Measuring Primary Production, P vs. I curves, shade acclimation, Model P vs. I approach, SSCM

Class 17, 10/28/08

EEOS630

Slide 1 Measuring Primary Production, P vs. I curves, shade acclimation, Model P vs. I approach, SSCM

NOTES:

Wimba Sessions

Tonight, Tuesday 10/28, 7 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
- Due date: papers due 4 weeks after projects posted.

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Slide 2 Wimba Sessions

NOTES:

Phytoplankton Readings

- My chapters:
  - Chapter 7 (μ, B, & P), 8 (C14 method), 9 (Light effects)
- Readings (on UMB E- Reserve)
  - μ, B, & P:
    - Eppley, R. W. 1972. Temperature and phytoplankton growth in the sea. Fish. Bull. *70*: 1063-1085.
    - Lorenzen, C. J. 1966. A method for the continuous measurement of *in vivo* chlorophyll concentration. Deep-Sea Res. *13*: 223-227.*[The classic paper describing the use of pumped water through a Turner Model III fluorometer with excitation peak at 445 nm and emission peak at >645 nm*
  - C14:
    - Peterson, B. 1980. Aquatic primary productivity and the $^{14}C\text{-}CO_2$ method: a history of the productivity problem. Ann. Rev. Ecol. Syst. 11: 359-385. [Just skim for now]
  - Light
    - Harrison, W. G., T. Platt, and M. K. Lewis. 1985. The utility of light-saturation models for estimating marine primary productivity in the field: a comparison with conventional "simulated: in situ" methods. Can J. Fish. Aquat. Sci. 42: 864-872.
    - Falkowski, P. G. and J. A. Raven. 1997. Aquatic Photosynthesis. Blackwell Science, Malden MA. 375 pp. *[Read Chapter 9, Read pp. 263-276, 282-288 on fast repetition rate fluorescence and nonphotochemical quenching; skim the rest of the chapter.]*

Slide 3 Phytoplankton Readings

NOTES:

Phytoplankton Readings

Nutrients and the spring bloom

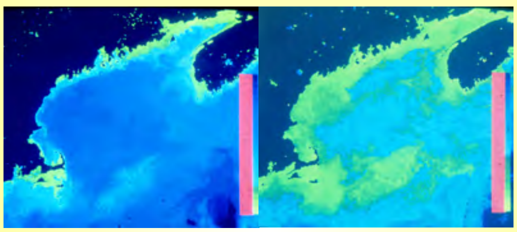
- Nutrient effects:
  - Chapter 10: Nitrogen cycle, nutrient limitation & chemostats
  - Howarth, R. W. 1988. Nutrient limitation of net primary production in marine ecosystems. Ann. Rev. Ecol. Syst. *19*: 89-110.
- Spring bloom
  - Chapter 11: Sverdrup's critical depth concept & the vernal phytoplalnkton
  - 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 4 Phytoplankton Readings

NOTES:

The Gulf of Maine bloom

Bill Hanlon (UMB M.Sc.): CZCS images, pre-bloom and bloom



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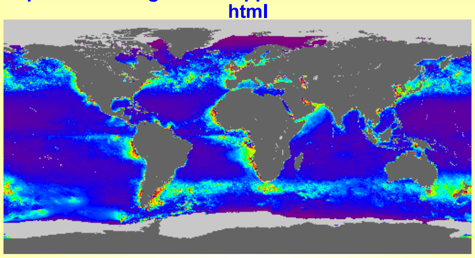
Slide 5 The Gulf of Maine bloom

NOTES:

Global Primary Production

VGPM Estimates of Global Primary Production
http://marine.rutgers.edu/opp/Production/Production1.html



October-December

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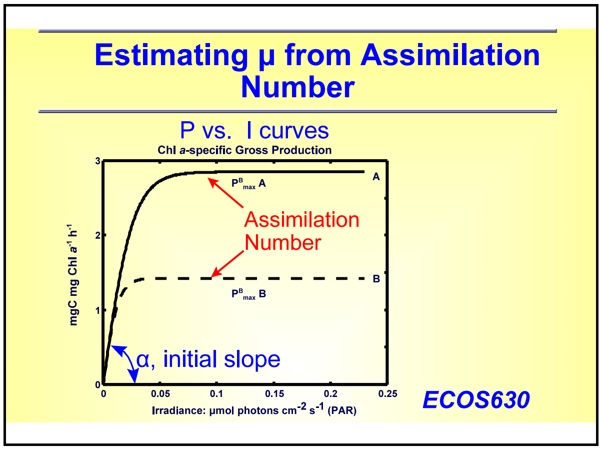
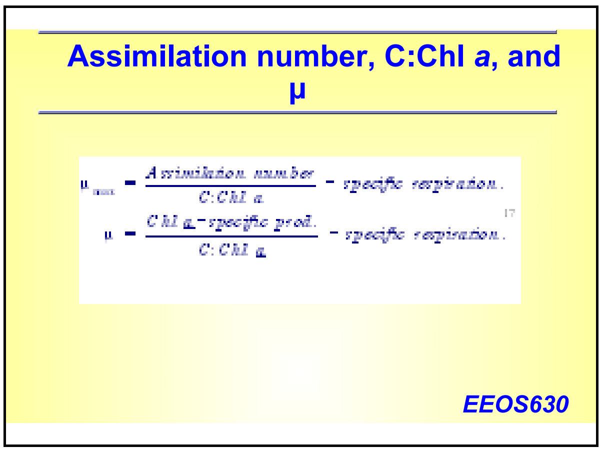
Slide 6 Global Primary Production

NOTES:



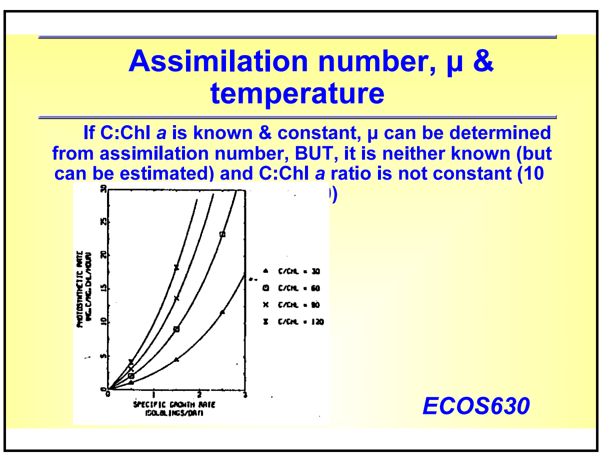
Slide 7 Estimating μ from Assimilation Number

NOTES:



Slide 8 Assimilation number, C:Chl a, and μ

NOTES:

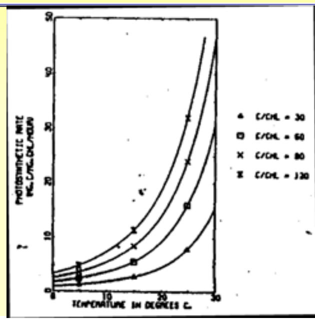


Slide 9 Assimilation number, μ & temperature

NOTES:

Maximum Chl-specific production, per hour, *vs.* Temperature

Assimilation Number



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Slide 10 Maximum Chl-specific production, per hour, vs. Temperature

NOTES:

Excursis on grazing & the dilution method

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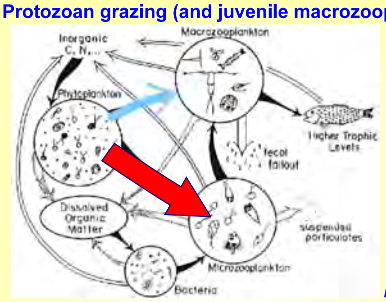
Slide 11 Excursis on grazing & the dilution method

NOTES:

Nano- and microzooplankton are usually the dominant grazers

Protozoan grazing (and juvenile macrozooplankton)



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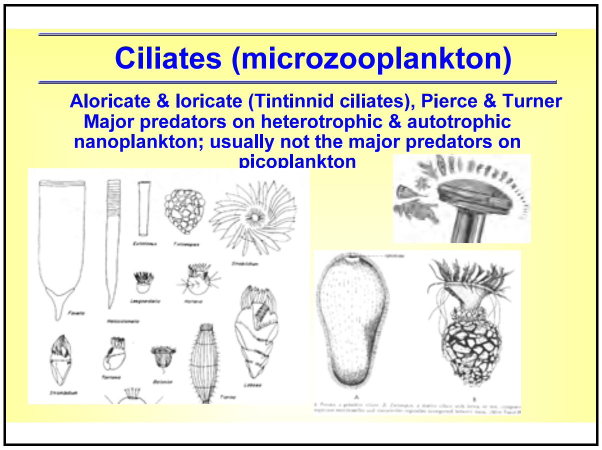
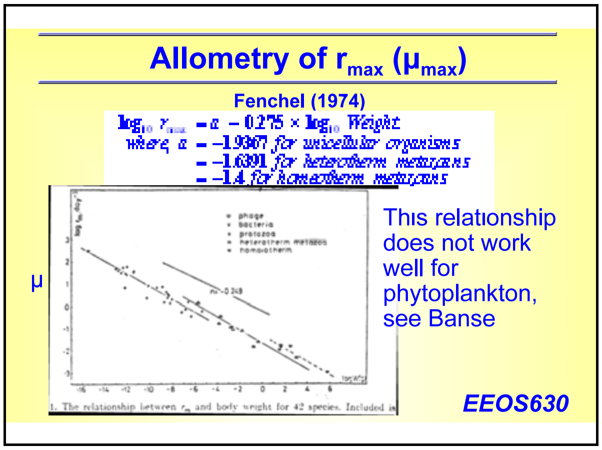
Slide 12 Nano- and microzooplankton are usually the dominant grazers

NOTES:



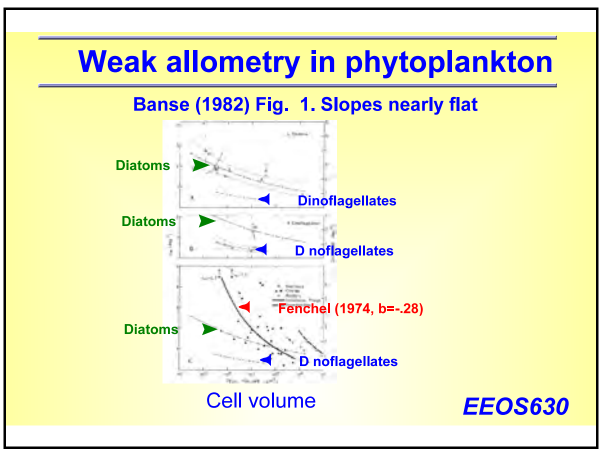
Slide 13 Ciliates (microzooplankton)

NOTES:



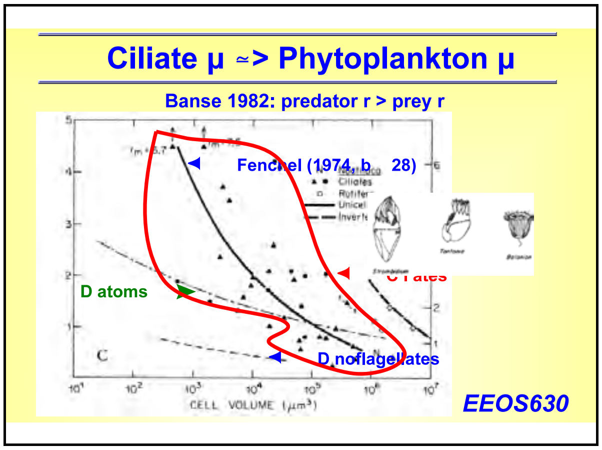
Slide 14 Allometry of rmax (μmax)

NOTES:



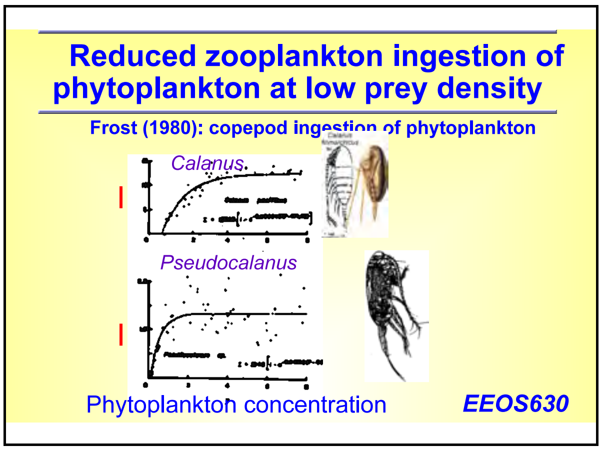
Slide 15 Weak allometry in phytoplankton

NOTES:



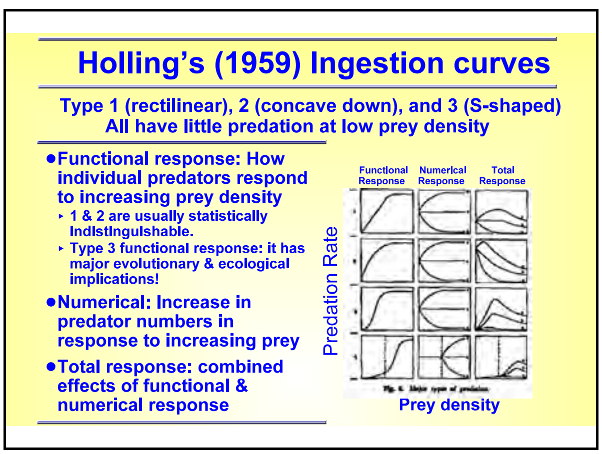
Slide 16 Ciliate µ ≈> Phytoplankton µ

NOTES:



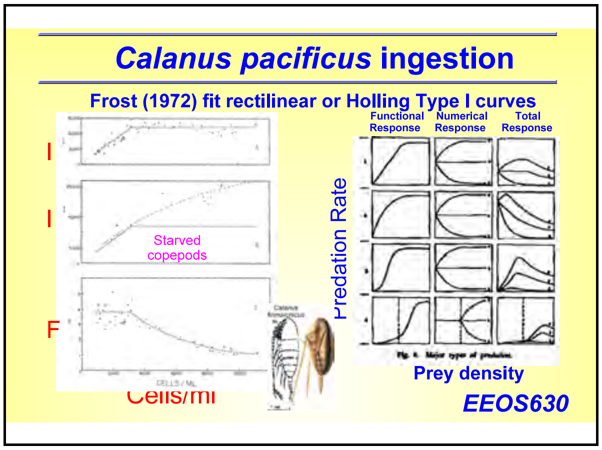
Slide 17 Reduced zooplankton ingestion of phytoplankton at low prey density

NOTES:



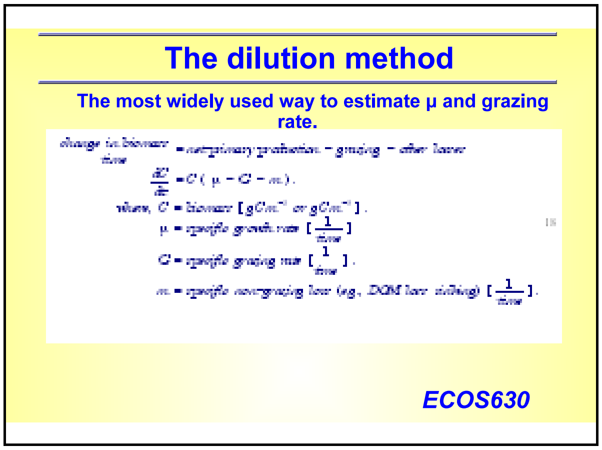
Slide 18 Holling's (1959) Ingestion curves

NOTES:



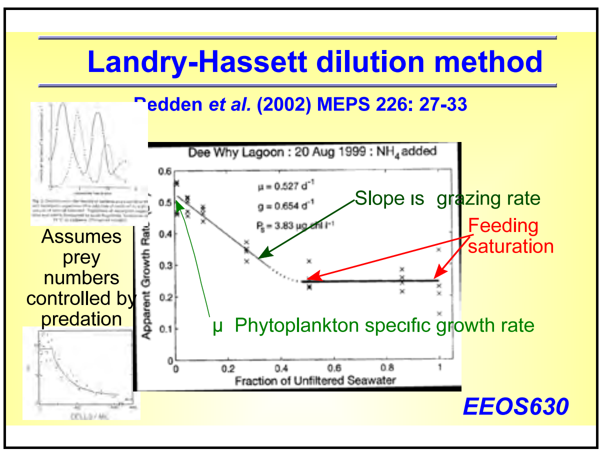
Slide 19 Calanus pacificus ingestion

NOTES:



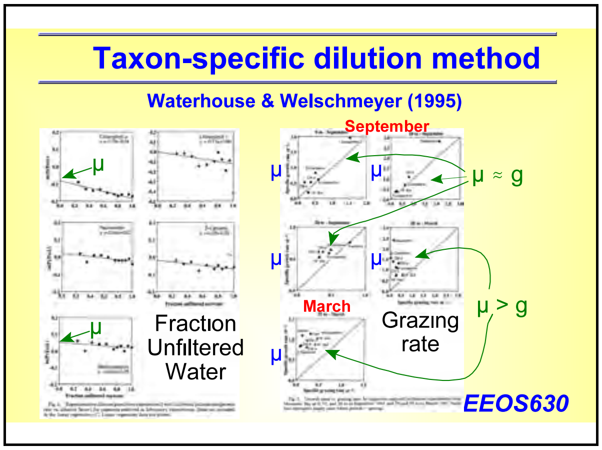
Slide 20 The dilution method

NOTES:



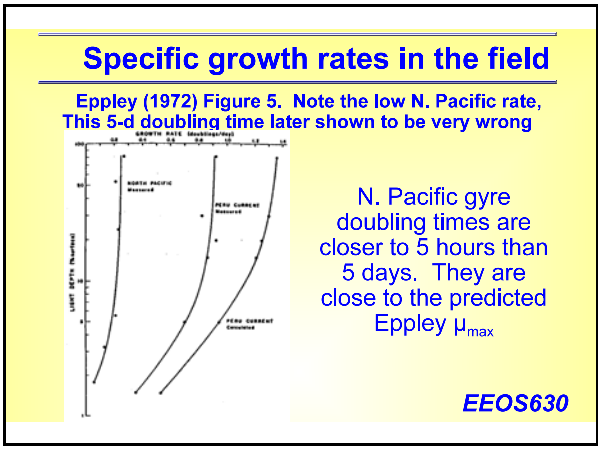
Slide 21 Landry-Hassett dilution method

NOTES:



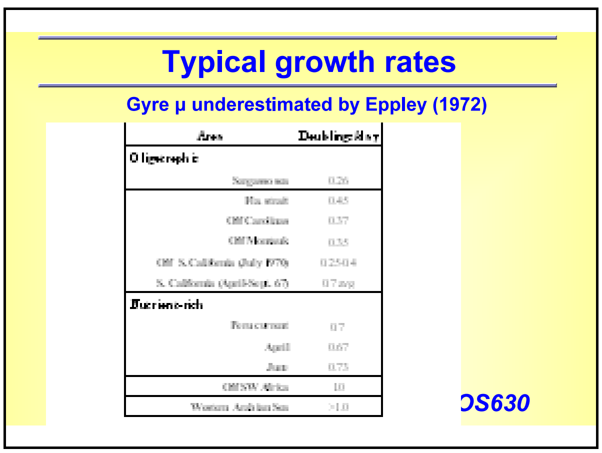
Slide 22 Taxon-specific dilution method

NOTES:



Slide 23 Specific growth rates in the field

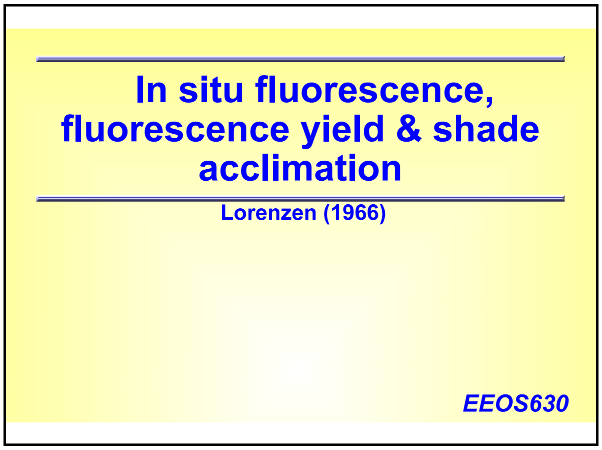
NOTES:



Area	Doubling/day
Oligotrophic	
Sargasso sea	0.26
Fla. strait	0.45
Off Carolinas	0.37
Off Montauk	0.35
Off S. California (July 1970)	0.25-0.4
S. California (April-Sept. 67)	0.7 avg
Nutrient-rich	
Peru current	0.7
April	0.67
June	0.73
Off SW Africa	1.0
Western Arabian Sea	>1.0

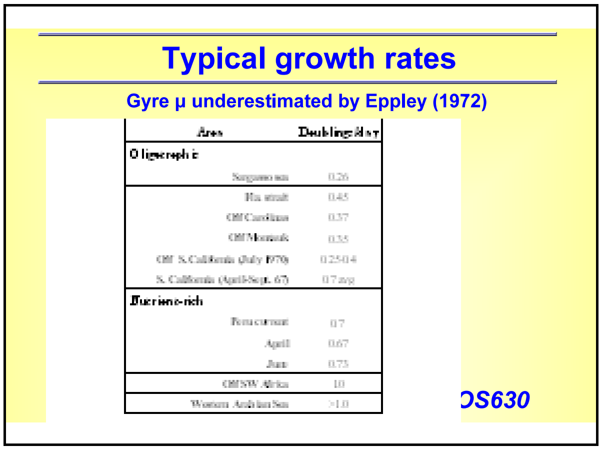
Slide 24 Typical growth rates

NOTES:



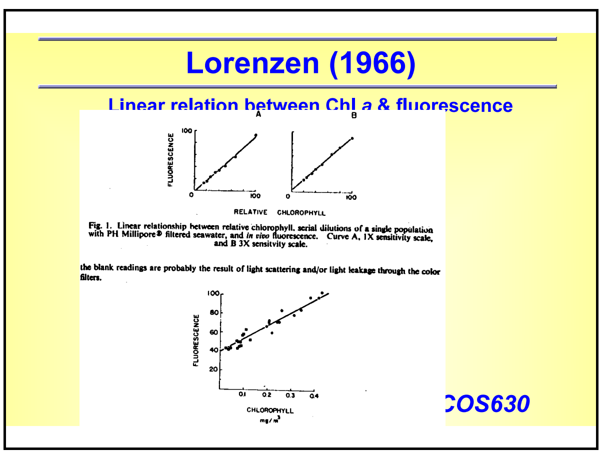
Slide 25 Typical growth rates

NOTES:



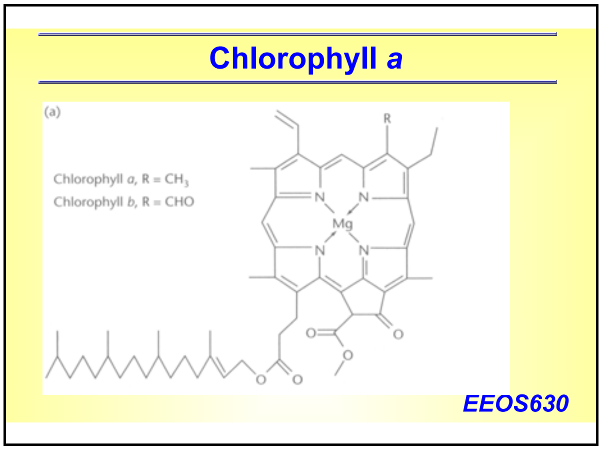
Slide 26 In situ fluorescence, fluorescence yield & shade acclimation

NOTES:



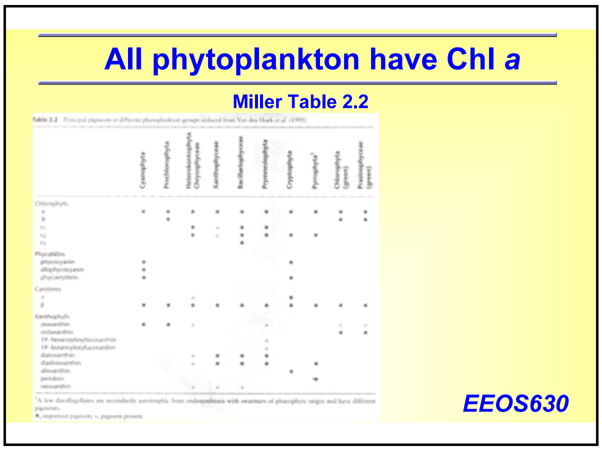
Slide 27 Lorenzen (1966)

NOTES:



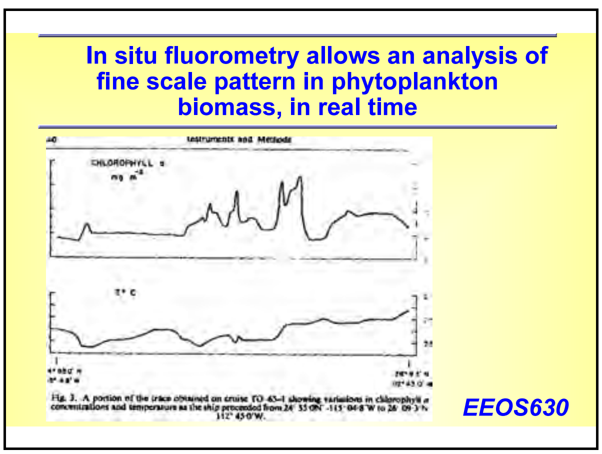
Slide 28 Chlorophyll a

NOTES:



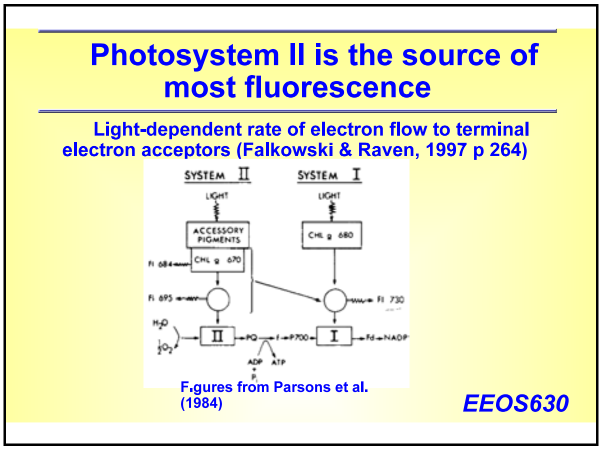
Slide 29 All phytoplankton have Chl a

NOTES:



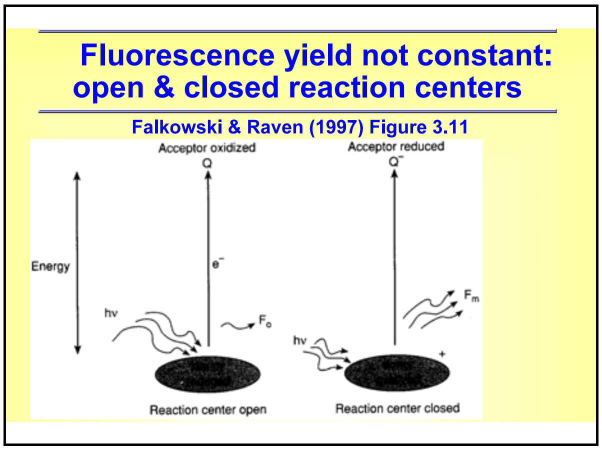
Slide 30 In situ fluorometry allows an analysis of fine scale pattern in phytoplankton biomass, in real time

NOTES:



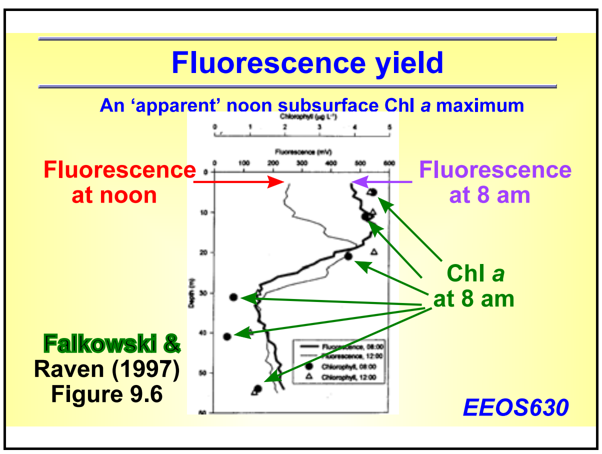
Slide 31 Photosystem II is the source of most fluorescence

NOTES:



Slide 32 Fluorescence yield not constant: open & closed reaction centers

NOTES:



Slide 33 Fluorescence yield

NOTES:

How do you measure production?

See Harrison & Platt; Choose a model

- *In situ* or simulated *in situ* incubations
  - *In situ* incubations account for light-quality effects, but not vertical mixing
  - Simulated *in situ*
    - Natural light
    - Artificial light source (photosynthetron)
- Model P vs. I approach
  - Obtain accurate estimates of initial slope of P vs. I curve, α, and the assimilation number
  - If the light field & **Chl *a* profiles** are known, primary production throughout the water column can be estimated from the P vs. I parameters

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Slide 34 How do you measure production?

NOTES:

Productivity methods

Choose a method

- ^{14}C *vs.* O_2 method
  - Sensitivity & variability in photosynthetic quotient pose problems for the O_2 method
- ^{18}O primary production
- Incubations: short vs. Long
  - Eppley used 24-h incubations
  - Most authors recommend short incubations, but
    - Photoacclimation a problem
    - Redalje: Sum of multiple short incubations < long incubation
  - Large *vs.* Small incubation bottles
    - Bottle effects
    - Noted especially by Gieskes & Kraay (1979)

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Slide 35 Productivity methods

NOTES:

C-14 method

See Chapter 2 & references for details

- Prepare a $H^{14}CO_3^-$ solution of known activity
- Obtain samples from the appropriate depth and light conditions. Don't expose samples to direct sunlight.
- Split samples between experimental and control bottles. Add ^{14}C spike to both experimental and control bottles.
- Controls: A variety have been used: Time-0, dark-bottle, DCMU, DCMU & dark-bottle

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Slide 36 C-14 method

NOTES:

Estimating productivity

- Incubate using *in situ* (preferred, but not possible with many licenses for ^{14}C) or simulated *in situ* methods for 2 to 24 hours
- Gently filter the particulate matter for later laboratory analysis (a 0.4-μm filter is now common). A sample of the medium can be obtained to estimate DOC production.

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Slide 37 Estimating productivity

NOTES:

Estimating productivity

After the incubation

- Determine radioactivity of POC (& DOC) and the amount of Chl *a* in the sample bottles
  - Estimate or measure the specific activity of the DIC in the incubation bottle [dpm/ g DIC].
  - Measure the ^{14}C activity in the particulate (and dissolved) organic phases. The filtered samples or liquid samples (for DOC) are first acidified to drive off unfixed ^{14}C, then the sample's radioactivity is determined by liquid scintillation counting.

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Slide 38 Estimating productivity

NOTES:

Esimating ^{14}C productivity

Note the isotopic discrimination factor (1.05)

$$\frac{dC}{dt} = \frac{1.05\, A^*}{I^*\, T}.$$

where, A^* = activity of ^{14}C in sample POC (& DOC) $\left[\frac{dpm}{sample}\right]$.

I^* = specific activity of DIC in bottle $\left[\frac{dpm}{g\,C\ DIC}\right]$.

T = Incubation time $[h]$.

1.05 = Isotopic discrimination factor.

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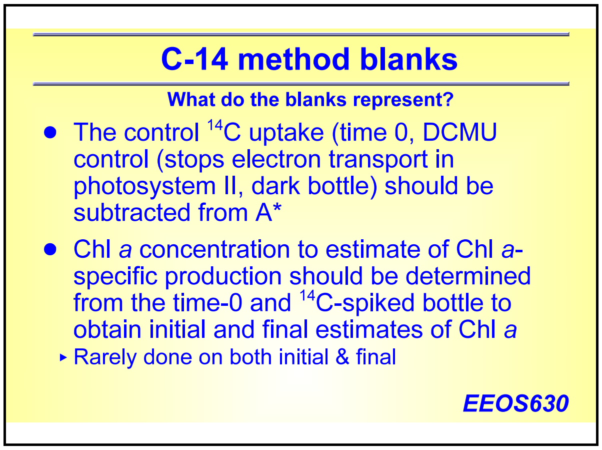
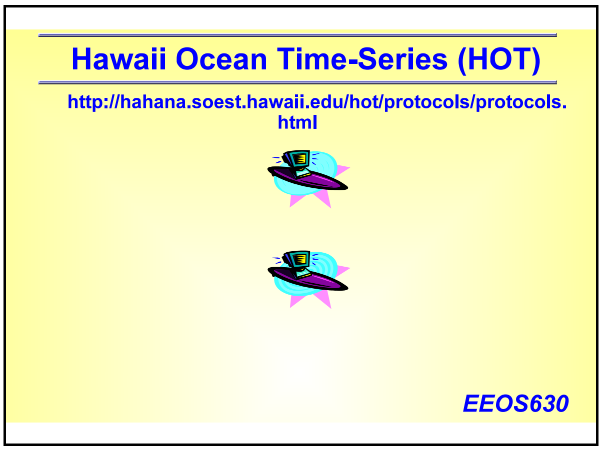
Slide 39 Esimating 14C productivity

NOTES:



Slide 40 C-14 method blanks

NOTES:



Slide 41 Hawaii Ocean Time-Series (HOT)

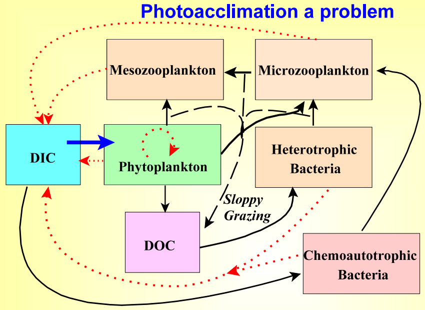
NOTES:

Slide 42 Gross primary Productivity

NOTES:

Carbon flow in bottles (& the sea)

Are short incubations the best solution?
Photoacclimation a problem



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Slide 43 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 44 The oxygen method

NOTES:

O_2 *vs.* ^{14}C

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

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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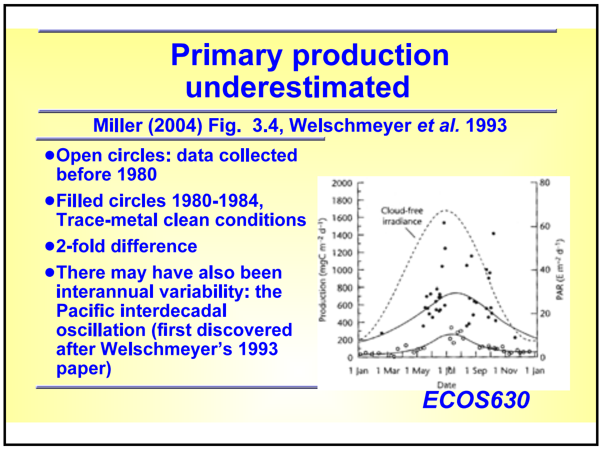
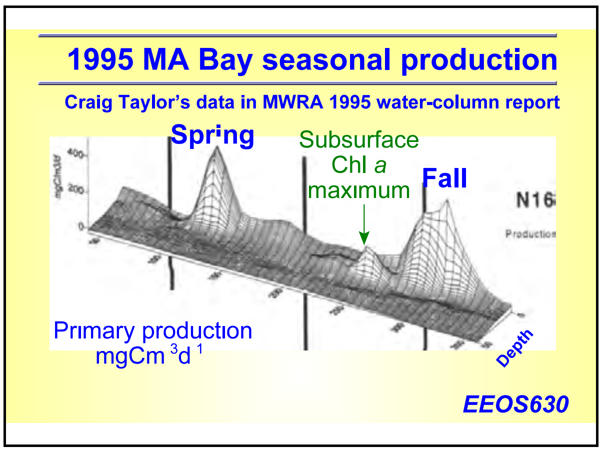
Slide 45 O2 vs. 14C

NOTES:



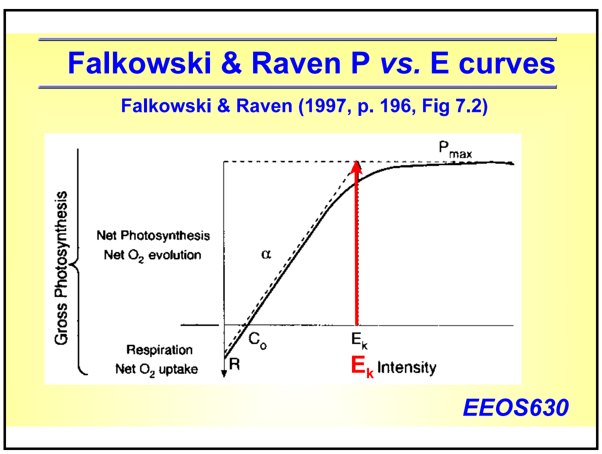
Slide 46 Primary production underestimated

NOTES:



Slide 47 1995 MA Bay seasonal production

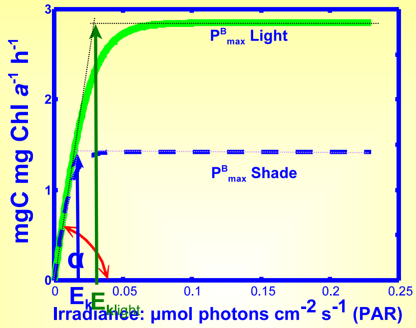
NOTES:



Slide 48 Falkowski & Raven P vs. E curves

NOTES:

Chl *a*-specific gross productivity



Slide 49

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).
- To convert to energy, 550nm light assumed

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Slide 50 PAR & units of light intensity

NOTES:

Converting units of light intensity

- Ein=mol photon
  - so the units of light should be in terms of a flux
    - μEin $cm^{-2}s^{-1}$ in the PAR
    - PSR<PUR<PAR (Photosynthetically active radiation or Photo. available radiation wavelengths from 300 to 720 nm)
    - Ein=6.02 * 10^{23} quanta=2.86 x 10^{8}/Angstroms g cal where Angstrom= 10^{-10} m
    - 1 g cal =4.185 x 10^{7} ergs=4.185 watt*sec
    - 1 g cal/cm^2 =1 langley
    - For average wavelength of visible light 550 nm, 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

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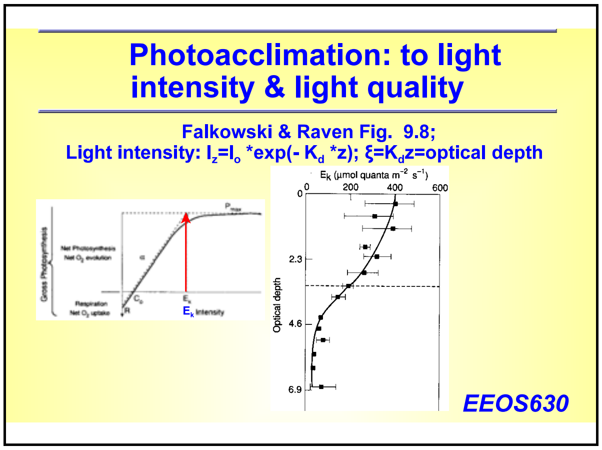
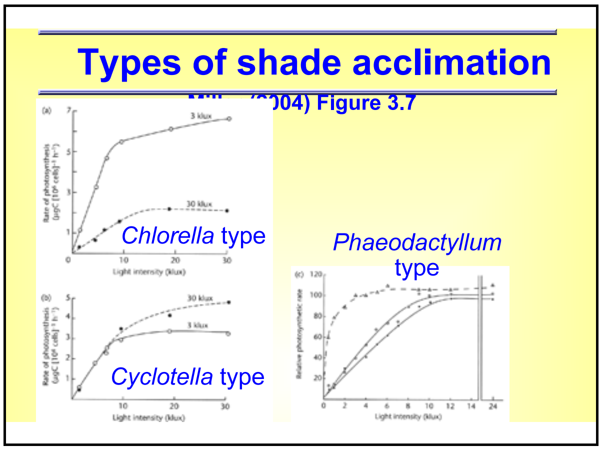
Slide 51 Converting units of light intensity

NOTES:



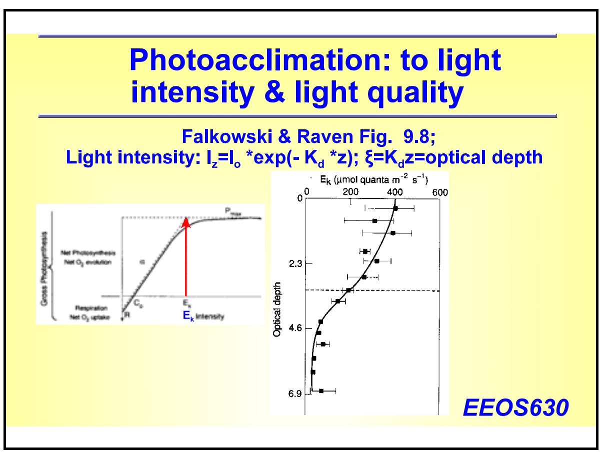
Slide 52 Photoacclimation: to light intensity & light quality

NOTES:



Slide 53 Photoacclimation: to light intensity & light quality

NOTES:



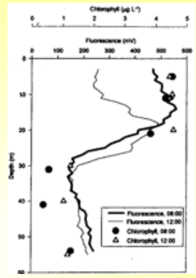
Slide 54 Types of shade acclimation

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 55 Measuring the Chl a profile

NOTES:

Shade acclimation (adaptation)

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

- Changes in the amount of photosynthetic pigment per cell (*e.g.*, changes in C:Chl *a* ratio)
- Changes in the ratios of photosynthetic pigments
- Changes in the size and number of photosynthetic units (Chl *a*:P700 size)
- Changes in chloroplast size & orientation
- Changes in the enzyme activities of both the light and dark reactions

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Slide 56 Shade acclimation (adaptation)

NOTES:

Shade acclimation (adaptation)

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

- Changes in the amount of photosynthetic pigment per cell (*e.g.*, changes in C:Chl *a* ratio)
- 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 57 Shade acclimation (adaptation)

NOTES:

Quenching

Refers to both scintillation counting and fluorescence yield

Quenching and quantum yield for fluorescence

$$\varphi_F = \frac{k_F}{(k_F + k_d + k_p)}, \text{ where}$$

φ_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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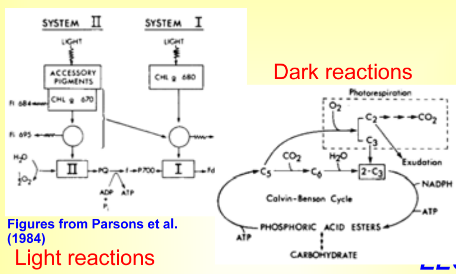
Slide 58 Quenching

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)

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Slide 59 Gross primary productivity

NOTES:

Jassby & Platt's (1976) Equation

Without photoninhibition

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

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

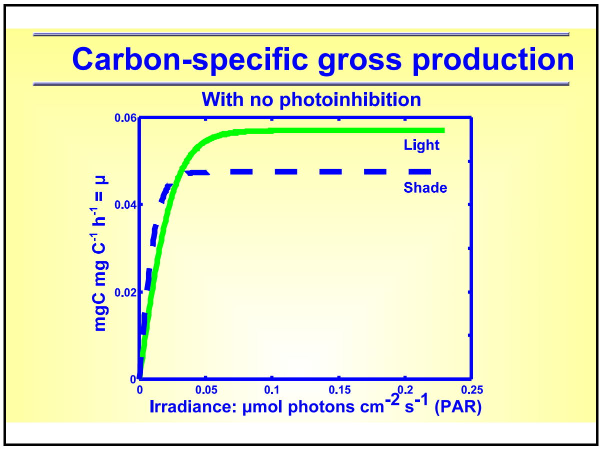
P^B_m = Max. rate at light saturation.
= Assimilation number
= the maximum photosynthetic rate at light saturation.

α = initial slope of the P vs. I curve.
$= \left[\frac{mg\ C}{mg\ Chla\ h\ (W\ m^{-2})}\right]$ or
$= \left[\frac{mg\ C}{mg\ Chla\ h\ (E\ m^{-2}\ h^{-1})}\right]$

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

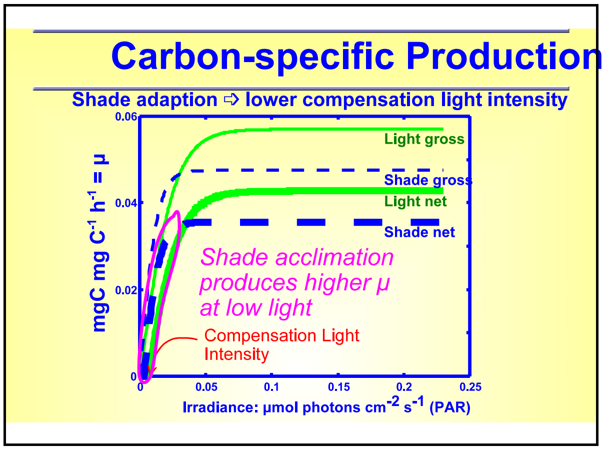
Slide 60 Jassby & Platt's (1976) Equation

NOTES:



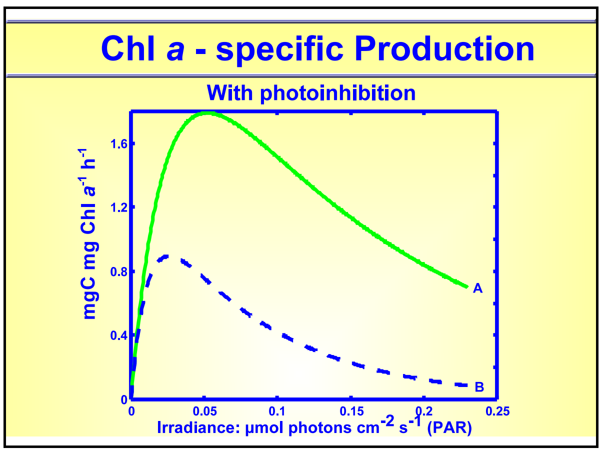
Slide 61 Carbon-specific gross production

NOTES:



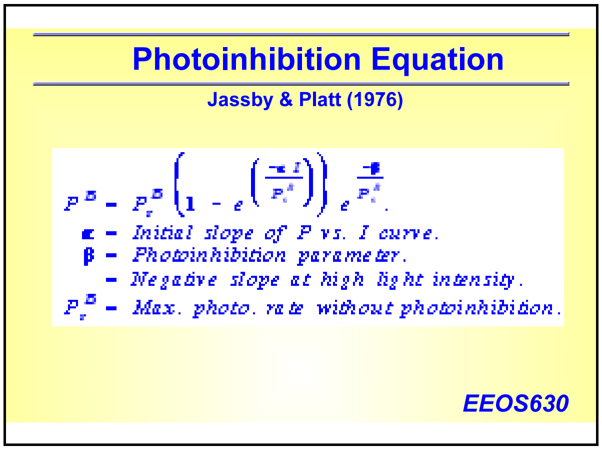
Slide 62 Carbon-specific Production

NOTES:



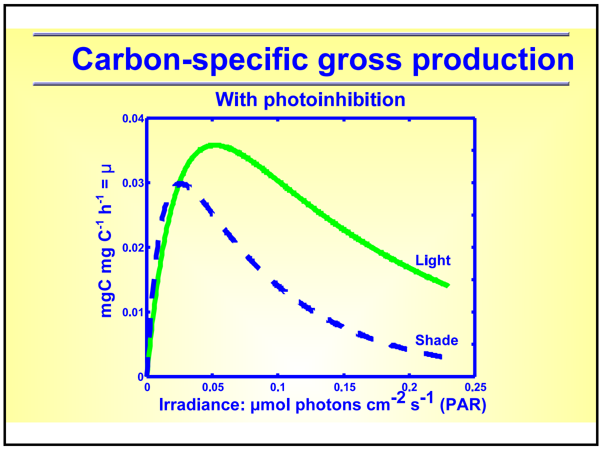
Slide 63 Chl a - specific Production

NOTES:



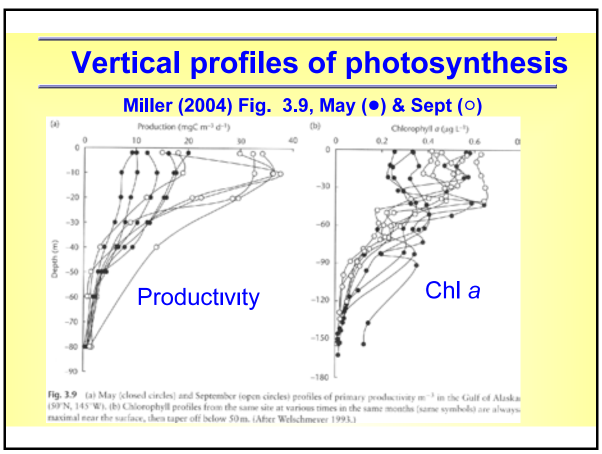
Slide 64 Photoinhibition Equation

NOTES:



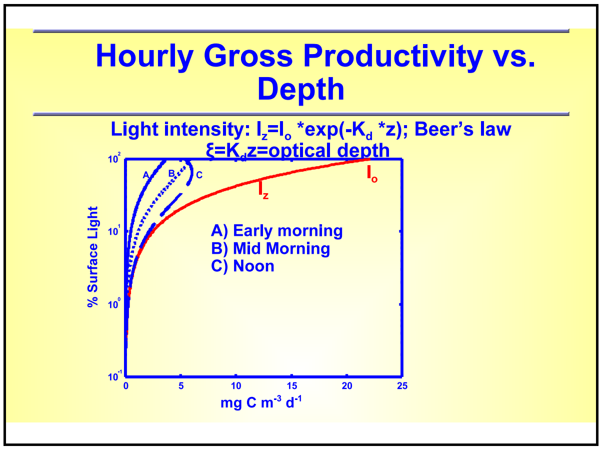
Slide 65 Carbon-specific gross production

NOTES:



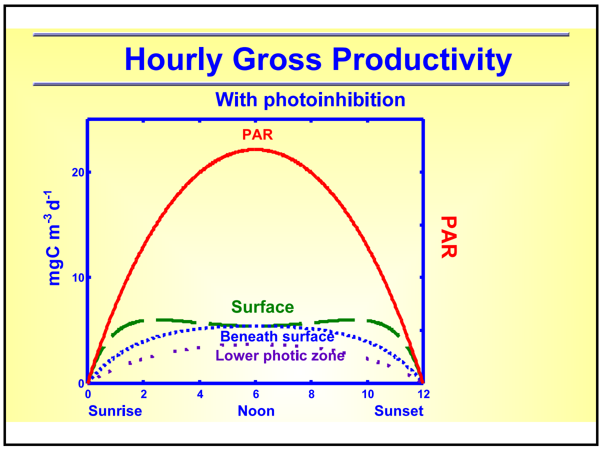
Slide 66 Vertical profiles of photosynthesis

NOTES:



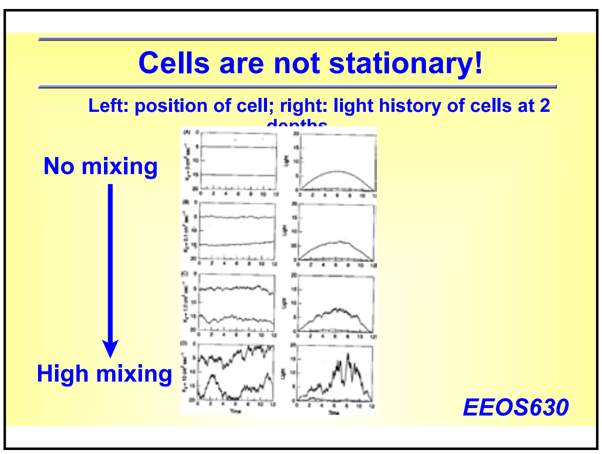
Slide 67 Hourly Gross Productivity vs. Depth

NOTES:



Slide 68 Hourly Gross Productivity

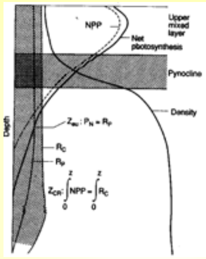
NOTES:



Slide 69 Cells are not stationary!

NOTES:

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



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Slide 70 Euphotic zone (≈1% light depth), mixed layer depth, and critical depth

NOTES:

Non-dimensional production

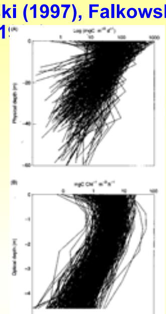
Behrenfeld & Falkowski (1997), Falkowski & Raven (1

Production vs. Depth

Meters

Chl-specific P vs. Depth

Optical depth



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Slide 71 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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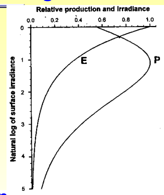
Slide 72 The model P vs I approach vs. SIS

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**



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

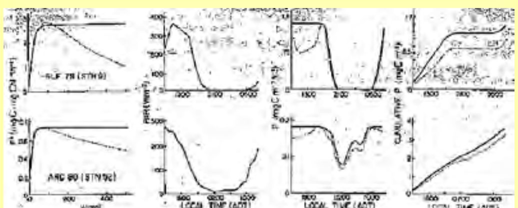
$$P_T = \sum_{t=1}^{24} P(t).$$

Slide 73 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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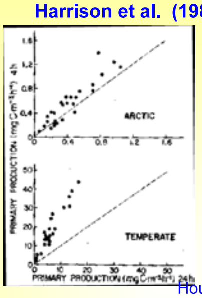
Slide 74 Model P vs. I approach

NOTES:

4- *vs.* 24-h incubations

Harrison et al. (1985) Figure 2

Hourly production (4-h)



Hourly production (24-h)

Nighttime productivity, midnight sun

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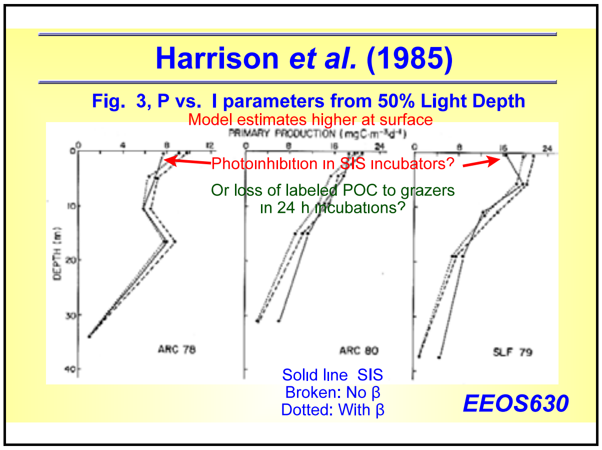
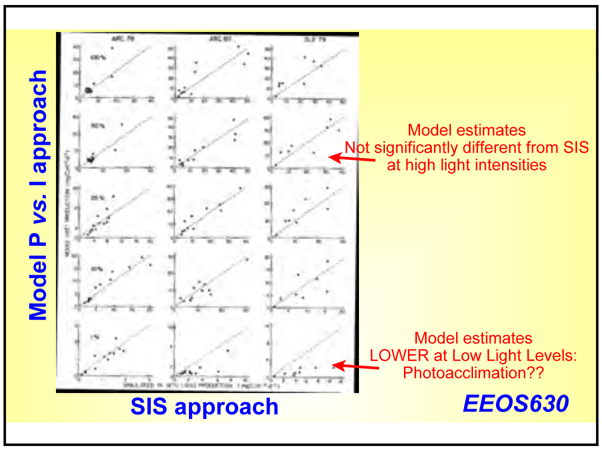
Slide 75 4- vs. 24-h incubations

NOTES:



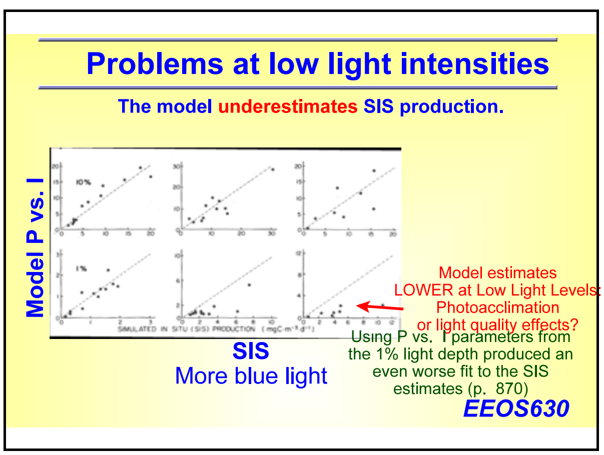
Slide 76 Harrison et al. (1985)

NOTES:



Slide 77

NOTES:



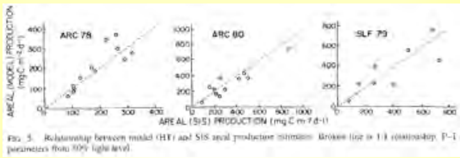
Slide 78 Problems at low light intensities

NOTES:

Areal production accurate

Harrison et al. (1985) Fig. 5

Model P vs. I



SIS

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Slide 79 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)	0.0016 (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 80 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

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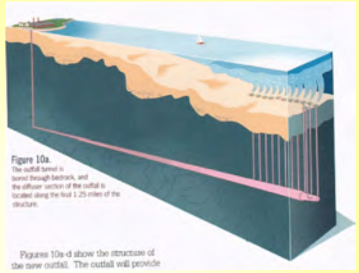
Slide 81 Applications

NOTES:

The MA Bay Outfall

From MWRA State of the Harbor Report



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Slide 82   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: 6-8 mg C mg Chl *a* h^{-1}

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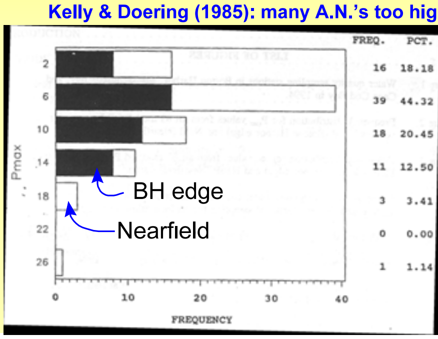
Slide 83   Realistic P vs. I parameters

NOTES:

MA Bay P vs. I parameters

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



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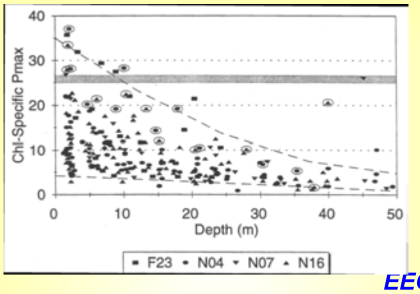
Slide 84   MA Bay P vs. I parameters

NOTES:

MA Bay assimilation numbers

Including Falkowski's theoretical maximum= 25



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Slide 85 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
  - Failure to subtract controls

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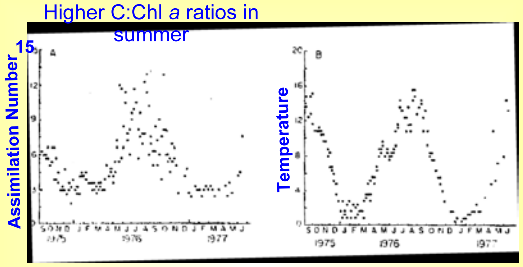
Slide 86 Why might assimilation numbers be too high?

NOTES:

Seasonal variation in A.N.

Harrison & Platt (1980), max. AN < 15

Higher C:Chl *a* ratios in summer



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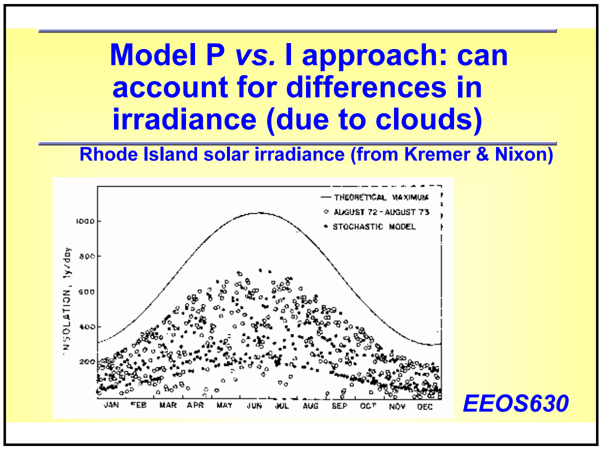
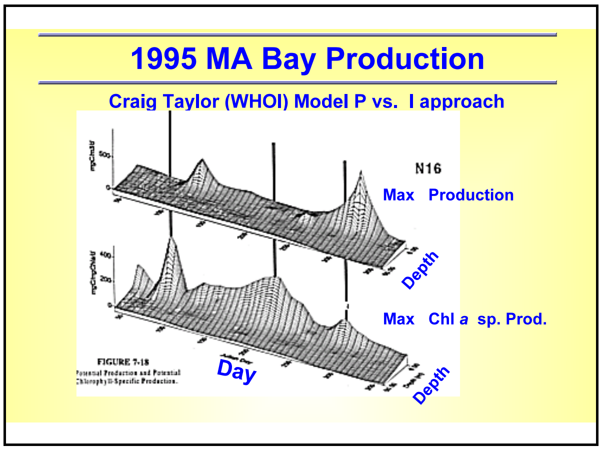
Slide 87 Seasonal variation in A.N.

NOTES:



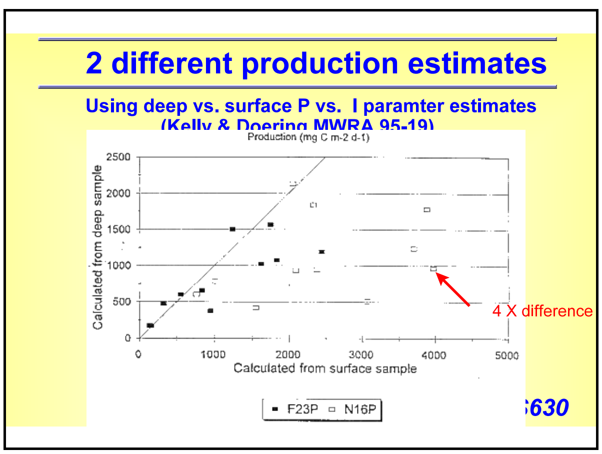
Slide 88 Model P vs. I approach: can account for differences in irradiance (due to clouds)

NOTES:



Slide 89 1995 MA Bay Production

NOTES:



Slide 90 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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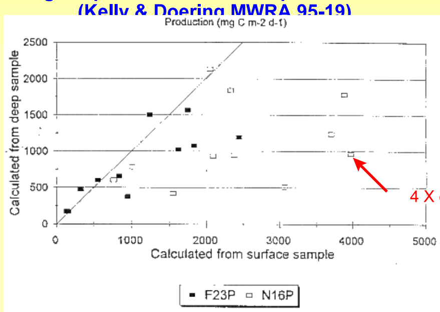
Slide 91 2 different production estimates

NOTES:

2 different production estimates

Using deep vs. surface P vs. I paramter estimates (Kelly & Doering MWRA 95-19)



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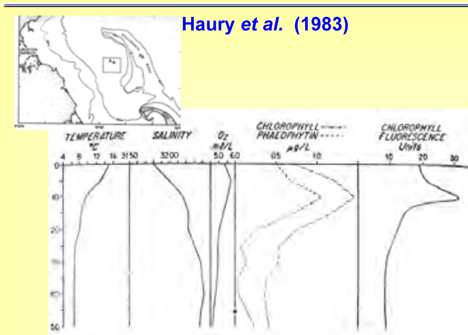
Slide 92 Excursis on the Subsurface Chlorophyll maxima

NOTES:

MA Bay subsurface Chl *a* maxima

Haury *et al.* (1983)



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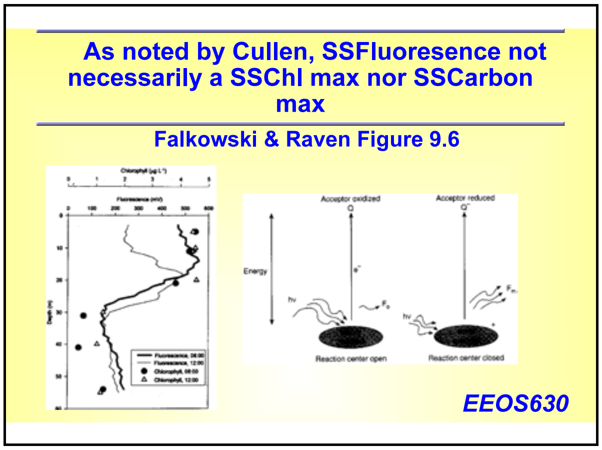
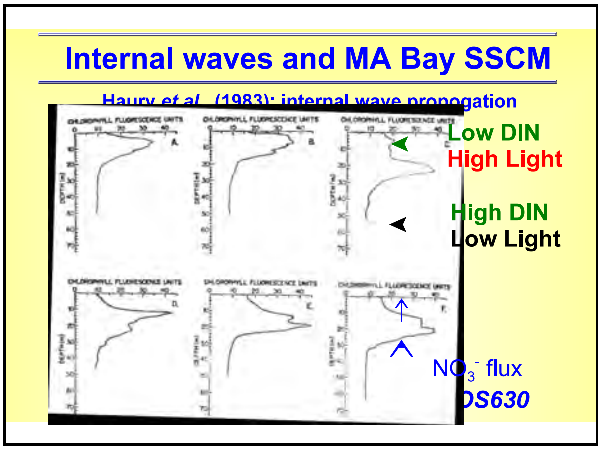
Slide 93 MA Bay subsurface Chl a maxima

NOTES:



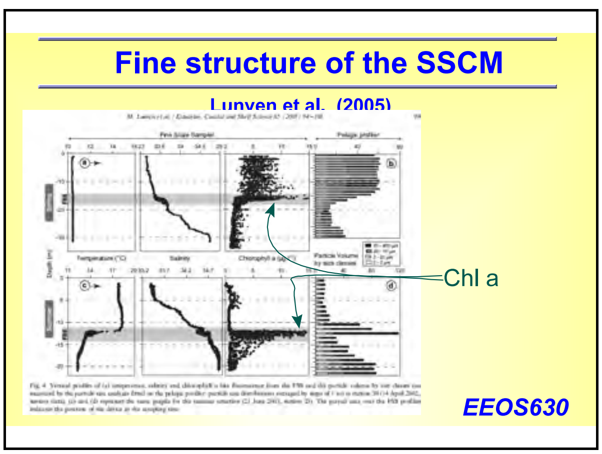
Slide 94 As noted by Cullen, SSFluoresence not necessarily a SSChl max nor SSCarbon max

NOTES:



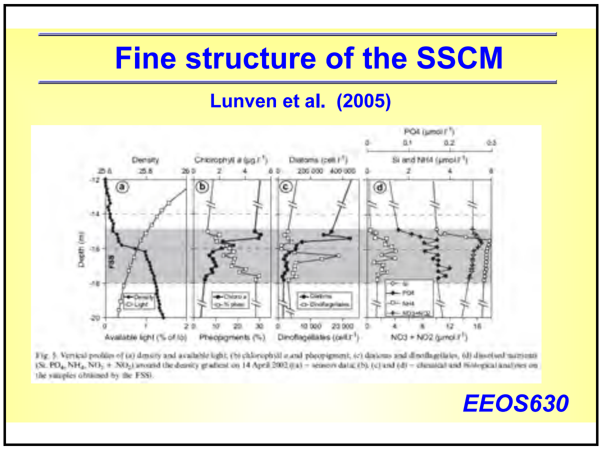
Slide 95 Internal waves and MA Bay SSCM

NOTES:



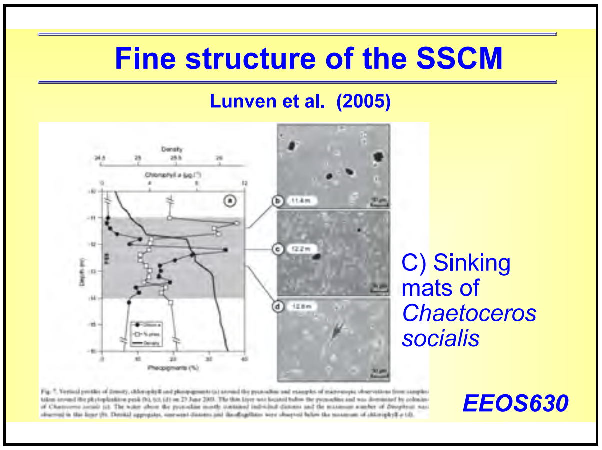
Slide 96 Fine structure of the SSCM

NOTES:



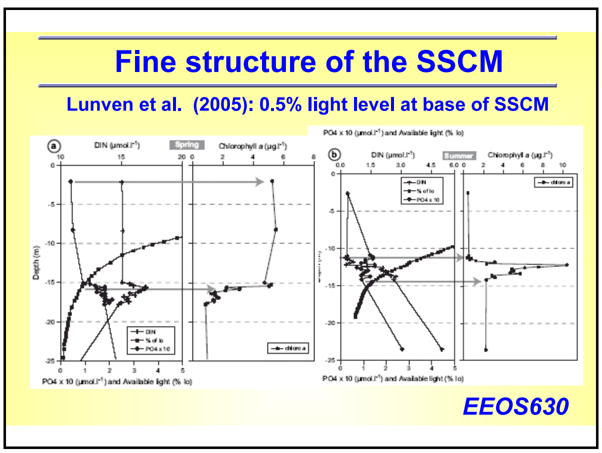
Slide 97 Fine structure of the SSCM

NOTES:



Slide 98 Fine structure of the SSCM

NOTES:



Slide 99 Fine structure of the SSCM

NOTES: