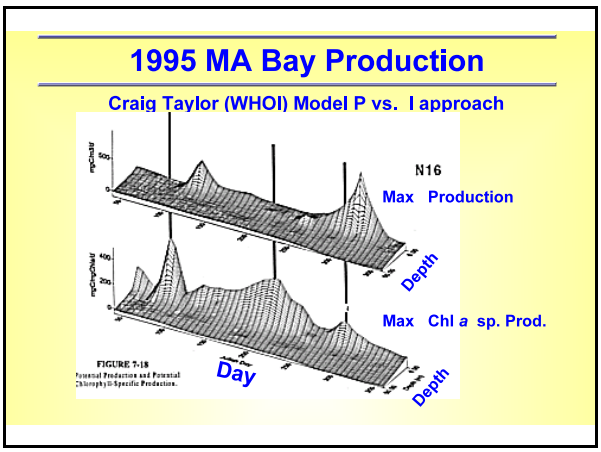
Slide 48 Seasonal variation in A.N.

NOTES:



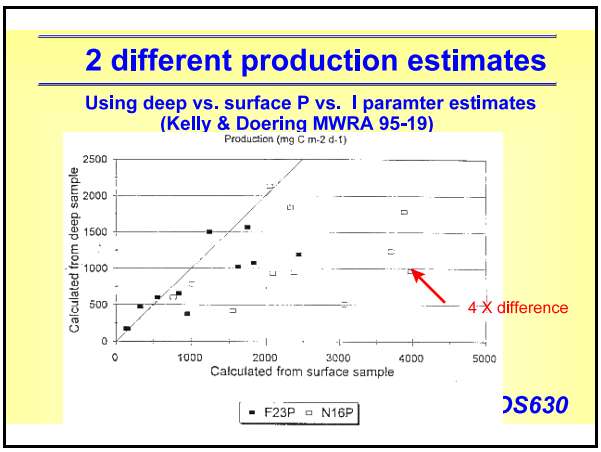
Slide 49 Model P vs. I approach: can account for differences in irradiance (due to clouds)

NOTES:



Slide 50 1995 MA Bay Production

NOTES:



Slide 51 2 different production estimates

NOTES:

Excursis on the Subsurface Chlorophyll maxima

Prevalent in Gulf of Maine (and MA Bay) from April through early September, many coastal zones (including the Washington-Oregon-California shelf) & oligotrophic gyres (called the Typical Tropical Structure)

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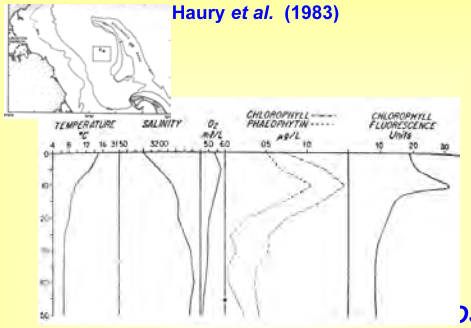
Slide 52 Excursis on the Subsurface Chlorophyll maxima

NOTES:

MA Bay subsurface Chl *a* maxima

Haury *et al.* (1983)



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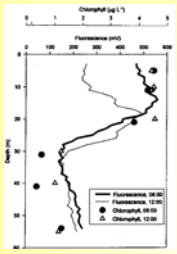
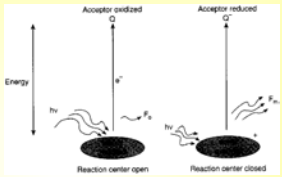
Slide 53 MA Bay subsurface Chl a maxima

NOTES:

