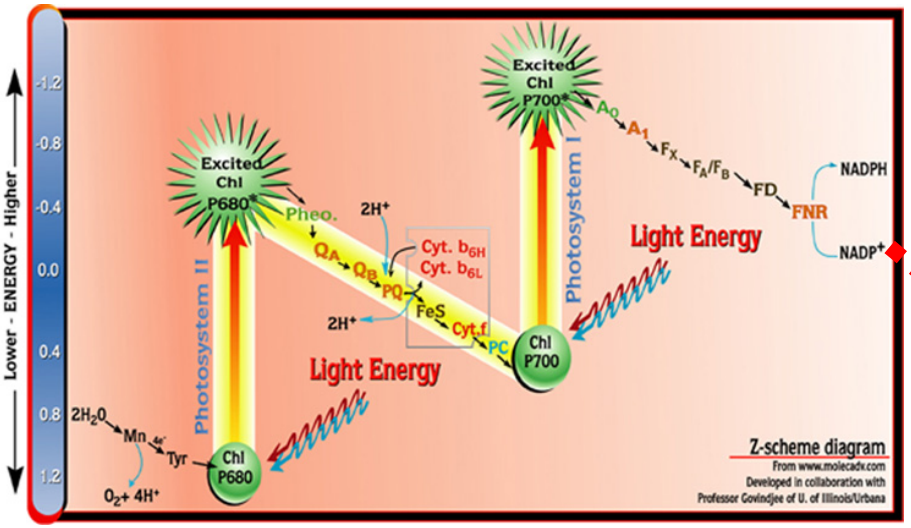
Marine Photosynthesis & Primary Production in the Ocean

Roadmap for this class session:

1. Photosynthesis (refresher) & primary production (some terminology)
2. PS & PP vs. irradiance relationships (P-I curves)
3. PS & PP vs. nutrient concentrations (Michaelis-Menten et al.)
4. PS & PP vs. temperature (Eppley curves)
5. 4 common approaches for measuring primary productivity
6. Some discussion on Martin et al.1994

Refresher slide photosynthesis: light & dark rxns

" $6\ H_20 + 6\ CO_2 \rightarrow 6\ (CH_2O) + 6\ O_2$ "



Light reactions

4 quanta

$H_2O + NADP \longrightarrow \frac{1}{2}\ O_2 + NADPH_2$

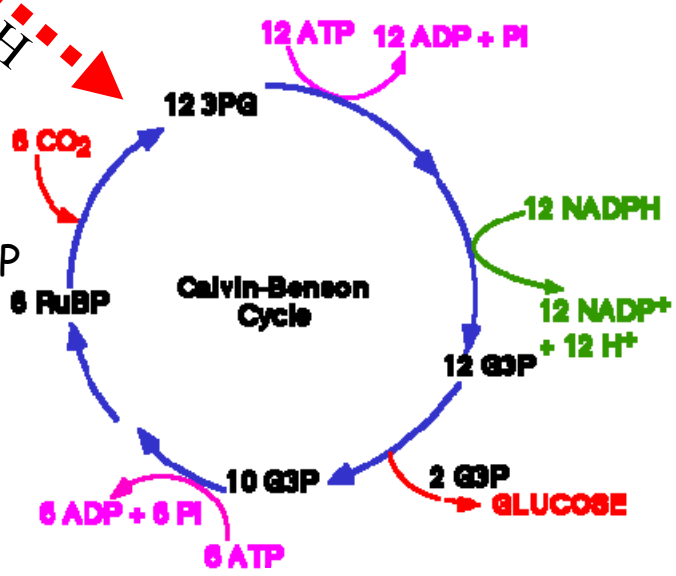
2 ADP + 2 P ATP

ATP
NADPH

"Dark" reactions

$CO_2 + 2\ NADPH_2 \rightleftharpoons CH_2O + H_2O + NADP$

3 ATP 3 ADP + 3 P



CO_2 actually taken from bicarbonate
Zn requirement for carbonic anhydrase

http://www.life.uiuc.edu/govindjee/ZSchemeG.html
http://www.blc.arizona.edu/courses/181gh/rick/photosynthesis/Calvin.html

Primary production, productivity are ecological processes

Some very basic definitions:

Primary production – an <u>amount</u> of photosynthate produced by photosynthesis (e.g., amt of CH_20)

Primary productivity – a <u>rate</u> of this production (e.g., total C fixed by photosynthesis, volume^{-1} time^{-1})

Gross & Net primary productivity

Net primary productivity = Gross - autotrophic respiration

(as with photosynthesis: net = gross – respiration)

Can quickly get more complicated….

Table 1. Different meanings associated with general terms. Because these general terms can be interpreted in many different ways, it is essential to be explicit and precise when discussing the factors that might influence primary production or the growth of phytoplankton.

General term	Specific terms	Comments (references*)
Primary production	Gross primary production	Important for understanding light limitation (1)
	Net primary production	Net rate of synthesis of the organic constituents of plant material in water (2)
	New production	Net accumulation plus export (3)
	Net small particle production	Measured in bottle incubations (4, 5)
	Net community production	Equivalent to new production (4, 6)
Growth	Standing crop of phytoplankton	Net result of phytoplankton growth; definitions of biomass differ (7)
	Potential standing crop	Terminal yield of bioassays (8)
	Specific growth rate of phytoplankton	Omits mortality and dispersal (9)
	Net growth rate of phytoplankton	Includes mortality and dispersal (10)
	Standing crop of plankton or net growth rate of plankton	Includes bacteria and grazers (4)
Control of primary production or control of phytoplankton standing crop†	Direct limitation of phytoplankton specific growth rate	Blackman concept (11, 12)
	Limitation of primary standing crop	Liebig-type (3) or a complex response (12)
	Colimitation of rate process	e.g. Ni and N (13)
	Proximate control	Direct regulation (14)
	Ultimate control	Indirect action through links in the ecosystem (12, 14)

* 1—Smetacek and Passow 1990; 2—Strickland 1965; 3—Dugdale and Goering 1967; 4—Platt et al. 1984; 5—Siegel et al. 1989; 6—Minas et al. 1986; 7—Cullen 1982; 8—Martin and Fitzwater 1988; de Baar et al. 1990; Banse 1990; 9—Lande et al. 1989; 10—Hecky and Kilham 1988; Banse 1991*b*; 11—Blackman 1905; 12—Thingstad and Sakshaug 1990; 13—Morel et al. 1991; 14—Cullen et al. 1992.
† Thingstad and Sakshaug 1990.

Cullen 1991

"…essential to be explicit and precise…"

Primary production done by phytoplankton

Phytoplankton (& all plants) in unusual situation, that

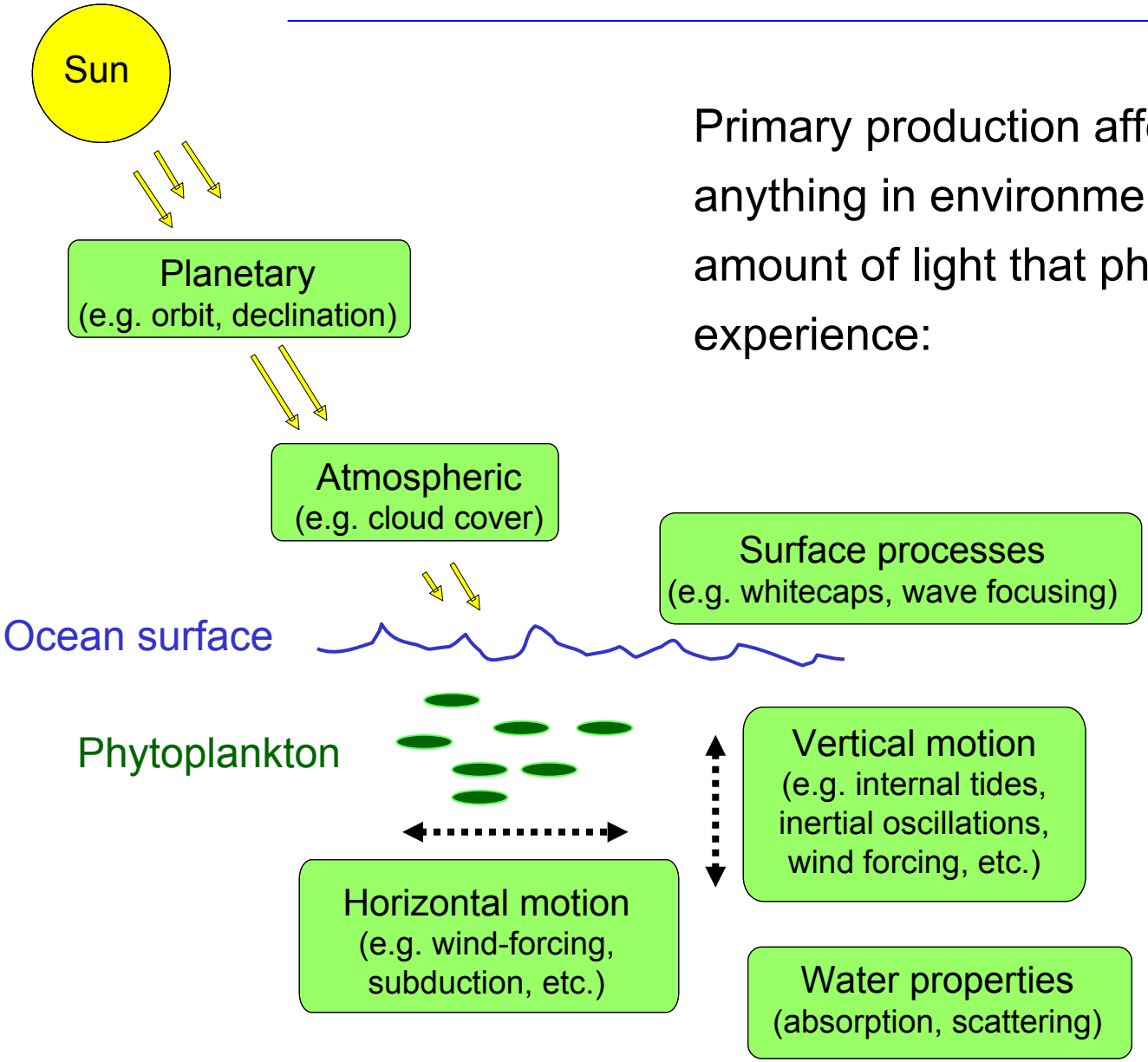
energetic & material resources come from different sources (unlike with heterotrophs)

With photosynthesis → fn (qty of light + nutrients)

With PP = → fn (qty & distributions of light + nutrients)

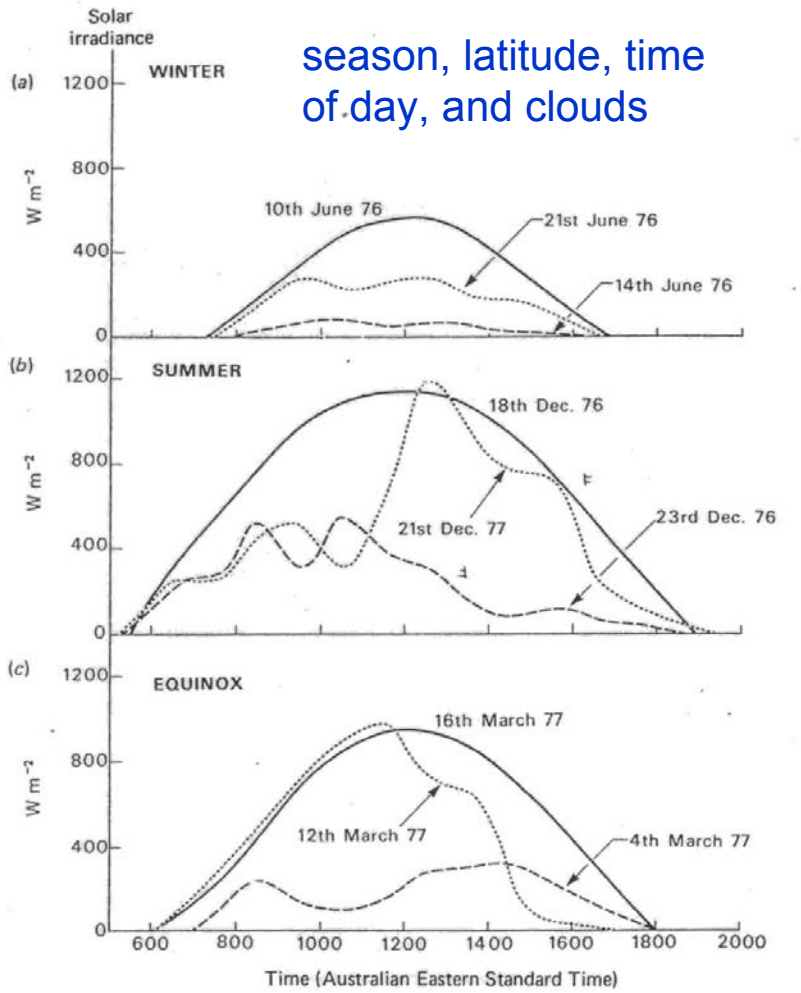
Spatial and temporal uncoupling of material & energetic resources in the ocean is fundamental issue in primary production & phytoplankton ecology.

Energy: sunlight (E or I)



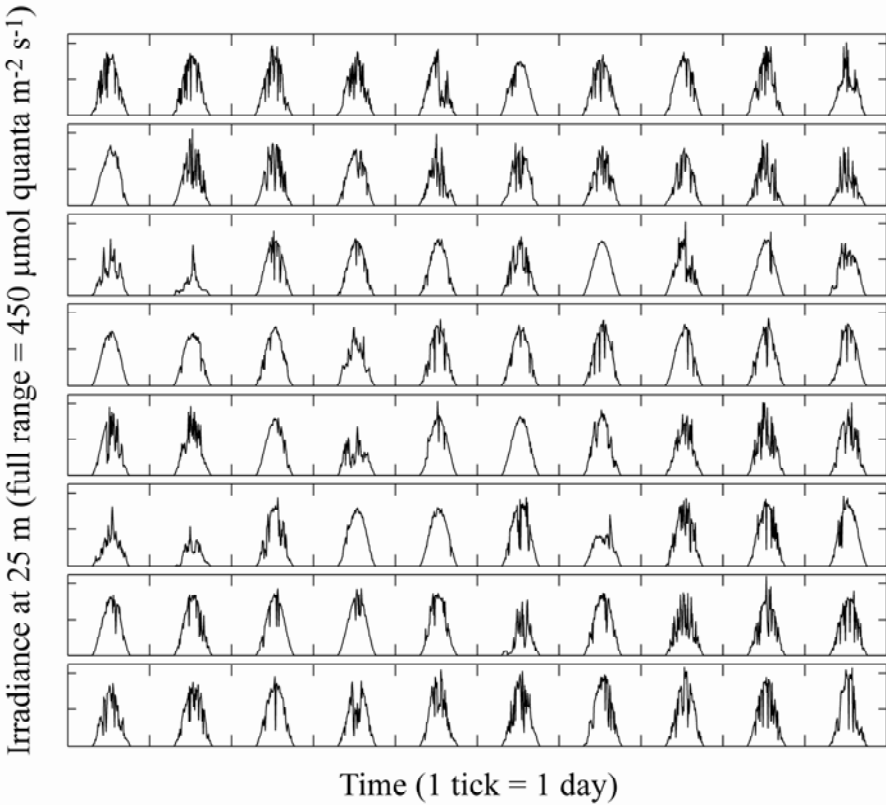
Primary production affected by anything in environment that affects amount of light that phytoplankton experience:

Strong variability: seasonal, latitude, time of day, clouds, etc.



season, latitude, time of day, and clouds

& intermittent, high-frequency clouds…



HALE-ALOHA mooring

Scales & magnitudes of variability in E
Organisms with lifespans of O(days)

JTO Kirk 1994

What about light after it enters the water column?

Seawater affects the light field strongly:

In both intensity and spectral composition

K_{water} = 0.02 m^{-1}, K_{PAR} ALOHA = ?

Red light preferentially absorbed.

Blue light preferentially scattered.

H_2O minimum abs ≈ 460 nm.

With depth color shifts bluer.

(loses red first, green later)

SCUBA diver? Color of blood?

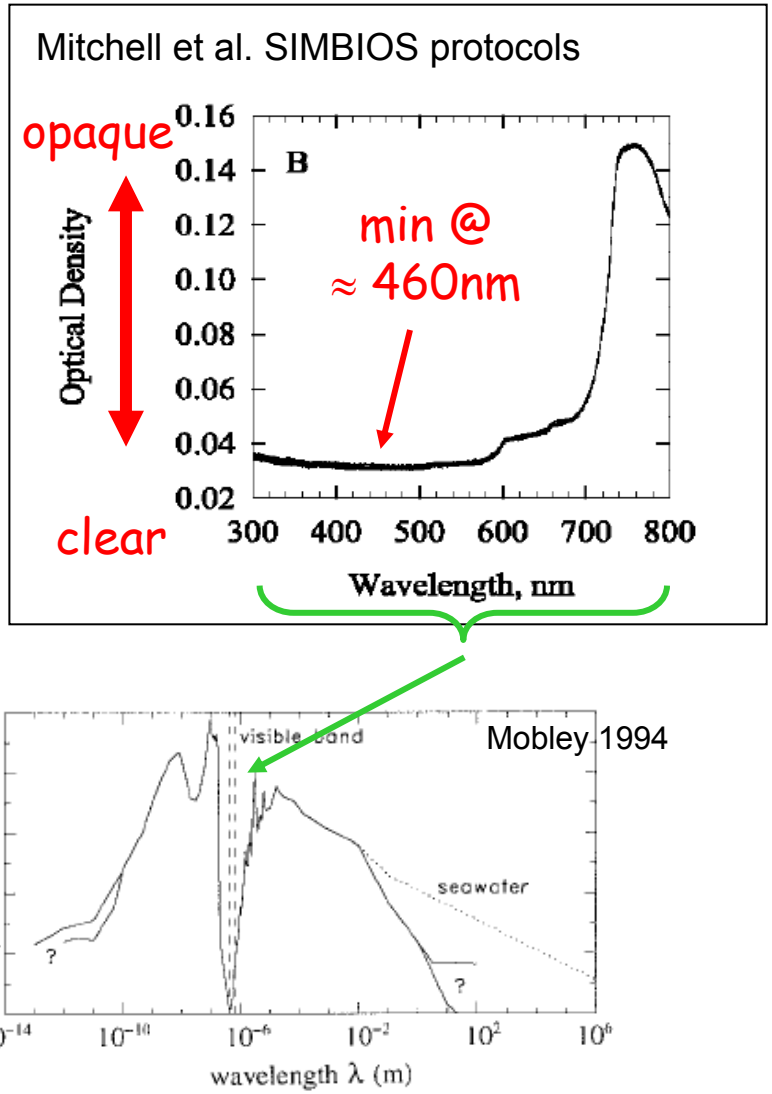
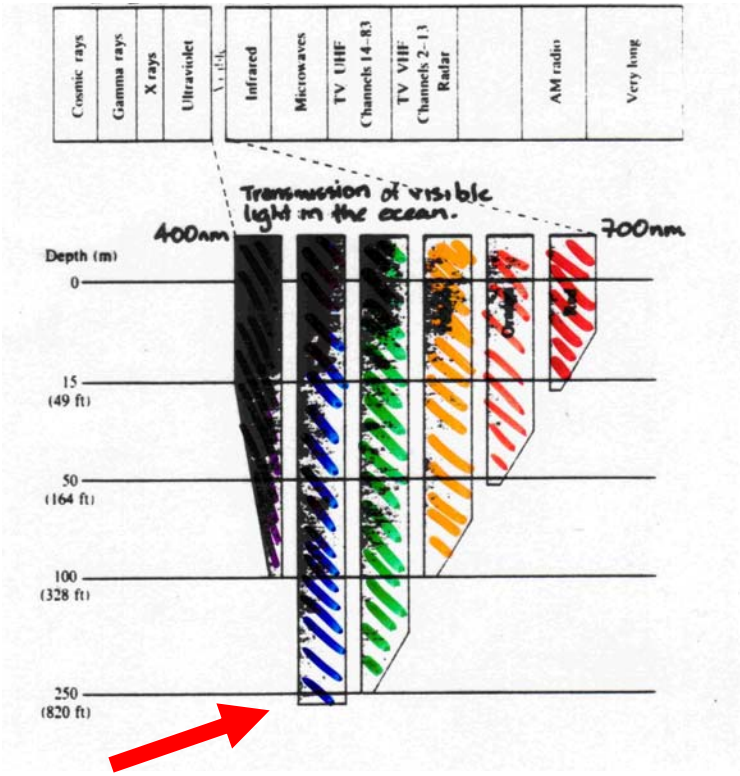
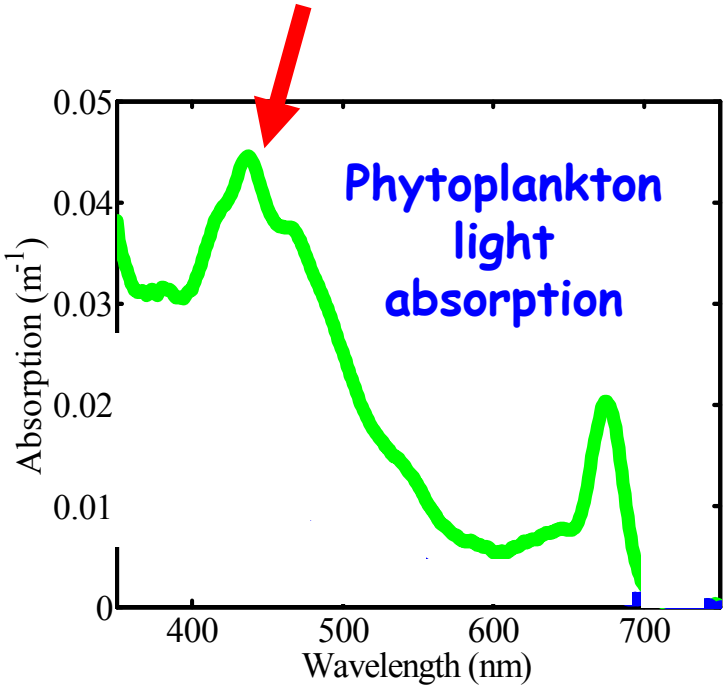


Fig. 3.4. Spectral absorption coefficient of pure water (solid line) and of pure sea water (dotted line) as a function of wavelength. [drawn from data compiled in Hale and Querry (1973), Jackson (1975), Smith and Baker (1981), and Zoloratev and Demin (1977)]

Evolutionary selection to absorb E(λ) = where photons are

E.g., spectral irradiance vs. z → Maximum abs of chl ~ 465 nm





L&P Fig. 2.4

Shouldn't be surprising that chlorophyll *a* absorption max in the blue.

Accessory pigments fill the abs gap (carotenoids, phycobiliproteins).

Yet, evolved differences in algal pigment complements

Implications for the so-called “paradox of the plankton”?

All species occupying identical, homogenous environments?

Fisheries & Allied Aquacultures Image Gallery

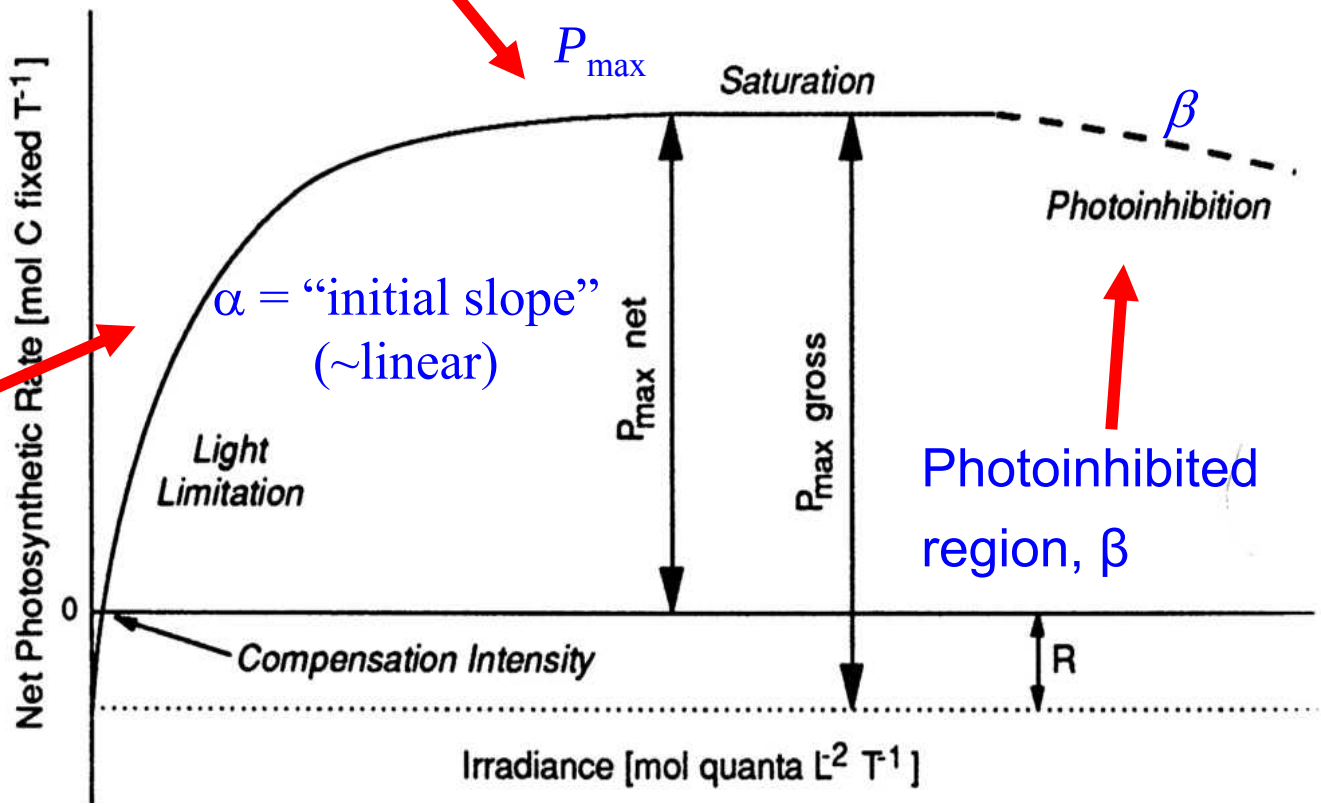
Quantifying photosynthesis-light relationships

Photosynthesis-Irradiance curves: "P-I (or P-E) curves"

P_{max}, α, β
(eqn Miller Ch3)

Saturation maximal rate (limited by dark rxns, P_{max})

Linear, light limited region (limited by light rxns, α)

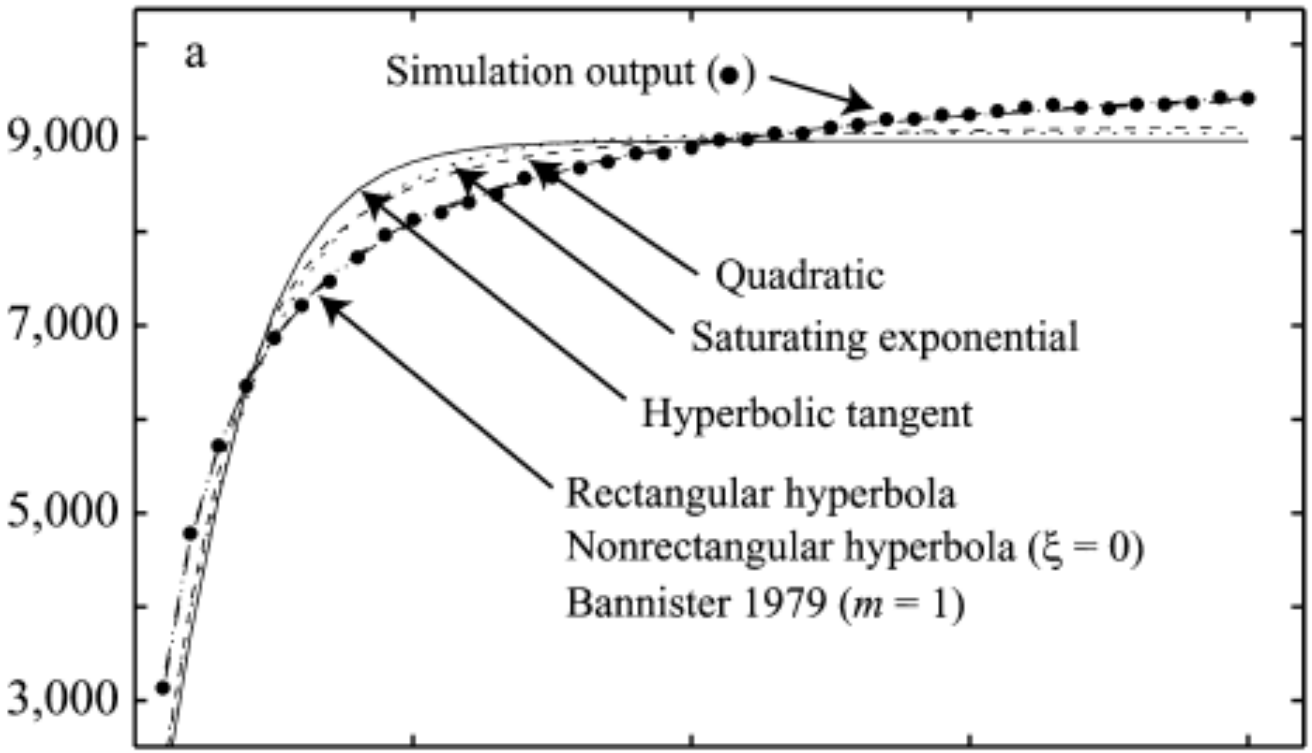


$$P = P_{max}(1 - e^{-\alpha I/P_{max}})e^{-\beta I/P_{max}}$$

$E_K \equiv P_{max} / \alpha$ → light lim to light sat

Many models to describe the linear-saturating phase

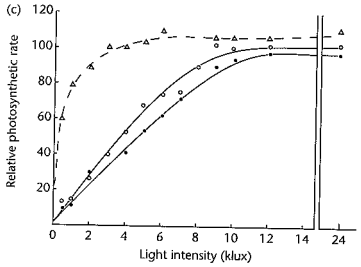
$$P = P_{max}(1 - e^{-\alpha I/P_{max}})e^{-\beta I/P_{max}}$$

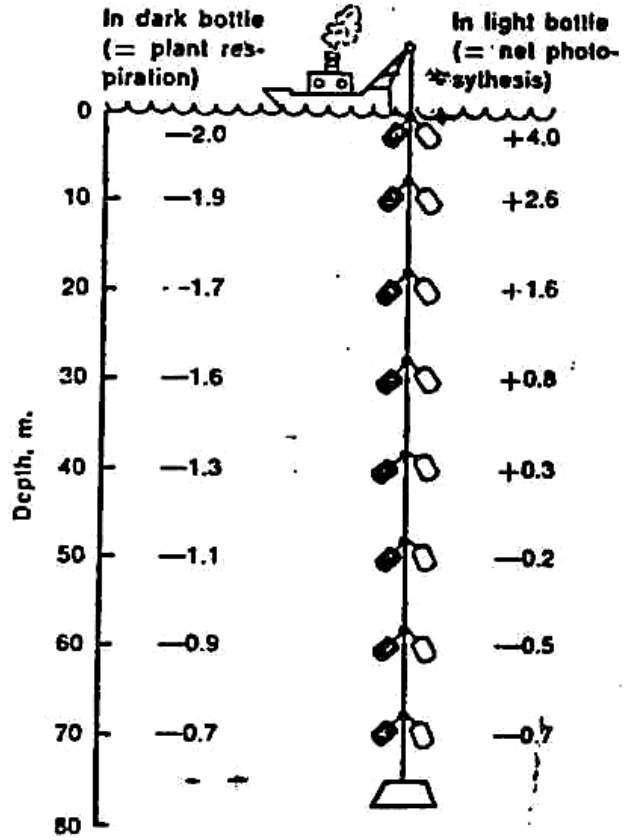


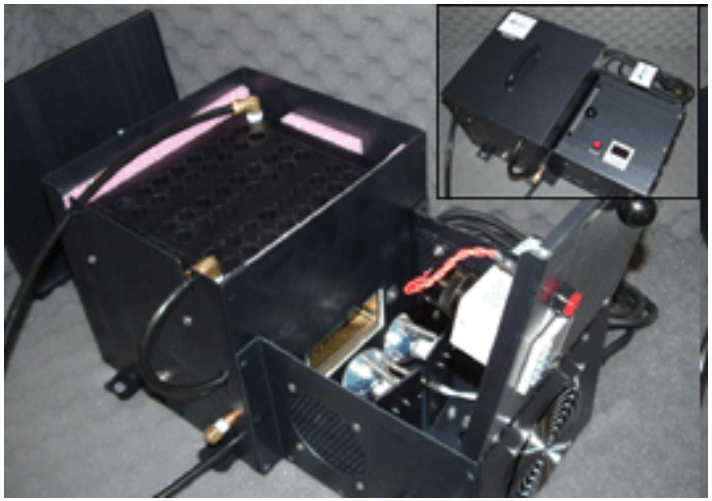
Purely empirical → semi-analytical → fully mechanistic

Laney & Letelier 2009

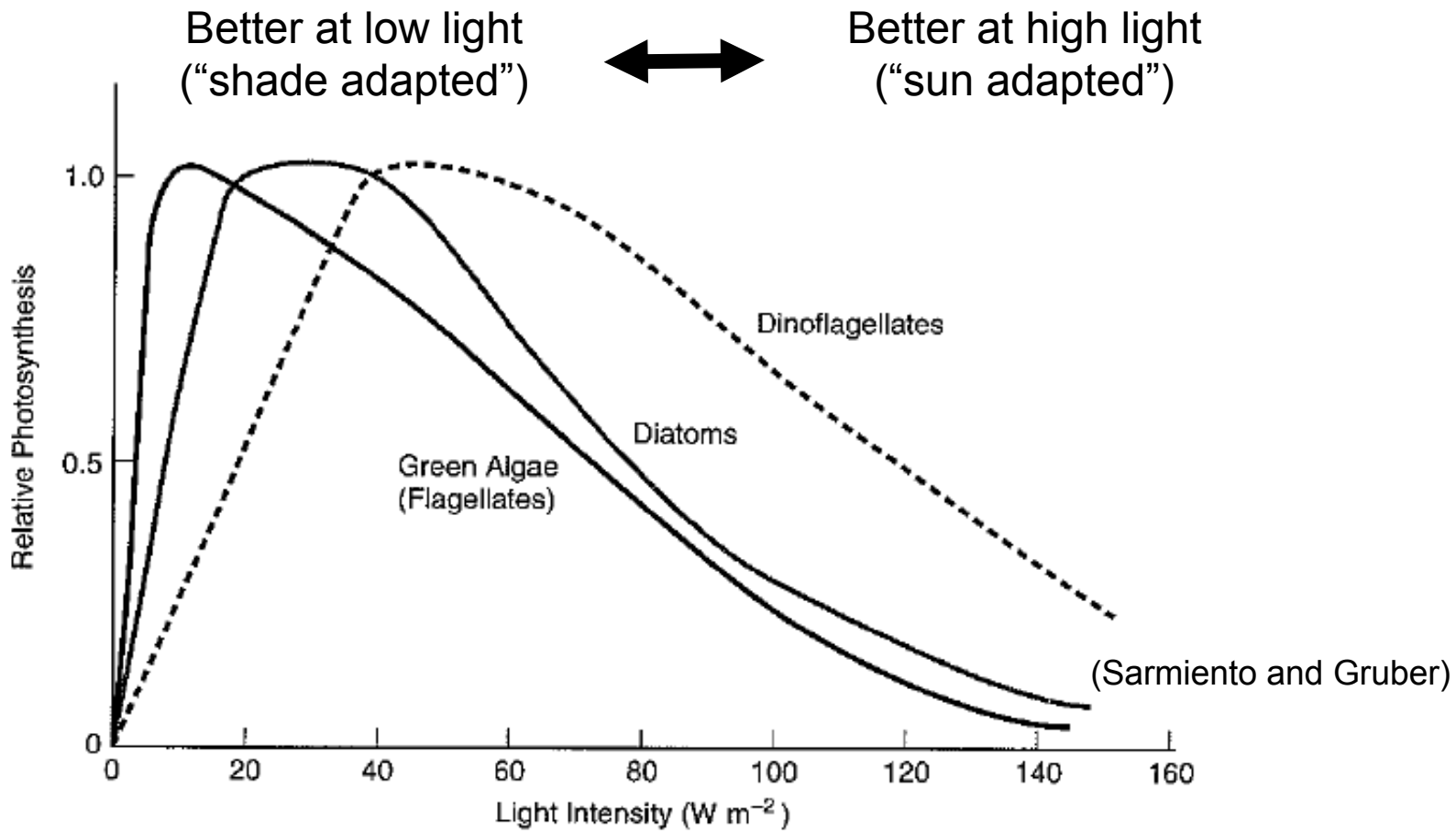
Generating P vs. I: photosynthetrons, incubators, *in situ*







P vs. I curves reflect *adaptation* (evolutionary) to light



(Sarmiento and Gruber)

FIGURE 4.2.9: Schematic P-I curves for various major phytoplankton groups. Based on *Parsons et al.* [1984].

Physiological differences in P-E relationship allow niche partitioning. Paradox?

P-E can also indicate *acclimation* to changes in light

Use curve fitting to estimate:

α (init slope)

P_{max} (sat level)

& compare these

1 vs. 3?
1 vs. 2?

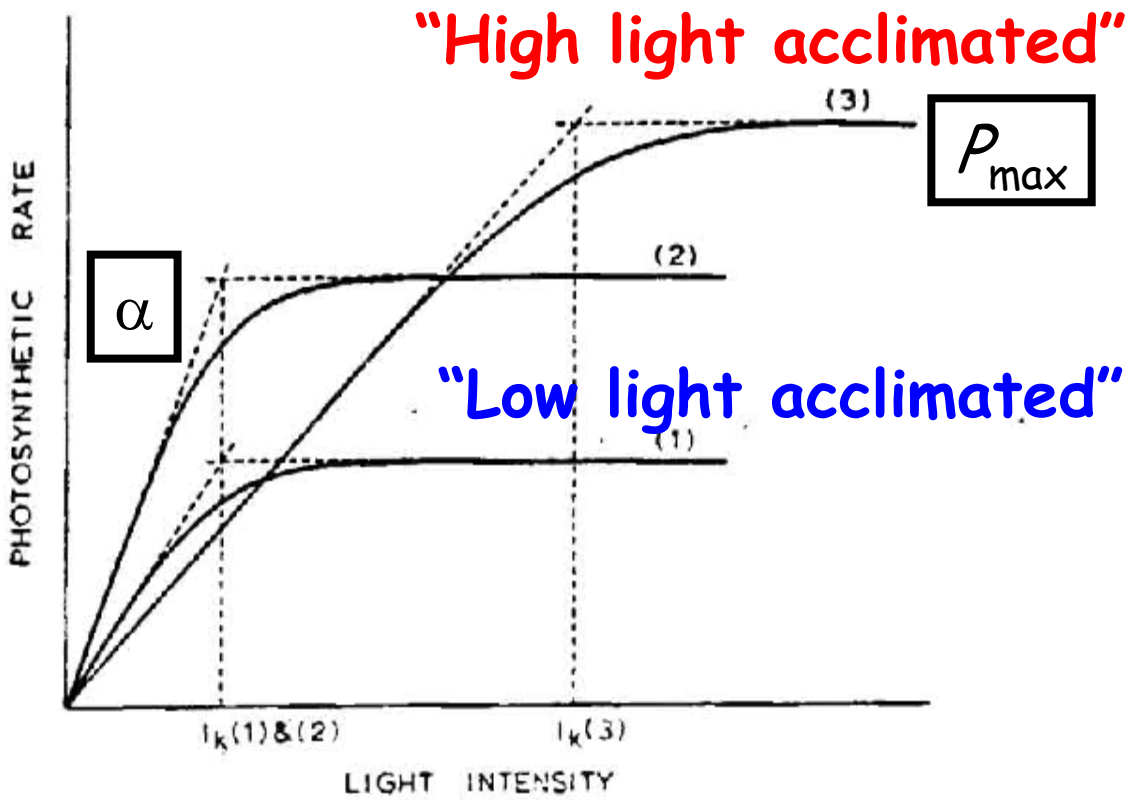


FIG. 30. Three types of *P* vs. *I* curves. (1) and (2) shade type algae showing similar I_k values but with higher photosynthetic efficiency in (2) than (1). Sun-type community (3) showing lower photosynthetic efficiency than (1) or (2) at lower intensity.

Reflecting different investment/structuring of photosynthetic components

Acclimation strategies

Broad taxonomic groups exhibit different photoacclimation strategies.

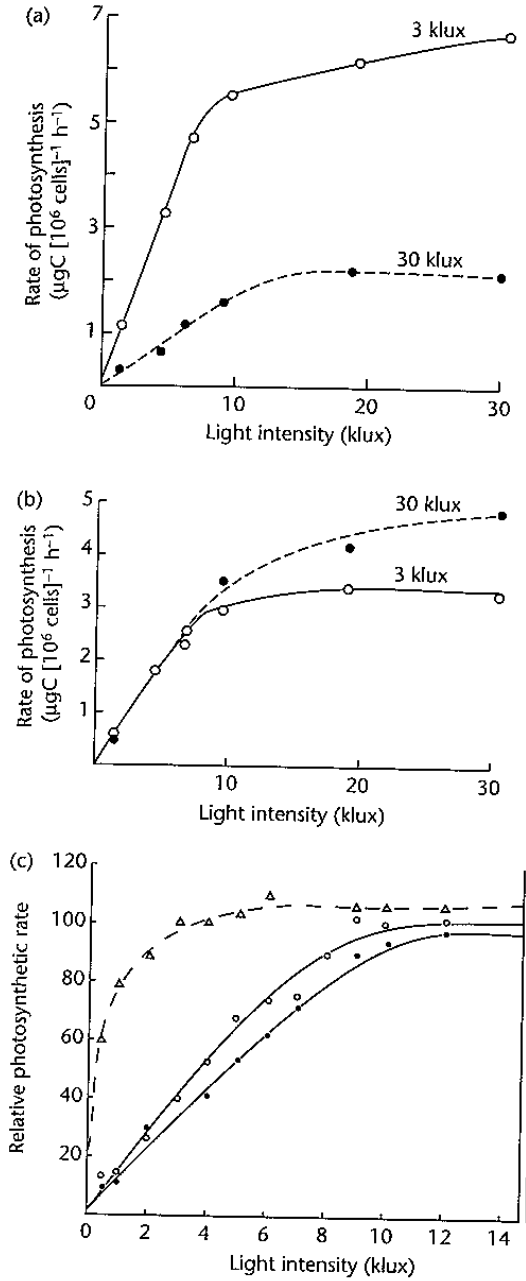
"acclimation" → an organism's individual response to a change in the environment.

"*Photoacclimation*": adjustments to

• Light harvesting capacity

• "Turnover" of photons into useful energy

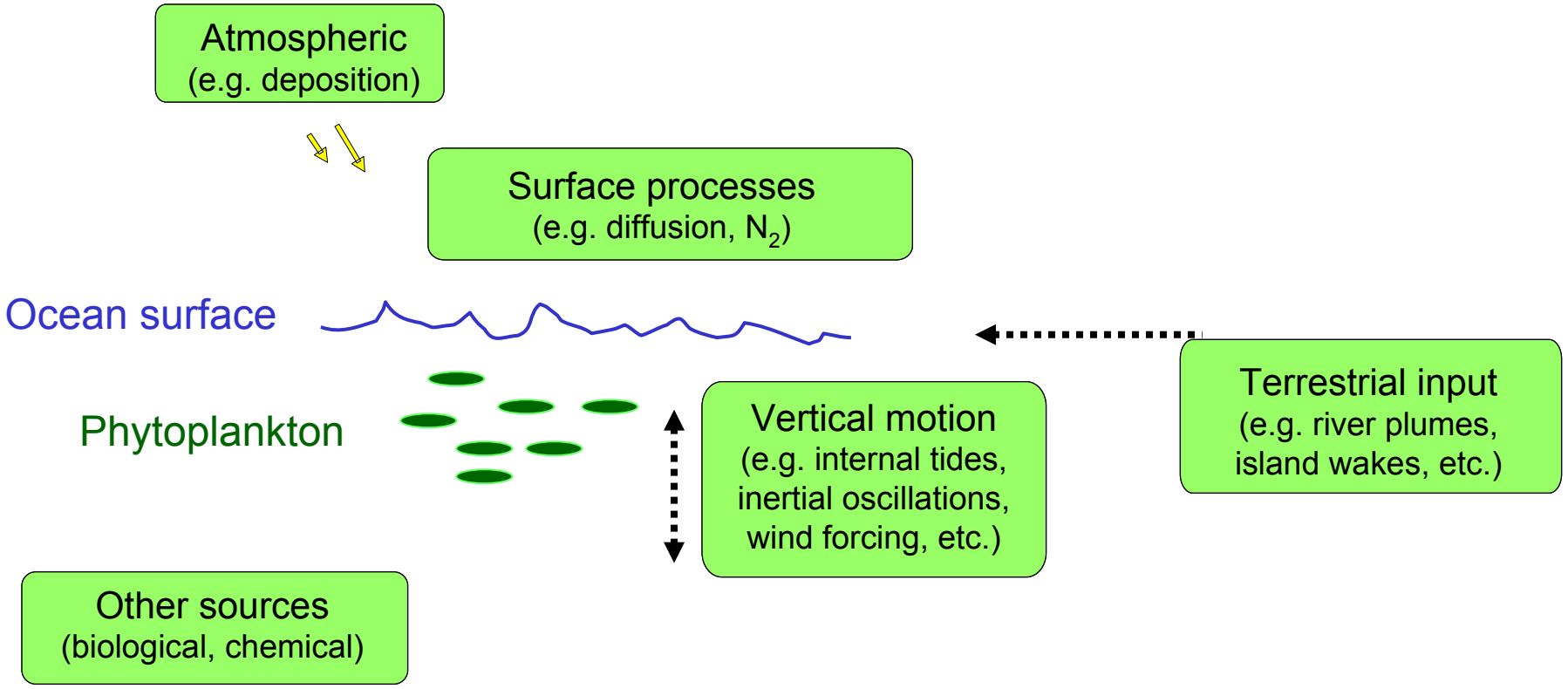
$$P = P_{max}(1 - e^{-\alpha I/P_{max}})$$



Miller Ch3

Effect of nutrients on the P-I relationship

As with light, different processes in the ocean control availability of nutrients to phytoplankton:



Michaelis-Menten kinetics for effect of [nuts] on PS, PP, μ

Hyperbolic function with asymptote μ_{max}
When $\mu = \frac{1}{2}\mu_{max}$, $K_N \equiv [N]$

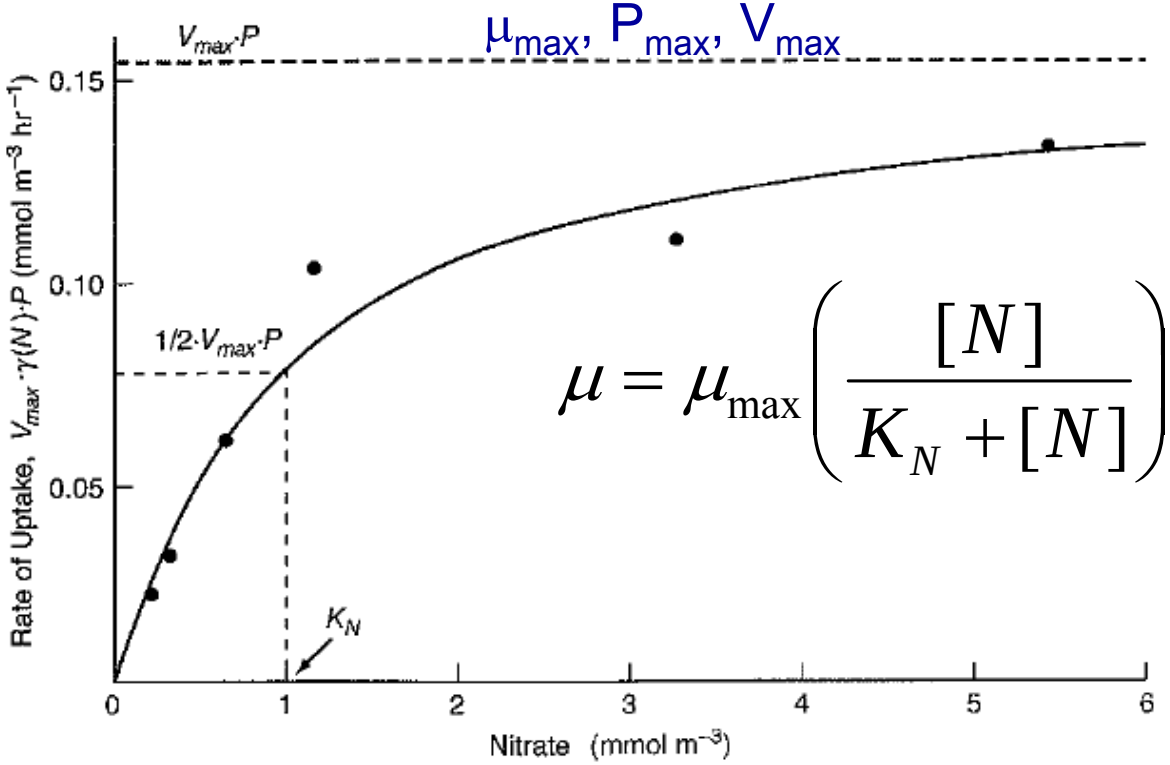


FIGURE 4.2.6: Rate of nitrate uptake versus nitrate concentration. Taken from *Dring* [1982]; original reference is *MacIsaac and Dugdale* [1969]. V_{max} is $V_P(T)$ and $\gamma_P(I) = 1$.

Relates phytoplankton growth rates to the availability of a specific nutrient (or multiple).

Derived from simple enzyme kinetic model.

Not appropriate for all nutrients (any?). Not how it actually "works" in cells (with active transporter sites, multiple limiting steps in uptake, etc).

Still, the most widely used parameterization.

Effect of nutrient concentration on P-I

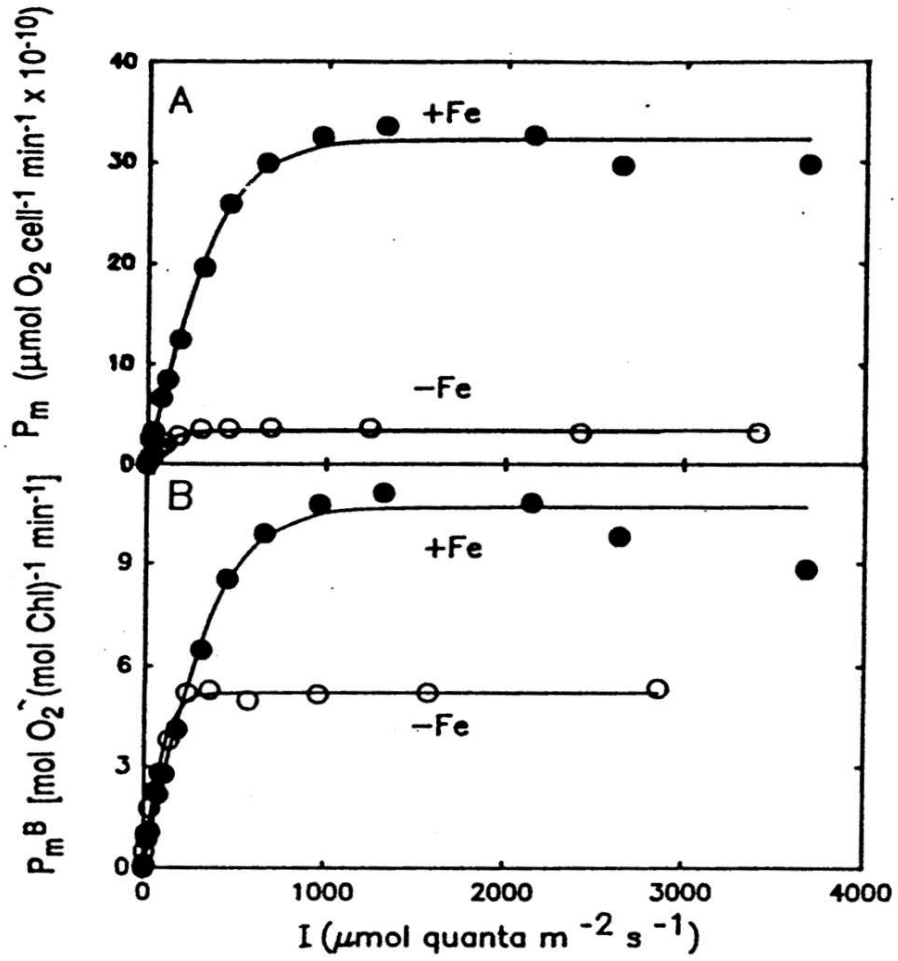


Fig. 1. Representative curves of cell-specific (A) and Chl *a*-specific (B) photosynthesis vs. irradiance for Fe-replete and Fe-deficient cultures of *Phaeodactylum tricornutum*.

Here P_{max} increases with increasing [Fe]. Any change in initial slope?

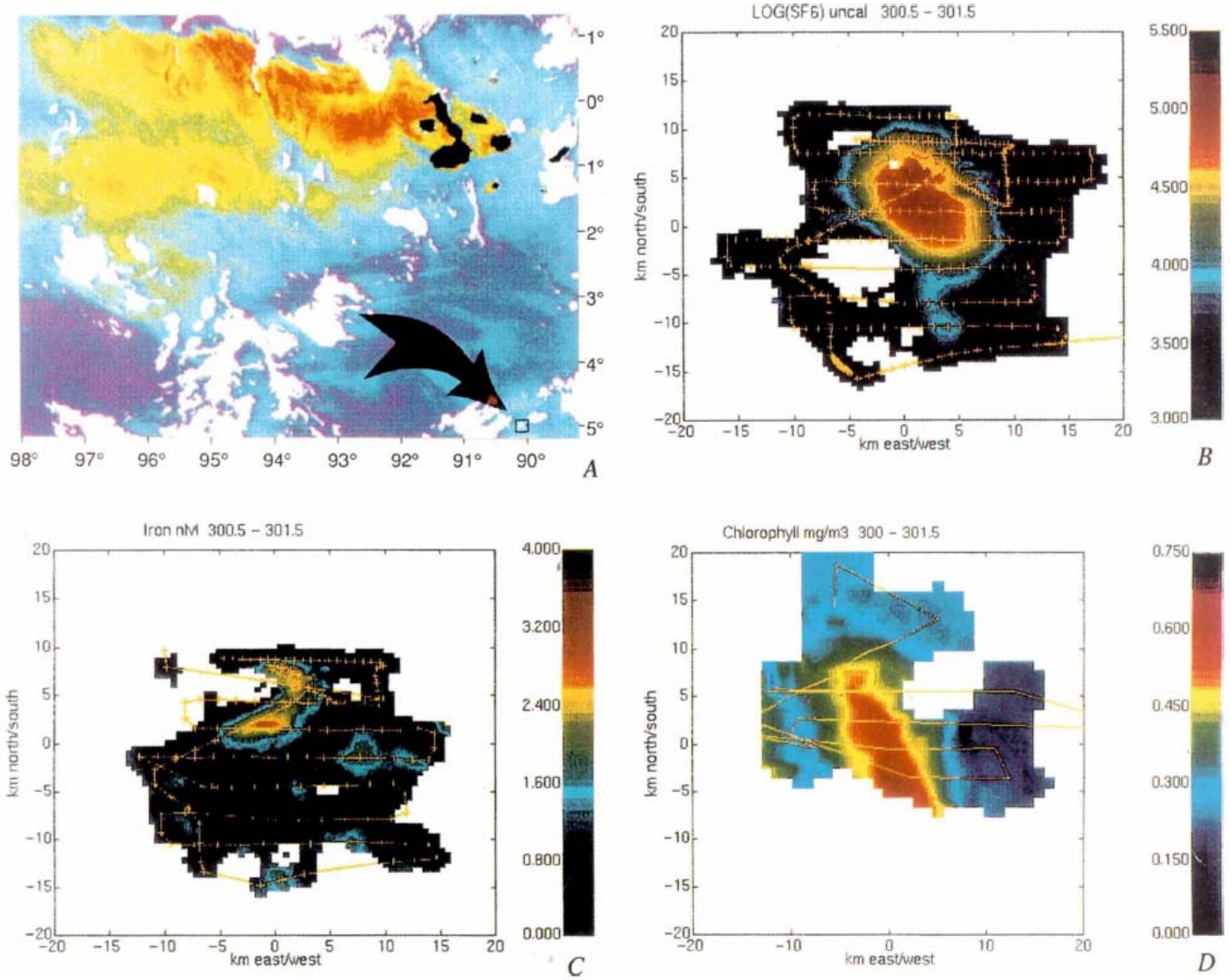
Specific effect depends on nutrient studied, species, & experimental treatment.

Are these good fits?
Why lower P at high E & [Fe]?

When might increases in a nutrient decrease P_{max}?

Greene et al. 1991

Open-ocean Fe enrichment & primary production



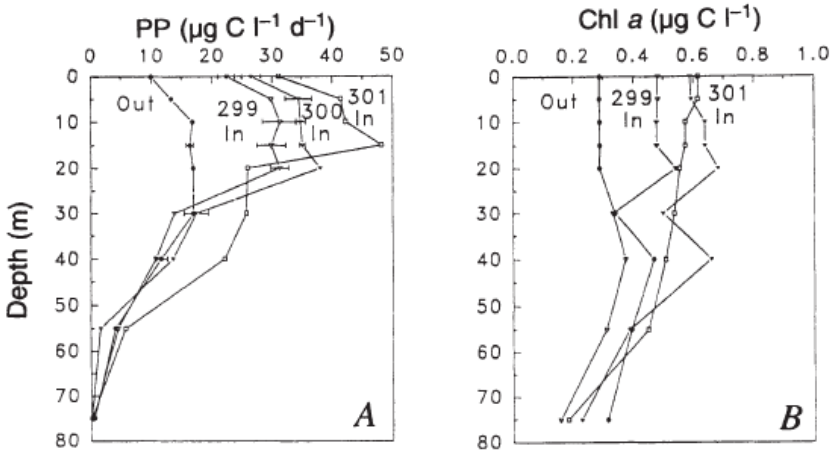


FIG. 3 Vertical profiles, for the 3 days following fertilization, of primary production, PP, (*A*) chlorophyll *a* concentrations, Chl *a*, (*B*) as a function of time inside and outside the patch. Outside values are depicted for YD 299. Primary production was measured using $H^{14}CO_3^-$ uptake determined at various light levels, in incubations on board the ship. Chlorophyll was determined from filtered and extracted samples as in Fig. 1*D*. The errors associated with the chlorophyll analyses are generally <0.02 µg C l^{-1}. The depth to which the water column was enriched was ~35 m up to YD 301 (just before subduction). It is in the upper 35 m that the differences are most pronounced. Productivity and chlorophyll both converge by 75 m.

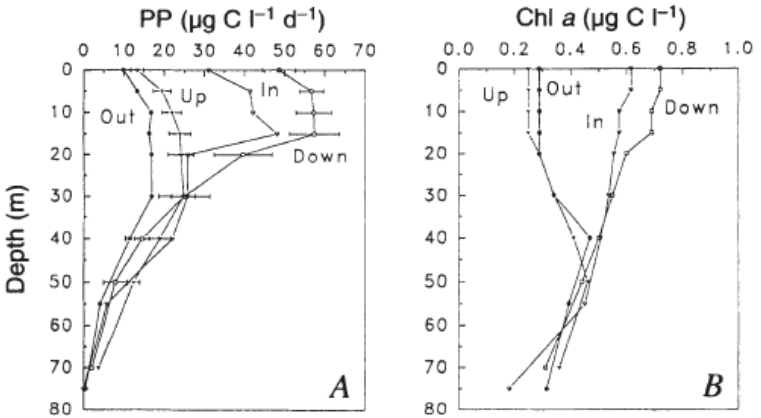


FIG. 4 Comparison of vertical profiles of primary production (*A*) and chlorophyll *a* concentrations (*B*) for stations inside and outside the fertilized patch, and stations upstream (westward) of the Galapagos Islands and downstream (eastward) of the Galapagos Islands.

Does P or N limit overall production in the ocean?

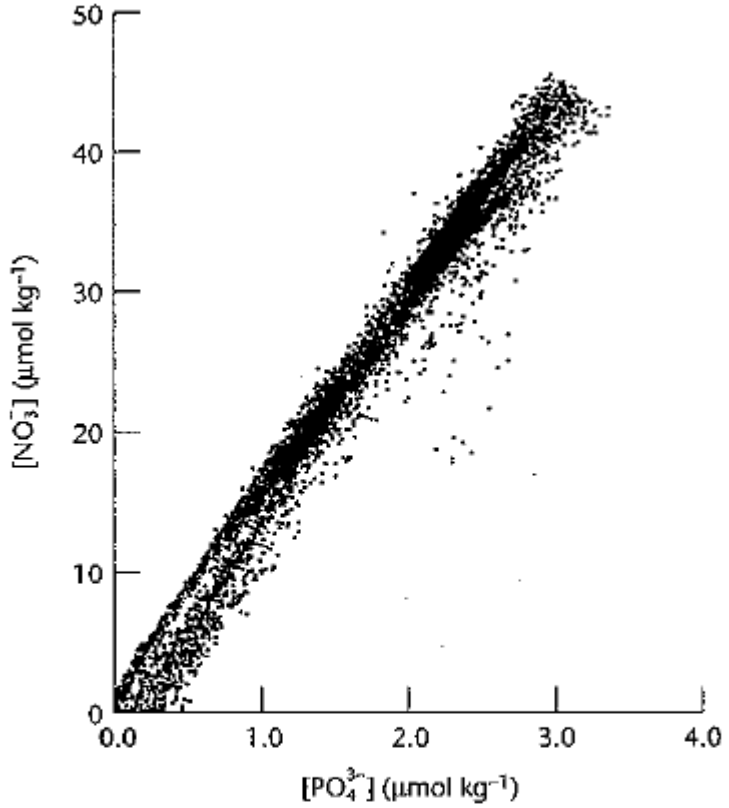


Fig. 3.13 A scatter plot from a series of global sampling sections (GEOSECS) of nitrate (NO_3^-) vs. phosphate (PO_4^{3-}). Some phosphate is usually left when nitrate is depleted below levels detected by standard techniques. (After Tyrrell 1999.)

What forms of P, N are available to phytoplankton in the ocean?

What might be misleading about this plot?

Lacustrine systems → high P inputs. What algae thrive in lakes & why?

← What is the N:P ratio?

Miller Ch3

Response to temperature

Dark reactions are primary chemical (enzymatic) and T dependent.

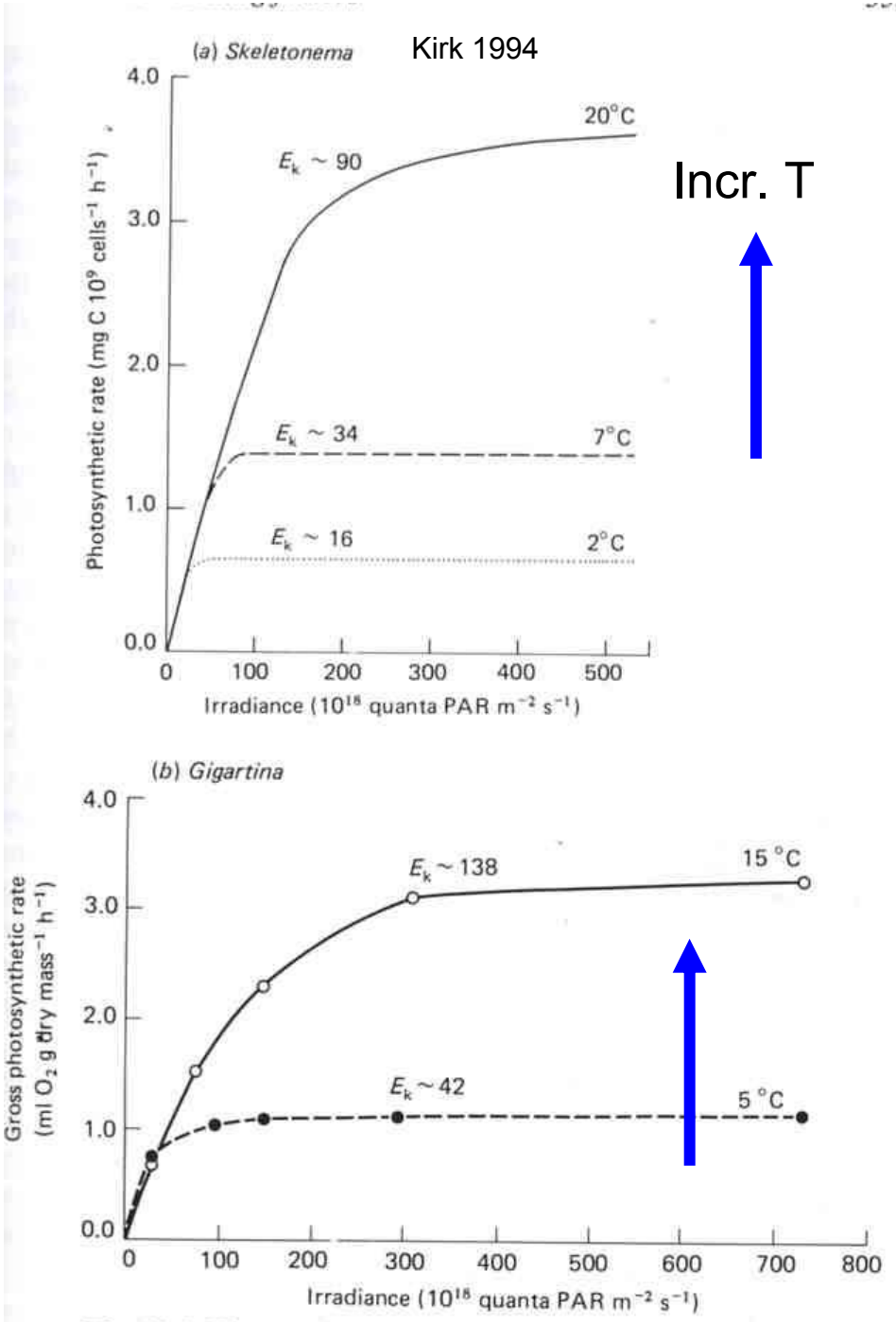
Increasing T leads to greater P_{max}, up to a point.

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{10/(T_2 - T_1)}$$

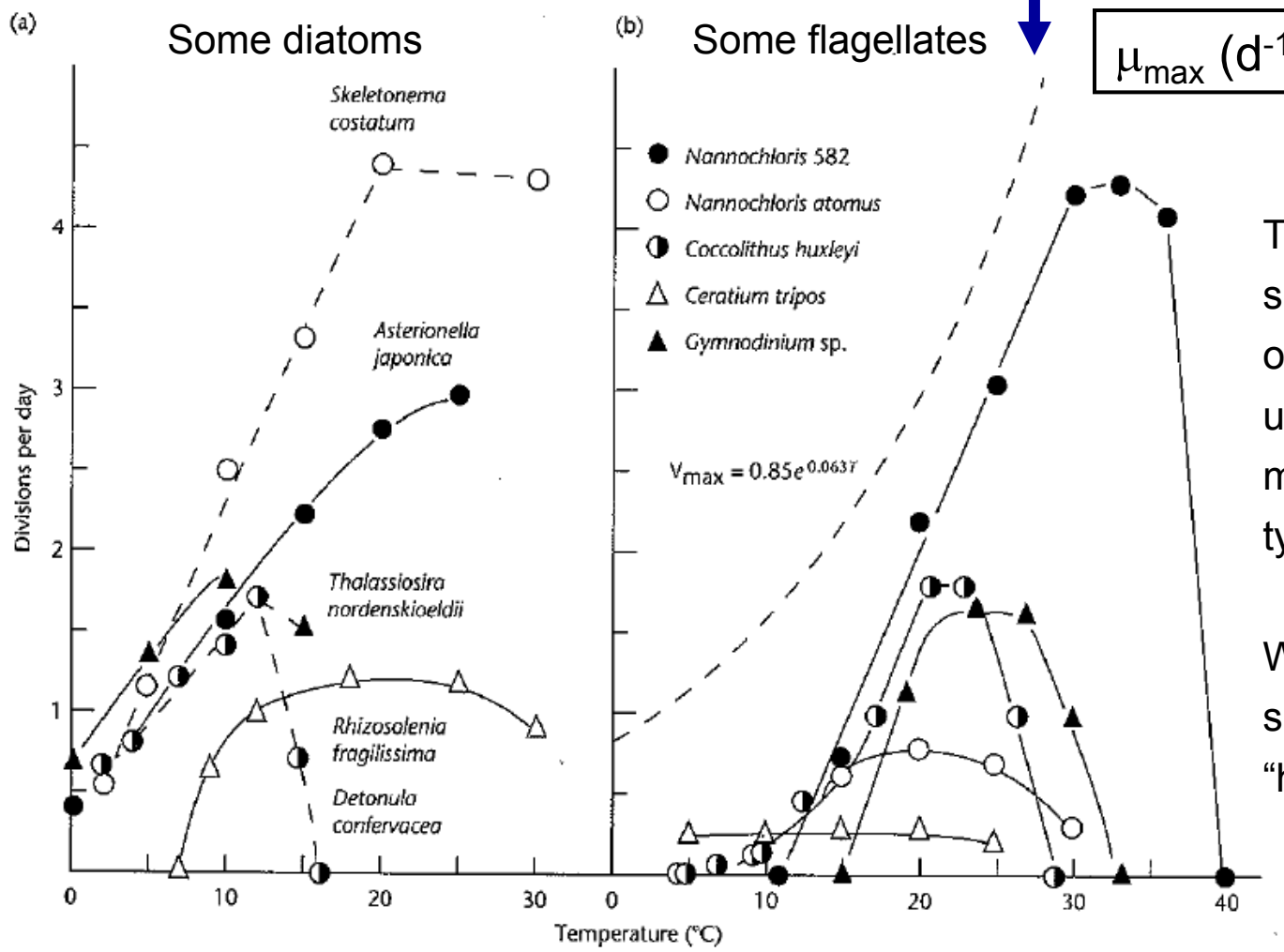
What is the Q_{10} of *Gigartina*?

A change in P_{max} or α?

Kirk 1994



The “Eppley curve” of temperature-dependent growth



μ_{max} (d^{-1}) = $0.85e^{0.063T}$

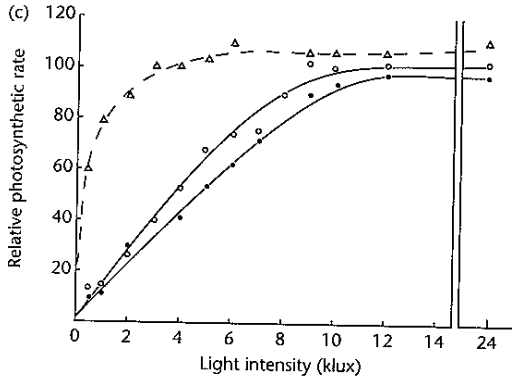
The Eppley curve should be considered only a maximum upper limit of how T might affect P, not a typical response.

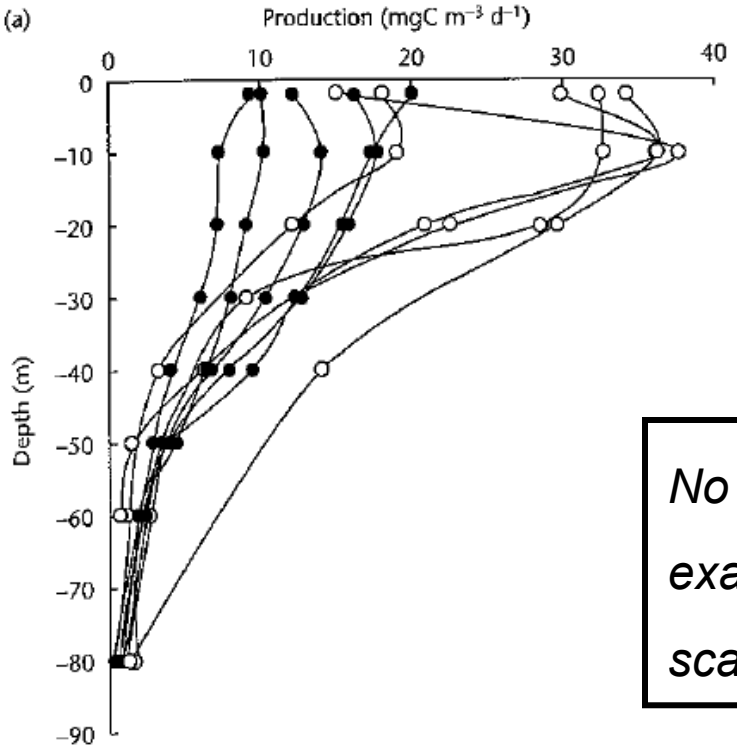
What causes the sharp drop-off at “high” temperatures?

Fig. 3.14 Temperature effect on phytoplankton growth rate for several species: (a) diatoms, and (b) flagellates. The dashed line in (b) is the “Eppley curve”, μ (doublings day^{-1}) = $0.85e^{0.063T}$. (After Smayda 1976.)

Miller Ch3

3+ methods for “measuring” primary productivity (-tion)



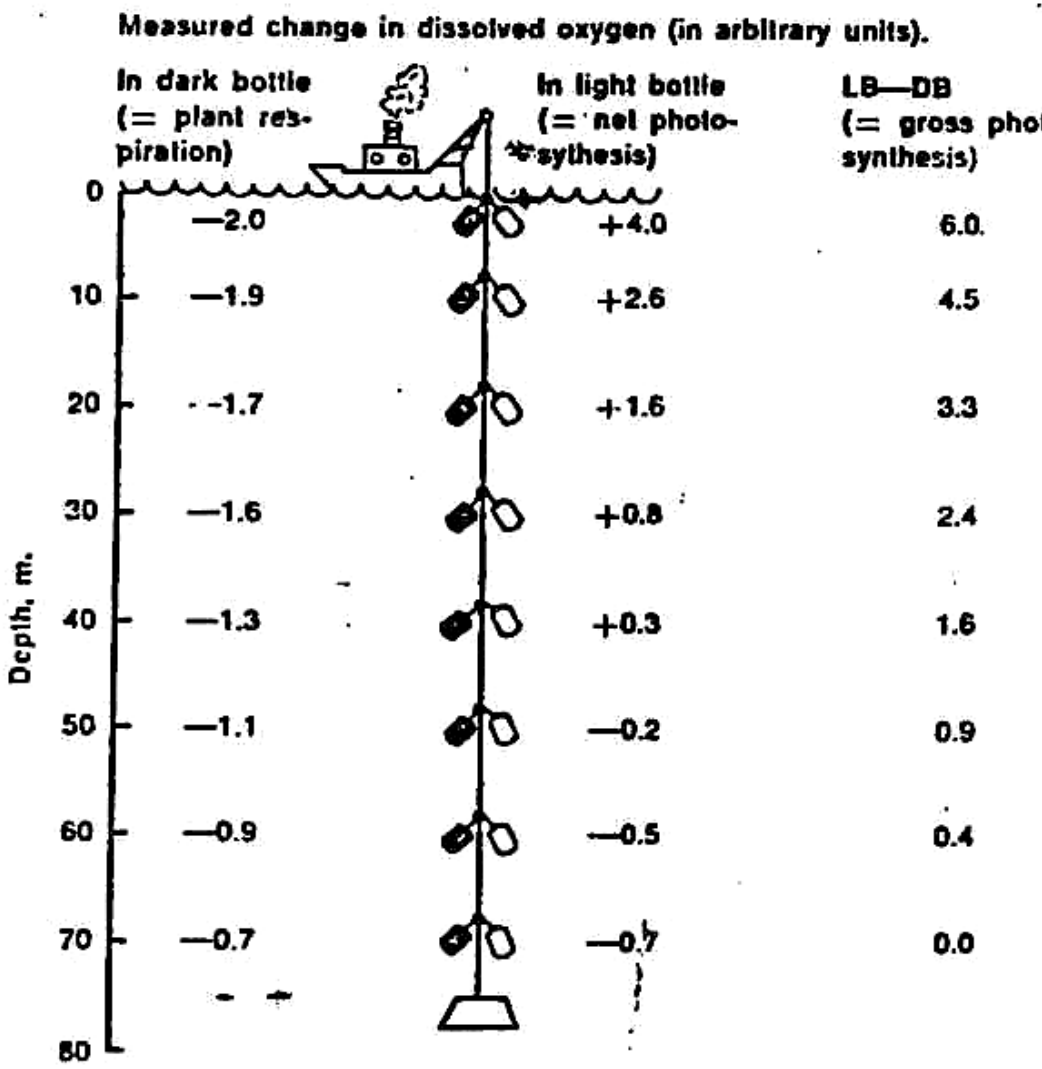


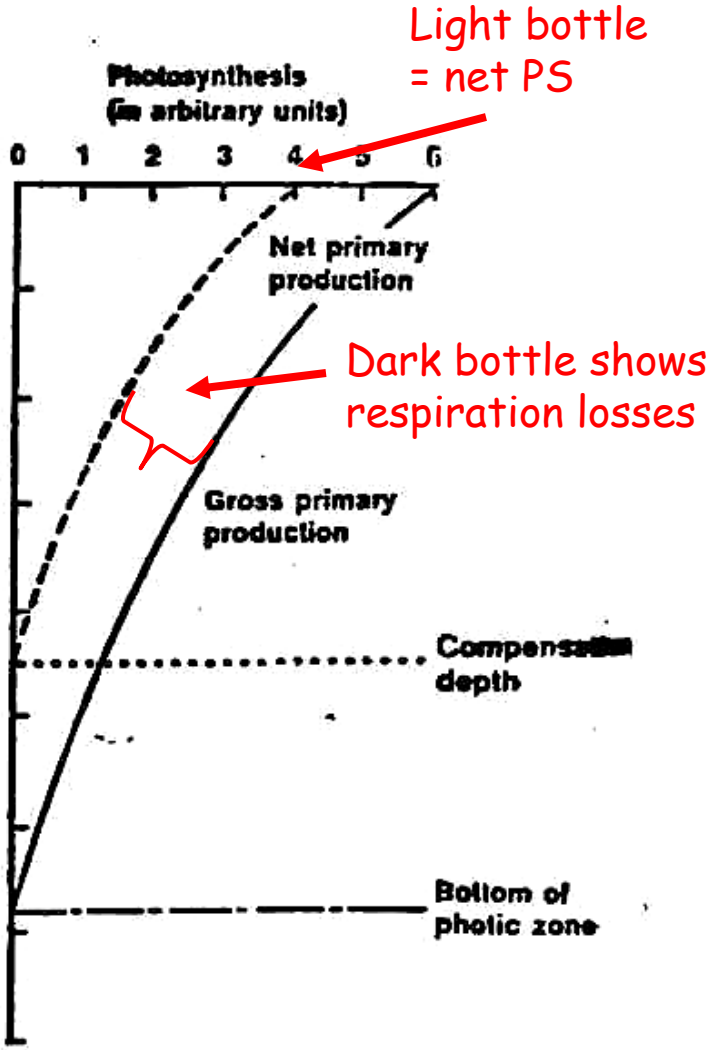
- O_2 evolution
- ^{14}C (radiocarbon) incorporation
- Ocean color remote sensing
- Others (^{18}O, C, ^{15}N, ^{32}P, etc.)

No one “best” method – different suitability for examining primary production on different scales, in different oceanographic contexts, etc.

I. Measuring the O_2 "out"

(Winkler titration. "light" & "dark" bottles to estimate gross PS)





How deep should we bother measuring P vs. I?

Euphotic zone: "well-lit" → near ocean surface

Where net photosynthesis occurs

Assumed to be depth of 1% light level (or 10% light level).

Just say all production happens above that, roughly proportional to $E_{PAR}(z)$ except in very near-surface (why?)

Compute 1% (or 10%) from $E_{PAR}(z)$ with Beer's Law:

$$I_z = I_0 e^{-kz}$$

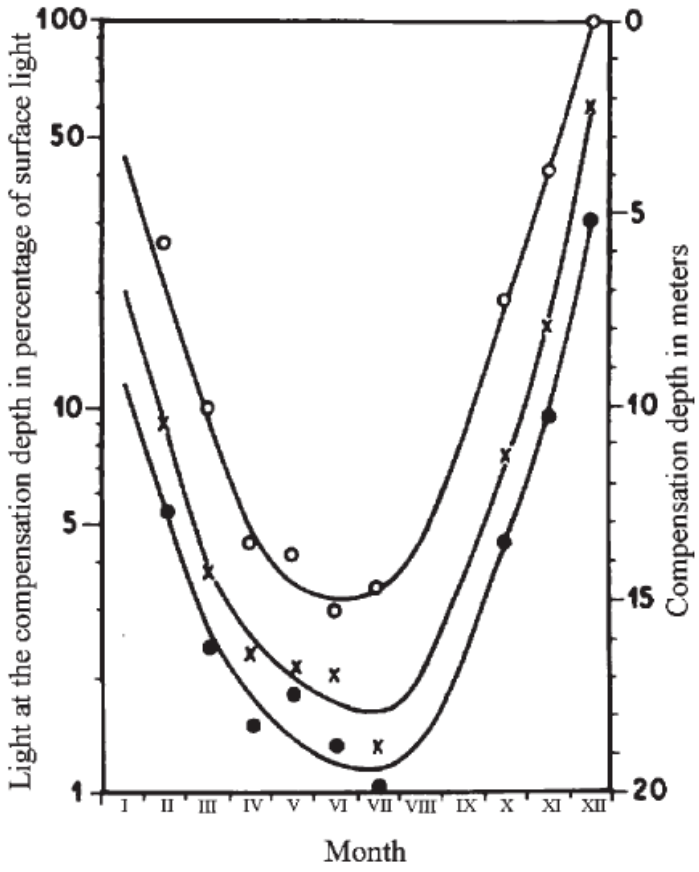
k = extinction coefficient (k_{PAR})

Continuing source of controversy

SHOULD WE CONTINUE TO USE THE 1% LIGHT DEPTH CONVENTION FOR ESTIMATING THE COMPENSATION DEPTH OF PHYTOPLANKTON FOR ANOTHER 70 YEARS?

Karl Banse, School of Oceanography, Box 357940, University of Washington, Seattle, WA, 98195-7940 USA; banse@ocean.washington.edu

Figure 1. Seasonal change of phytoplankton compensation depth in Danish waters (56°N) for dark (open circles), average (crosses), and bright (filled circles) days on right-hand ordinate and percent of incident PAR on left-hand ordinate. (Figure 7 in Steemann Nielsen and Hansen, 1961, with permission.)



II. Measuring the CO_2 "in"

Can use the same light-dark bottle approach

" 6 H_20 + 6 $^{14}CO_2$ → 6 ($^{14}CH_2O$) + 6 O_2 "

1- Collect samples, filter out grazers (you try…)

2- Incubate in situ after spiking with ^{14}C labeled bicarbonate

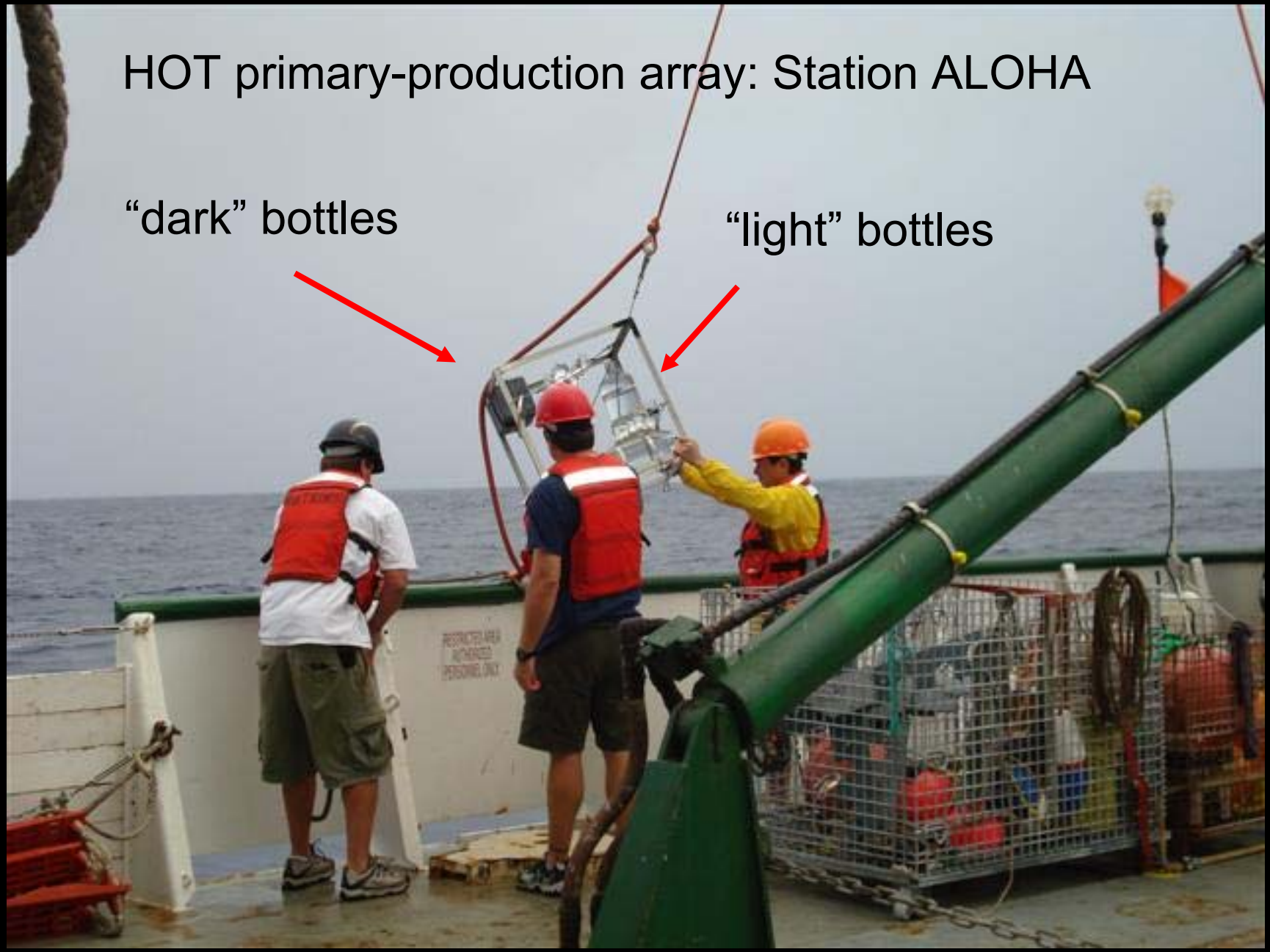
3- After time T, filter out phytoplankton & acidify

4- Calculate specific radioactivity by scintillation counting

Approximates: Net primary productivity (sum of dissolved and particulate organic matter plus ^{14}C labeled organic carbon that is respired)

Classic paper: Steemann-Nielsen (1952)

50^{th} year conference proceedings, Wales (2002)



http://hahana.soest.hawaii.edu/hot/

Problems with (but not unique to) ^{14}C method:

- “Bottle effect”: phytoplankton photosynthesize differently in a bottle (e.g. no turbulence)

- Micro- herbivores! (same size classes as phytoplankton)

- Bacterial uptake might differ b/w light and dark bottles

- Assumption that only new photosynthate (with ^{14}C) is respired during the incubation

- Isotope uptake might differ between species

- Errors in measuring total carbonate

- Trace metal contamination (accidental spikes in Fe, e.g.)

- Cell breakage on filters

- others…

Continuing source of controversy

SHOULD WE CONTINUE TO MEASURE ^{14}C-UPTAKE BY PHYTOPLANKTON FOR ANOTHER 50 YEARS?

Karl Banse, School of Oceanography, Box 357940, University of Washington, Seattle, WA 98195-7940 USA; banse@ocean.washington.edu

L&O Bull. 2002

<u>Remember:</u>

Photosynthesis is a complex process, & so is primary production

All methods have associated problems

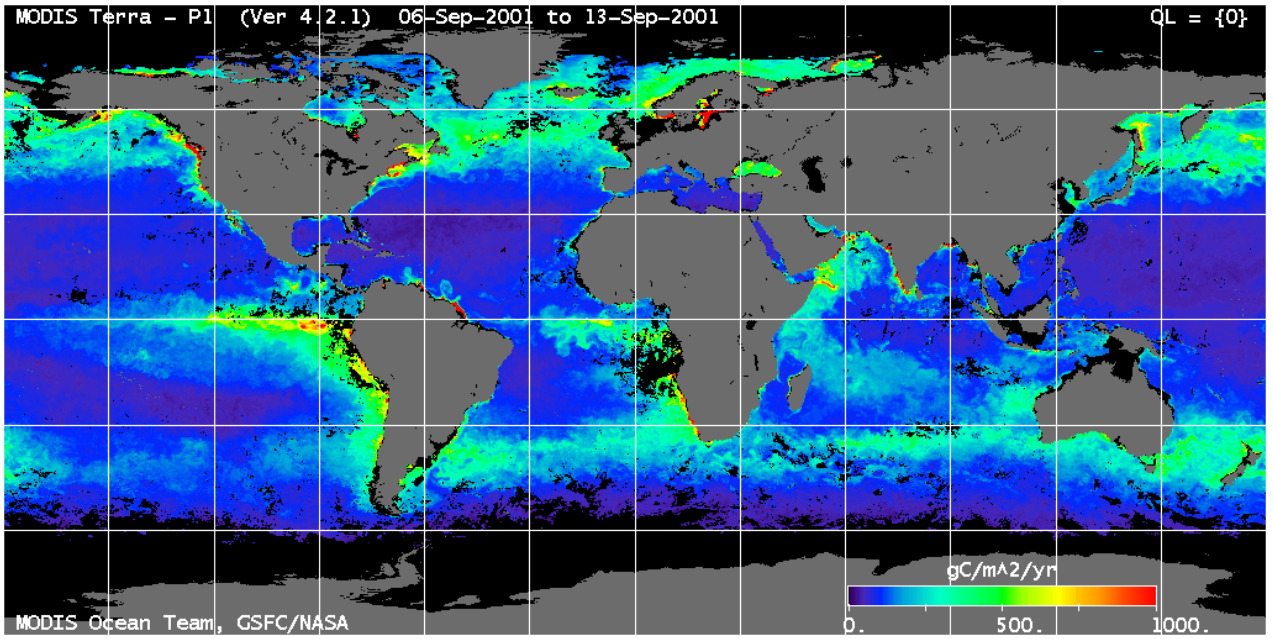
No economy is easy to quantify (especially physiological ones)

Make sure the method is appropriate to the question of interest

III. Satellite methods ("ocean color")

More green → more chl

Convert chl → PriProd



- **CZCS** (1978): Coastal Zone Color Scanner
- **SeaWiFS** (1997-2011): Sea-viewing Wide Field of view Sensor
- **MODIS** (1999, 2002): Moderate Resolution Imaging Spectroradiometer (instrument aboard Terra and Aqua satellites)

Top of the Atmosphere Radiances (L_{sat})

↓

Radiative Transfer Models

↓

Normalized Water Leaving Radiances (nL_w) **10%!!!**

↙ ↓ ↘

Photosynthetic Available Radiation (PAR)

Chlorophyll Empirical or Semi-analytical Algorithms

↓

Sea Surface Chl a concentrations

↓

Empirical SST Algorithm

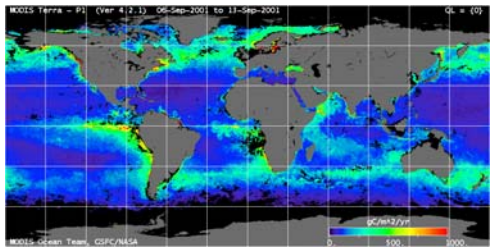
↓

Empirical Photosynthetic Efficiency (Φ_p)

↘ ↓ ↙

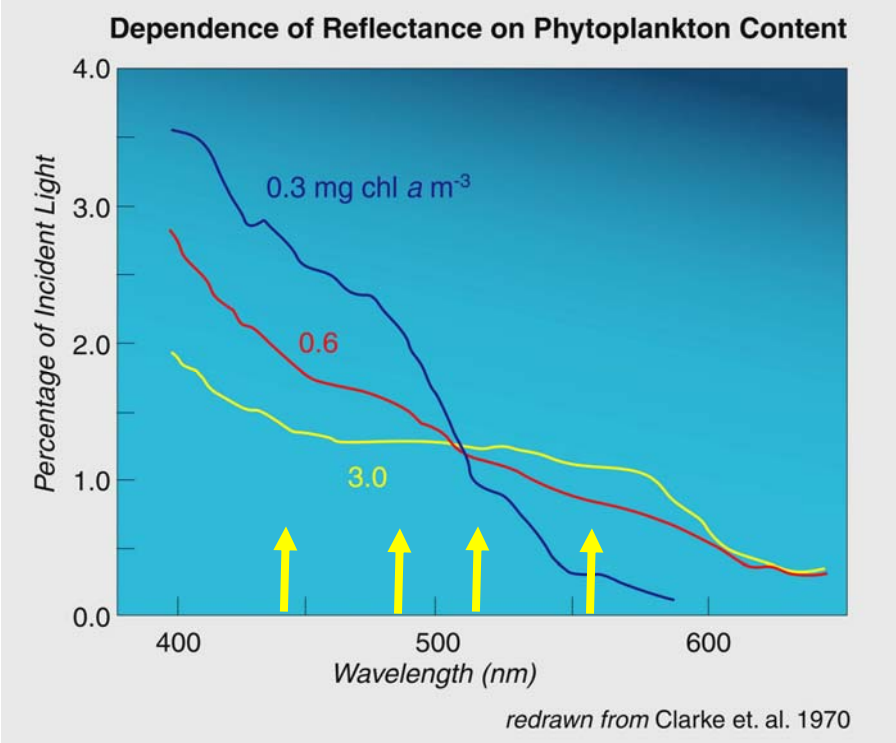
Primary Productivity model

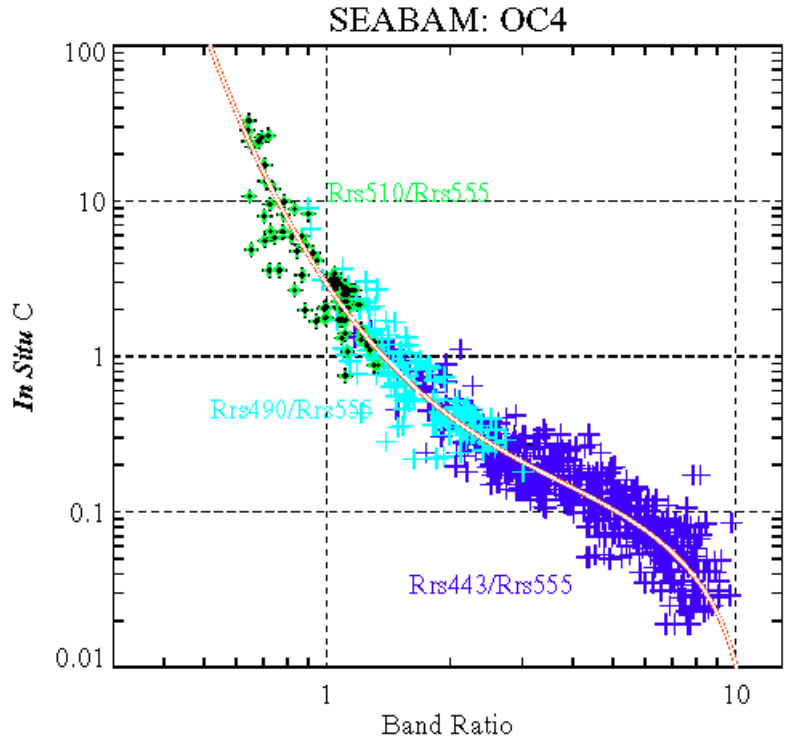
↘



Algorithms for chl biomass

Choose some wavelengths, do a fit. “greener” = more chl





“Ocean Chlorophyll 4” (i.e., OC4)

[Chl] = 10^(a0 + a1*R + a2*R^2 + a3*R^3) +a4

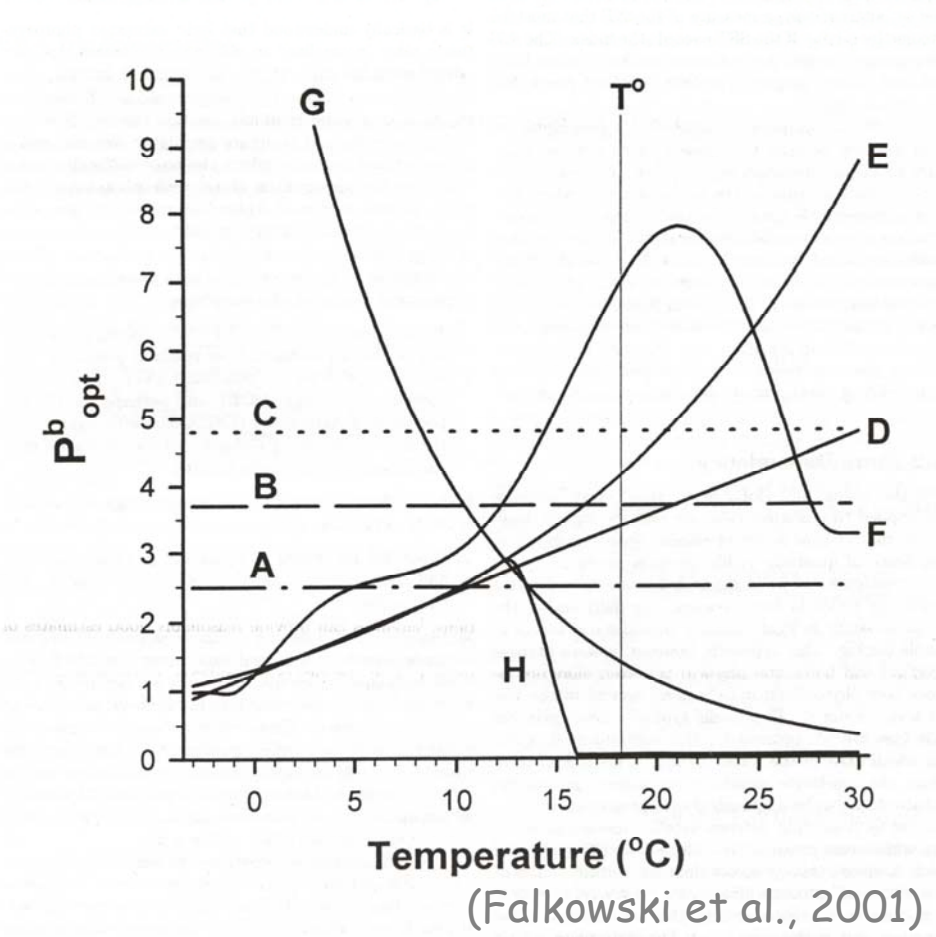
R = Log((Rrs443>Rrs490>Rrs510)/Rrs555)

e.g., O’Reilly et al. 1998

Use chl, PAR, daylength, SST to calc primary production →

$$P = 0.66 P^{B}_{opt} \left(\frac{E_0}{E_0 + 4.1}\right) Z_{eu} C_{opt} D$$

$$P^{B}_{opt} = f(T)$$



(Falkowski et al., 2001)

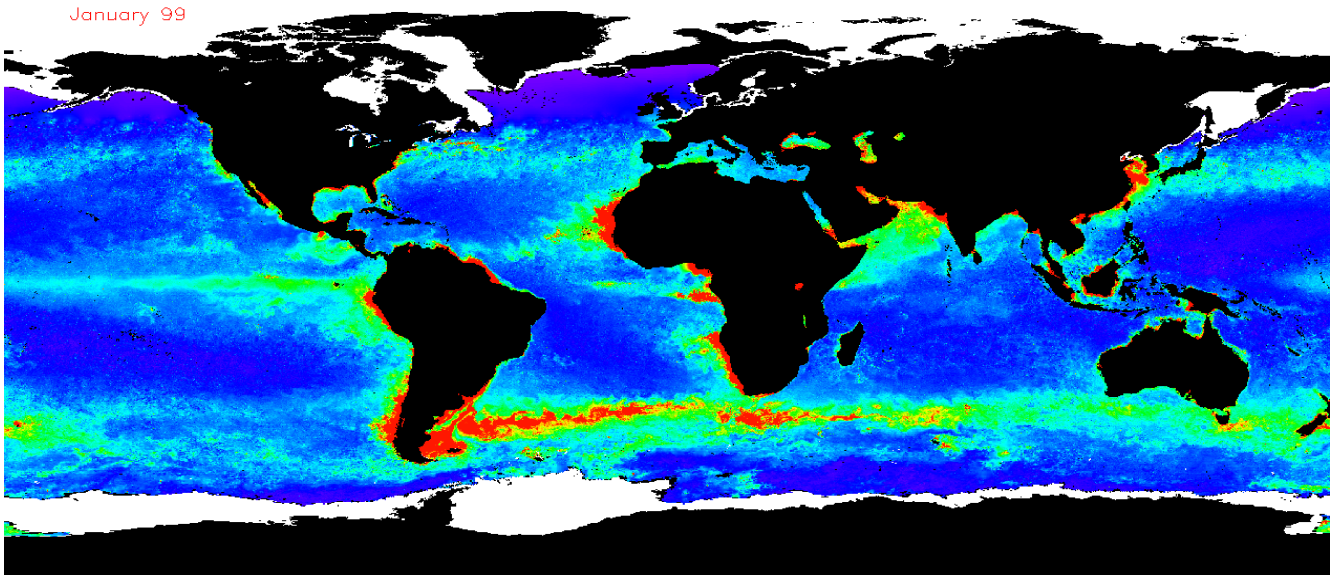
What's this P^{B}_{opt}?

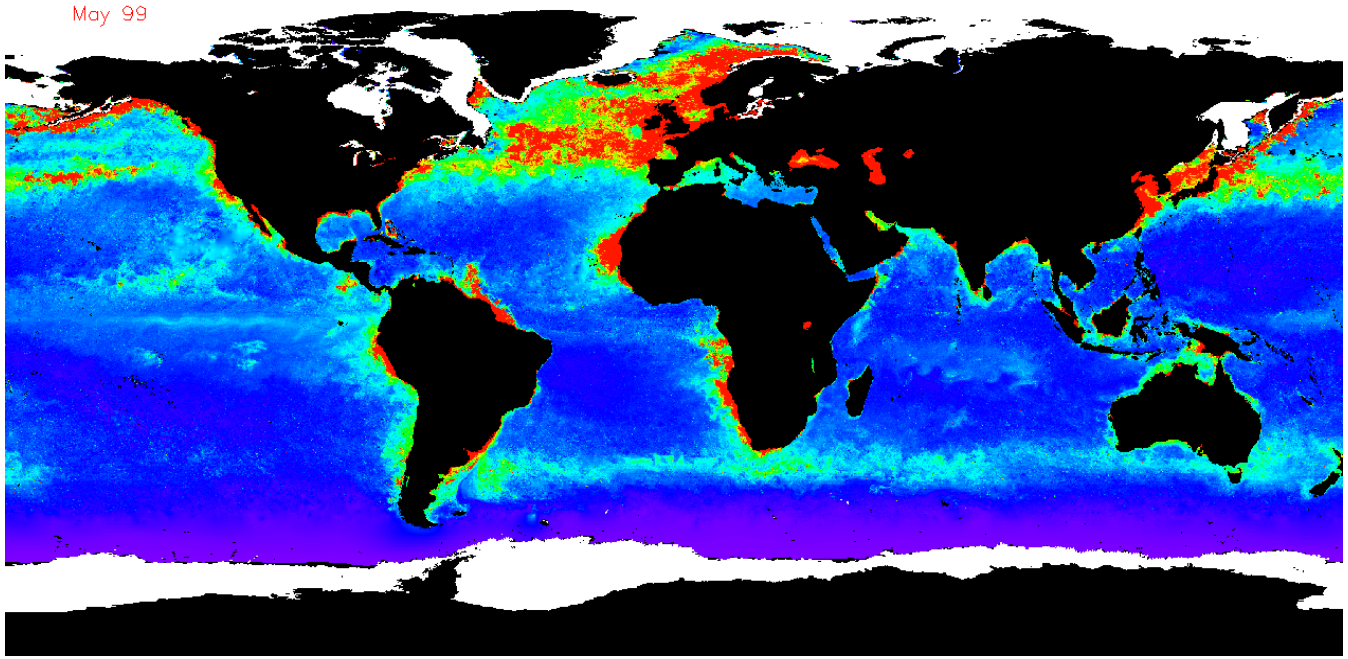
A 7th order polynomial function of temperature (a fit).

Idea: Use remote sensing SST to help constrain quantum yields.

Theory: Enzymatic rates, e.g. carbon fixation, should scale with temperature.

Problem: Not a clear relationship between SST and Φ_p even in surface waters alone.





Produces surprisingly realistic patterns in global PP.

January

May

Behrenfeld, http://marine.rutgers.edu/opp/