EFFECTS OF LIGHT ON PHYTOPLANKTON

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Assignment

Topics

"How does light quantity and quality affect phytoplankton growth in the sea?"

Required Readings

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. *[Model P-I curves are calculated and compared with actual field measurements of production.]*

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.]*

Supplemental

Behrenfeld, M. J. and P. J. Falkowski. 1997. A consumer's guide to phytoplankton primary productivity models. Limnol. Oceanogr. *42*: 1479-1491. *[They don't focus on the methods used to generate productivity estimates, but on the conceptual models for the correlates of productivity: biomass, depth, light, etc.]* [?]

Miller, C. B. 2004. Biological Oceanography. Blackwell Science, Malden MA. 402 pp. Chapter 3, especially pp. 52-56.

P *vs.* I curves and the effects of light adaptation

P *vs.* I curves, called P vs. E curves in **Falkowski & Raven (1997)** are described by the **Jassby-Platt (1976)** equation. **Jassby & Platt (1976)** chose this equation because with just two parameters, it could express the asymptotic approach to a maximum value:

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

where, P^B = *Chl a-specific production* $\left[\frac{mgC}{mgChl\,a\ h}\right]$.

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.*
= $\left[\frac{mgC}{mgChl\,a\ h\ (W\ m^{-2})}\right]$, *or*
= $\left[\frac{mgC}{mgChl\,a\ h\ (E\ m^{-2}\ h^{-1})}\right]$

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

The two parameters for this equation are the light-saturated photosynthetic rate, P^B_m, now called the assimilation number, and the initial slope, α.

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 (*e.g.*, Chl *a*)
- 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

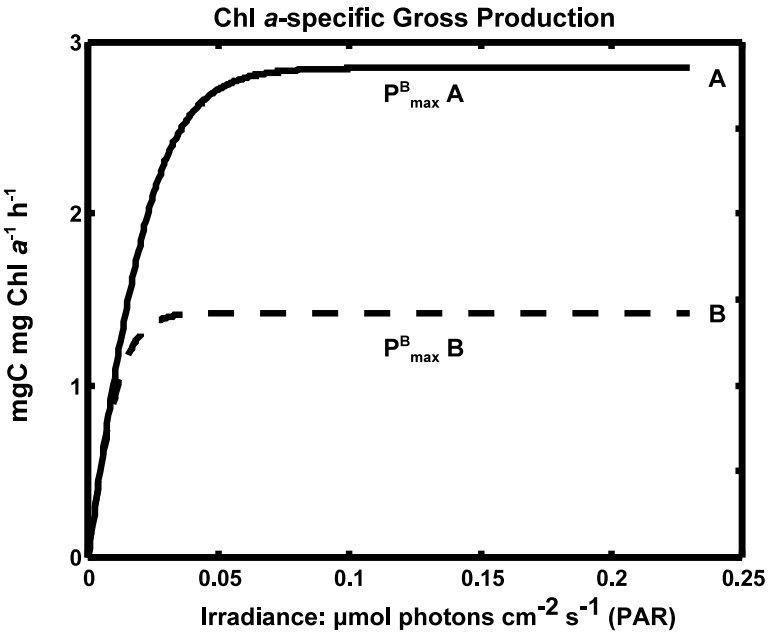

Figure 1. An idealized P *vs.* I curve showing the effects of shade adaptation. Curves A and B represent the effects of incubating subsamples of the same phytoplankton culture for two days at high and low light, respectively, before doing a short-term P *vs.* I incubation with subsamples from each culture.

Figure 1 shows what might occur with identical phytoplankton cultures that had been split and grown at two different light intensities for two days, prior to their production being determined with a one-hour P *vs.* I incubation.

Figure 1 shows what **Rhee (1980)** calls the *Cyclotella*-type of photoadaptation.

The initial slope of the Chl-specific production *vs.* Light intensity curve remains the same, but the asymptote or assimilation number increases with adaptation to higher light intensities. The fundamental units of photosynthesis are the Photosystem I and Photosystem II units, which are tightly integrated and linked suites of photosynthetic pigments and enzymes. To adapt to low light, phytoplankton cells should increase the probability that they will capture photons of light. This can be done by either increasing the amount of photosynthetic pigment within each photosynthetic unit, or increase the number of photosynthetic units per cell. **Perry *et al.* (1981)** showed that five phytoplankton species increased the amount of Chl *a* per photosynthetic unit in response to low light.

The time scale of photoadaptation is generally regarded as ranging from a few minutes to less than a doubling time. **Huntsman & Barber (1977)** showed how this could be used to determine the mixing history of phytoplankton cells. In the Peruvian upwelling system under high wind, cells collected from the top and bottom of the euphotic zone appeared to have similar P *vs.* I curves. After adaptation to high light, these cells showed roughly the same initial slope, α, but a much higher P^B_m . The cells under high wind had become shade-acclimated, since the average light intensities experienced were very low. Under stratified conditions, the P *vs.* I curves from the surface and base of the euphotic zone are quite different. However, the differences may be due to differences in phytoplankton species composition as well as physiological adaptation.

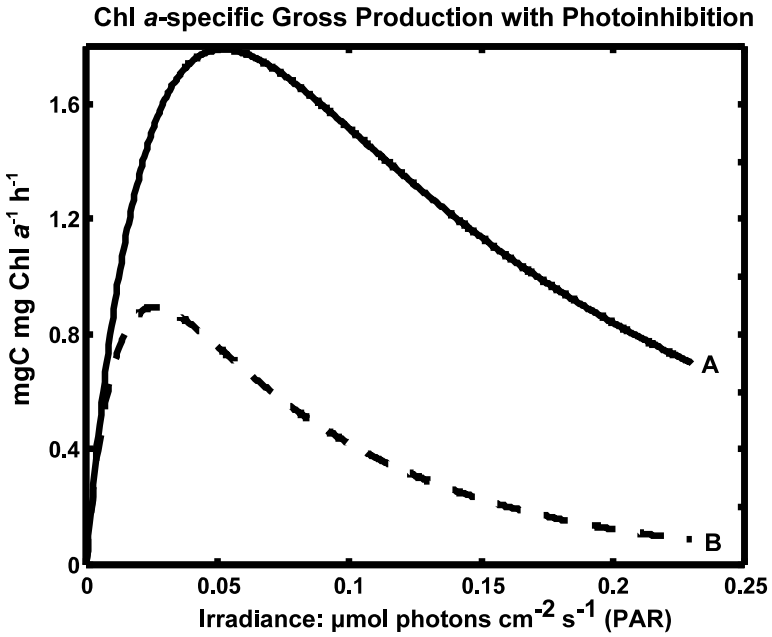

Figure 2. The same α and P^B_m parameters as Fig. 1, but now with a large photoinhibition parameter (β).

One of the problems with the simulated *in situ* technique is that it doesn't simulate the light fields experienced by phytoplankton cells as they are mixed meters or tens of meters vertically each day. Phytoplankton cells exposed to high light intensities near the sea surface can experience photoinhibition. As reviewed by **Neale (1987)**, photoinhibition can occur in milliseconds if the light is bright enough. The major cause of photoinhibition is the destruction of electron-transport enzymes of Photosystem II. Photoinhibition is reversible.

Jassby & Platt (1976) modeled the reduced photosynthetic rate at high light intensities with a third parameter, β, in the P *vs.* I curve:

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

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.*

Figure 2 shows a P *vs.* I curve with the same α and P^B_m as Fig. 1 but with a relatively high photoinhibition parameter, β. Photoinhibition can pose some severe problems in interpreting the results of P *vs.* I incubations. Phytoplankton cells, unlike bottles, do not remain at one light intensity throughout the day. They can be mixed throughout the surface mixed layer. If the time of exposure to photoinhibiting light levels is very short, then the P *vs.* I curves from fixed light intensities might underestimate production. Incubations bottles exposed to continuous high light will be strongly photoinhibited, while cells in the "real" mixed layer are not. If most phytoplankton cells are mixed close enough to the surface to experience photoinhibition, then water-column production estimates based on P *vs.* I curves could overestimate production. In the "real" water column, most cells would be photoinhibited, but in the production bottles, cells exposed to continuous low light would not be photoinhibited.

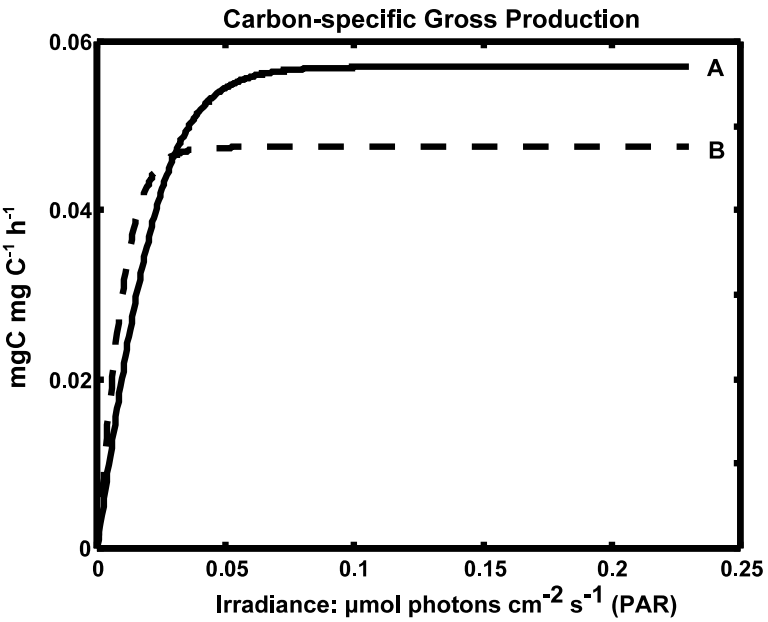

Figure 3. The same data shown in Fig. 1 are plotted as carbon-specific production rates. The shade-adapted cells (**B**) have a lower C:Chl *a* ratio.

What are the advantages of shade adaptation? One potential advantage results from the decreased C:Chl *a* ratios in shade-adapted cells. Figures 3 and 4 show the same data shown in Figs. 1 and 2, but now the data are plotted as the carbon-specific gross production rates. The lower C:Chl *a* ratios typical of shade adapted cells confers a growth advantage for these cells at low light intensities.

Shade adaptation isn't as simple as phytoplankton cells increasing their Chl *a* content in order to increase the probability of absorbing light. Chl *a* in cells is found in tightly integrated units called Photosystems I and II. Photosystem I has an electron trap called the P700 unit, composed of Chl *a*, accessory pigments, and electron-transport proteins. Photosystem II has an electron trap called the P680 unit. Each photosynthetic unit can process one photon of light, without need for chemically recharging the reaction center. Phytoplankton at low light should be adapted to increase the probability of capture of photons of light. **Perry *et al.* (1981)** showed that five phytoplankton species accomplish this by increasing the amount of Chl *a* in each photosynthetic unit, rather than increasing the number of photosynthetic units. Falkowski & Owen (1980) found two different types of adaptation to low light, based on the Chl:P700 ratio. *Skeletonema costatum* adapted to low light increase the photosynthetic unit size while the reaction centers for PS I (P700) per cell decrease. *Dunaliella* decreased the size of the photosynthetic unit but increased the number of P700 reaction centers. They concluded that either adaptation increases the efficiency of transfer or light energy from reaction centers under low light. They found that the efficiency of light utilization per unit of Chl *a* (the slope of a P *vs.* I curve) did not increase as the Chl/P700 ratio increased.

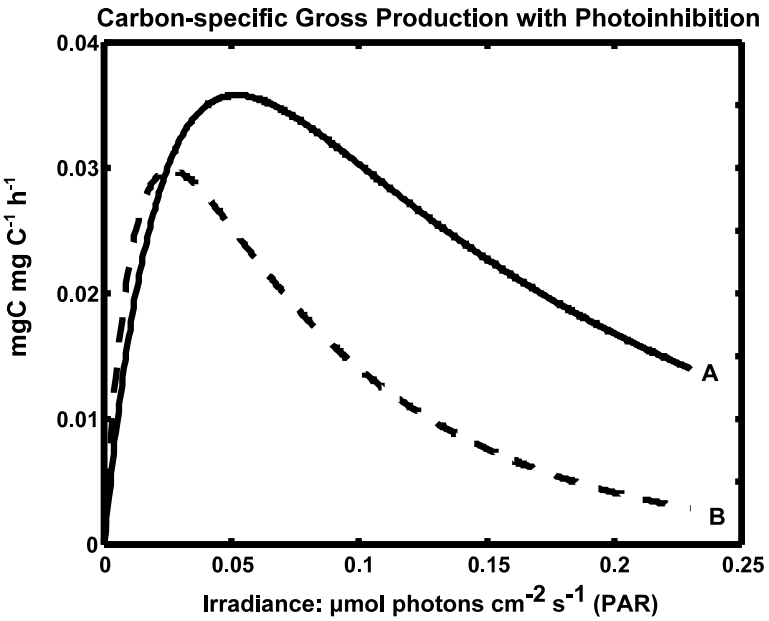

Figure 4. Carbon-specific gross photosynthesis with photoinhibition (same α and P^B_m as Fig. 2)

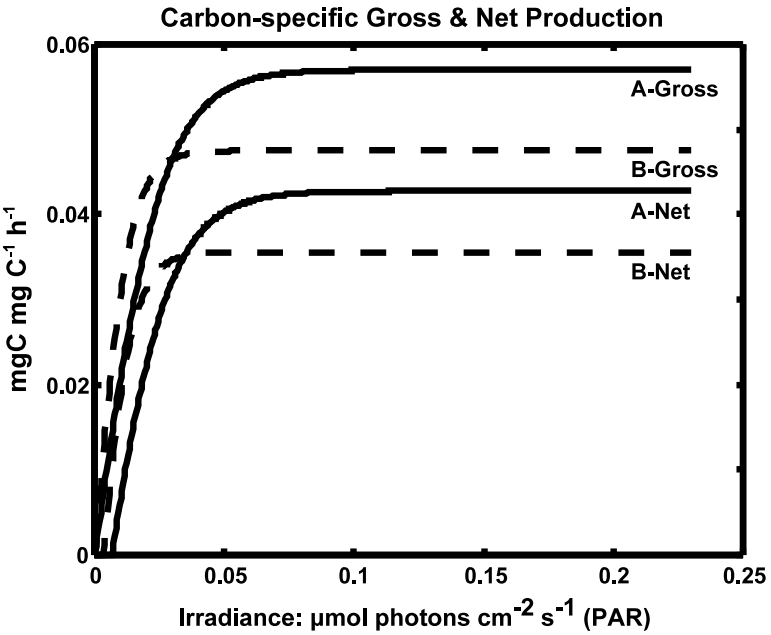

Figure 5. Gross and net carbon-specific photosynthetic rate for shade (B) and light (A) adapted phytoplankton. Respiration is usually assumed to be about 10% of P^B_m , but 20% is used here to show the difference between gross & net carbon-specific production.

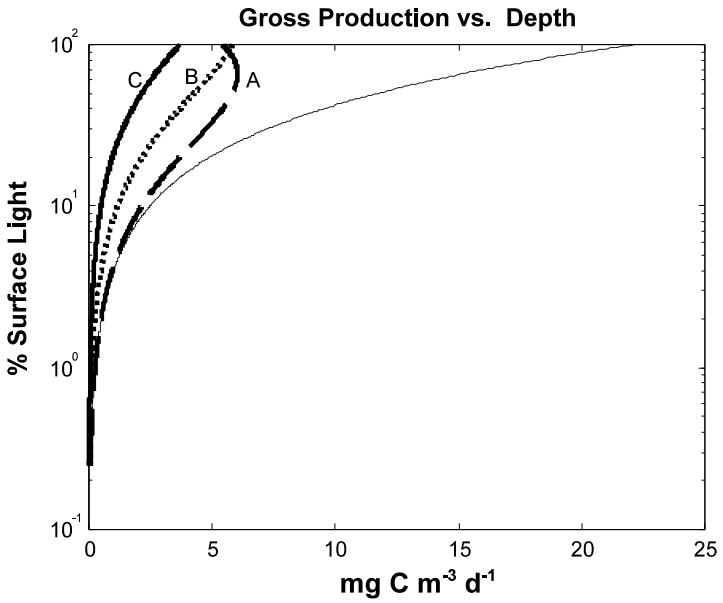

Figure 6 Vertical distribution of gross production in a vertically mixed water column (thus, algal concentrations do not change with depth) (A) around noon on a bright day with light inhibition (the broken line would hold if there was no inhibition); (B), mid-morning on a bright day; (C), early in the morning, or on a strongly overcast day at noon. Ordinate: Percent of blue-green light immediately below water surface.

Figures 1-4 show gross photosynthetic rate. Figure 5 shows the gross and net photosynthetic rate. Respiration rate is usually modeled as being approximately 10% of P^B_m. Slight differences in respiration rate can have profound effects on certain aspects of phytoplankton ecology, especially the timing of the spring bloom. Smetacek & Passow (1990) show the dramatic increase in the critical depth for phytoplankton capable of growing with respiration rates of only 5% of P^B_m instead of 10% of P^B_m.

Figure 6 shows how the photosynthetic parameters shown in Figs. 2 and 4 translate into depth-dependent gross production.

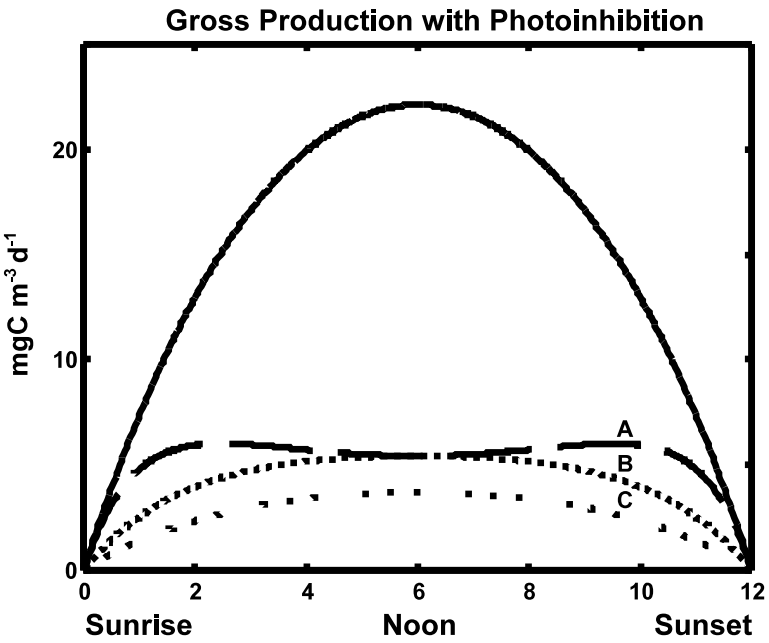

Figure 7 Gross production against time of day in a somewhat stratified water column without nutrient limitation on a bright day, to show effect of light inhibition around noon and of afternoon depression. (A) surface (broken line as in Fig.6); (B) at a light level slightly below saturation intensities around noon; © in the lower part of the photic zone. The upper-most line is the gross production integrated over the photic zone.

Figure 7 shows the consequences of the same

P *vs.* I curve parameters from the previous figures on hourly production rates. Note the noon-time dip in production in the surface layer, due to photoinhibition (Curve **A** in Fig. 7). **Mann & Lazier (1996)** note another confounding factor controlling "real" hourly production rates in the field. If the wind is constant throughout the day, solar heating will warm the surface layer slightly each day, shallowing the mixed layer by a few meters. All else being equal, phytoplankton cells will spend more time near the surface later in the day than in the morning. At night, the water column cools slightly, increasing the mixed layer thickness.

Outlines of papers

ASSIGNED

Harrison *et al.* 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.

1.Abstract:
- 1.1.Simulated in situ method tested in stratified water.
- 1.2.model v. direct measurements

2.Introduction
- 2.1.Different methods, *in situ* method the best
- 2.2.Simulated *in situ* used most commonly
- 2.3.Modeling method.
- 2.4.biological profiling information, in situ fluorometry.
- 2.5.This paper a comparison of methods.

3.Methods
- 3.1.3 cruises.
- 3.2.water samples taken at 100, 50, 25, 10 and 1% light depths.
  - 3.2.1.based on Secchi disk.
  - 3.2.2.PAR was 45% of pyranometer value
- 3.3.24 h 200-ml incubations on board deck for P v. I incubations
  - 3.3.1.model P *vs.* I curves used 30-50 100 ml samples, for 2-4 h.
  - 3.3.2.P *vs.* I measurements made at 2 depths: 1% and 50%
  - 3.3.3.Natural sunlight used.
  - 3.3.4.time-zero or "dark bottles" used as blanks
- 3.4.**Jassby-Platt (1976)** relationship:

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

where, P^B = *Chl a specific production*
= $[mgC\ (mgChl\ \underline{a})^{-1}\ h^{-1}]$.
P^B_m = *Assimilation number.*
= *the maximum photosynthetic rate at light saturation.*
α = *the initial slope of the P vs. I curve.*
= $[mgC\ (mgChl\ \underline{a}\ h)^{-1}\ (W\ m^{-2})^{-1}]$, *or*
= $[mgC\ (mgChl\ \underline{a}\ h)^{-1}\ (E\ m^{-2}\ h)^{-1}]$
I = *the light intensity of PAR*: $[Watts\ m^{-2}]$, *or* $[Einsteins\ m^{-2}\ h^{-1}]$.

- 3.5.photoinhibition equation:

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

where, α = *Initial slope of P vs. I curve.*
β = *photoinhibition parameter.*
= *negative slope at high light intensity.*
P^B_s = *max. photo. rate without photoinhibition.*

3.6.Hourly primary productivity rates computed

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

$$P(t) = P^B (I(t))*B. \quad (3)$$

3.7.Rates for each depth were computed using 100, 50, 25, 10 and 1% surface light values. Daily rates were calculated by summing hourly rates.

$$P_v = \Sigma P(t) \quad (4)$$

3.8.Trapezoidal integration of P_v over the total depth interval samples.

4.**Results and Discussion**

4.1. Data used to compute model estimated production (Fig. 1)

Fig. 1. Computational scheme. Dotted lines use photoinhibition model. Hourly and cumulative production

4.2.Arctic waters show nearly linear diel photosynthesis (Fig 1. bottom right), Figure 2 top.

Fig. 2. Relationship between PP measured using 4-h and 24-h incubations. In Arctic waters, uptake is nearly constant over the 24-h period.

4.3.Model and SIS predicted estimates showed good agreement (Fig. 3).

Fig. 3.Mean primary production rates in the euphotic zone, comparing SIS with model estimates. Solid line SIS, broken HT, dotted line, photoinhibition model. There is more recycling in the surface layer (*e.g.*, phytoplankton to zooplankton)

4.3.1.2-4 hr P *vs.* I *vs.* 24 hr SIS

4.3.2.Slight discrepancies due to the use of tungsten lamps.

model estimates used tungsten lamps

Fig. 4.Relationship between model and SIS production rate estimates for individual depths. (Model tends to greatly overestimate production at the 1% light depths, but note change in scale).

4.3.3.light quality differences.

4.3.4.or differences in phytoplankton populations or adaptations

Fig. 5. Relationship between model (HT) and SIS areal production estimates.

Fig. 6. Effects of spectral differences.

5.Conclusions

5.1.model estimates close

5.2.get P vs. I parameters from upper mixed layer (ANOVA in Table 6)

5.3.More work needed on the effects of spectral quality on production

5.4.

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*]

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.* (3.8)

k_f = *de-excitation of singlet to fluorescence*

k_d = *heat.*

k_p = *photochemistry.*

9. Photosynthesis and primary production in nature
    i. Large number of photochemical responses that occur on short and long scales.
    ii. Acclimations vs. adaptations
  b. Estimating photosynthesis in aquatic systems (p. 264)
    i. Gross photosynthesis: the light-dependent rate of electron flow from water to terminal electron acceptors (e.g., CO_2)
      (1) oxygen evolution modified by the Photosynthetic Quotient.
    ii. et photosynthesis
    iii. Net primary production

Figure 9.1

    iv. Community respiration
  c. Measurements of rates of gas exchange
    i. The ^{18}O method
      (1) Addition of $^{18}O_2$ and measurement of light dependent production of ^{18}O -labeled water
      (2) tedious and expensive
    ii. The ^{14}C method
      (1) Introduced by Steemann-Nielsen 1952
      (2) ambient DIC about 2 mM
      (3) After steady-state achieved, rate of incorporation equals net production
      (4) Incubation problems
        (a) Incubation time remains an issue
        (b) trace metal contamination a problem for measurements prior to 1980 in open-ocean incubations

Scintillation counters

        (c) Natural light vs. simulated *in situ* approaches
  d. Integrated water-column photosynthesis (p. 269)
    i. Euphotic zone

Figure 9.2. A schematic diagram showing the vertical profile of photosynthesis.

    ii. Non-dimensional P vs. z

Figure 9.3. A simulation model showing the effect of vertical motons on the light environment

  e. Phytoplankton respiration (p. 272)

Figure 9.4 A schematic diagram showing the relationship between density, net photosynthesis, net primary production, dailiy integrated photoautotrophic respiration (Rv), daily integrated total community respiration, the depth of the euphotic zone and the critical depth.

f. The effect of photoautotrophic biomass

Figure 9.5 One thousand vertical profiles of carbon fixation as a function of physical and optical depth.

g. Temporal variations in light in aquatic ecosystems (skim only for 9/17 class)

h. Diel cycles and Circadian rhythms

i. P vs. E curves and bio-optical models

j. ***In Vivo*** **Fluorescence approaches** (p. 282)

In vivo fluorescence
Variable quantum yield of fluorescence
-fluorescence yields higher during day than at night
-Appearance that there is a subsurface chlorophyll maximum, when this is not so.

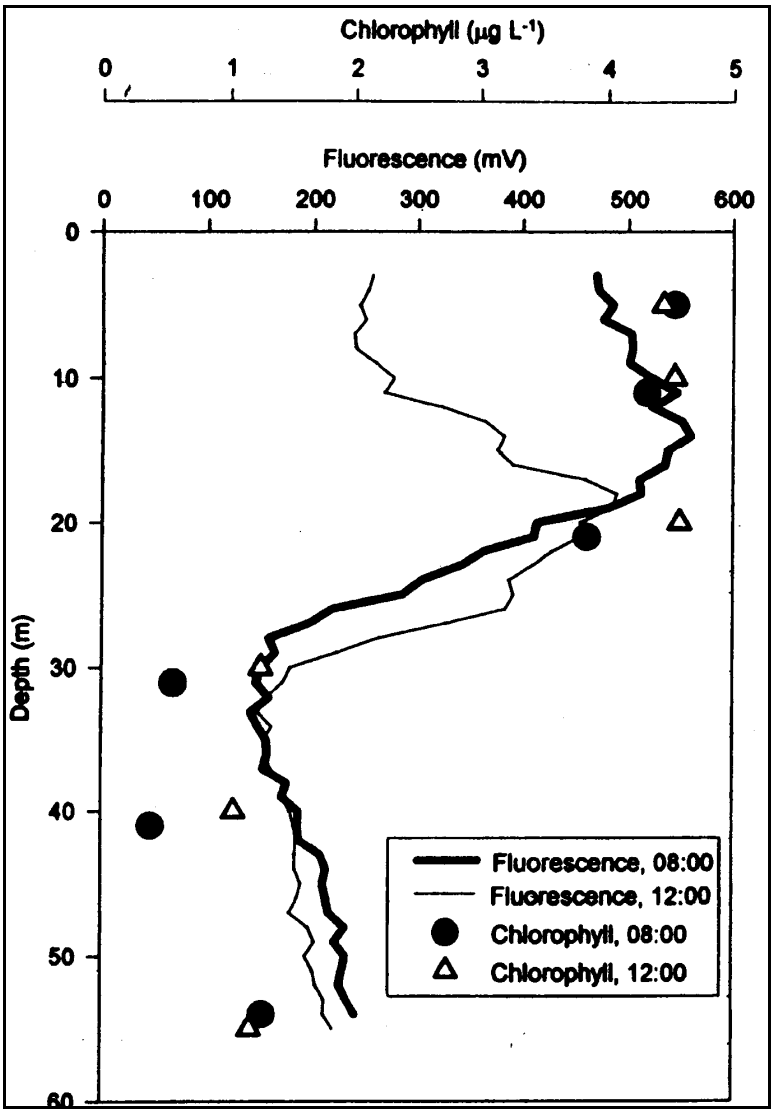

Figure 9.6. An example of non-photochemical quenching of in vivo fluorescence in the ocean from the NW Atlantic in April. The subsurface fluorescence maximum does not correspond to a subsurface Chl *a* maximum.

Nonphotochemical quenching due to the antennae and the reaction center

i. Profiles of fluorescence with a fast repetition rate fluorometer

k. Integrated water-column light utilization efficiency.

SUPPLEMENTAL

Parsons, T. R, M. Takahashi & B. Hargrave. 1984. Biological Oceanographic processes, 3d edition. Pergamon Press pp. 61-80.

1.Light quality
- a.Wavelengths
  - i.usable between 300 and 720 nm PAR (photo. available radiation)
  - ii.PUR, photo. usable radiation, fraction available being used
  - iii.PSR, amount stored as chemical energy
- b.Chromatic adaptation:adaptation in sessile benthic algae, light quantity not quality (Rhee, p. 50)

2.Measurement of light quantity
- a.units: µEin =microEinsteins

3.Extinction in the water column
- i.Secchi disk
- ii.light meters

4.light adaptation
- a. P *vs.* I curves: Banse's figures (6.1 - 6.5)
  - i.Prezelin's relationship (Rhee p. 52, shown in Fig. 6.1 of HO6)
  - ii.Photoinhibition: depression in P *vs.* I curve
  - iii.*Chlorella* type
    - increase cellular Chl *a*
  - iv.*Cyclotella* type
    - cellular Chl *a* content unchanged
- b.Perry showed increase in photosynthetic unit size at low light
- c.Falkowski measures Chl/P700 ratio

5.Time scales
- a.rate of adaptation/rate of mixing important: 1st order kinetics (Falkowski found 2 days)

6.Diel rhythms
- a.Falkowski (1984) picosecond to month scales

7.Respiration rates:
- a.function of P_{max}; approximately 10%

8.photorespiration may be important

9.Interactions between light and N. limitation:Interactions are neither additive nor multiplicative

10.Temperature
- a.affects distribution and seasonal succession of species
- b.Eppley's equation assumes that Temp affects on µ-max, not K_s,
  - recent studies show effects on K_s

11.Temperature-light interactions
- -photochemical reactions insensitive to temperature

12.Conclusions
- a.threshold nutrient concentrations set by RKR -type relationships.
- b.Relationships well understood for steady state
- c.Interactions between environmental variables important

OTHERS

Rhee, G.-Yull. 1982. Effects of environmental factors and their interactions on phytoplankton growth. Adv. microb. Ecol. *6*: 33-74.

1. Introduction
   -a review of nutrients, light and temperature effects
2. response of species to changing environmental stresses are the driving forces behind succession and species distribution.
3. Nutrients.
   - a. Nutrient limitation inferred
     - i. from field sampling, elemental composition: Redfield (1958) atomic ratio: 106:16:1

ii. for photoautotrophs carbon is rarely limiting (Schindler 1977, Parsons *et al.* , 1978
iii. Redfield ratio is generally found in oceanic and neritic regions *[? evidence]*
iv. Ryther & Dunstan (1971): N is the limiting nutrient in seawater
v. Freshwater: P is limiting (Thomas 1969, Fuhs *et al.* , 1972, Line and Schelske 1979)
vi. *[G. P. Harris argues that N & P are both limiting in freshwater & marine]*
vii. Si limitation: Smayda (1974), Kilham (1975).
Si:P ratio is 8:1 to 12:1 (D'Elia *et al.* , 1979)

b. Limiting nutrients: growth and uptake
i. external concentrations and growth

Equation (1) is wrong. The correct equation is:

$$N_t = N_o e^{\left(\frac{\ln(2)\, t}{t_d}\right)} = N_o e^{\mu t}, \qquad (1)$$
$$\textit{where, } t_d = \textit{the population doubling time.}$$

(1) Monod equation:

$$\mu = \frac{\mu_{max} S}{K_s + S}. \qquad \textbf{(7)}$$

(2) threshold concentrations
(3) in the field, S cannot be related to growth.

ii. intracellular concentrations and growth

Droop (1968) equation:

$$\mu = \mu'_{max}\left(1 - \frac{q_o}{q}\right).$$
$$\textit{where, } q = \textit{cell quotient.}$$
$$q_o = \textit{cell quotient at } \mu = 0. \qquad \textbf{(8)}$$
$$\mu = \textit{specific growth rate.}$$
$$\mu'_{max} = \textit{asymptotic growth rate (at } q = \infty).$$
$$> \mu_{max} \textit{ (from Monod equation).}$$

Caperon (1968):

$$\mu = \frac{\mu_m' (q - q_o)}{K_q + (q - q_o)}. \qquad (6, \text{p. } 38)$$

(1) Droop's equation is the simplest
(2) μ_m' is always greater than μ_m (p. 39)
(3) *"Under steady-state conditions, the Monod and cell-quota models are mathematically equivalent in describing growth rate (Burmaster 1979)"*. p. 40

iii. **nutrient uptake and growth**

(1) $dq/dt = v - \mu q$, where v is uptake rate (8)
(2) $v = \mu q$ (9)
(3) $v = V'_{max} S(K_m + s)$ (10)
(4) One cannot used K_m as a substitute for K_s

c. **Optimum N:P ratios and multinutrient limitation**
i. Liebig's law of the minimum
ii. Experimental results (Rhee 1974, 1978, Droop 1974) showed that growth is controlled by the nutrient in shortest supply.
(1) N:P ratio of 30
(2) optimum N:P ratio is the same as the ratio of minimal cell quotas for N and P q_{oN}/q_{oP} (Rhee 1978)

4. **Light**

a. **Growth and Photosynthesis**

growth rate

(1) **compensation light intensity**: the light intensity required to maintain the viability of the population without net growth.

(2) p. 46. When growth is expressed as a function of the absorption rate of light energy (q_E) one can obtain the efficiency of an organisms to convert light energy to growth. The rate q_E may be expressed as$(dE/dt)/((1/X)$, where X is biomass. q_*e has units of time^{-1}. The relationship between μ and q_E is linear:

$$\mu = c*q_E + \mu_e \quad (15)$$

(3) *[See Laws latest 1990 models for this]*

(4) Efficiency varies between species, highest for the green algae and lowest for the cyanobacteria.

(5) **Succession:**species differences in the efficiency factor and the compensation rate play an important role in phytoplankton succession.

Green algae===> cyanobacteria (low compensation rates of absorption)

(6) K_i, the light required to support half maximal growth

(7) μ *vs.* I relationship should be predictable from plots of P *vs.* I. The disagreement is not surprising since cells excrete organic carbon (Nalewajko and Marin 1969), Berman and Holm-Hansen 1974, Hellbust 1974, Berman 1976, Mague *et al.* , 1980)

ii. Photosynthesis: light and dark reactions.

light:photochemical reactions generate ATP and reducing power with evolution of O_2
dark:CO_2 is enzymatically reduced to carbohydrates and other products using the energy and electrons generated in the light reactions.

(1) slope of the P *vs.* I curve dictated by light reactions, asymptote by dark reaction

(2) Light:

(a) Ψ & II: each has its own set of light-absorbing pigments,

(b) P700, a special Chl *a* pigment assembly serves as a an electron trap in Ψ

(i) electrons in the trap are expelled.

(c) PSII: P680 photosystem instead of P700

(i) electrons expelled from the trap and pass through redox carriers, generating ATP from ADP by photophosphorylation. The electrons come to rest at P 700. The electron in PS II comes from H_2O with release of O_2

(d) C_3 *vs.* C_4:*Skeletonema costatum* and *Phaeodactylym tricornutum* is primarily of the C_4 type: [This may not be the case]

(e) -*Dunaliella tertiolecta* assimilates CO_2 primarily through the C3 pathway during exponential growth and by both C3 and C4 during stationary phase (Glover *et al.* , 1975, Beardall *et al.* , 1978, Mukerji *et al.* , 1978, Glover and Morris 1979, Morris 1980)p. 48

[Dark: plateau of P *vs.* I curves reflects limitations by dark reactions.

Calvin Bensen cycle: CO_2 carboxylated to ribulose 1,5 bisphosphate by RuBP carboxylase to yield 2 molecules of phosphoglycerate.

C_4: CO_2 incorporated into phosphoenolpyruvate by PEP carboxylase. The net CO incorporation in C_4 plants take place through the Calvin cycle.]

[Question for the class:Why would a plant have a C_4 metabolism?]

iii. Effects of light quality (p. 49)

(1) Light quality can be important. Some species showed maxima in blue and red light (Wallen and Geen 1971, Brown and Geen 1974)

(2) The enhancement of protein synthesis appears to be related to the enhanced PEP carboxylase activity under blue light (Miyachi *et al.* 1978, Rutyers, 1980)

(3) *Excretion depends on spectral composition of light* is least under blue and red light, and the nature of the products varies with the spectral composition of the light under which the cells are grown (Soeder and Stengel 1974, Brown and Geen 1974).

(4) Pigmentation changes with respect to light quality.

(5) Distribution of benthic algae (green to brown to red) explained in terms of light quality.
(6) Photosynthesis per unit quanta showed no correlation with their depths.

iv. Photoinhibition
(1) Disruptions of both light and dark reactions.
(2) precedes the destruction of chlorophyll
(3) processes implicated:(page 50)
(a) action of UV light
(b) inhibition of dark respiration
(c) stimulation of chlorophyllase activity
(d) enhancement of photorespiration (Tolbert *et al.* , 1974, Li *et al.* , 1980)

v. **Cell composition:**
(1) cellular contents of Chl a and accessory pigments (*e.g.*, Chl b, c, biliproteins and carotenoids) increase
(2) Cell RNA and protein content increased.

(3) **Light adaptation**

Light changes seasonably, daily, with depth and with turbidity.
-Jørgensen (1969,1970) proposed 2 types of adaptation:

vi. **Chlorella type adaptation.**

organisms increase their cellular Chl *a* content with decreasing light: little difference in photosynthetic rates at adapted light intensity between high- and low-light adapted cells.

Net photosynthetic rate per cell appears to be constant during steady state regardless of the level of light, but the rate per unit Chl a follows a saturation function.

vii. **Cyclotella type of adaptation.**

cellular Chl *a* content remains unchanged, and only the light-saturated photosynthetic rate varies.
(1) Mechanisms:
(a) *Scenedesmus obliquus*: regulation of redox carriers
(b) initial slope of P (per cell) *vs.* I was little different
(c) light saturation level changes.: difference in the amount of redox carriers (*i.e.*, when low-light adapted cells are exposed to high light, the concentration of redox carrier (plastoquinone) becomes limiting to photosynthesis.)
(d) *Glenodinium*: adapts by increasing the efficiency of light absorption.: *Glenodinium* model plotted in Banse's figure 6.1.
(2) Falkowski and Owen (1980): suggested 2 strategies, based on the Chl:P700 ratio
(a) *S. costatum* adapted by increasing the photosynthetic unit size while the reaction centers for PS I (P700) per cell decreased.
(b) *Dunaliella*, the photosynthetic unit size decreases, but the number of reaction centers increased.
(c) Conclusion: either change will yield an increase in the efficiency of light energy transfer to reaction centers under low light conditions. In theory, an increase in number would increase photosynthetic capacity, whereas an increase in size would enhance the efficiency of light utilization. However they found that the efficiency of light utilization per unit of Chl *a* (the slope of a P *vs.* I curve) did not increase, while the Chl/P700 ratio increased.
(3) Perry *et al.* (1981) reported an increase in the photosynthetic unit size in five marine species at low light intensities.
(a) Perry *et al.* (1981) suggest that organisms with intrinsically larger photosynthetic unit sizes may adapt more readily to the rapid fluctuations of light that occur in the mixed layer. [K-selected species]
(4) Time scale of adaptation:
(a) If the rate is slower that the rated of displacement, light adaptation would not be manifested as a function of depth.
(b) Regulation can occur in less than one generation
(c) p. 54: When shade adapted cells are exposed to strong light, the fluorescence yield measured as the ratio of *in vivo* fluorescence to Chl *a* decreases. This decrease reflects energy spillover (Govindjee *et al.* ,

1973) *i.e.*, the energy absorbed by PSII is directed away from its reaction center to the reaction center of PS I. This change, which would reduce O_2 production as well as noncyclic electron transport, takes place within a few minutes. Therefore it has been suggested that energy spillover is a short term mechanism of adaptation, which may be of particularly significance for organisms subject to wide fluctuations of light in a short time period.

(d) Depressed fluorescence yield observed in near-surface waters of lakes. Depression inversely related to light intensity and was reversible. Similar depressions have been noted by Kiefer 1973. Decrease attributed to the contraction of chloroplasts.

(e) fluorescence yield also varies with nutrient limitation Kiefer (1973)

b. Interactions of light with nutrient limitation and uptake.

i. Nutrient limitation decreases photosynthetic rate per cell or per dry weight.

ii. Seft (1978) $P'_m = P_m(1-[q_o/q])$ (17)

iii. *"Under light limitation, nutrient requirements increase."*
"...in CO_2-limited A. nidulans...the maintenance concentration of CO_2, the concentration below which no growth can occur, increases with decreasing irradiance, and the CO_2 requirement to maintain growth rate also increases (Young and King, 1980)"

iv. The interaction effects of light and nutrient limitation are greater than the sum of their individual effects. The interaction effects are therefore not additive, nor are they multiplicative.

v. Under severe nutrient limitation, an otherwise optimal light intensity can be lethal.

vi. The stimulation of N uptake by photosynthesis can be explained by the availability of photogenerated electrons and ATP

vii. When N-limited *Chlorella fucusa* was given nitrate or nitrite, the CO_2 fixation rate decreased. DCMU decreased nitrite reduction (but not nitrate) by about 50%. About half the electrons used for nitrite reduction are generated photochemically.

5. **Temperature**

a. Growth

i. Growth rate

(1) Arrhenius equation
$A=Ae^{-E/RT}$ (18)
R is the gas constant, T is absolute temperature, E is activation energy'

(2) Relationship between ln μ and 1/T is inversely linear.

(3) single-species growth is rarely linear

ii. Cell composition

(1) cell quotas change [See Goldman for critique]

b. Temperature adaptation

c. Interactions with Nutrient limitation and uptake

i. Optimum is rarely achieved because of nutrient limitation.

ii. temperature effects minimum cell quota

d. Temperature-Light interactions (p. 62):

i. Photochemical reactions are insensitive to temperature.

ii. The slope of the P *vs.* I curve (per Chl a) are little affected. When light is limiting, photosynthetic rate is unaffected by changes in temperature. The plateau changes

6. **Concluding remarks**:

a. Threshold-type control lays a foundation

Growth rate: saturation functions.

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