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

Falkowski & Raven Figure 9.6





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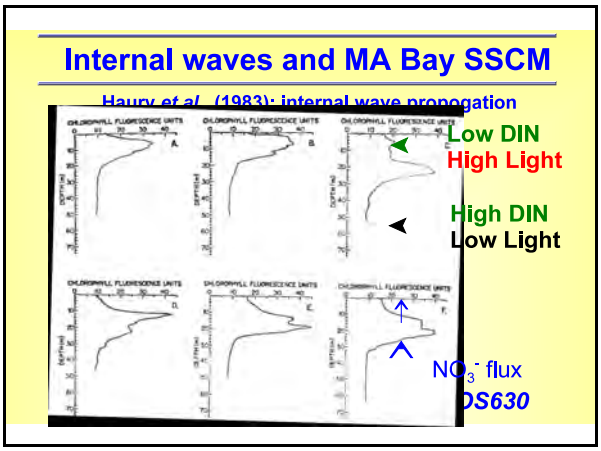
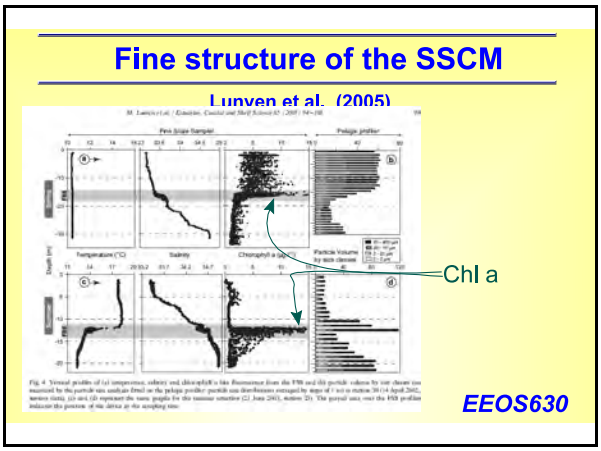
Slide 54 As noted by Cullen, SSFluoresence not necessarily a SSChl max nor SSCarbon max

NOTES:



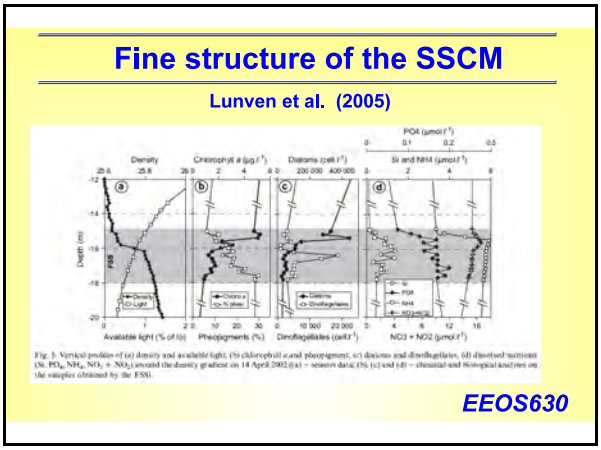
Slide 55 Internal waves and MA Bay SSCM

NOTES:



Slide 56 Fine structure of the SSCM

NOTES:

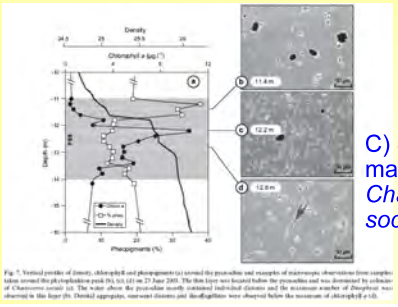


Slide 57 Fine structure of the SSCM

NOTES:

Fine structure of the SSCM

Lunven et al. (2005)



C) Sinking mats of *Chaetoceros socialis*

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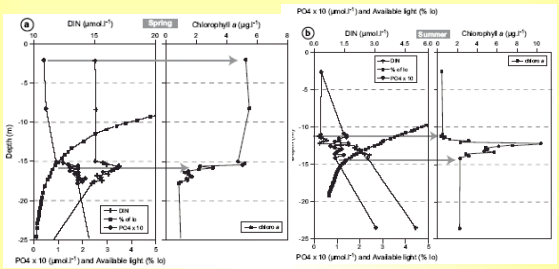
Slide 58 Fine structure of the SSCM

NOTES:

Fine structure of the SSCM

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



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Slide 59 Fine structure of the SSCM

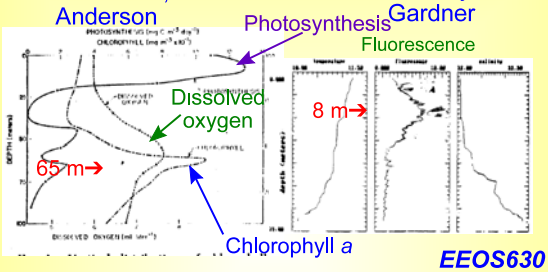
NOTES:

SSCM off the Washington-Oregon Coast, also off California

West coast *vs.* MA Bay

WA Coast, Anderson

MA Bay, Gardner



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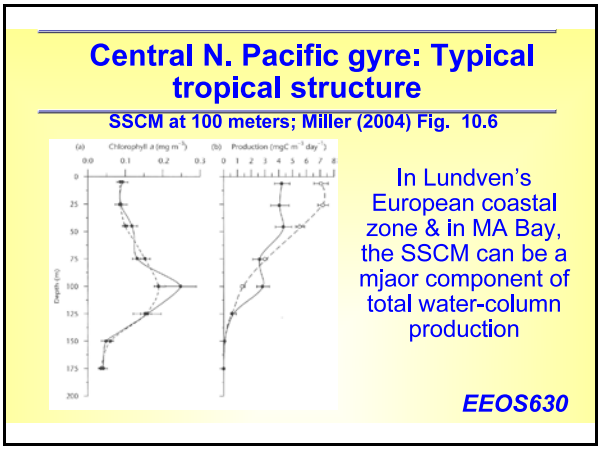
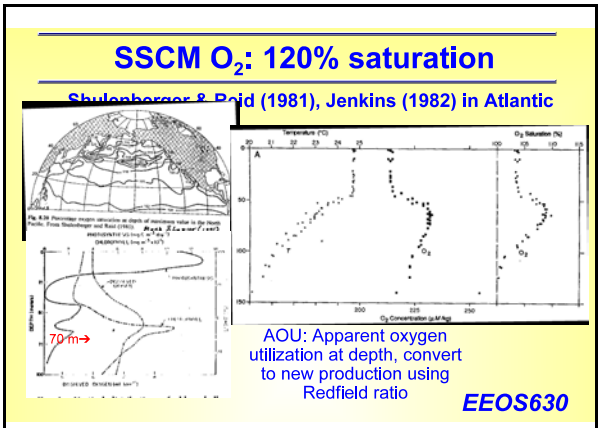
Slide 60 SSCM off the Washington-Oregon Coast, also off California

NOTES:



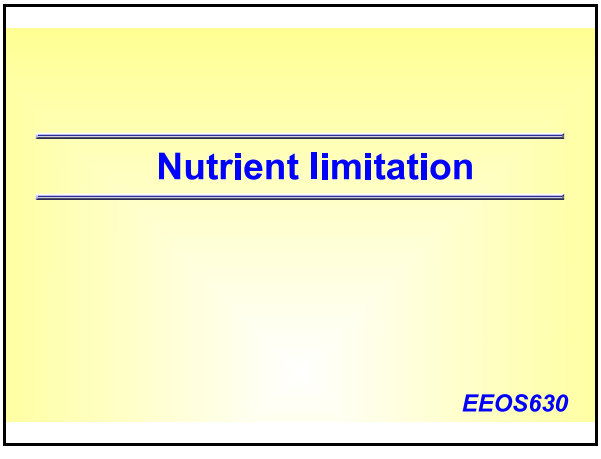
Slide 61 Central N. Pacific gyre: Typical tropical structure

NOTES:



Slide 62 SSCM O2: 120% saturation

NOTES:



Slide 63 Nutrient limitation

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 μ
- 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 64 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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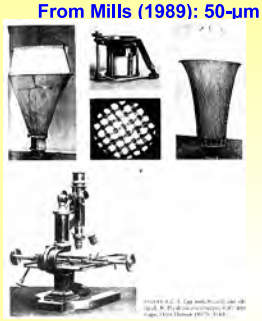
Slide 65 Terms & concepts

NOTES:

Hensen's Nets & major cruise

From Mills (1989): 50-μm nets, 1889 National cruise



Slide 66 Hensen's Nets & major cruise

NOTES:

Hensen's "Blood of the Ocean"

Uniformly distributed phytoplankton!

- The German Hensen introduced quantitative Plankton sampling to oceanography (1840s-1880s)
  - Hensen introduced quantitative plankton sampling (50-µm silk mesh)
  - Phytoplankton are uniformly distributed
- Conclusions from 1889 National Cruise
  - Within a biogeographic province, phytoplankton are uniformly distributed in the ocean, like oxygen and other chemical constituents
  - The oceans were in general very poor in plankton standing stocks, especially the tropics.

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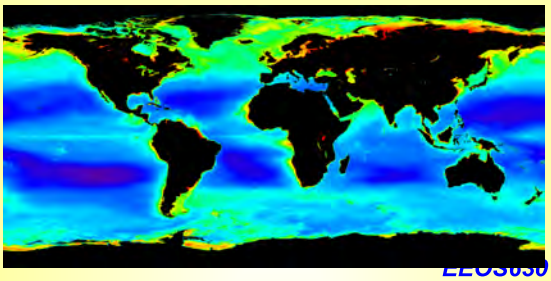
Slide 67 Hensen's "Blood of the Ocean"

NOTES:

SeaWiFS Average Chl *a*

Oct 1997 -April 2002

http://seawifs.gsfc.nasa.gov/SEAWIFS/IMAGES/SEAWIFS_GALLERY.html



Slide 68 SeaWiFS Average Chl a

NOTES:

Brandt's denitrification hypothesis

Proposed in 1899

- Nitrogen is the Liebigian (1876) limiting nutrient in the ocean
  - Liebig proposed 50 agricultural laws, the law of the minimum was #33 (de Baar 1994)
  - The law was proposed for monospecific crops
- Why (according to Brandt, 1899)?
  - Land is the major source of nitrogen to the sea
  - Denitrifying bacteria have higher activities at higher temperatures
  - Nitrogen should be scarcer in warmer waters
  - Phytoplankton production should be less in tropical waters.

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Slide 69 Brandt's denitrification hypothesis

NOTES:

The refutation of Brandt

Mixing & methodological problems

- Brandt assumed a terrestrial source for N. Terrestrial sources are not the major source of Nitrogen fueling coastal production
  - the Norwegians proposed vertical mixing from deep, N-rich water
  - More vertical mixing in coastal waters, less in the tropics
- Methodological problems:
  - DIN could not be measured (until the 20s & 30s)
  - Denitrifying activity not measured until the 70s (Seitzenger)
  - Nitrifying bacterial activity not measured accurately until the 80's (Olson, Ward)

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Slide 70 The refutation of Brandt

NOTES:

Brandt abandons his hypothesis

In 1929, opts for vertical mixing (Mills 1989, p. 161)

"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 **"that denitrifying bacteria break down an excess of nitrogen compounds and that it is they that maintain the existing equilibrium in nature."**

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Slide 71 Brandt abandons his hypothesis

NOTES:

Brandt's strengths & weaknesses

- Brandt was correct, but before his time in emphasizing:
  - Liebig's law of the minimum.
    - This has been tested experimentally, and it is usually only 1 nutrient, a rate-limiting nutrient that controls primary production
    - Multiple nutrient limitation not a major factor
  - Denitrification
    - Largely responsible for low N:P in marine waters
    - Phosphorus may be a limiting nutrient over geologic time scales & during glacial periods (Fe & N fixation)
- Major flaws
  - Overestimated terrestrial input of nitrogen
  - Ignorance of vertical mixing
  - Overemphasis of temperature effects

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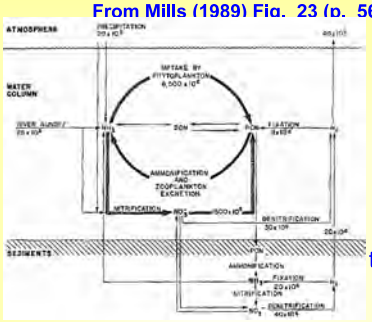
Slide 72 Brandt's strengths & weaknesses

NOTES:

The Nitrogen cycle

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



Fluxes in metric tons per year

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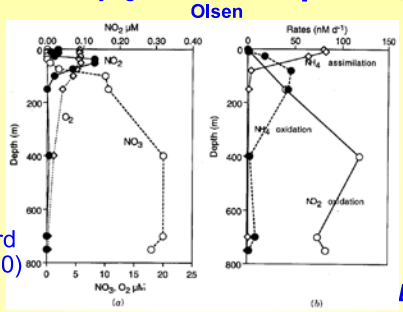
Slide 73 The Nitrogen cycle

NOTES:

Subsurface NO_2^- maximum

Produced by light inhibition of NO_2^- oxidizers; Ward & Olsen



Ward (2000)

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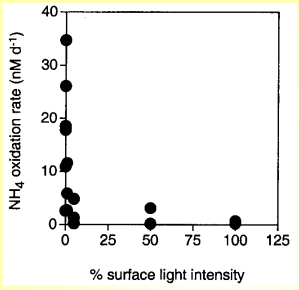
Slide 74 Subsurface NO2- maximum

NOTES:

Light inhibition of NH_4^+ oxidation

Ward (2000), NO_2^- oxidizers more inhibited than NH_4^+ oxidizers



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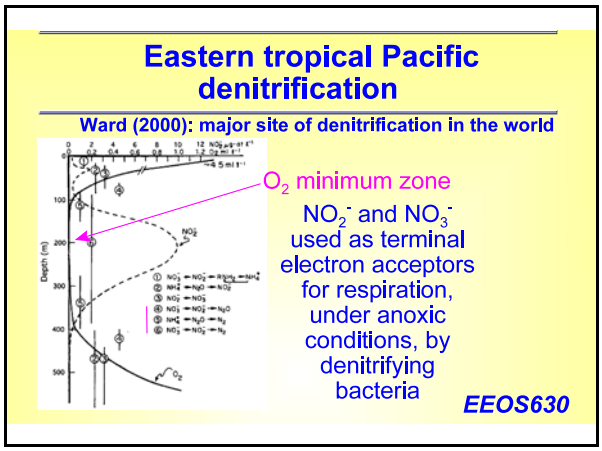
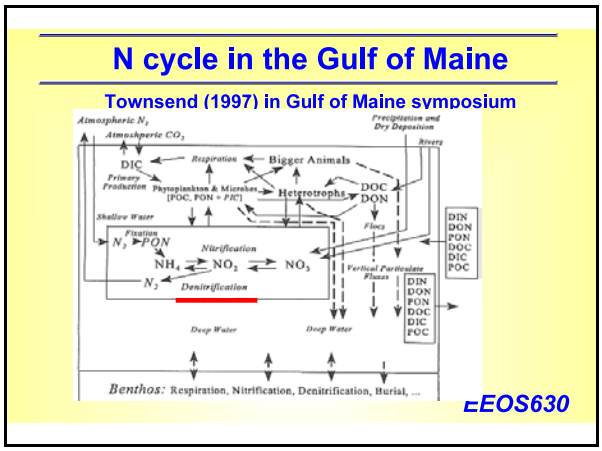
Slide 75 Light inhibition of NH4+ oxidation

NOTES:



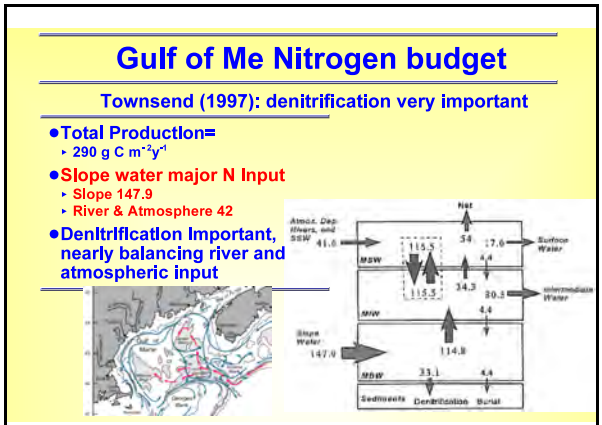
Slide 76 Eastern tropical Pacific denitrification

NOTES:



Slide 77 N cycle in the Gulf of Maine

NOTES:



Slide 78 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

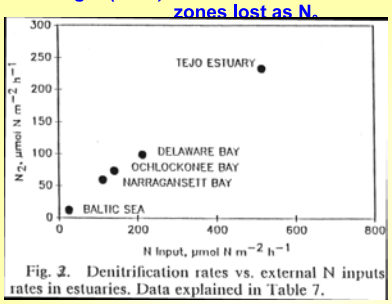


Fig. 3. Denitrification rates vs. external N inputs rates in estuaries. Data explained in Table 7.

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Slide 79 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, units: μmol N m⁻² h⁻¹.

Location	N input	N input removed by denitrification (%)	Notes*	Time interval
Lakes				
ELA 227†	3,200	1.4	1	Annual
Eviod sø†	1,327	7	2	Annual
Bryrup Langsø†	690	25	2	Annual
Arreso	81	14	3	Annual
Okeechobee	46	9–23	4	Annual
Meadotal	45	36	5	Annual
Rivers				
Potomac	632	35	6	Fall
Delaware	1,452	20	7	Summer
Estuaries				
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	35	40	12	Annual
Baltic Sea	35	55	13	Annual
Four League Bay‡		20	14	Annual

0

Slide 80 About 40-50% of N load lost as N2

NOTES:

Denitrification in Boston Harbor sediments: *Ampelisca* mats

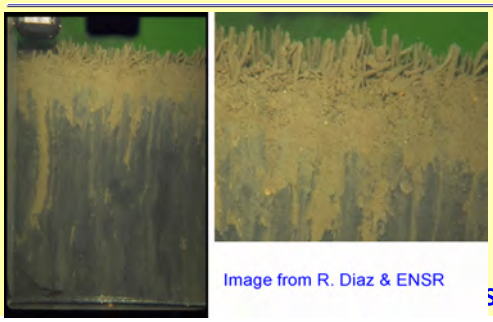

Image from R. Diaz & ENSR

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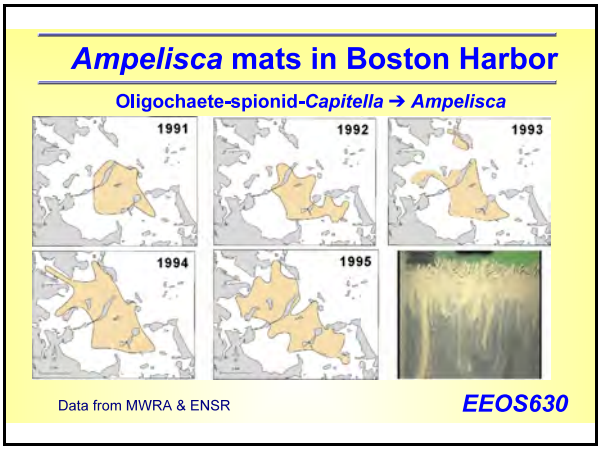
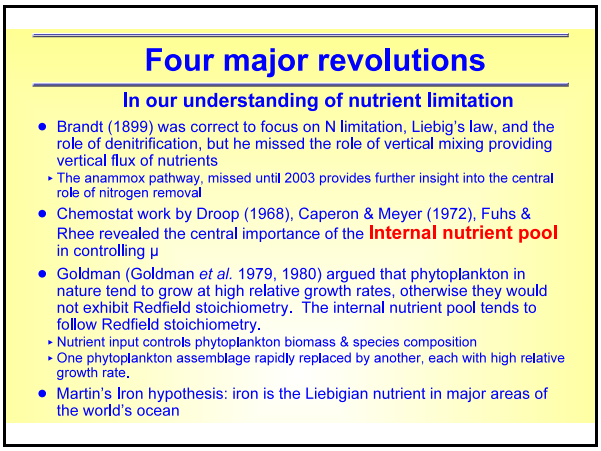
Slide 81 Denitrification in Boston Harbor sediments: Ampelisca mats

NOTES:



Slide 82 Ampelisca mats in Boston Harbor

NOTES:



Slide 83 Four major revolutions

NOTES: