SMS 598: Calibration and Validation for Ocean Color Remote Sensing

**Lecture 25 Primary Productivity**

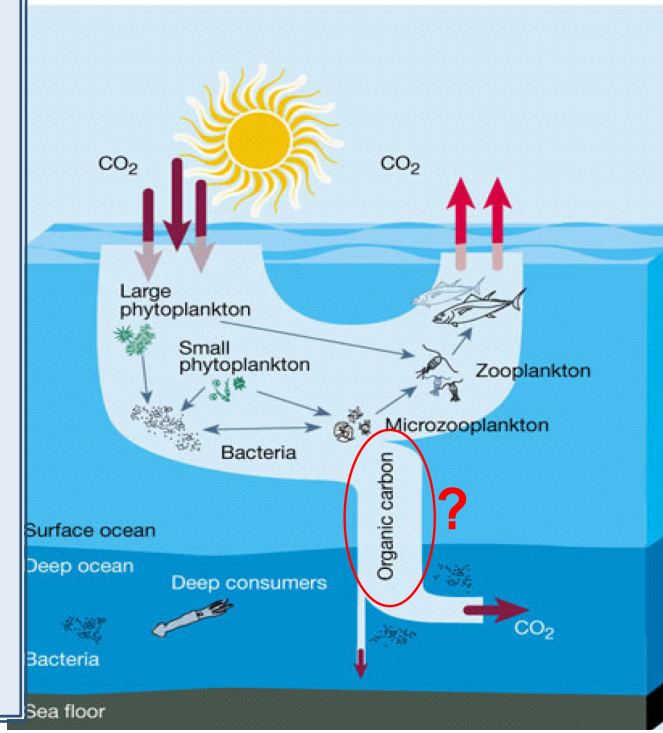
Mary Jane Perry ~ 27 July 2015

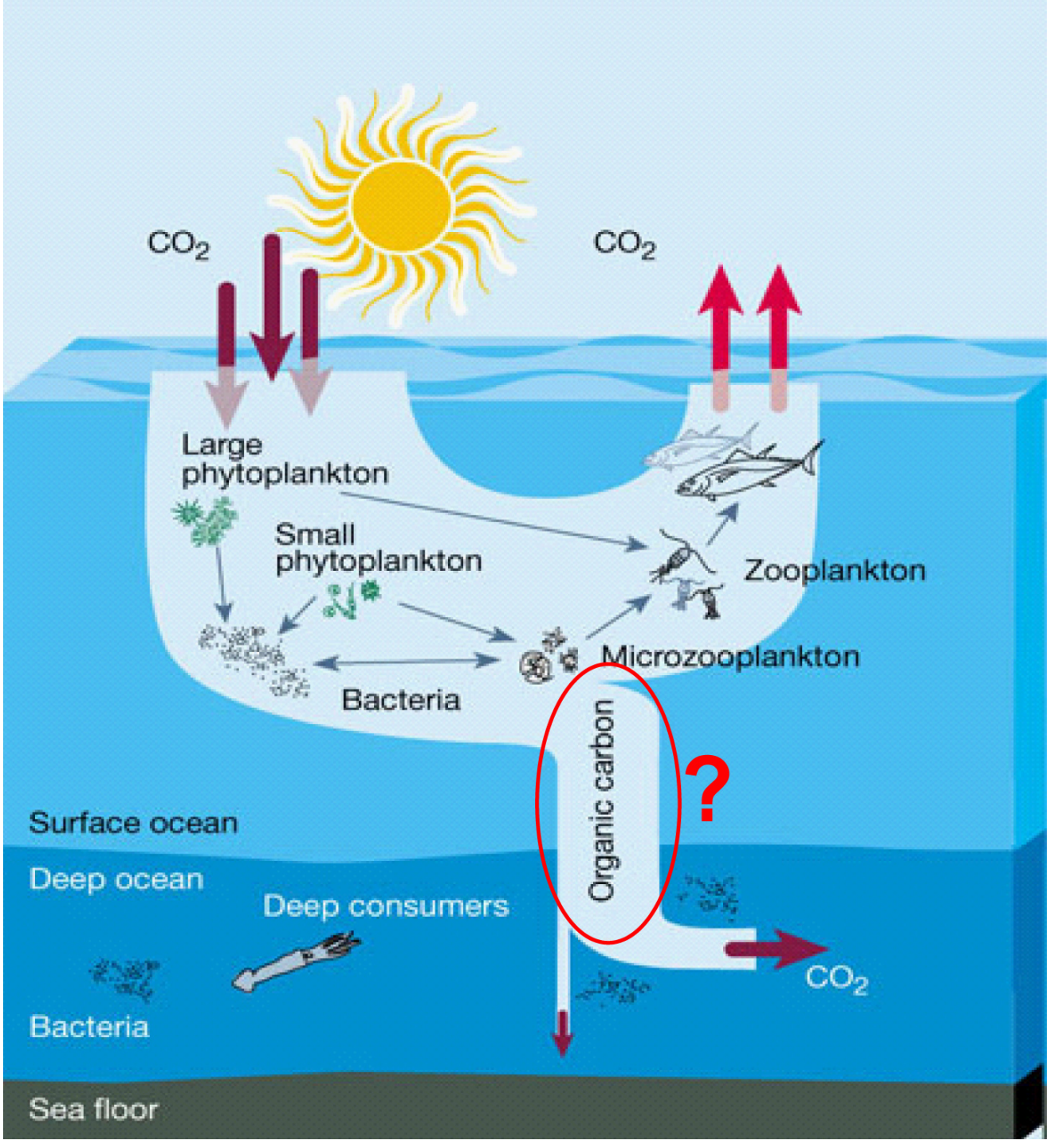
Photosynthesis – charge separation leading to production of high-energy chemical reductants

Primary productivity – rate, typically of organic carbon production (g C/area or volume/t)

Measurement – O2 evolution or POC production

Models – often optically based




$CO_2$
$CO_2$
Large phytoplankton
Small phytoplankton
Zooplankton
Microzooplankton
Bacteria
Organic carbon
?
Surface ocean
Deep ocean
Deep consumers
Bacteria
$CO_2$
Sea floor

# What is photosynthesis?

(in text books, all terms  shown times 6; reflects synthesis of simple sugar):


$$CO_2 + H_2O \rightarrow -(CH_2O)- + O_2$$

Respiration is reverse.

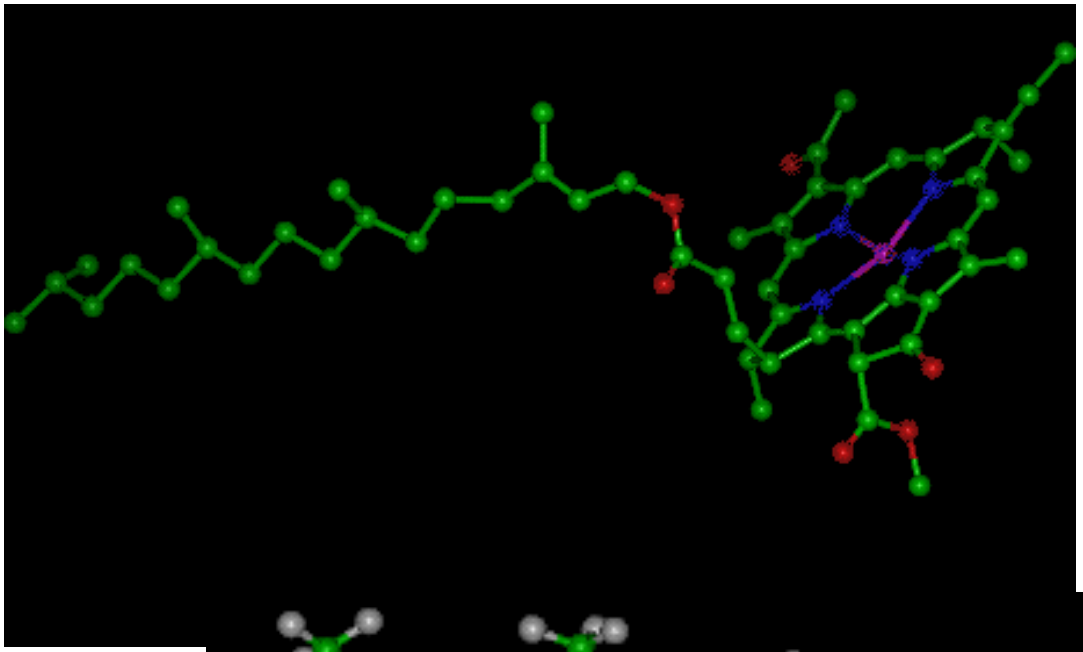
**Photosynthesis – process and products (**Should you expect stoichiometry between **C** and **$O_2$** ?)

1. **photon absorption** - Light Harvesting chlorophyll & accessory pigments
2. **exciton (energy) transfer** from LH pigments to reaction center
3. **PSII trans-membrane charge separation**: high energy electron is transferred from P680 across membrane to plastoquinone (electron acceptor)
4. **Electron is transported** to PSI, replacing electron lost by PSI's $P700^+$ (see # 5); **ATP** is produced
5. **PSI trans-membrane charge separation**: high energy electron is transferred from P700 across membrane to pre-ferrodoxin (electron acceptor); **NADPH** is produced. (Lost electron resupplied from PSII)
6. **$H_2O$ split (PSII)**
   – replace electrons lost by PS II ($P680^+$) during charge separation
   – produces **$O_2$ as waste product**
   – produces $H^+$; $H^+$ gradient couples with electron transport from PSII to PSI leading to **ATP** production
7. **ATP & NADPH** used to reduce **$CO_2$, $NO_3^-$ and drive biosysnthesis, etc**

https://www.youtube.com/watch?v=bxWI6HEvyDQ

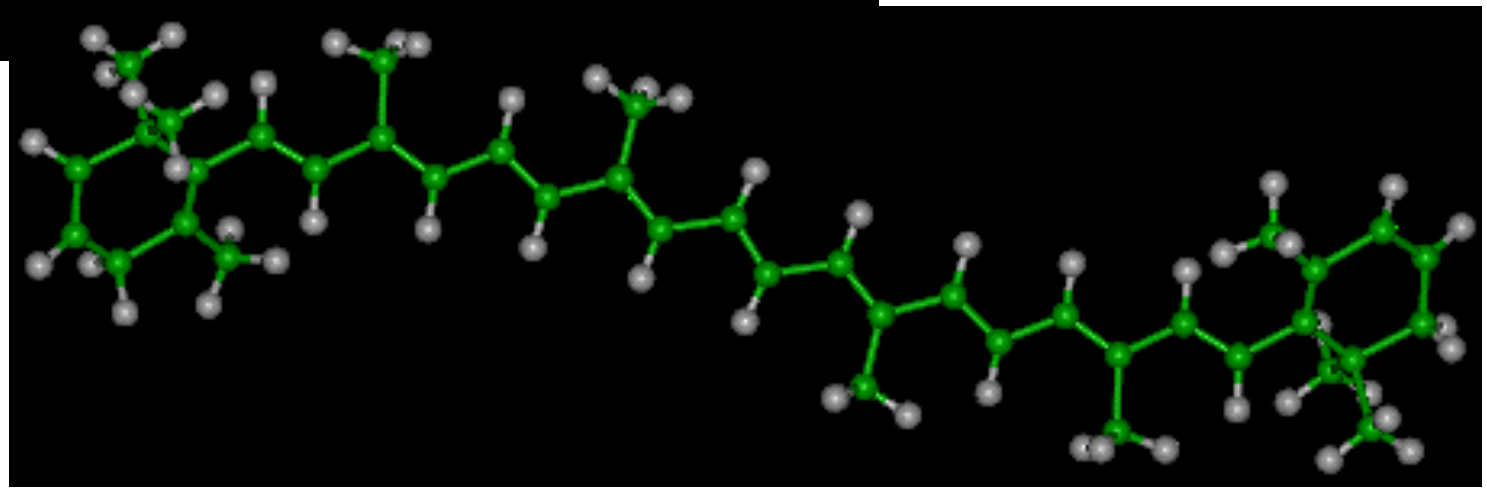
**Jimmy Stewart on Solar Energy: 1938 - YouTube**

1. photon absorption by chlorophyll & light harvesting accessory pigments (fucoxanthin, chlorophylls b & c, etc.)

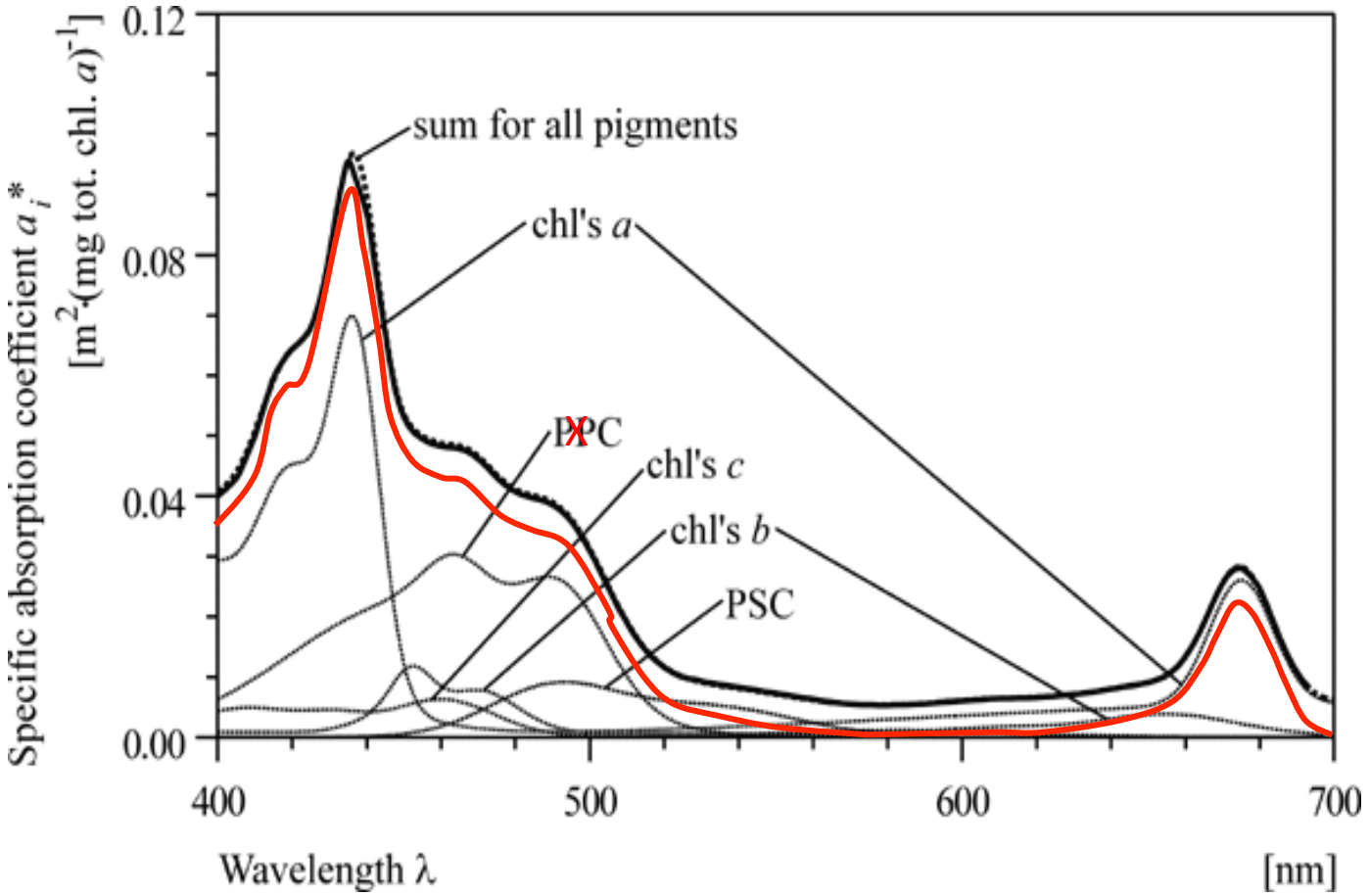


chlorophyll a

carotenoid



# 1. photon absorption by chlorophyll & light harvesting accessory pigments (fucoxanthin, chlorophylls b & c, etc.)




http://www.iopan.gda.pl/rbdo/fizyka/mbo_lab/tab_gauss.htm

**Chlorophyll molecule is attached to binding protein.**

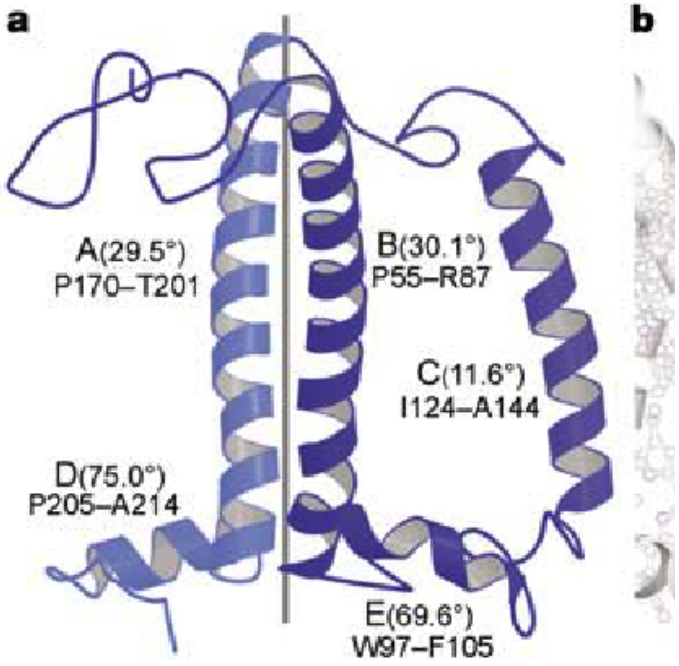
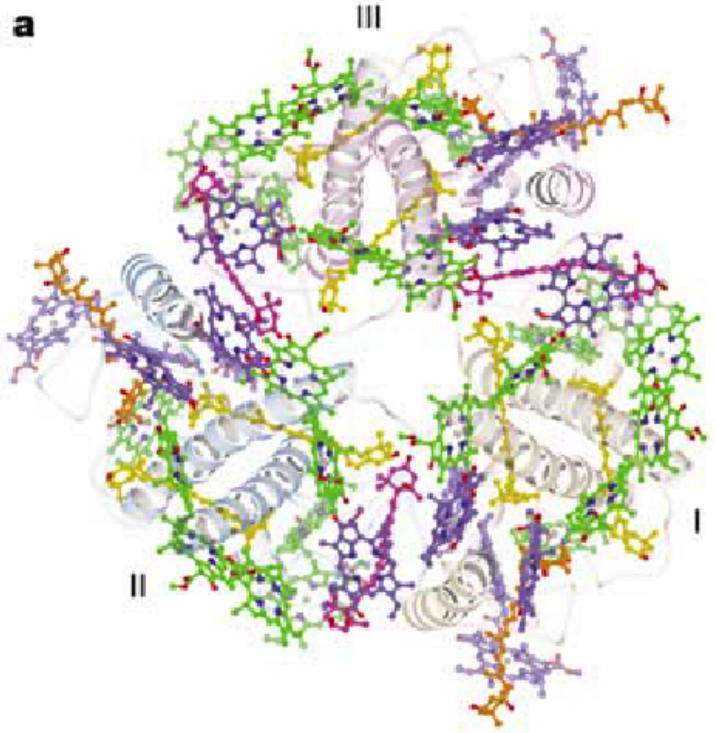



**Figure 3** Secondary structure of monomeric LHC-II

protein backbone of monomeric LHC-II protein complex, from electron density mapping

**Trimeric complexes of Chl and binding protein.**




3 monomers = 1 trimer

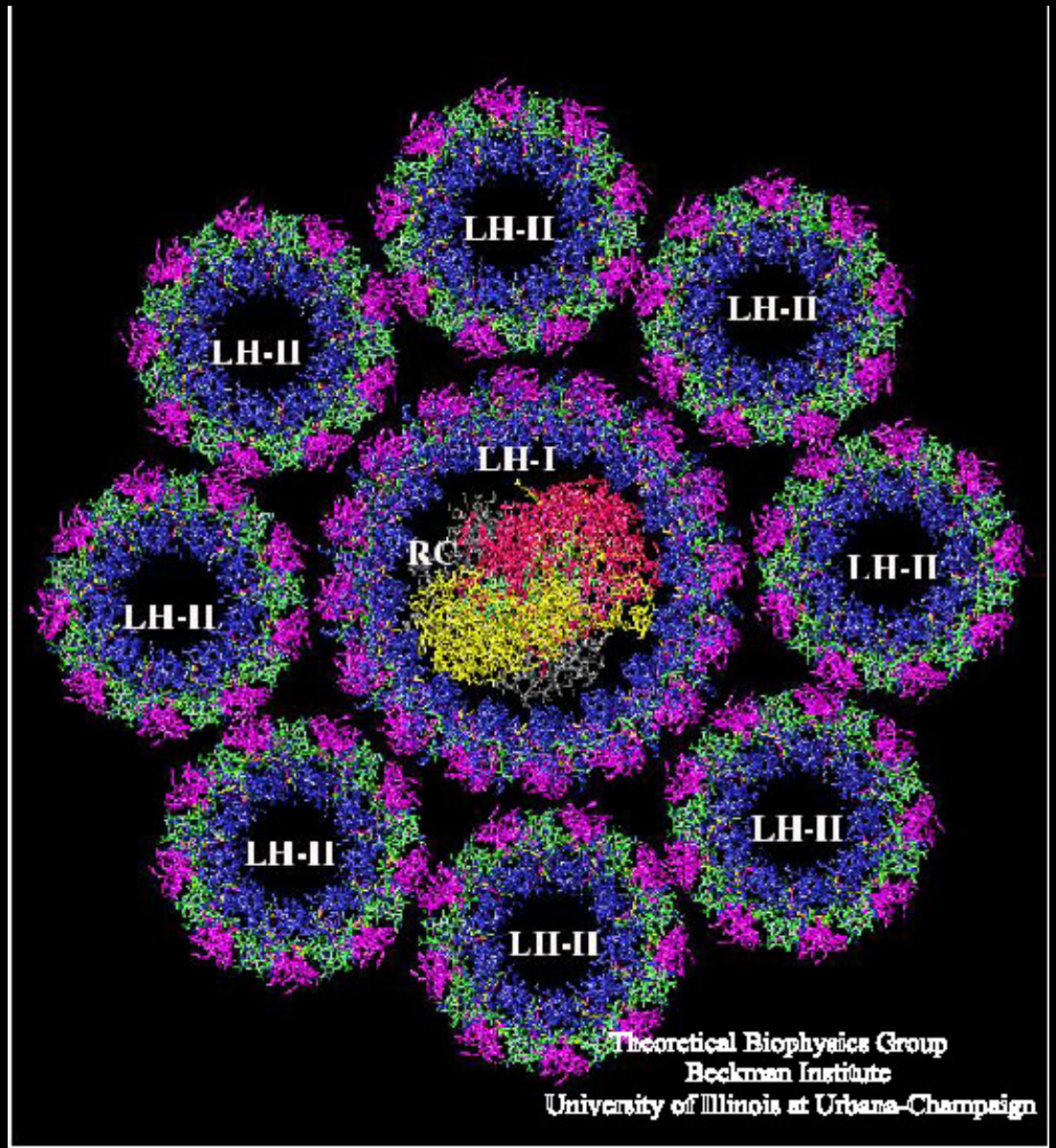
green: chl *a*; blue: chl *b*

yellow/orange: P carotenoids

magenta: PP carotenoids

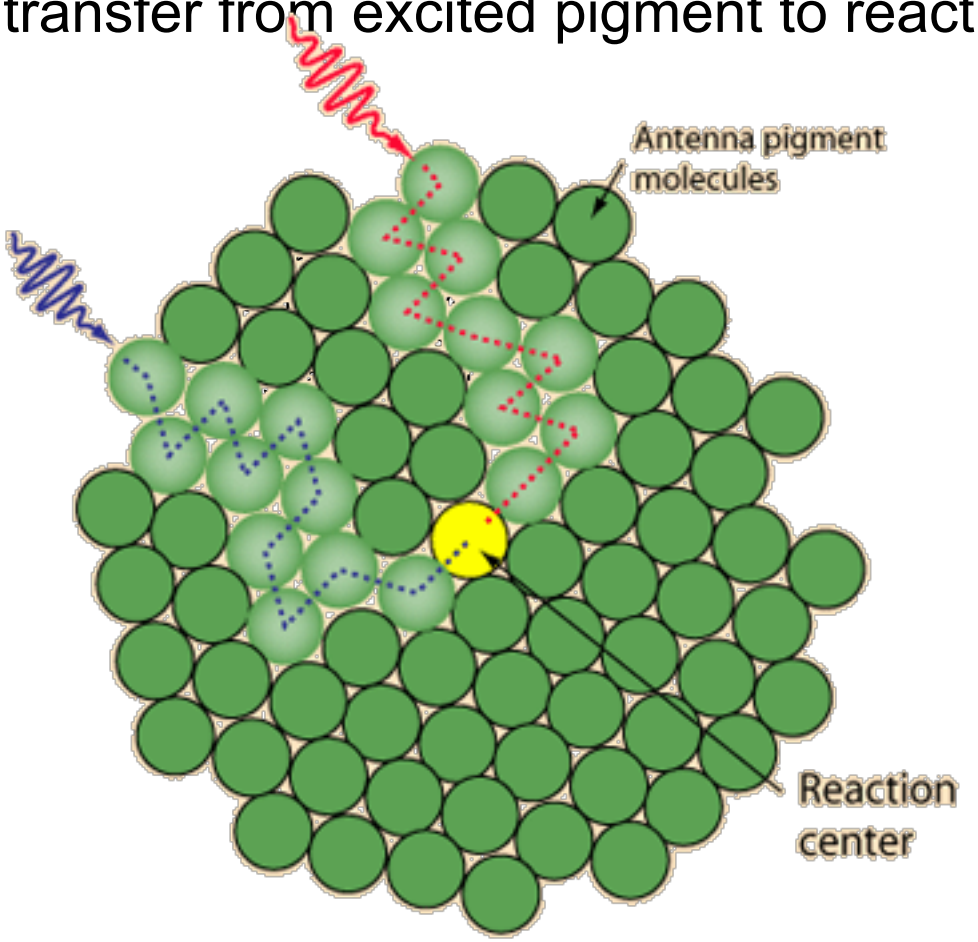
Lui et al., 2004, Nature 428: 287ff for spinach LHC-II

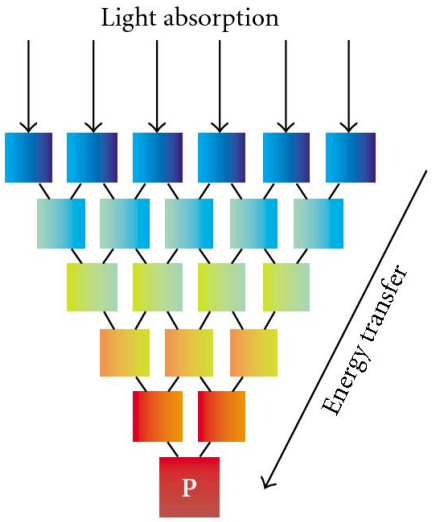
Many light harvesting trimers around reaction center (PS II)
to form a light harvesting complex.




Lui et al., 2004

2. exciton (energy) transfer from excited pigment to reaction center

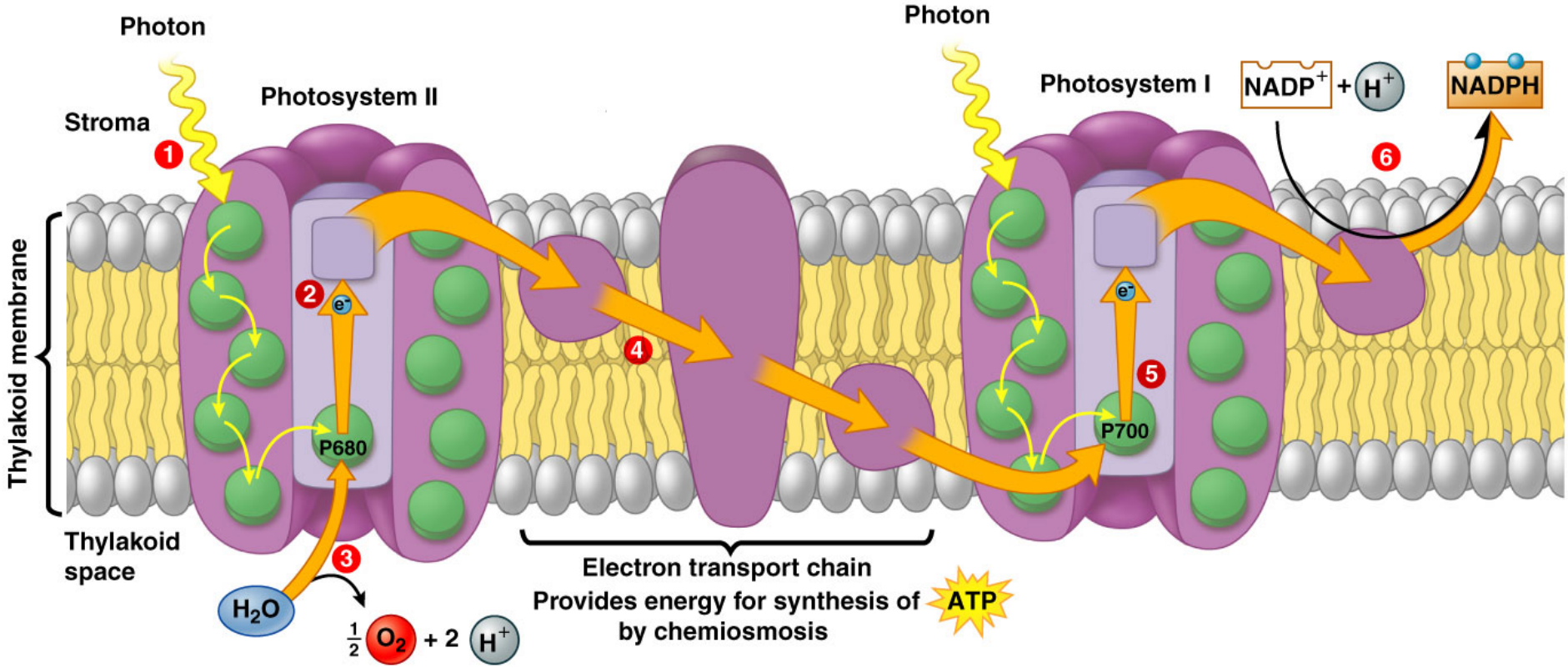



Energy transferred down gradient to reaction center

International Journal of Photoenergy, Volume 2009, Article ID 434897, 21 pages

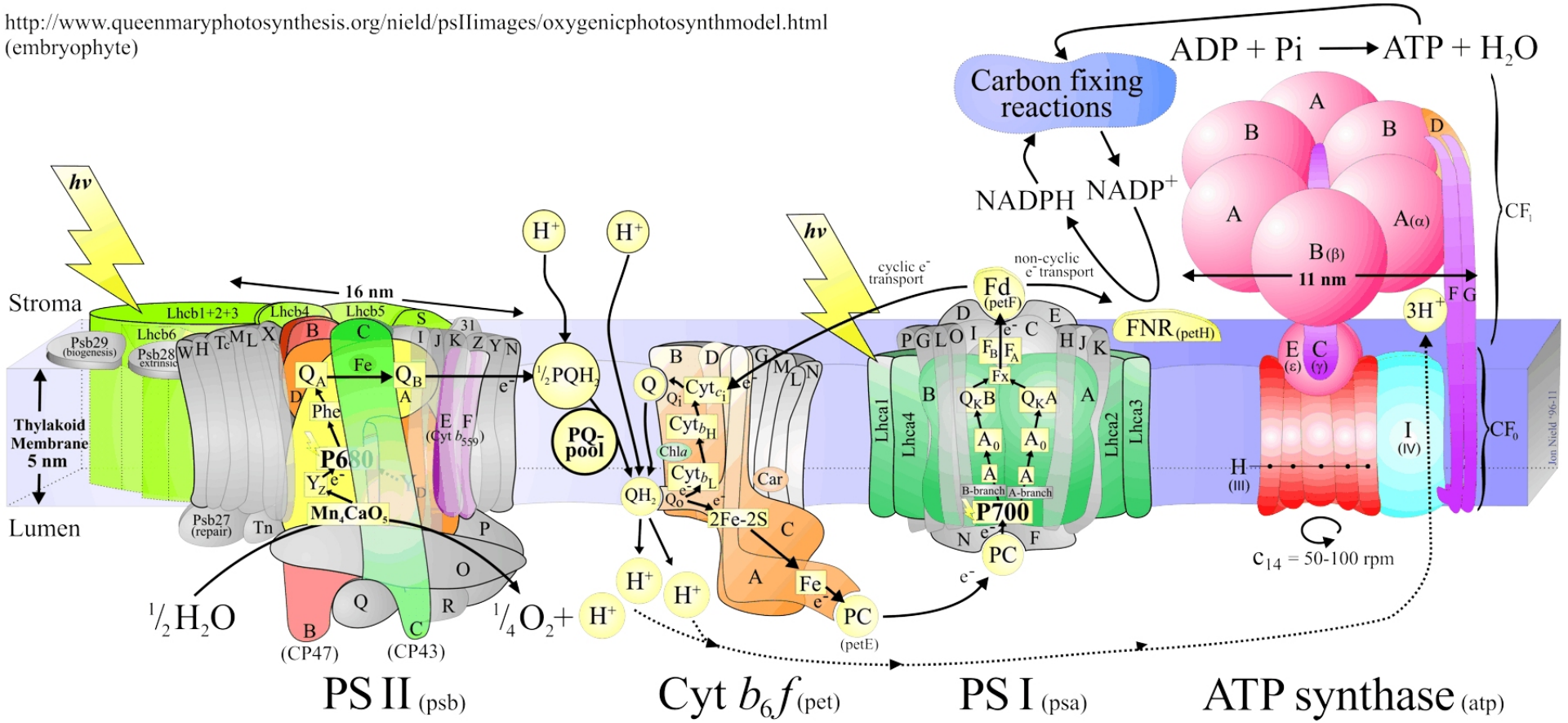
# Excited electrons move from Photosystem II to Photosystem I





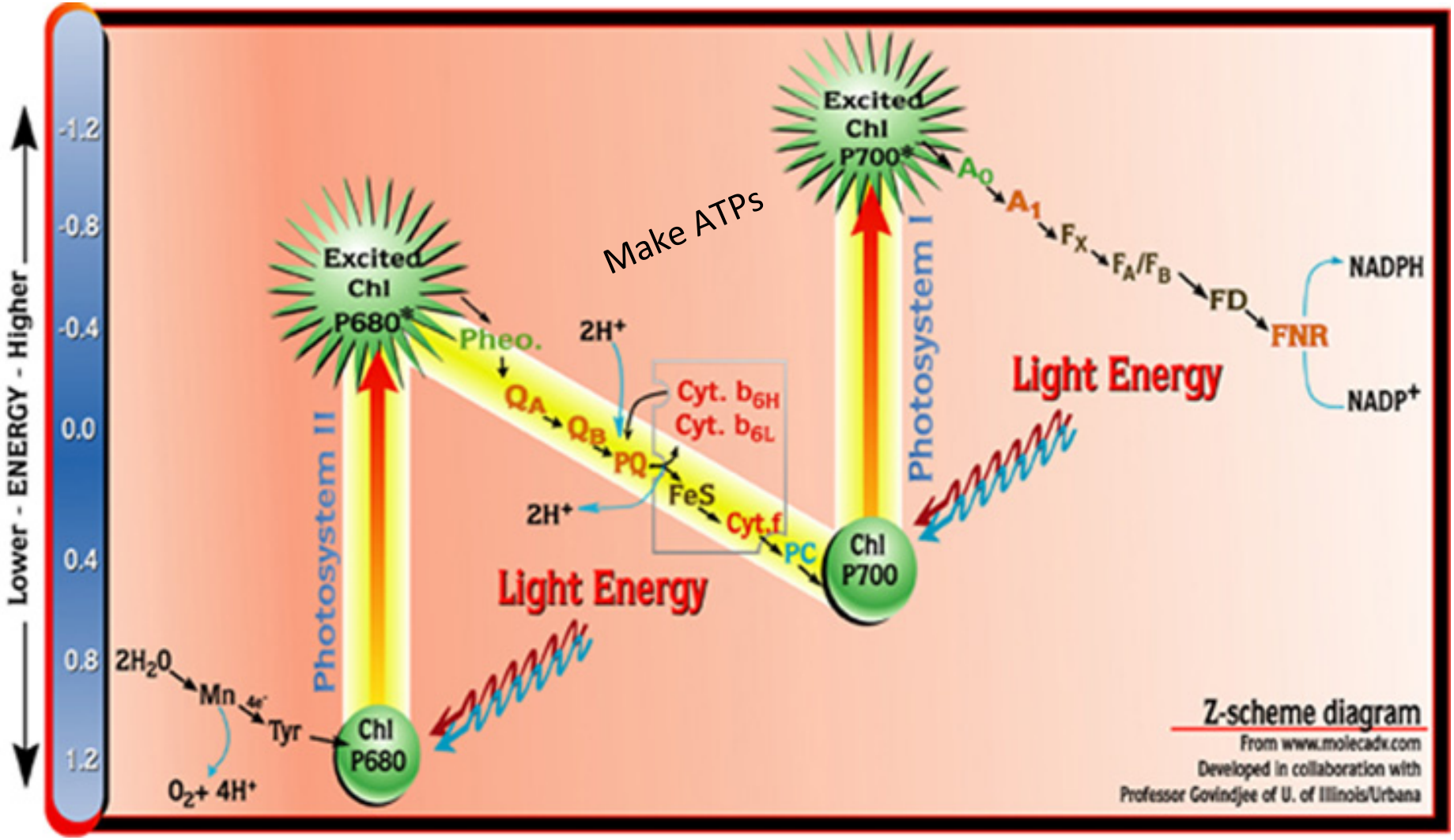

http://smirkbioacc8.blogspot.com/2015/03/light-reactions-photosynthesis-diagram.html

# A more detailed view




http://macromol.sbcs.qmul.ac.uk/resources/AllComplexes_25Nov2011_1800px.gif

3. trans-membrane charge separation at PSII
4. electron transport PSII to PS I (**ATP** is produced; P700 electron replaced)
5. trans-membrane charge separation at PSI (**NADPH** is produced)



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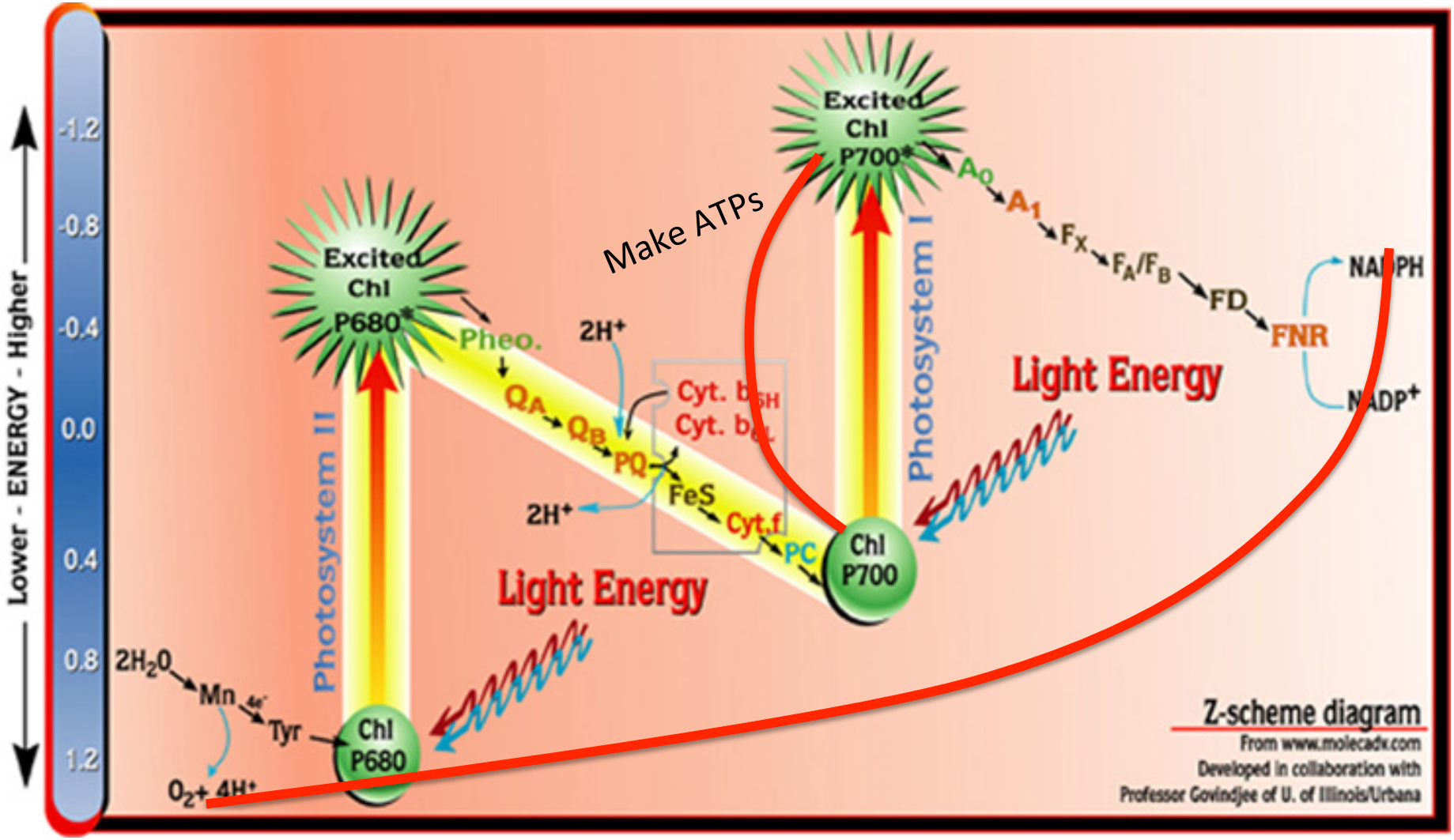
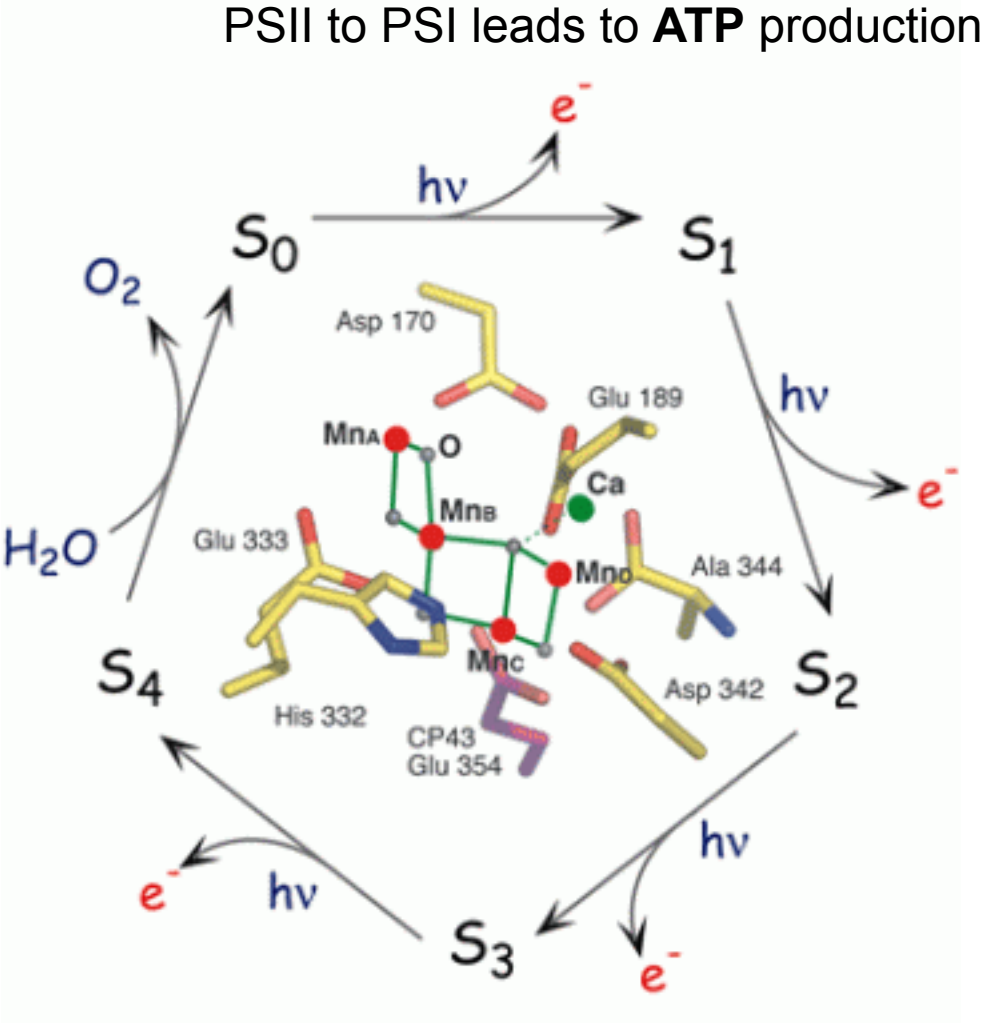
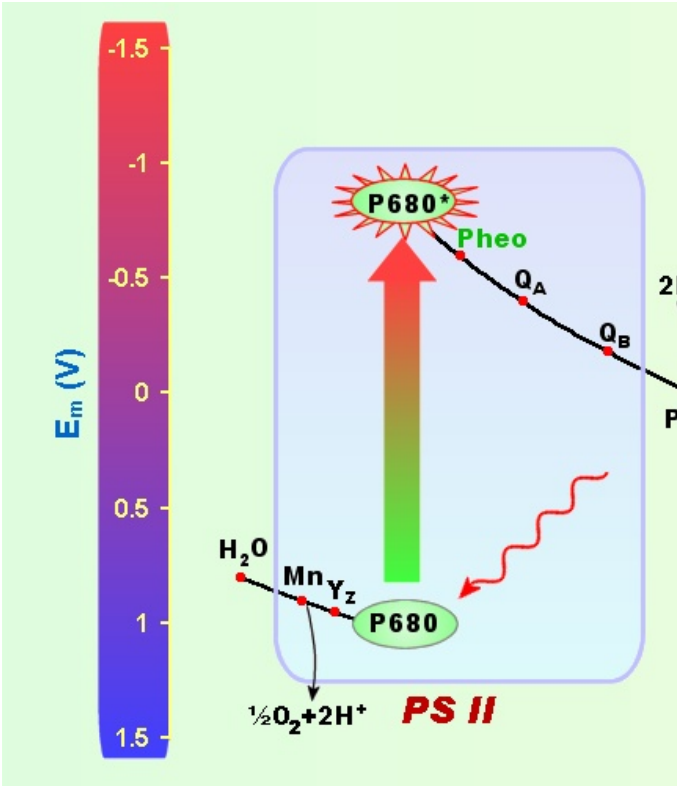


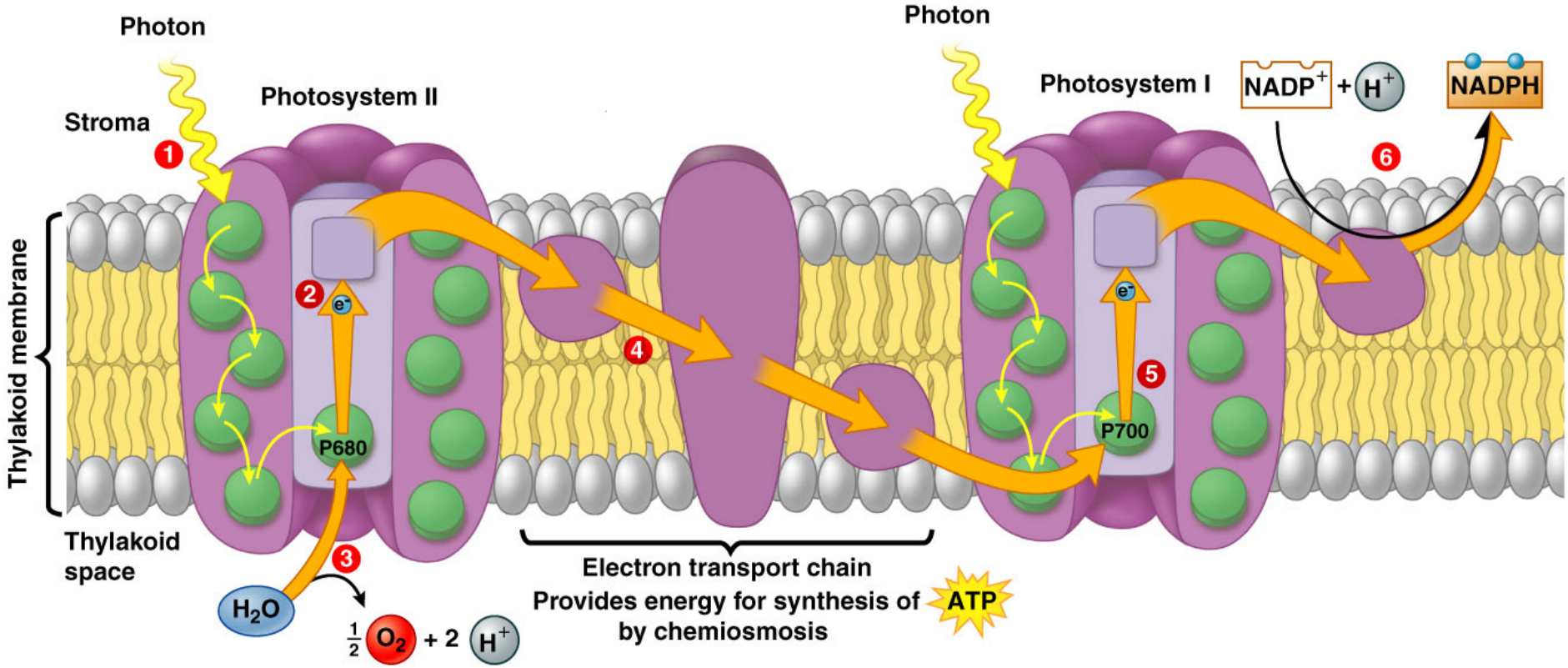

Ratio of ATP & NADPH: Cyclic PS I makes ATP; Mehler reaction consumes O2 & NADPH

6. $H_2O$ is split at PSII
   - – generate electrons to replace those lost by PS II ($P680^+$) during charge separation;
   - – produces **$O_2$ as waste product**;
   - – $H^+$ is produced; $H^+$ gradient coupled with electron transport from PSII to PSI leads to **ATP** production



# All these process happen on the thylakoid membrane, but where's the carbon?

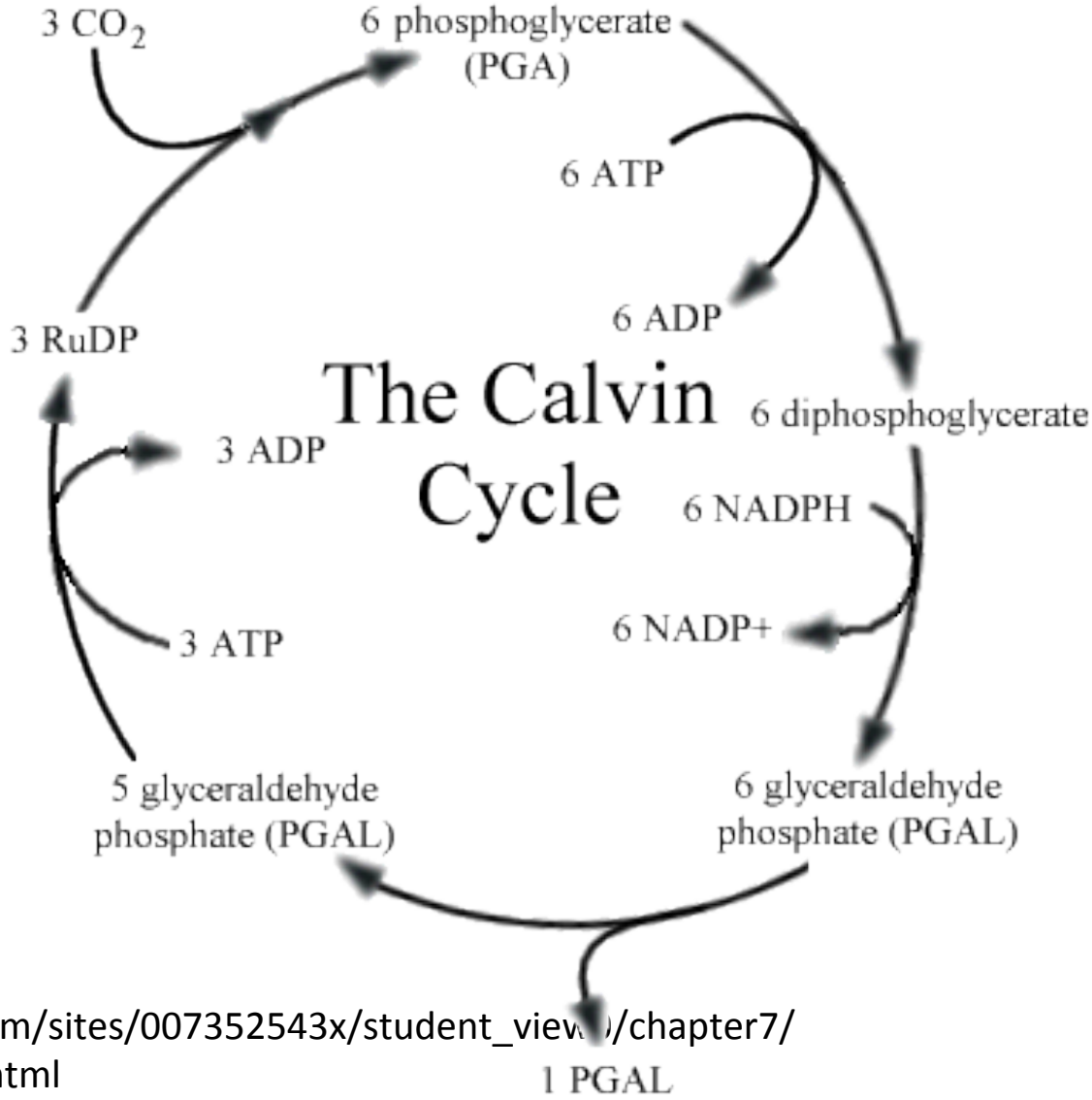




http://smirkbioacc8.blogspot.com/2015/03/light-reactions-photosynthesis-diagram.html

7. **ATP & NADPH** used to reduce **$CO_2$, $NO_3^-$, $SO_4^{-2}$** and provide energy for **biosynthesis of proteins, lipids, nucleic acids, etc., etc.**

Here's the carbon




http://highered.mcgraw-hill.com/sites/007352543x/student_view0/chapter7/how_the_calvin_cycle_works.html

## Summary of "Light" reactions of PS:

absorption of **8 photons** produces **2 ATP, 2 NADPH**, **1 $O_2$**

PS quantum yield ($\Phi$): mol $O_2$ produced / mol photon absorbed;

$\Phi$ max ~ 0.125 at low light; $\Phi$ lower at higher light

## Summary of "Dark" reactions: use products of photosynthesis (ATP and NADPH):

1. Reduce $CO_2$ to –[**$CH_2O$**]– (fixed C increases biomass, used at night in respiration, excreted as DOC)

2. Directly use as energy source in biosynthesis;
   **lipids, proteins, complex carbohydrates** require more energy – ATP, NADPH.

3. Reduce **$NO_3^-$**, **$SO_4^{-2}$, synthesize molecules**, etc.

$CO_2$ reduction requires **10 photons** (**3 ATP, 2 NADPH**)

PS quantum yield: mol C produced/mol photon absorbed;
$\Phi$ max ~ 0.10; $\Phi$ lower at higher light;
Also lower if ATP and NADPH used for nitrate reduction, etc.

**Photosynthetic quotient:** $O_2$ evolved to C fixed. >1; 1.5 & higher.
Leads to some uncertainty in mass balance calculations.

# What is productivity?

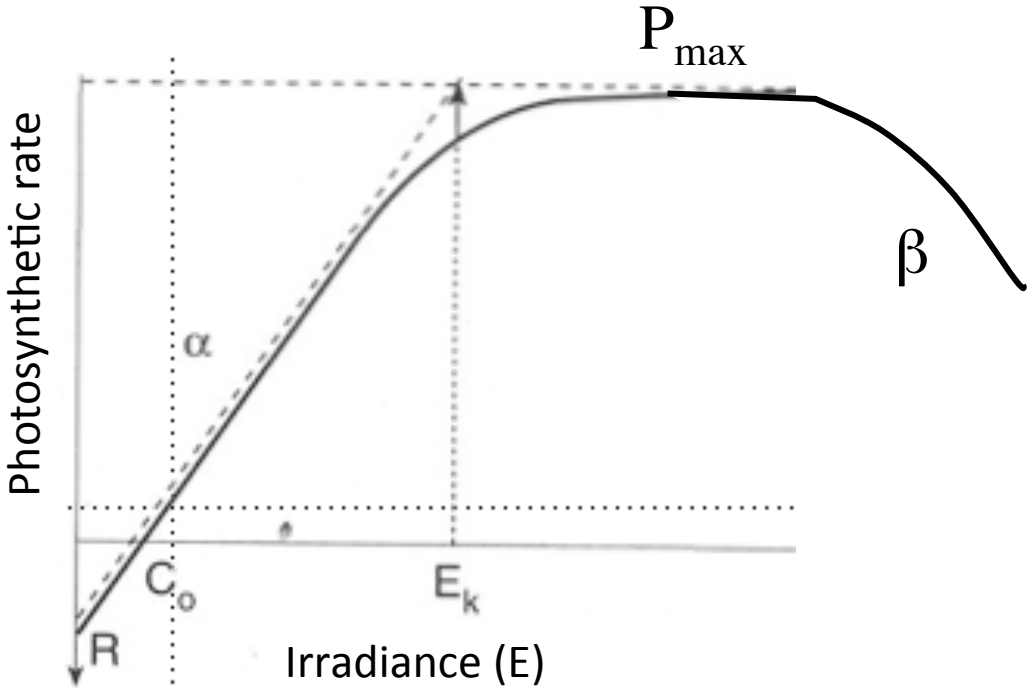
$$CO_2 + H_2O \longrightarrow -(CH_2O)- + O_2$$

Rate / area or volume / time

# Basic light response:

Photosynthetic coefficients are normalized to phytoplankton biomass, are a function of light, and incorporate physiology (photo-adapatation, nutrient limitation, etc.)

$$P = P_{max}(1 - e^{-(E/Ek)})\, e^{-(E/E\beta)}$$




E (light)

$P^b_{max}$ (normalized rate – usually to Chl); product is C or $O_2$

α (slope)

$E_K = P_{max} / \alpha$

β (light inhibition)

$E_\beta = P_{max} / \beta$

R = respiration

**There is more than one type of productivity**

1. **GOP:** gross photosynthesis as oxygen evolution.
   Bottle 18O, *in situ*: triple O

2. **NPP:** net primary productivity, rate of phytoplankton fixation of carbon minus phytoplankton respiration (24 h). What about DOC?
   Bottle 14C; *in situ*: diel changes in biomass

3. **NCP:** NPP minus local heterotrophic consumption: (grazing by protoza and zooplankton; microbial respiration).
   *In situ:* mass balance Ar/O2, O2 corrected for air/sea flux, NO3

4. **EP:** export production, need to boundary conditions – sinking of organics, zooplankton vertical transport, DOC subduction, resource harvesting.
   *In situ:* mass budgets, traps, cameras, etc.

5. **SP:** sequestration production, what gets through the twilight zone
   *In situ:* deep traps, sediment cores

6. **Secondary P:** production of heterotrophic biomass

## Measurements

1) **Incubations** – short time scales (typically < 1 day); bottle effects?
   i. tracers: $^{14}C$, $^{18}O$, $^{15}N$, $^{33}P$, $^{68}Ge$ (for Si), $^{59}Fe$, etc.
   ii. "dilution" experiments – dilute grazers, measure increase in chl, other pigments (taxa specific), cell number, etc.
   iii. light/dark bottle (BOD) – changes in oxygen, pH, biomass

**2) Direct observations in environment** – integrate over different space and time scales – time scale makes a difference
   i. change in product over time (**$O_2$** evolution and **phytoplankton concentration)** – is that NCP?
      (how to measure phytoplankton? cells, Chl, absorption, scatter)
      (how to correct for air/sea exchange?)
   ii. change in reactant over time
   – drawdown of **N, P, $CO_2$**, **DIC**; apply Redfield ratios or P.Q. (correct?)

Tools: satellites, ships, moorings, floats, gliders. (Lagrangian vs. Eulerian)

3) Variants of probe fluorometry (pump and probe, PAM, FRRF) – provides terms for PS electron flow models

**Models** – validated how?

# Gross PP (GPP)

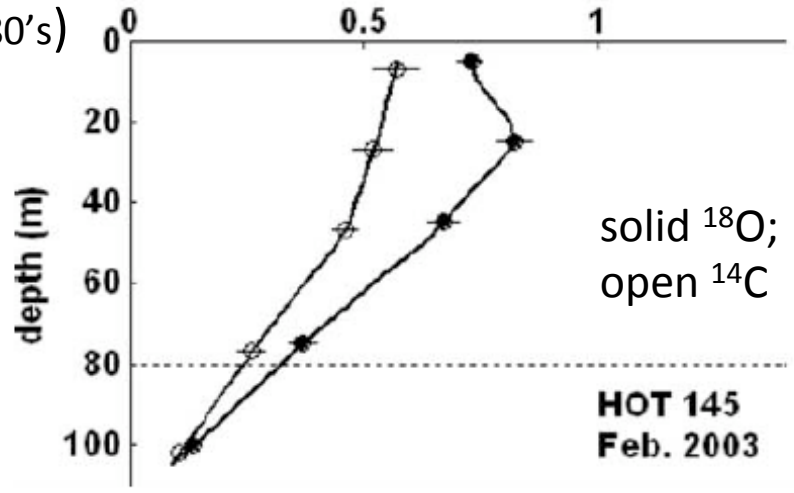
**Triple oxygen isotope** – direct in situ measurement. Photosynthetic production of O is mass dependent (produce less heavy isotope), while UV interactions among $O_2$, $O_3$, and $CO_2$ in atmosphere are mass independent (leads to equal lowering of fraction of $^{17}O$ and $^{18}O$).

Biologically-produced O is enriched in $^{17}O$ vs. $^{18}O$.
By measuring difference in $^{17}O/^{16}O$ and $^{18}O/^{16}O$ of $O_2$ between dissolved in seawater and in atmosphere (plus need estimate of air/sea gas transfer rate, advection, mixing, etc.), can estimate gross photosynthesis. Often much higher than carbon based estimates.

**Bottle tracer incubation methods** (Bender ~ 1980's)

$$\frac{H_2{}^{18}O}{H_2{}^{16}O} \sim \frac{{}^{18}O^{16}O \text{ evolved}}{{}^{16}O_2 \text{ evolved}}$$

$^{18}O$ is 1.5 to 2-fold higher than $^{14}C$ - or higher !
Also calls into question Photosynthetic Quotient.




solid $^{18}O$;
open $^{14}C$

Juranek & Quay (2005) BGC 19,GB3009

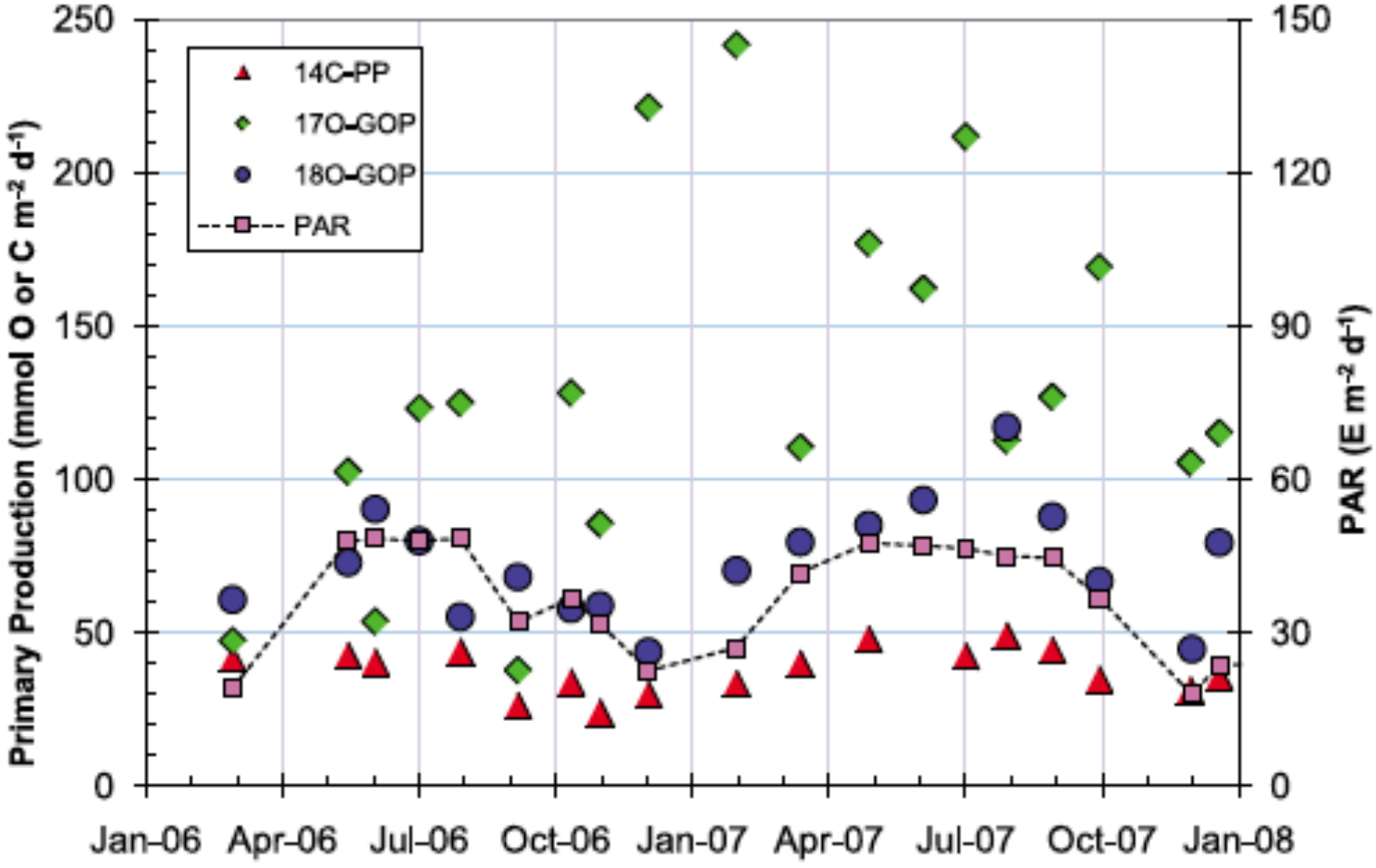
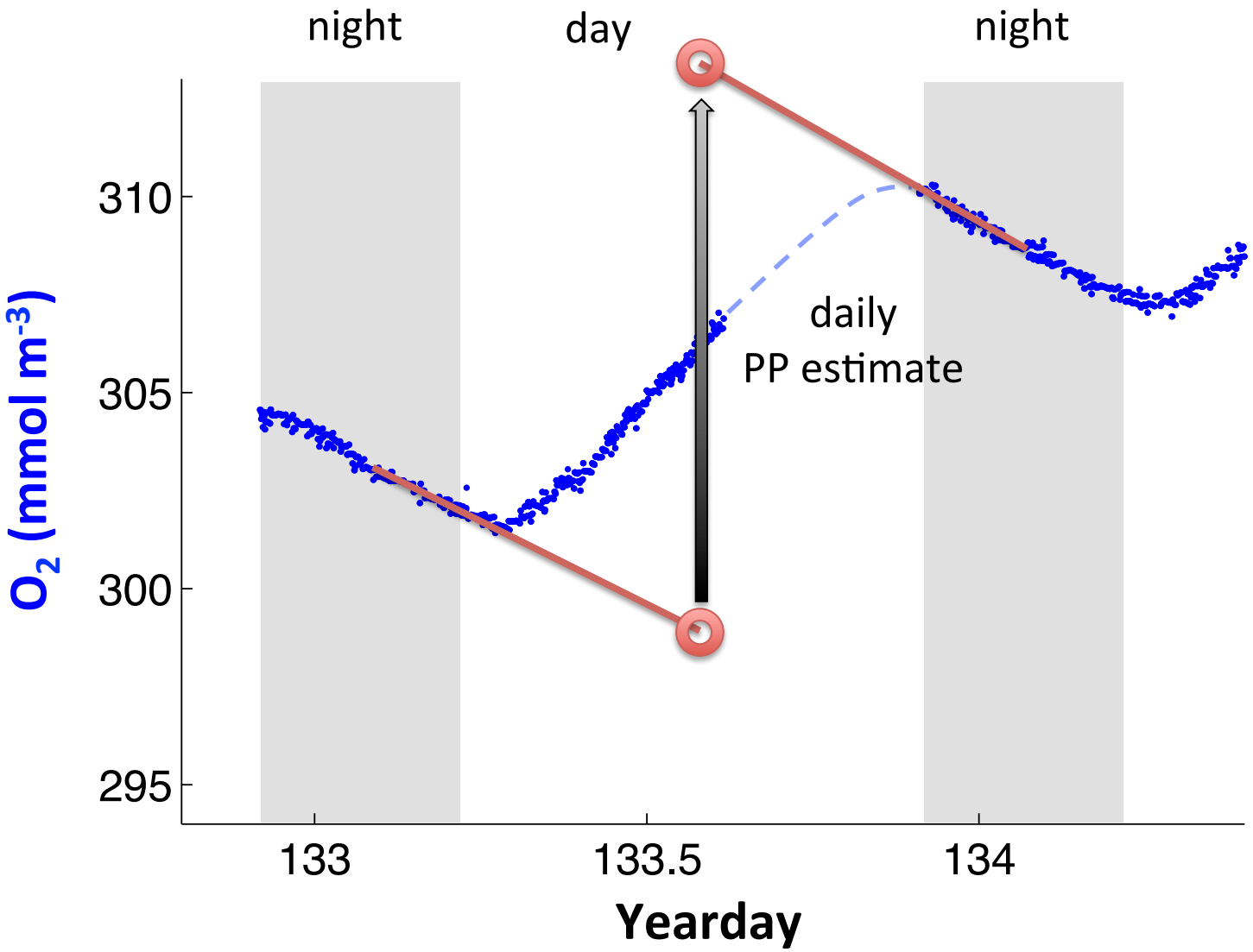



**Figure 3.** Monthly rates of GOP estimated from the $^{17}\Delta$-GOP and $^{18}$O-GOP (mmol $O_2$ $m^{-2}$ $d^{-1}$) and $^{14}$C-PP (mmol C $m^{-2}$ $d^{-1}$) methods depth-integrated to 100 m.

Quay et al. 2010. GLOBAL BIOGEOCHEMICAL CYCLES, VOL. 24, GB3014

# GPP (?)

Briggs PhD:
In situ measurements from Lagrangian float – diel cycles of O2



# Net PP (NPP)

**Bottle incubation**: **radio-labeled $^{14}C$ incorporation (tracer method)**

- introduced by E. Steeman Nielsen in 1950

*Of the 14C approach, Longhurst et al. (1995) wrote 'Rarely, in fact, can a technique have been so persistently criticized, but so consistently used.'*

$$CO_2 + H_2O \dashrightarrow -(CH_2O)- + O_2$$

$$\frac{^{14}HCO_3^-}{^{12}HCO_3^-} \sim \frac{^{14}C \text{ in new biomass}}{^{12}C \text{ in new biomass}}$$

$^{14}C$-labelled DIC (mostly $HCO_3^-$)

Photosynthetic energy leads to $CO_2$ reduction and incorporation of new POC in cells, biosynthesis of lipids, etc., nitrate reduction, photorespiration. DOC release of Calvin Cycle products is a high-light photo-protection mechanism (therefore, more DOC release near surface)

Does 14C POC reflect GPP or NPP? depends on length of incubation, etc.

# JGOFS protocols, Chapter 19. Primary Production by 14C

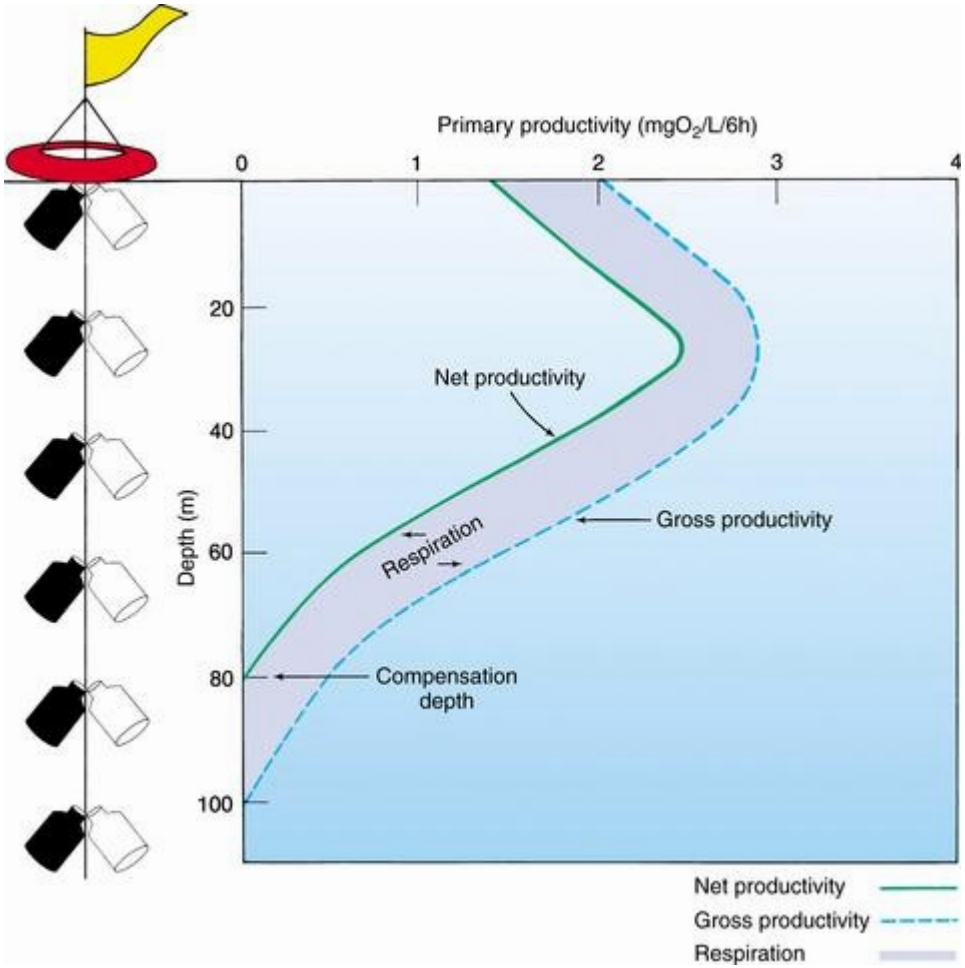
http://usjgofs.whoi.edu/protocols.html

$$PP\ (mg\ C\ m^{-3}\ d^{-1}) = \frac{SDPM}{V} * \frac{W * 0.25 \times 10^{-3}}{Tdpm} * \frac{1.05}{T}$$

| | | |
|---|---|---|
| SDPM | = | DPMs in filtered sample |
| V | = | volume of filtered sample (liters) |
| TDPM | = | Total $^{14}C$ DPMs (in 0.25 ml) |
| W | = | DIC concentration in samples (approx 25000 mg C $m^{-3}$; should be measured for non-oceanic habitats) |
| $0.25 \times 10^{-3}$ | = | conversion of pipette volume to liters |
| 1.05 | = | correction for the lower uptake of $^{14}C$ compared to $^{12}C$ |
| T | = | time (days) |

This measures POC, does not measure $^{14}$C DOC

Incubations – 1) *in situ*
(typically 24 hour incubations)




**Typically:**

Collect water pre-dawn from 5 or 6 depths, distributed throughout euphotic zone. Day or 24 hr?

Add $^{14}C$ to light and dark bottles

Put bottles at depth ('same' light level) and temperature to incubate.

Filter POC $^{14}C$ on filter.
Count dpm on LSC.

What's the effect of 'constant' light (yes, solar angle is changing and clouds) vs. light exposure in mixing layer?

Incubations – 1) *in situ*
(typically 24 hour incubations)

**Patterns:**

Surface photo inhibition

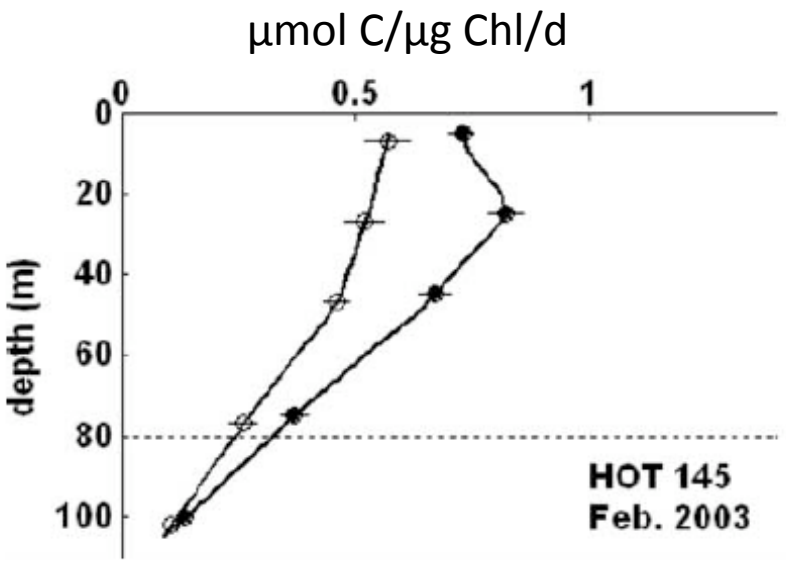
Rates normalized to Chl

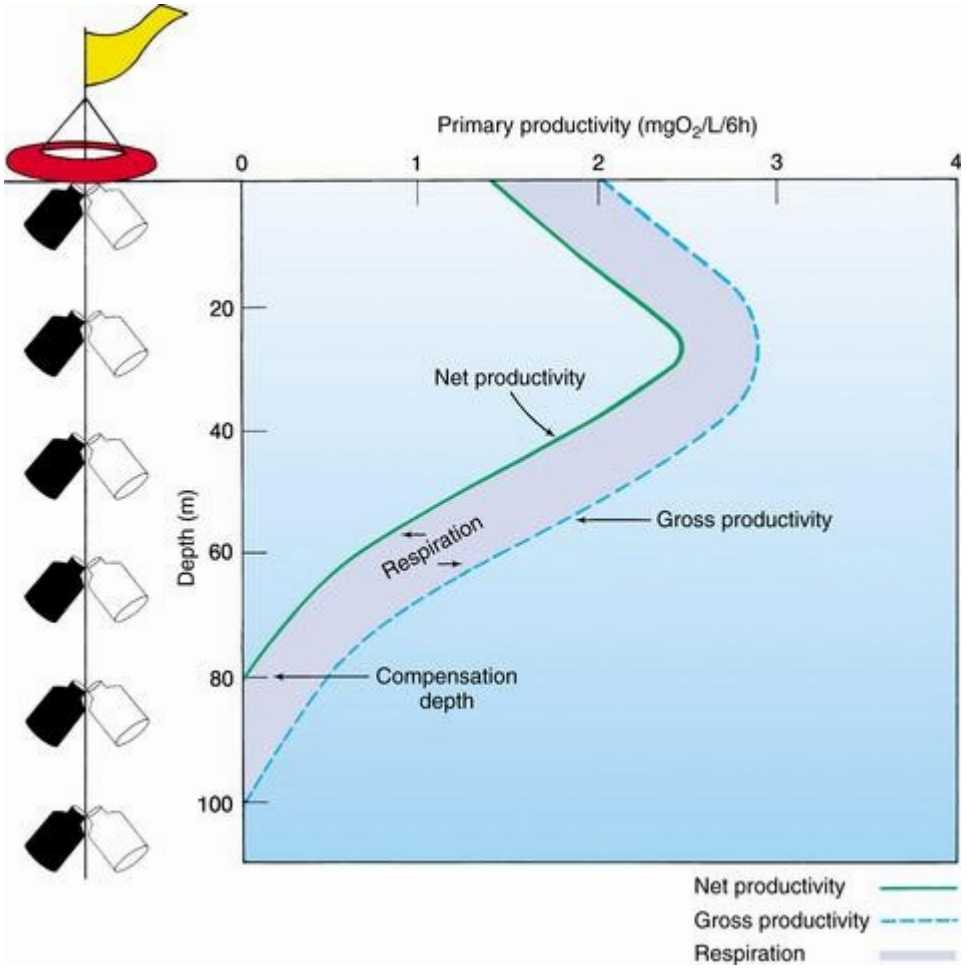
vary w/ depth

Effect of phytoplankton

respiration (Net PP)

Compensation depth




solid $^{18}O$; open $^{14}C$

Juranek & Quay (2005) BGC 19,GB3009.

# What does $^{14}C$ measure? GPP or NPP?

1. What happens in the cell during a 24-h period? (photosynthesis, synthesis, respiration)

2. What happens in the bottle? (nutrients, grazing, etc. ?)

3. Is it the same as the ocean? (mixing, light, etc.?)

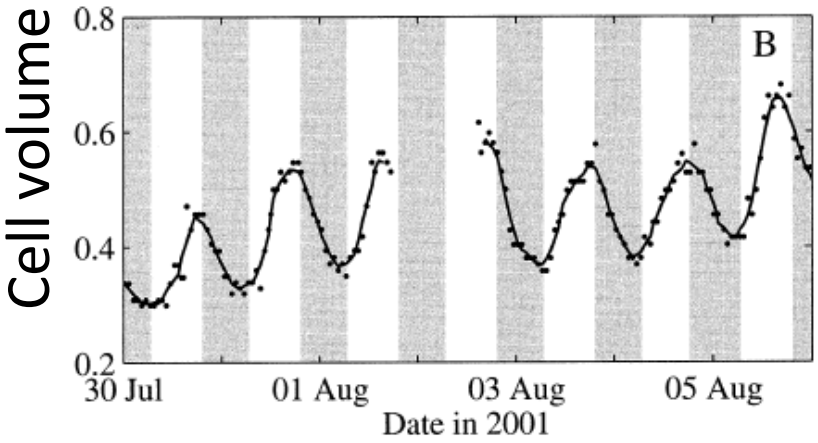
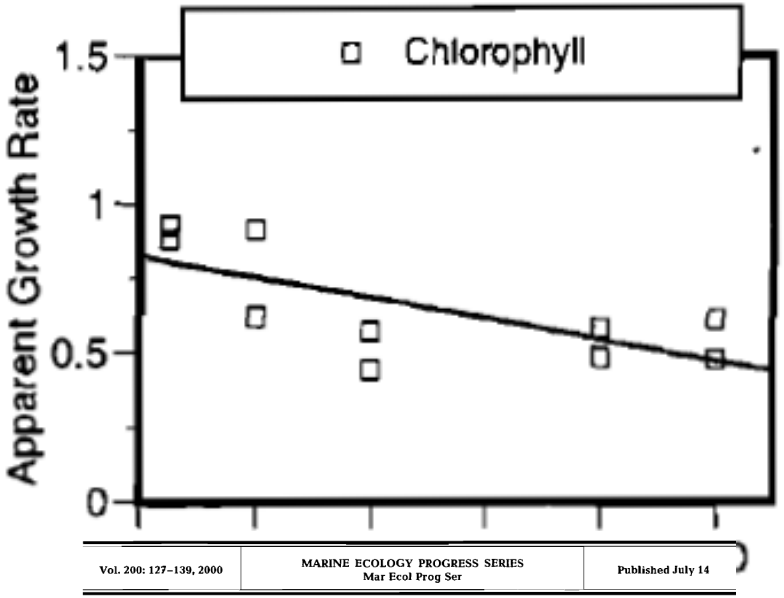



Fig. 3. *Synechococcus* properties for a 1-week subset of the time series shown in Fig. 2. Shaded bars indicate nighttime, and solid lines are four-point running means. Regular diel variations are not apparent in (A) cell concentration but are pronounced in (B) mode cell volume.

Sosik et al. 2003. L&O 48: 1756

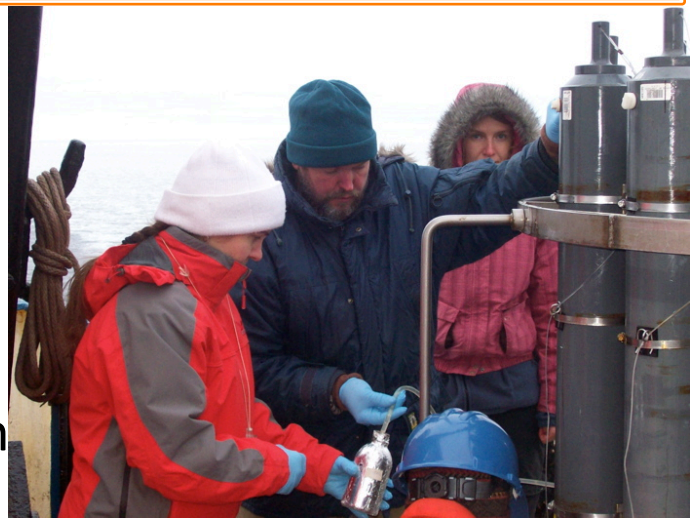



Vol. 200: 127–139, 2000 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published July 14

**Dilution effects on microzooplankton in dilution grazing experiments**

J. R. Dolan[1,2,*], C. L. Gallegos[1], A. Moigis[1,**]

# Incubations – 2) SIS (simulated in situ) incubations on deck, in natural sunlight



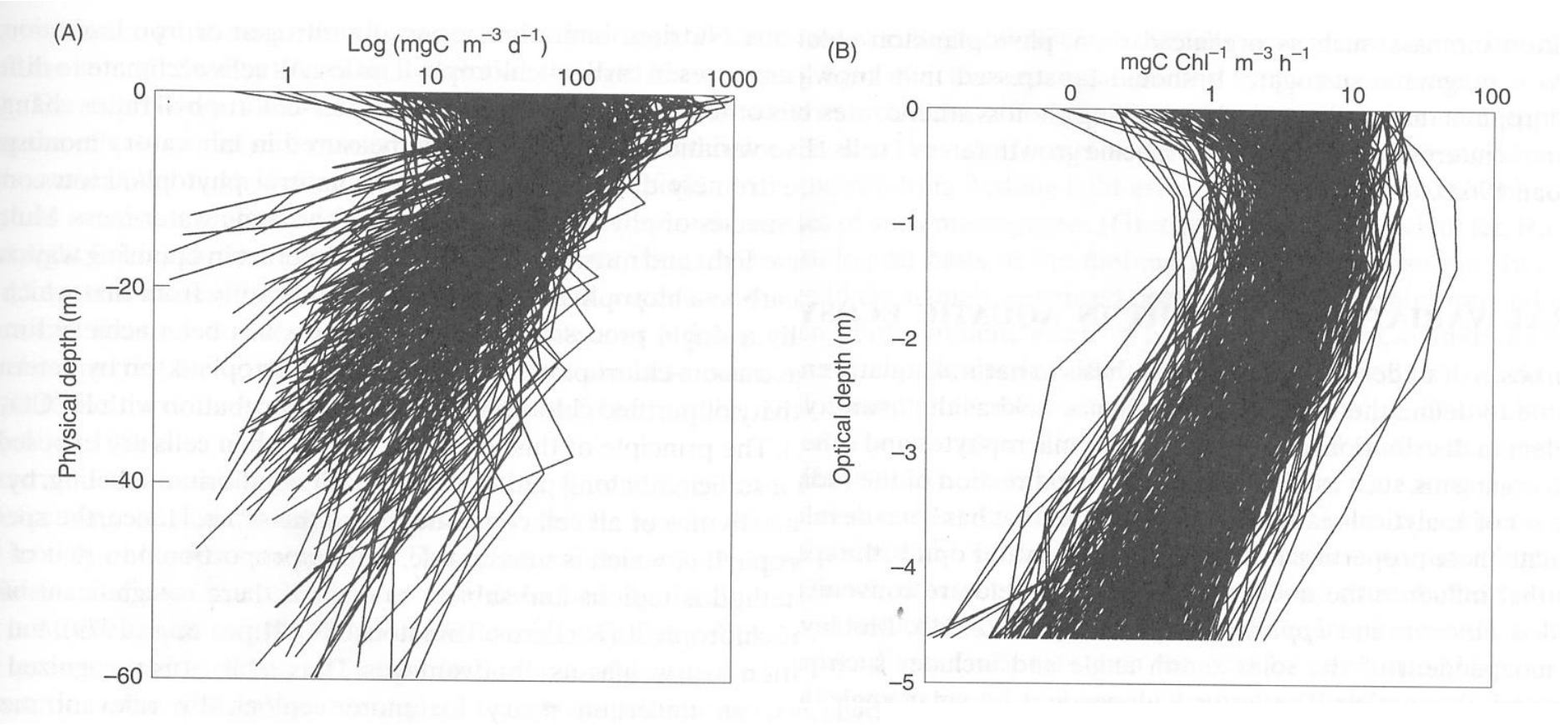
Collect water (typically predawn)
Add tracer
Place in screened incubator to
- simulate light at depth (hope you pick the right light/depth);
- temperature may not match that at depth

Incubate for ½ day, full day, 24 h day + night
Filter and count $^{14}C$ on filter

# Example of data from $^{14}C$ measurements

log C vs Z

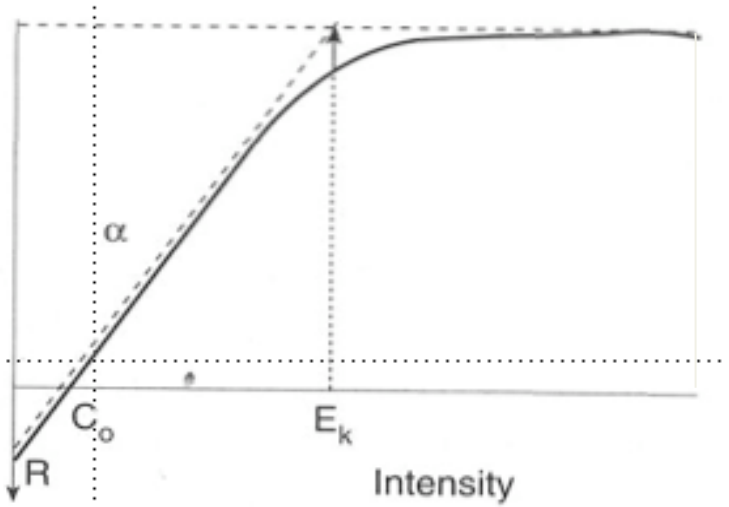
log C vs. log E



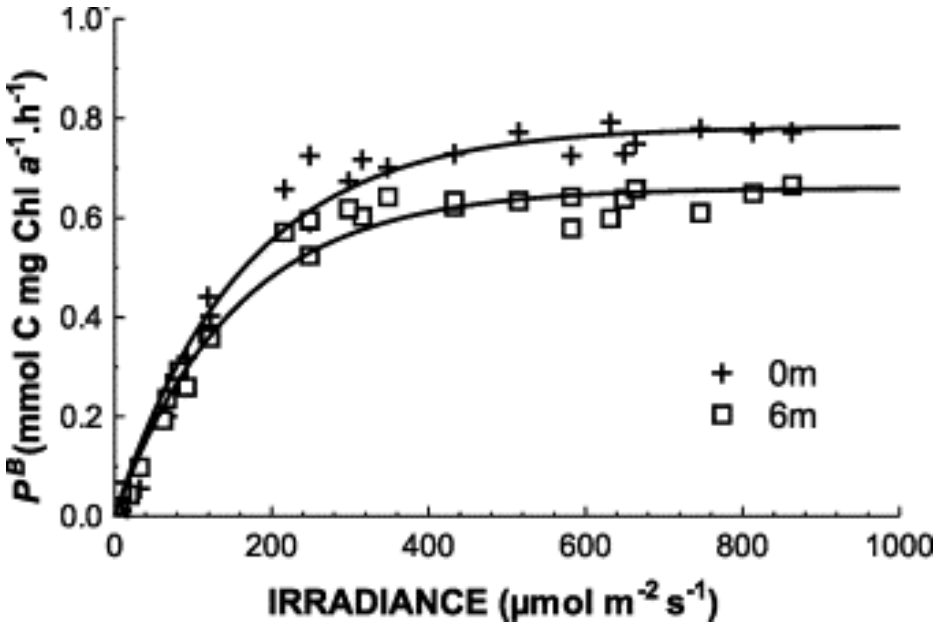
# Incubations – 3) P vs. E or photosynthesis vs. Irradiance incubations in the lab in artificial light

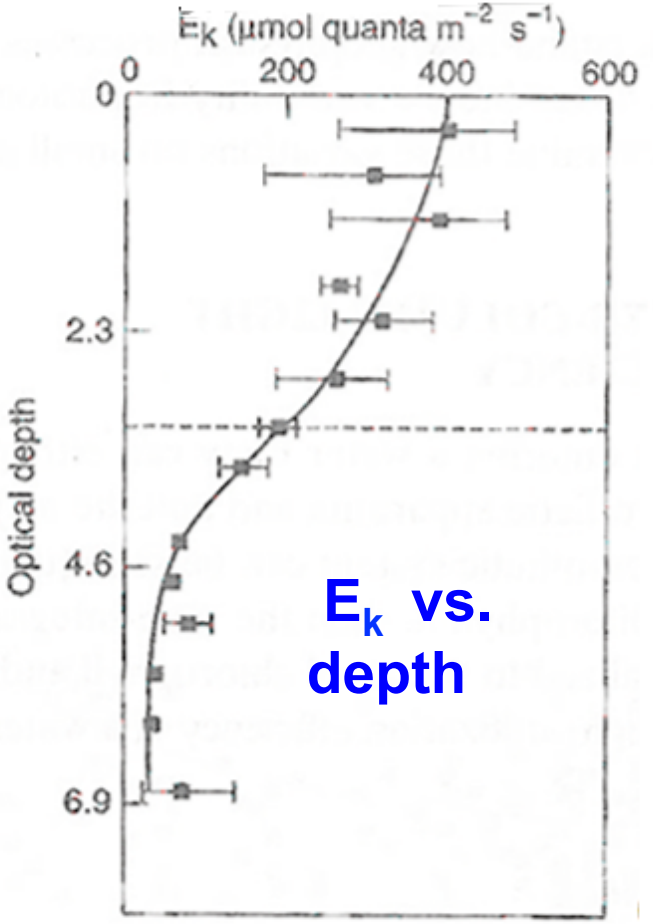
Collect water (any time of day)
Add tracer to 10 - 20 small bottles or vials
Place bottles in water jacketed incubator at range of irradiances
Incubate for 1- 2 hours; filter or analysis whole sample (acidify to degas DIC)

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




Incubations – 3) P vs. E or photosynthesis vs. Irradiance incubations in the lab in artificial light



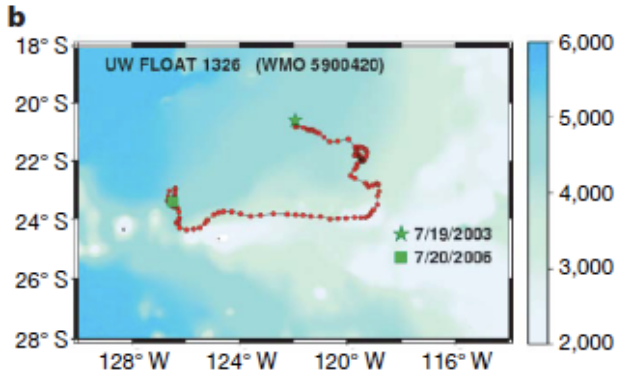



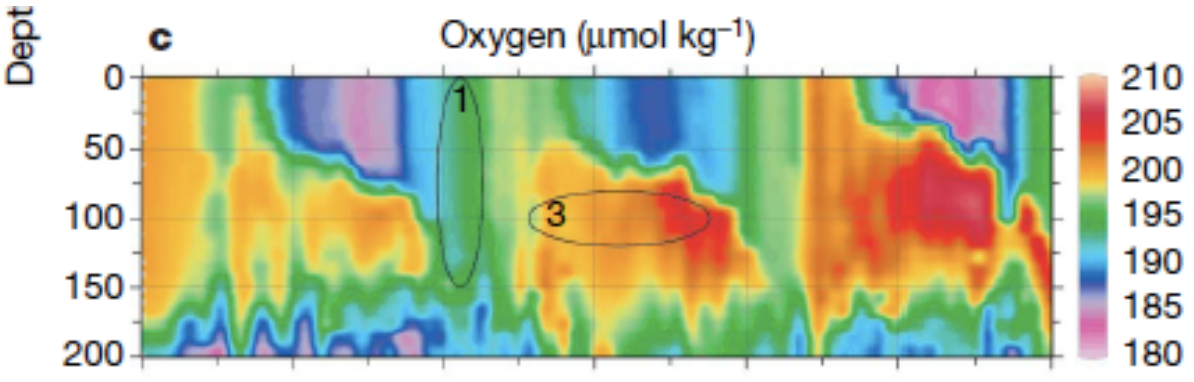
# **Net Community Production (NCP)** – direct in situ observations

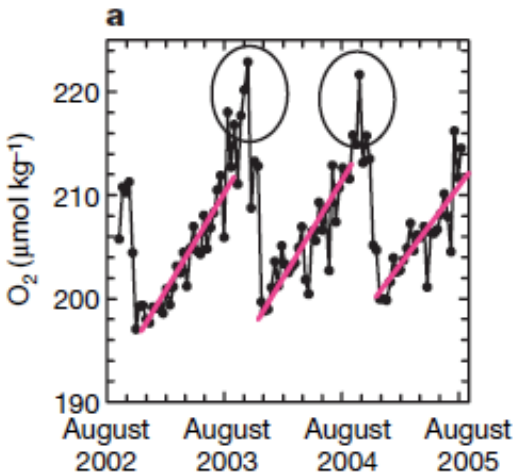
NCP = GPP minus all respiration (phytoplankton and heterotrophs)

**Dissolved oxygen/argon ($O_2$/Ar) ratios**
Argon corrects for disequilibrium of dissolved oxygen in mixed layer.

Changes in oxygen over time – Ken Johnson float.



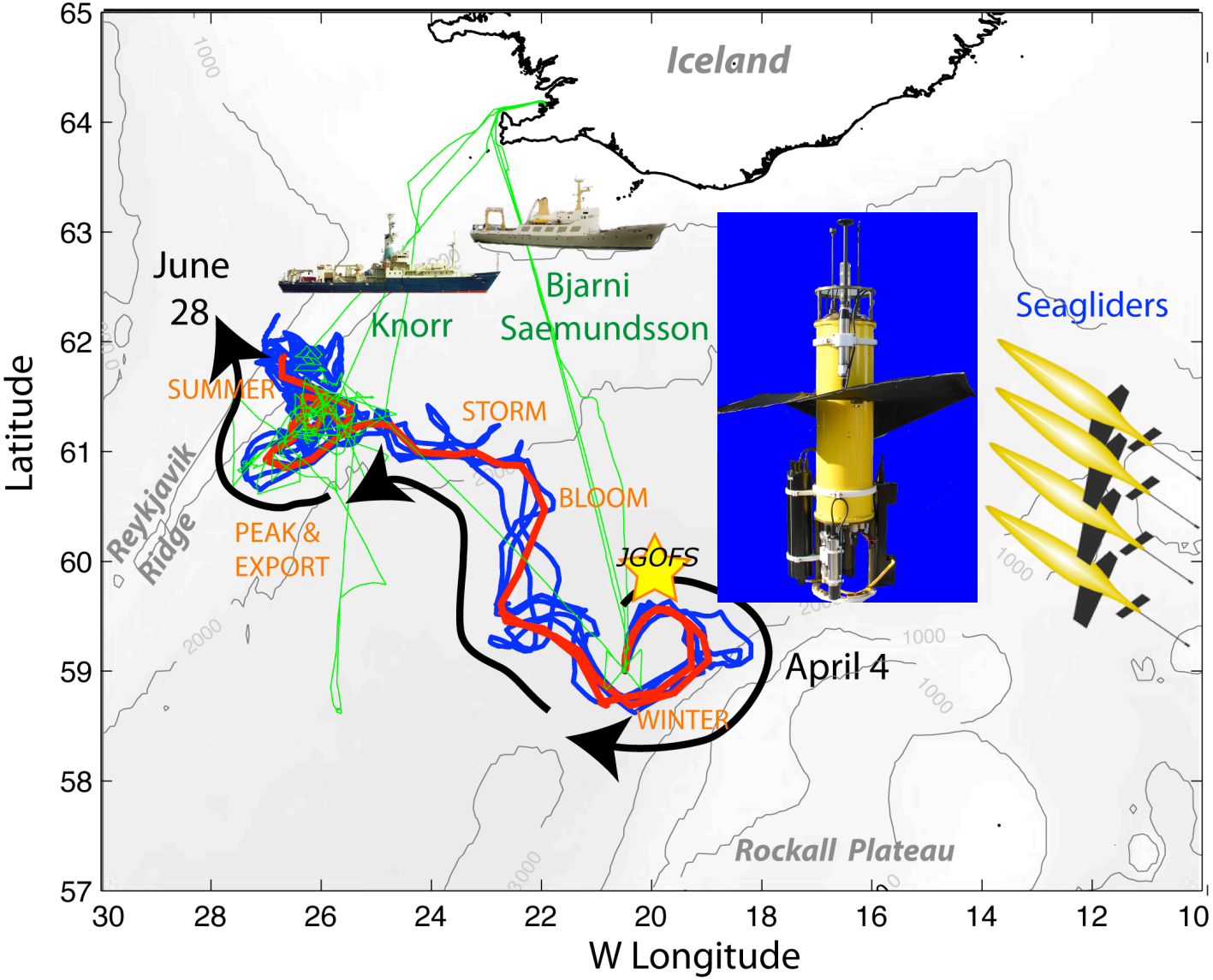



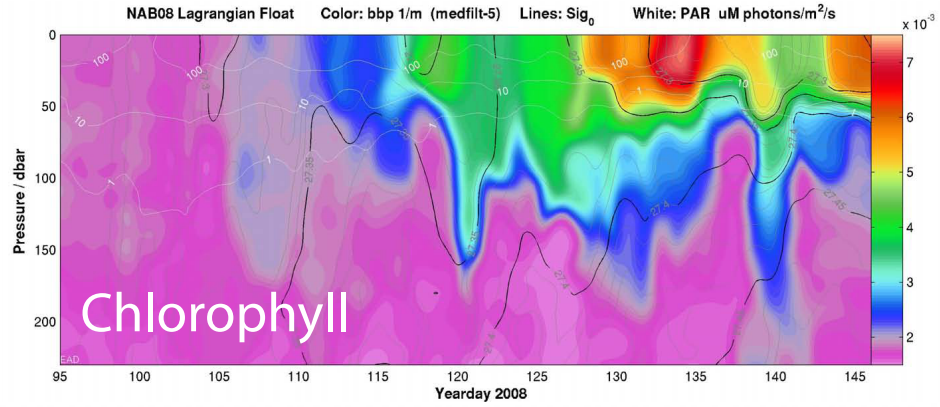

ARGO floats near Hawaii.

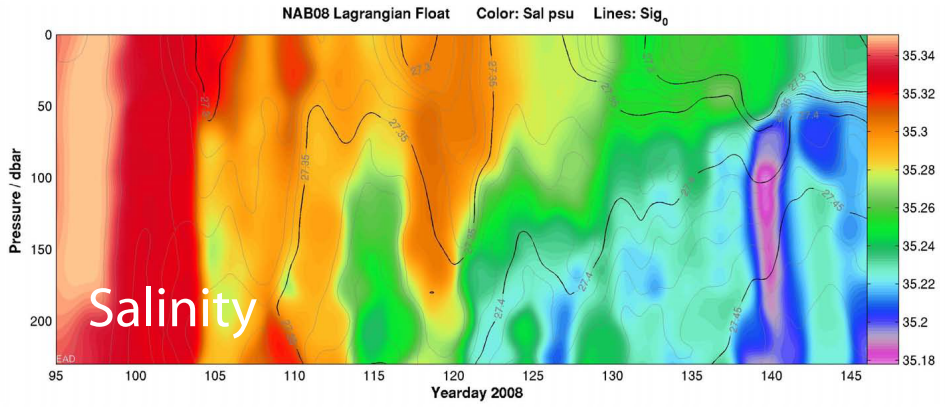
Riser & Johnson. 2008. Nature 451: 323

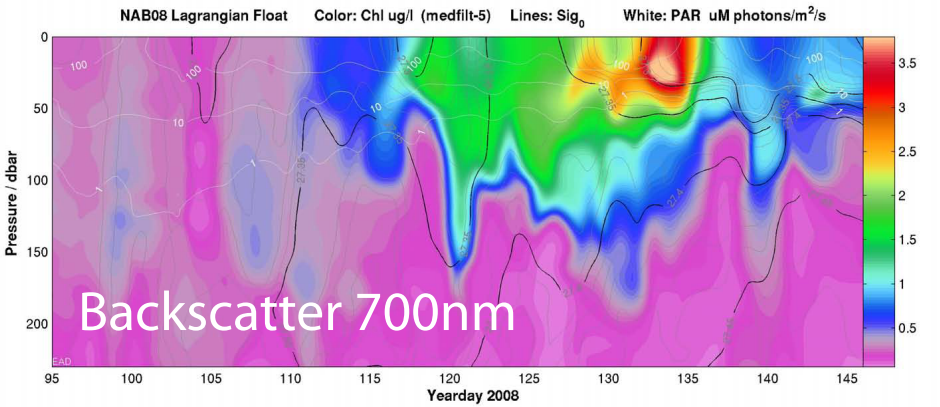
North Atlantic Bloom experiment 2008. Lagrangian float tracked a patch – evolution of O2, drawdown of NO3, accumulation of POC.

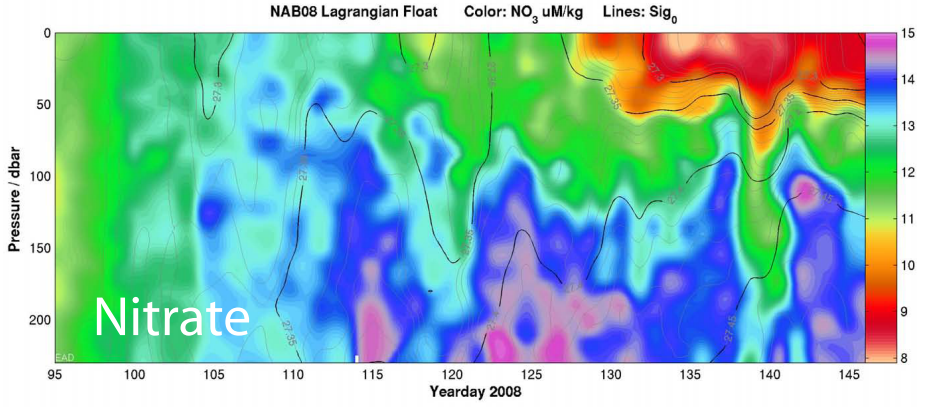


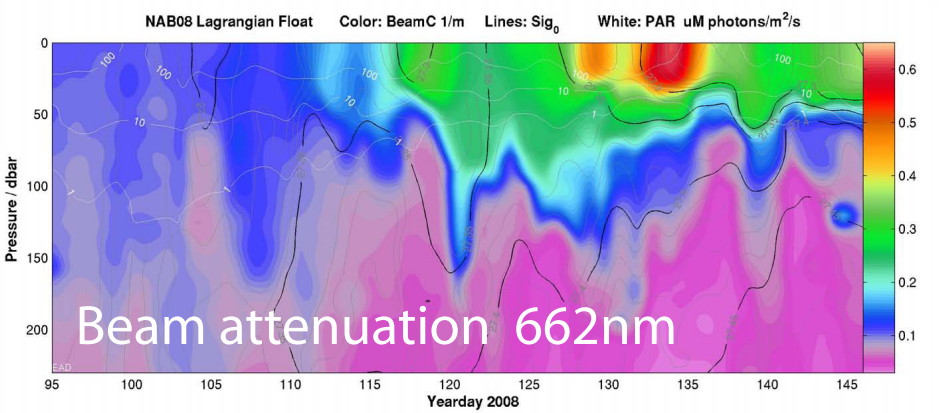

Float data, Alkire et al. 2012

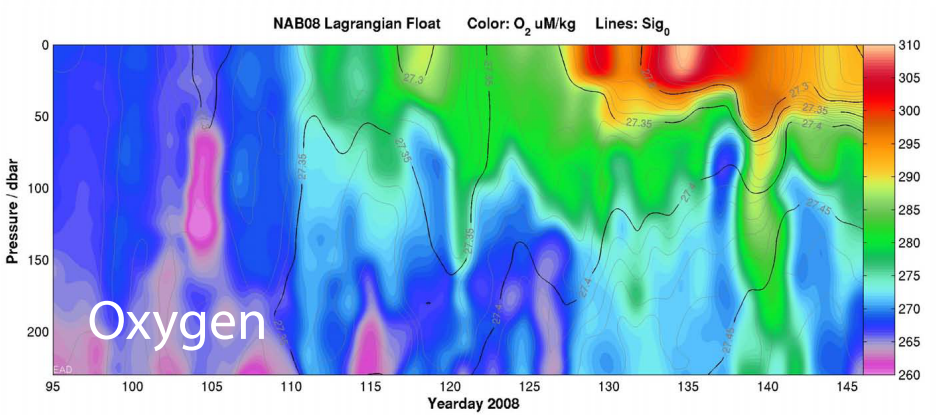


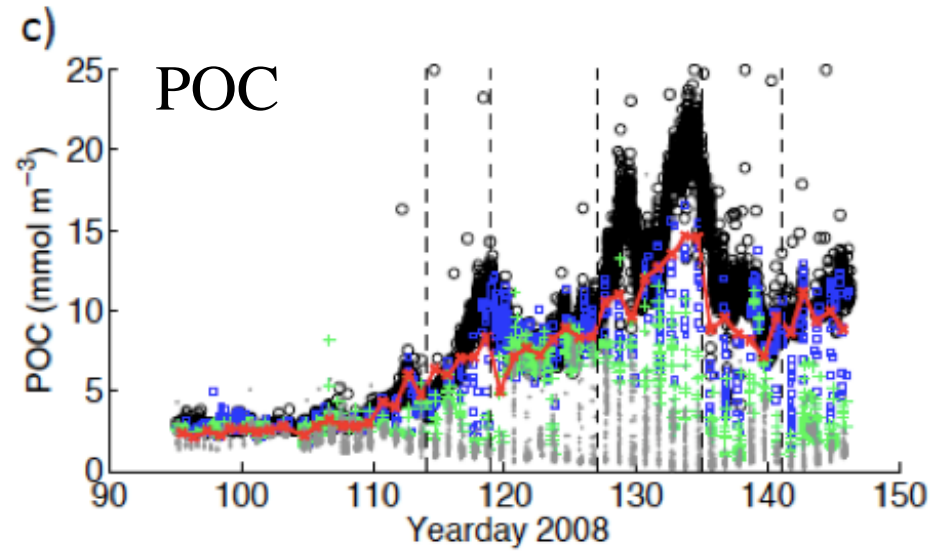



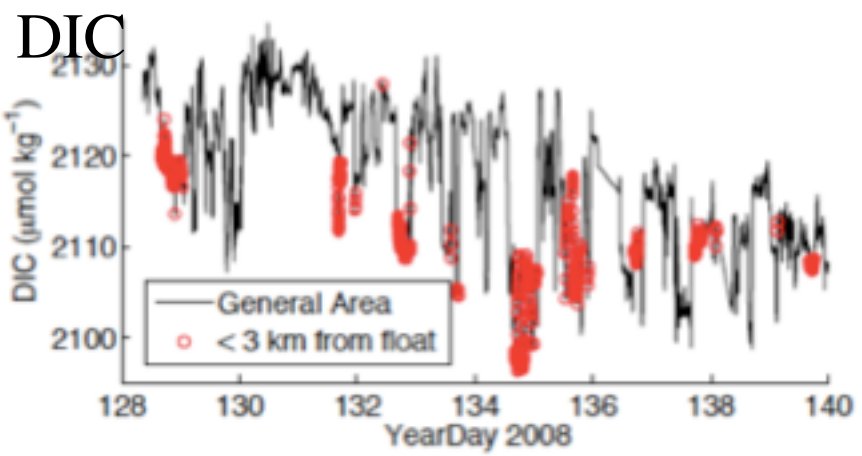



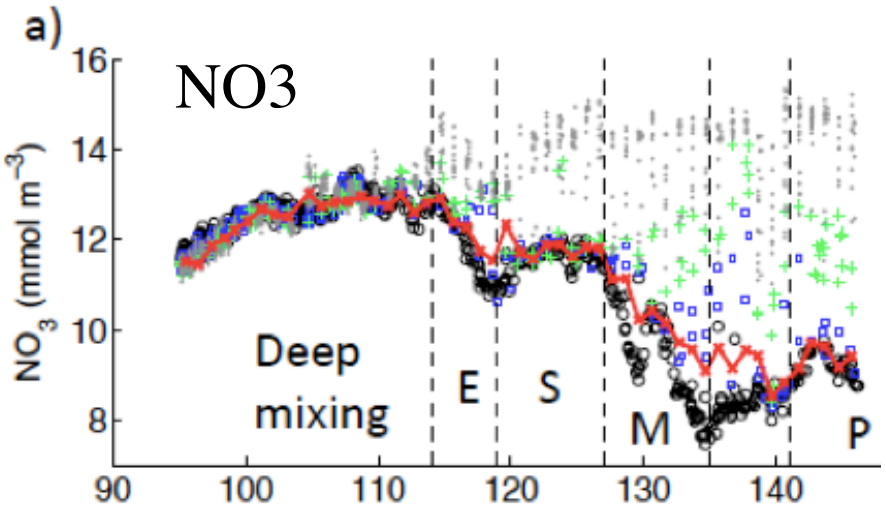



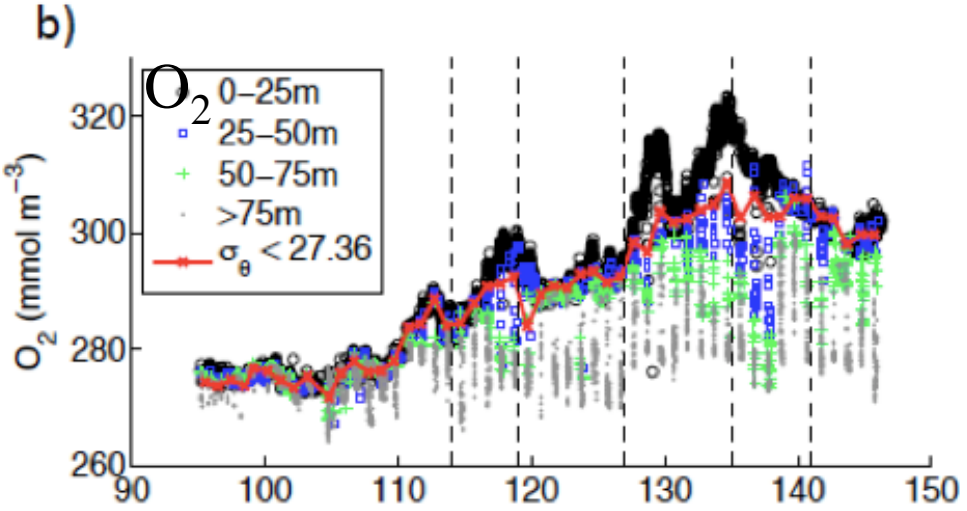




Float data, Alkire et al. 2012




POC from nitrate & O2, Redfield conversion does not equal POC biomass

Float data, Alkire et al. 2012

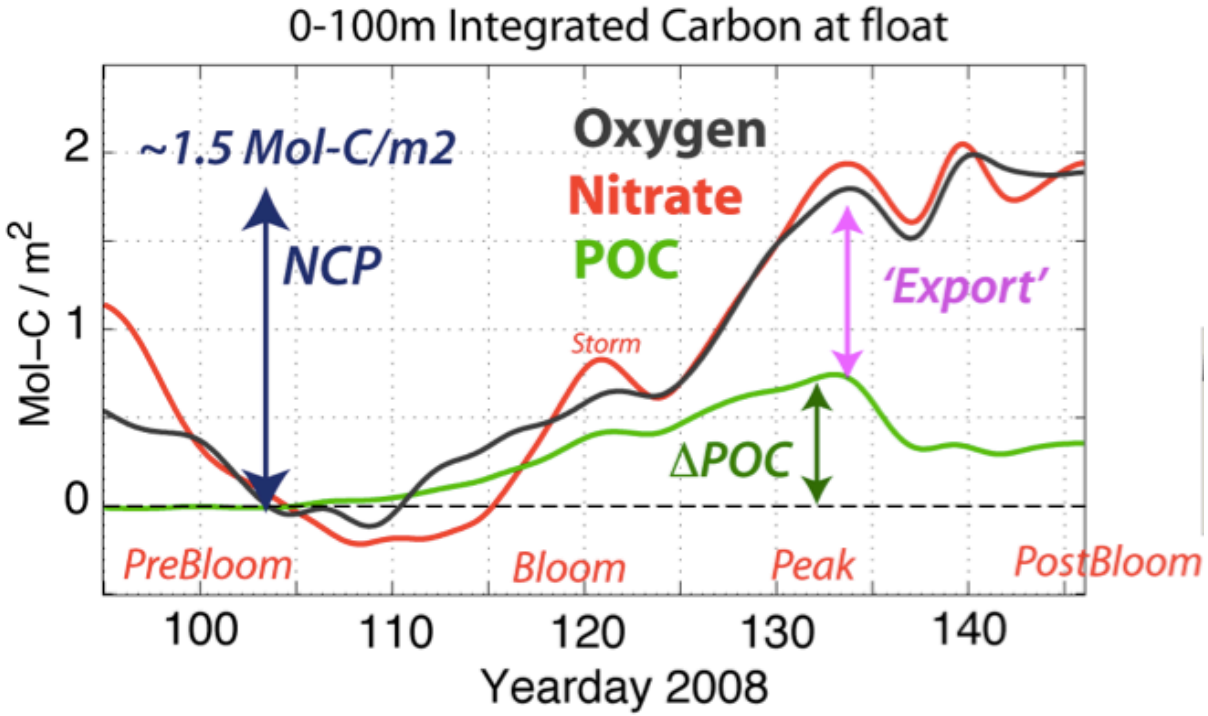
# NCP from Lagrangian O2 and NO3

*NCP= Primary Production - Respiration*

*= Decrease in $NO_3$ x C:N Redfield*

*= Increase in $O_2$ + $O_2$ loss to atmosphere x O:C (PQ)*

*= Increase in POC - Carbon Export + [ increase in DOC]*




D'Asaro, unpub.

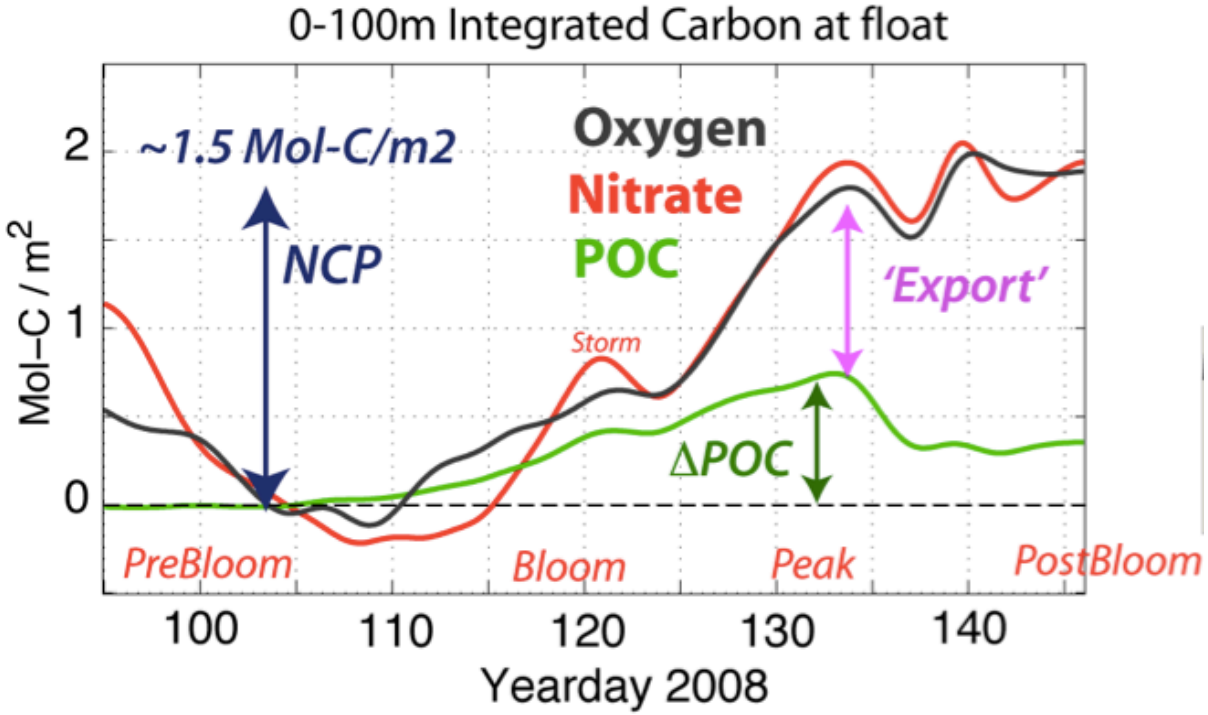
# Export Production from difference between NCP & POC accumulation

*NCP= Primary Production - Respiration*

*= Decrease in $NO_3$ x C:N Redfield*

*= Increase in $O_2$ + $O_2$ loss to atmosphere x O:C (PQ)*

*= Increase in POC - Carbon Export + [ increase in DOC]*

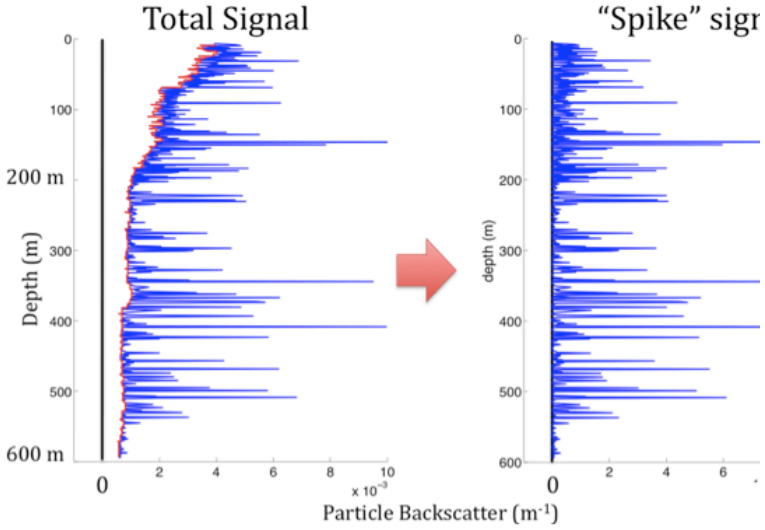


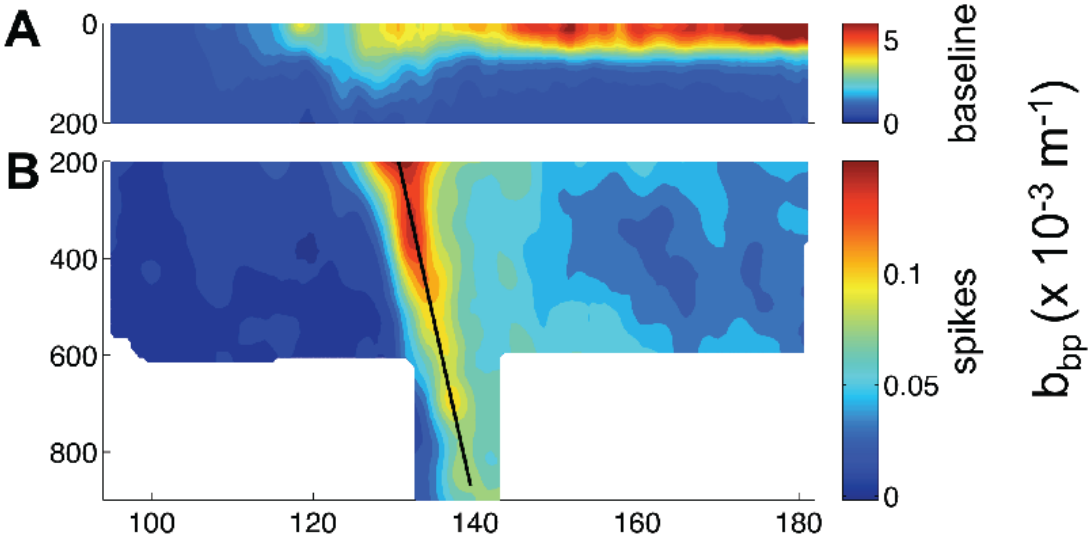

**Much of net fixed carbon is exported.**

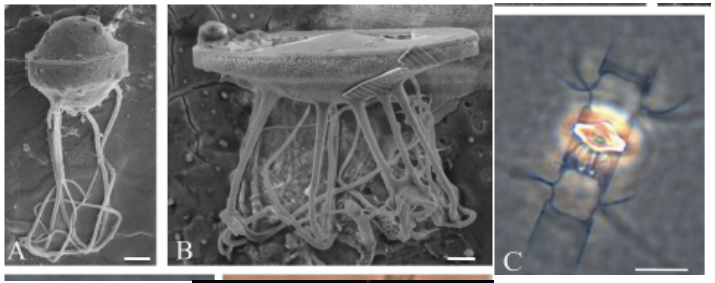
Export ratio
= Export / NCP
~ 30 – 70%

D'Asaro, unpub.

# Optical evidence of Export Flux – sinking aggregates



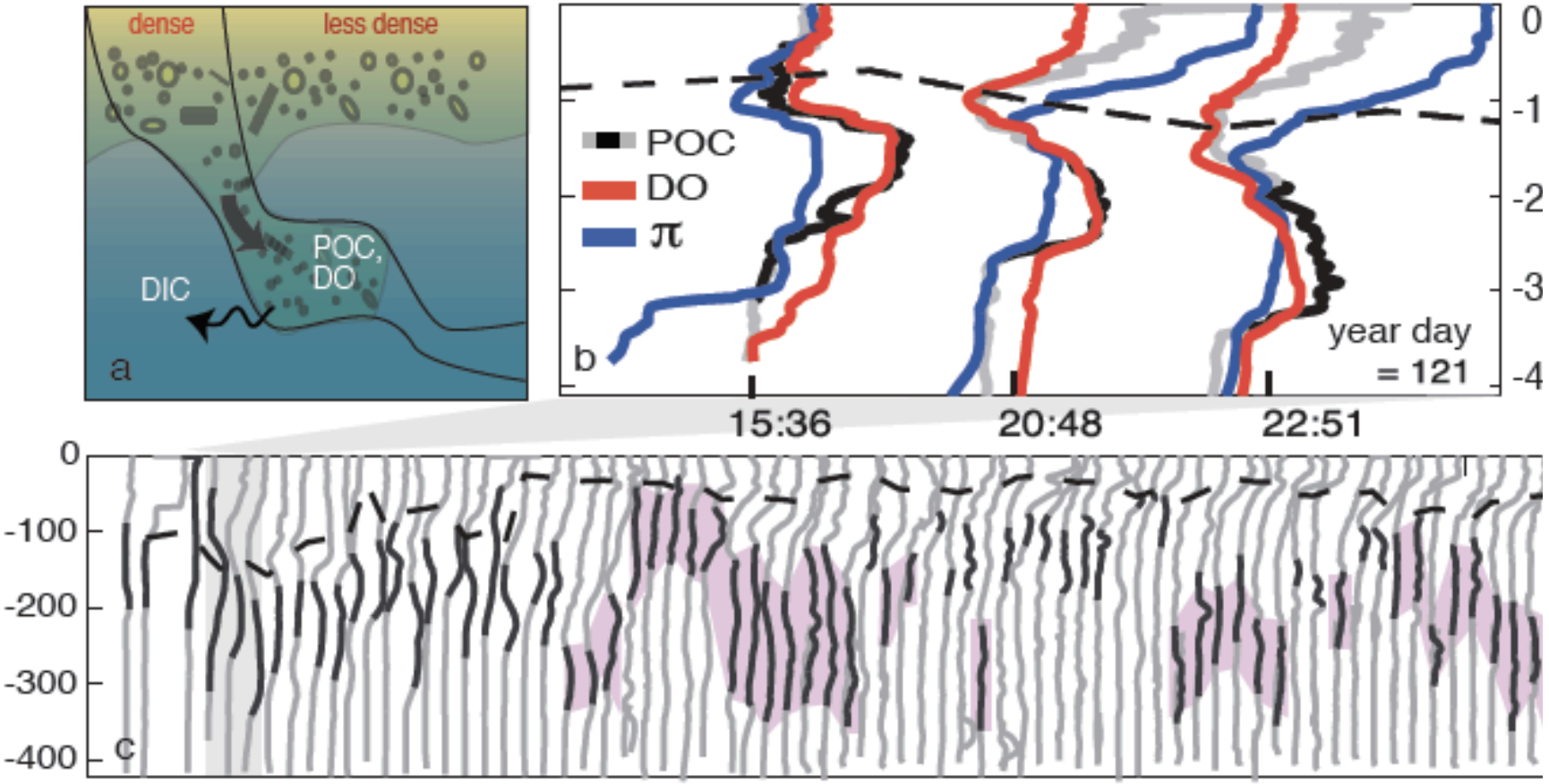




- Sinking of diatom aggregates (optical spikes).
- How much carbon passes through the twilight zone?
- Diatom spores are resistant.

Briggs et al., 2011
Martin et al., 2011
Rynearson et al., 2013

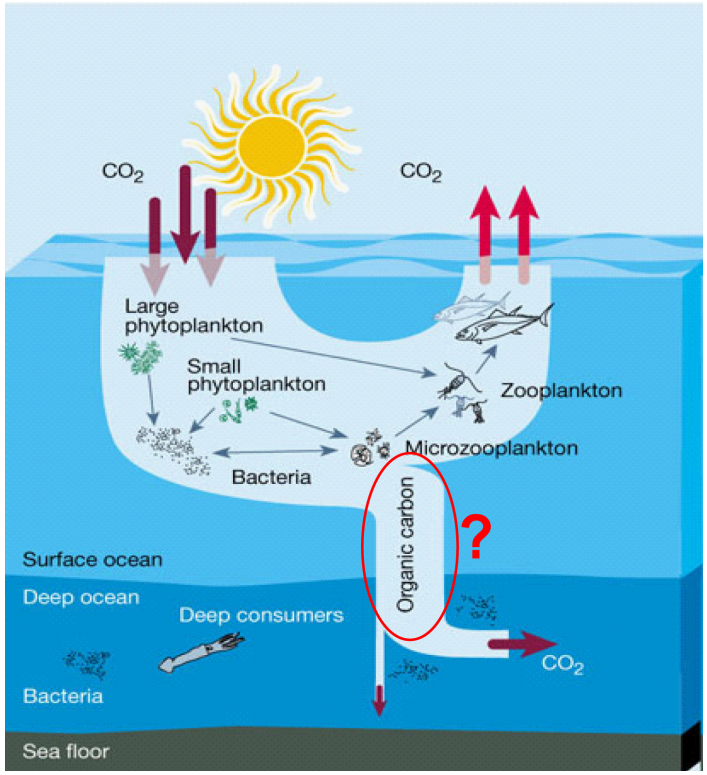
# Optical evidence of Export Flux – eddy driven subduction




Omand et al., 2015

Primary productivity =

light ($\lambda$) * phytoplankton biomass (chl? cell? carbon? or ?) * photosynthetic coefficients (normalized to phytoplankton; these vary w/light, growth, etc.)



# **Light:** surface or depth ?

**Profile** – typically one profile per location

**Mooring** – several depths,

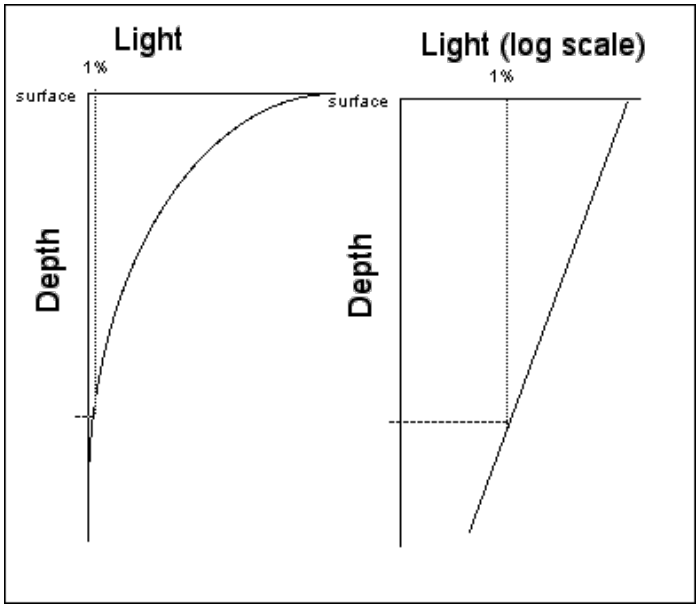
how is surface changing over time?

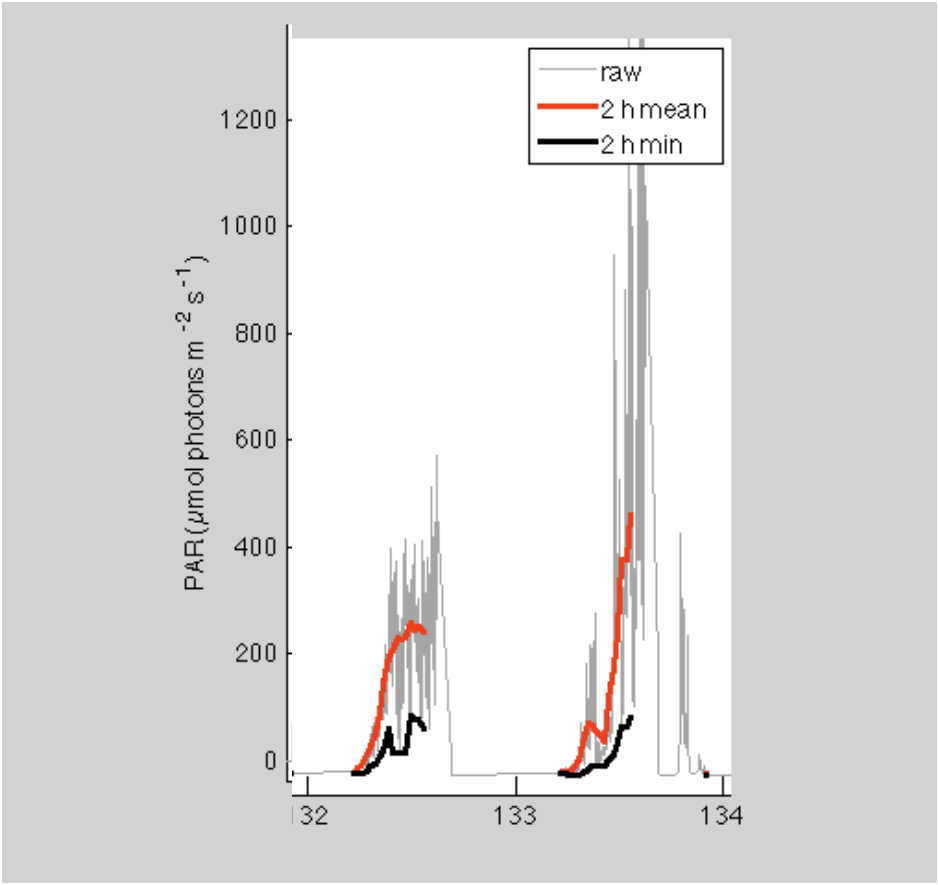
is Kd constant?

**Satellite** – surface only;

derive Kd – is it constant vs. z? λ?

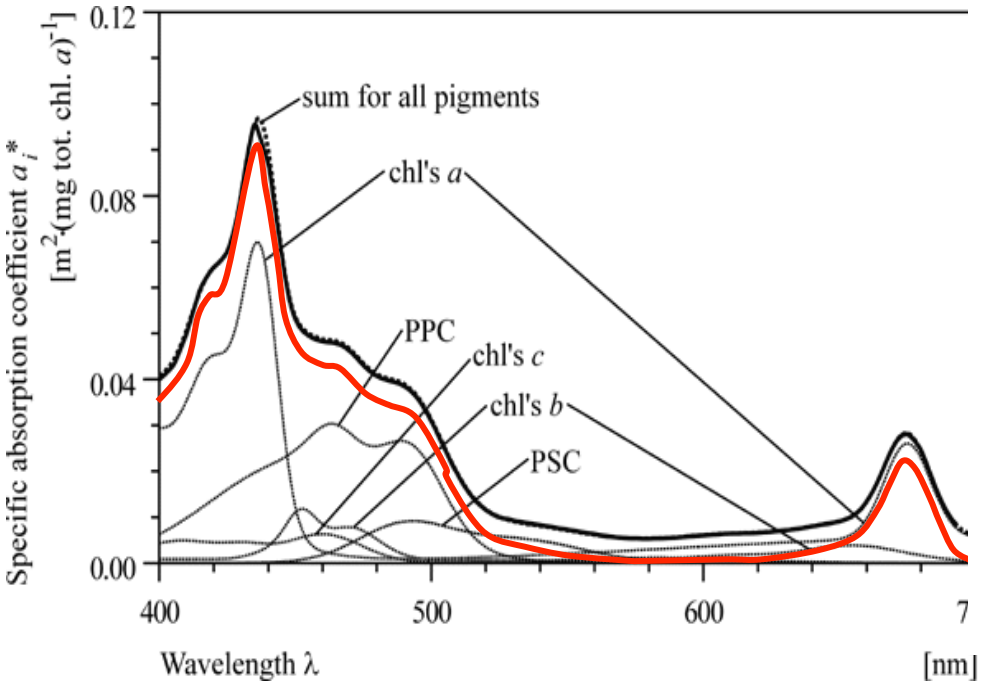
**Autonomous** – moving in x, y, z plane

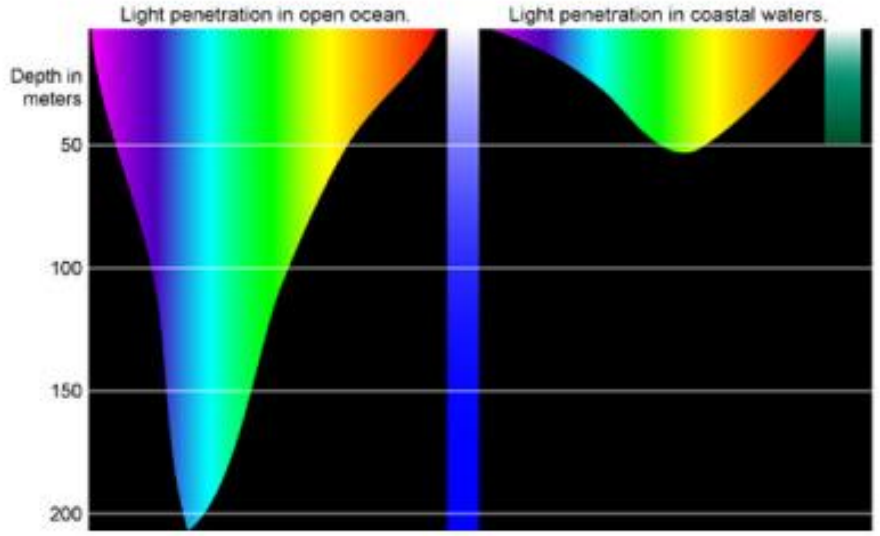


# **Light:** PAR or spectral?

Photon absorption for photosynthesis requires a **match between spectra of photosynthetic pigments ($a_{phyt}(\lambda)$) and spectra of underwater light field**.




http://www.iopan.gda.pl/rbdo/fizyka/mbo_lab/tab_gauss.htm

**Phytoplankton biomass:** chlorophyll, absorption coefficient, cell number, cell volume, phytoplankton carbon, other?

Note: Photosynthetic coefficients must be normalized to same units of phytoplankton biomass (biomass units cancel)

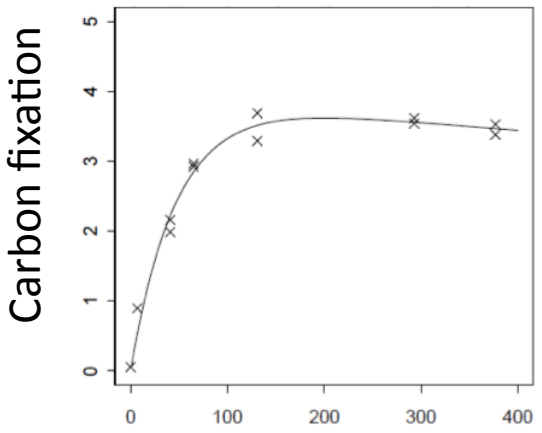
Primary productivity =

light ($\lambda$) * phytoplankton mass * photosynthetic parameter

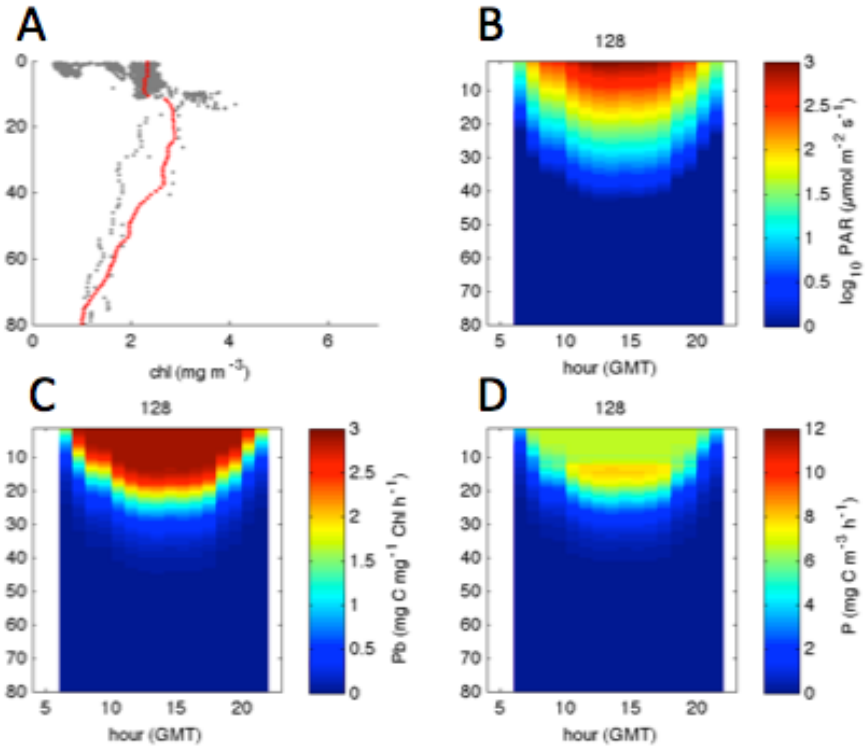
chl? cell? carbon? or? normalized to phytoplankton and function of light, growth, etc.

# Modeled NPP from ship P vs. E and float PAR & chlorophyll

Ship-based P vs. E
normalized to Chl




Hourly from float –
Chl, PAR, PP/Chl, PP




Daily estimates of water column PP

North Atlantic Bloom 2008
(K. Gudmundsson et al., in prep.)

# Alternative parameterization: PS = E(λ) * $a_{ps}(\lambda)$ * Φ

Photosynthetic quantum yield ($\Phi_{ps}$)

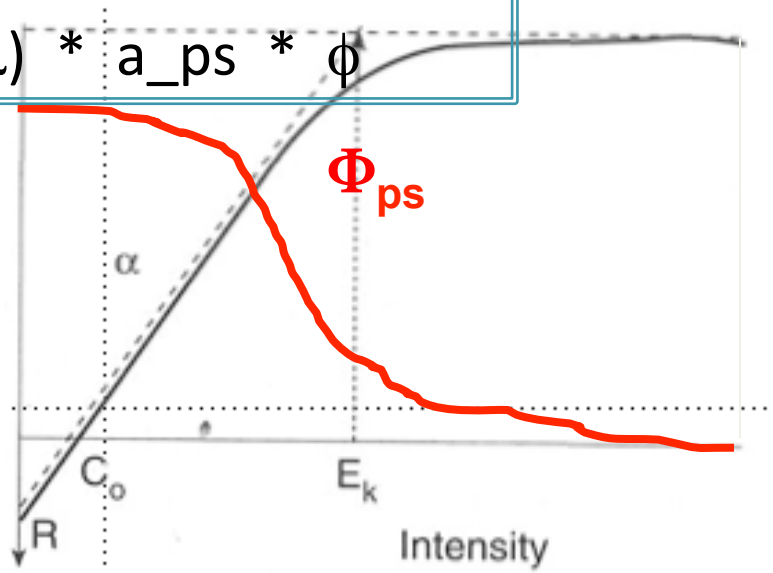
$$\Phi_{ps} = \frac{\text{moles product evolved}}{\text{moles photons absorbed}}$$

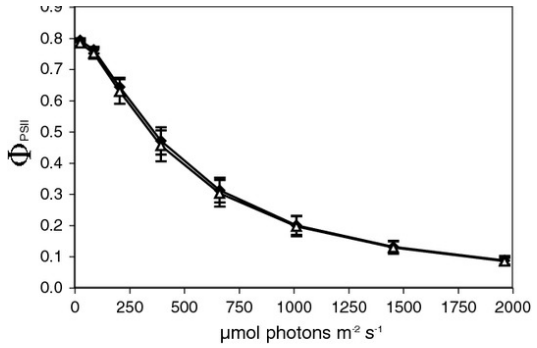
Φ is maximal at low irradiance, and decreases as irradiance increases ($E_k$ term regulates decrease of Φ)

Primary productivity

light (λ) * a_ps * ϕ

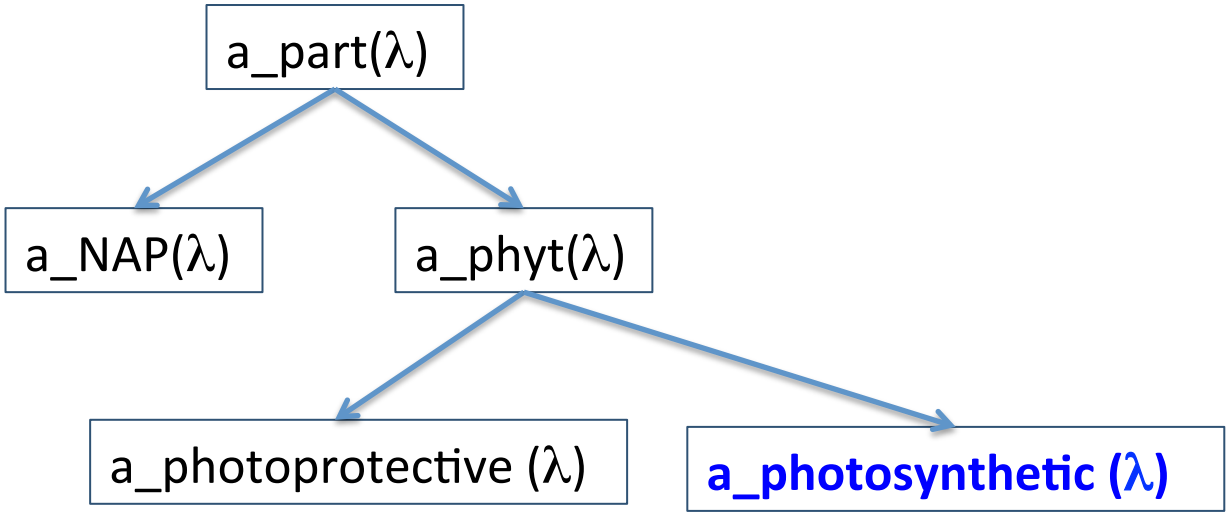
PS

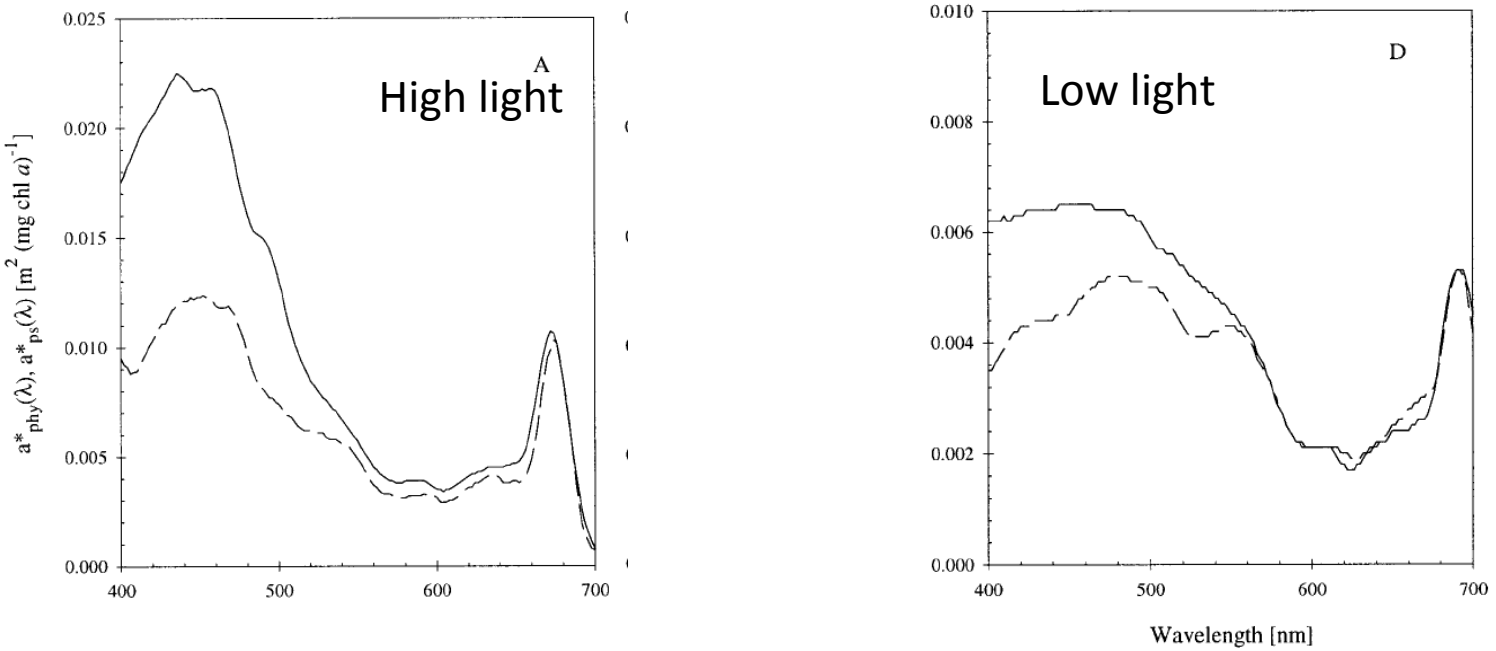



upper limits Φ for C is 0.10

For this model, need if use absorption, need $a_{PS}$ (λ):
Primary productivity = light (λ) * a_ps * ϕ




*Amphidinimum carterae* grown at (A) 700 and (D) 5 µmol photons $m^{-2}$ $s^{-1}$

I. Wavelength-resolved models (WRMs)

$$\sum PP = \int_{\lambda=400}^{700} \int_{t=\text{sunrise}}^{\text{sunset}} \int_{z=0}^{Z_{eu}} \Phi(\lambda, t, z) \times \text{PAR}(\lambda, t, z) \times a^*(\lambda, z) \times \text{Chl}(z)\, d\lambda\, dt\, dz - R$$

II. Wavelength-integrated models (WIMs)

$$\sum PP = \int_{t=\text{sunrise}}^{\text{sunset}} \int_{z=0}^{Z_{eu}} \varphi(t, z) \times \text{PAR}(t, z) \times \text{Chl}(z)\, dt\, dz - R$$

II. Time-integrated models (TIMs)

$$\sum PP = \int_{z=0}^{Z_{eu}} P^b(z) \times \text{PAR}(z) \times DL \times \text{Chl}(z)\, dz$$

IV. Depth-integrated models (DIMs)

$$\sum PP = P^b_{\text{opt}} \times f[\text{PAR}(0)] \times DL \times \text{Chl} \times Z_{eu}$$

Behrenfeld & Falkowski (1997) L&O 42: 1479-
A consumer's guide to phytoplankton primary productivity models

# Platt and Sathyendranath (1990's) based on P vs. E relationships, with fixed PE parameters for a given **province.**

| Method | Variables: Input | Variables: Output |
|---|---|---|
| **Analytic** | | |
| dwcpa | latitude | latitude |
| | longitude | longitude |
| | day number | day number |
| | initial slope, $\alpha^B$, for relationship of photosynthesis to irradiance | day length, $D$ |
| | assimilation number, $P_m^B$ | dimensionless noon irradiance, $I_*^m$ |
| | biomass, $B$ | daily production for a layer, $P_{Z_1,Z_2,T}$ |
| | attenuation coefficient, $K$ | |
| | depth to top of layer, $Z_1$ | |
| | depth to bottom of layer, $Z_2$ | |
| **Numerical** | | |
| dwcpn | latitude | latitude |
| | longitude | longitude |
| | day number | day number |
| | initial slope, $\alpha^B$, for the relationship of photosynthesis to irradiance | day length, $D$ |
| | assimilation number, $P_m^B$ | total daily irradiance, $I_T$ |
| | depth of phytoplankton maximum, $z_m$ | daily water-column production, $P_{Z,T}$ |
| | background biomass, $B_0$ | |
| | Gaussian height parameter, $h$ | |
| | Gaussian scale parameter, $\sigma$ | |
| **Empirical** | | |
| dwcpe | initial slope, $\alpha^B$, for the relationship of photosynthesis to irradiance | values (by various methods) for the canonical function, $f(I_*^m)$, as defined in Platt & Sathyendranath (1993) |
| | assimilation number, $P_m^B$ | |
| | peak (noon) surface irradiance, $I_0^m$ | |

Table 3.5: Input and output variables for daily water-column production programs.

chl
chl profile
daylength
E
K
$P_{max}$
$\alpha$

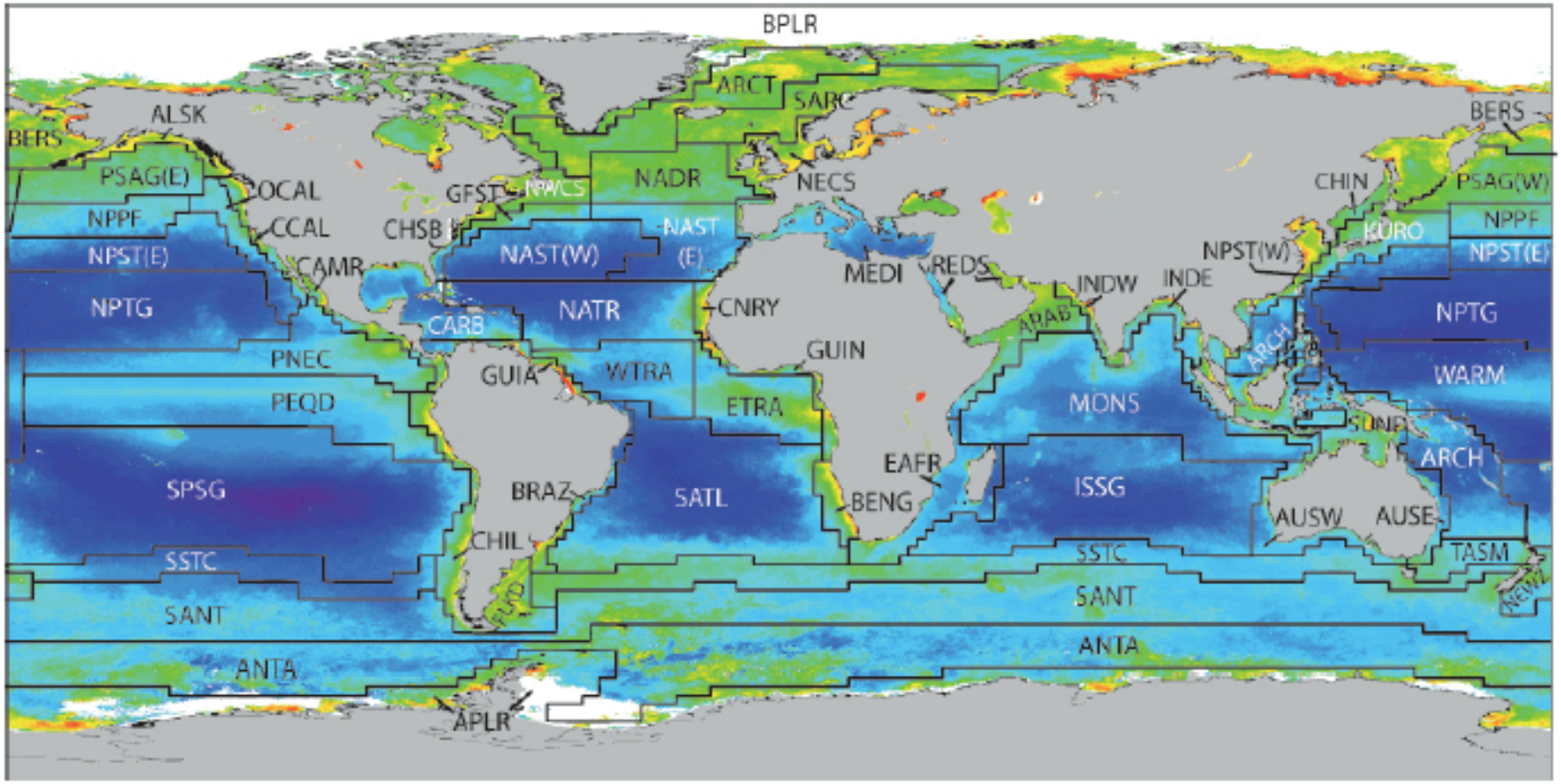



**Figure 6.4** Distribution of the Longhurst oceanographic provinces adopted for the global ocean. Definition and acronyms of the provinces are detailed in Longhurst (1998; 2006).

# Behrenfeld Variants of the VGPM
(Vertically Generalized Production Model )

| **Global Annual Production** | **Pg C/yr** |
|---|---|
| **1. Standard model** | 47.5 |
| **2. No surface photoinhibition** | 47.8 |
| **3. Surface irradiance ($I_o$) not cloud corrected** | 44.9 |
| **4. Clear sky and no photoinhibition** | 50.4 |
| **5. $P^B_{opt}$ estimated from Eppley temperature** | 40.6 |
| **6. $P^B_{opt}$ constant: 4.54 mg C/mg Chl/h** | 46.4 |

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www.biogeosciences.net/8/489/2011/
doi:10.5194/bg-8-489-2011


Biogeosciences

# An evaluation of ocean color model estimates of marine primary productivity in coastal and pelagic regions across the globe

V. S. Saba[1,2], M. A. M. Friedrichs[1], D. Antoine[3], R. A. Armstrong[4], I. Asanuma[5], M. J. Behrenfeld[6], A. M. Ciotti[7], M. Dowell[8], N. Hoepffner[8], K. J. W. Hyde[9], J. Ishizaka[10], T. Kameda[11], J. Marra[12], F. Mélin[8], A. Morel[3], J. O'Reilly[9], M. Scardi[13], W. O. Smith Jr.[1], T. J. Smyth[14], S. Tang[15], J. Uitz[16], K. Waters[17], and T. K. Westberry[6]

**Abstract.** Nearly half of the earth's photosynthetically fixed carbon derives from the oceans. To determine global and region specific rates, we rely on models that estimate marine net primary productivity (NPP) thus it is essential that these models are evaluated to determine their accuracy. Here we assessed the skill of 21 ocean color models by comparing their estimates of depth-integrated NPP to 1156 in situ $^{14}C$ measurements encompassing ten marine regions including the Sargasso Sea, pelagic North Atlantic, coastal Northeast Atlantic, Black Sea, Mediterranean Sea, Arabian Sea, subtropical North Pacific, Ross Sea, West Antarctic Peninsula, and the Antarctic Polar Frontal Zone. Average model skill, as determined by root-mean square difference calculations, was lowest in the Black and Mediterranean Seas, highest in the pelagic North Atlantic and the Antarctic Polar Frontal Zone, and intermediate in the other six regions. The maximum fraction of model skill that may be attributable to uncertainties in both the input variables and in situ NPP measurements was nearly 72%. On average, the simplest depth/wavelength integrated models performed no worse than the more complex depth/wavelength resolved models. Ocean color models were not highly challenged in extreme conditions of

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**Table 1.** Description of each region and study from which NPP measurements were recorded.

| General region | Program | Ecosystem type | *N* | Sampling time range | Spatial coverage | NPP method (incubation, tracer, incubation time) |
|---|---|---|---|---|---|---|
| Northwest Atlantic Ocean: Sargasso Sea | BATS* | Subtropical – Gyre | 197 | Dec 1988 to Dec 2003 | Single station | in situ, $^{14}C$, 12–16 h |
| Northeast Atlantic Ocean | NABE | Temperate – Convergence Zone | 12 | Apr 1989 to May 1989 | Multiple stations | in situ, $^{14}C$, 24 h |
| Northeast Atlantic Ocean | NEA (OMEX I, II), SeaMARC | Temperate – Convergence Zone | 52 | Jul 1993 to Jul 1999 | Multiple stations | on deck, $^{14}C$, 24 h |
| Black Sea | NATO SfP ODBMS | Temperate Anoxic Basin | 43 | Jan 1992 to Apr 1999 | Multiple stations | on deck, $^{14}C$, 24 h |
| Mediterranean Sea | DYFAMED, FRONTS, HIVERN, PROSOPE, VARIMED, ZSN-GN | Temperate Basin | 86 | Feb 1990 to Sep 2007 | Multiple stations | on deck, $^{14}C$, 24 h |
| Arabian Sea | Arabian Sea (Process Study) | Tropical – Monsoonal | 42 | Jan 1995 to Dec 1995 | Multiple stations | in situ, $^{14}C$, 24 h |
| North Pacific Ocean | HOT | Subtropical – Gyre | 139 | Jul 1989 to Dec 2005 | Single station | in situ, $^{14}C$, 12–16 h |
| Southern Ocean | Ross Sea (AESOPS, CORSACS) | Polar – Polynya | 133 | Oct 1996 to Dec 2006 | Multiple stations | on deck, $^{14}C$, 24 h |
| Southern Ocean | WAP (LTER-PAL) | Polar – Continental Shelf | 440 | Jan 1998 to Jan 2005 | Multiple stations | on deck, $^{14}C$, 24 h |
| Southern Ocean | APFZ (AESOPS) | Polar – Convergence Zone | 12 | Dec 1997 | Multiple stations | on deck, $^{14}C$, 24 h |

**Table 2.** Contributed satellite-based ocean color primary productivity models. Specific details for each model are described in Appendix A of the Supplement.

| Model # | Contributer | Type | Input variables used: | | | | Reference |
|---|---|---|---|---|---|---|---|
| | | | Chl-*a* | SST | PAR | MLD | |
| 1 | Saba | DI, WI | x | | | | Eppley et al. (1985) |
| 2 | Saba | DI, WI | x | x | x | x | Howard and Yoder (1997) |
| 3 | Saba | DI, WI | x | x | x | | Carr (2002) |
| 4 | Dowell | DI, WI | x | x | x | x | Dowell, unpublished data |
| 5 | Scardi | DI, WI | x | x | x | x | Scardi (2001) |
| 6 | Ciotti | DI, WI | x | x | x | | Morel and Maritorena (2001) |
| 7 | Kameda; Ishizaka | DI, WI | x | x | x | | Kameda and Ishizaka (2005) |
| 8 | Westberry; Behrenfeld | DI, WI | x | x | x | | Behrenfeld and Falkowski (1997) |
| 9 | Westberry; Behrenfeld | DI, WI | x | x | x | | Behrenfeld and Falkowski (1997); Eppley (1972) |
| 10 | Tang | DI, WI | x | x | x | | Tang et al. (2008); Behrenfeld and Falkowski (1997) |
| 11 | Tang | DI, WI | x | x | x | | Tang et al. (2008) |
| 12 | Armstrong | DR, WI | x | x | x | | Armstrong (2006) |
| 13 | Armstrong | DR, WI | x | x | x | | Armstrong (2006); Eppley (1972) |
| 14 | Asanuma | DR, WI | x | x | x | | Asanuma et al. (2006) |
| 15 | Marra; O'Reilly; Hyde | DR, WI | x | x | x | | Marra et al. (2003) |
| 16 | Antoine; Morel | DR, WR | x | x | x | x | Antoine and Morel (1996) |
| 17 | Uitz | DR, WR | x | | x | x | Uitz et al. (2008) |
| 18 | Mélin; Hoepffner | DR, WR | x | | x | | Mélin and Hoepffner (2011) |
| 19 | Smyth | DR, WR | x | x | x | | Smyth et al. (2005) |
| 20 | Waters | DR, WR | x | x | x | x | Ondrusek et al. (2001) |
| 21 | Waters | DR, WR | x | | x | x | Ondrusek et al. (2001) |

DI = Depth-integrated, DR = Depth-resolved, WI = Wavelength-integrated, WR = Wavelength-resolved.

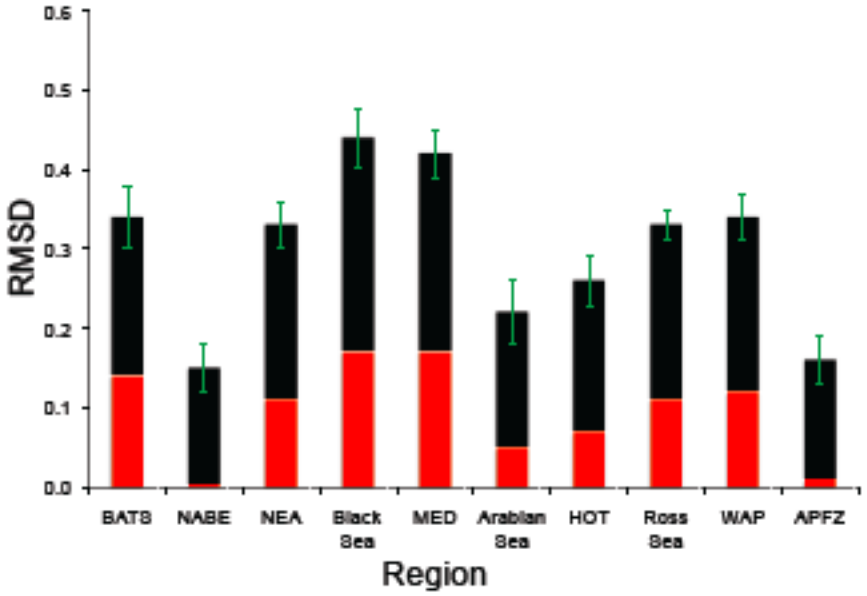



**Fig. 2.** Average RMSD for all 21 models at each region. Lower values of RMSD are equivalent to higher model skill. Green error bars are 2× standard error. Red bars represent the maximum reduction in RMSD (increase in model skill) when the uncertainty in both the input variables and in situ NPP measurements are considered.

**Table 3.** Uncertainties in each input variable at each region based on differences between satellite, modeled, and in situ data sources. Ocean color models were provided with 81 perturbations of input data for each NPP measurement based on these region-specific uncertainties.

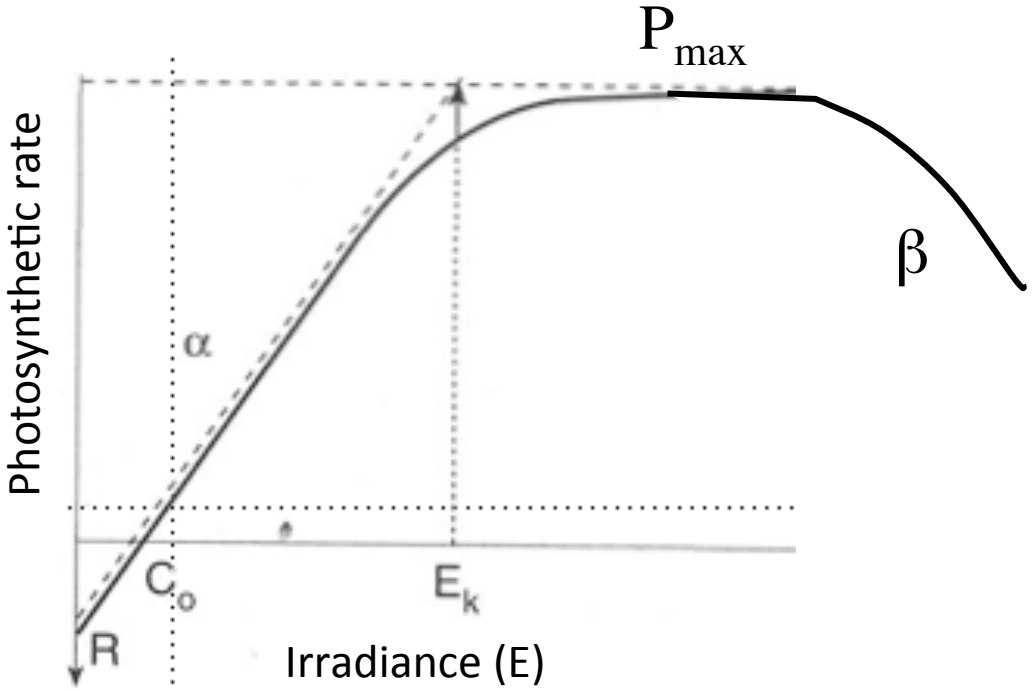
| Region | Chl-*a* ± | SST ± | PAR ± | MLD ± |
|---|---|---|---|---|
| BATS | 35% | 1 °C | 20% | 40% |
| NABE | 50% | 1 °C | 20% | 40% |
| NEA | 50% | 1 °C | 20% | 20% |
| Black Sea | 50% | 1 °C | 20% | 40% |
| Med. Sea | 65% | 1 °C | 20% | 40% |
| Arabian Sea | 50% | 1 °C | 20% | 40% |
| HOT | 35% | 1 °C | 20% | 40% |
| Ross Sea | 65% | 1 °C | 20% | 60% |
| WAP | 65% | 1 °C | 20% | 60% |
| APFZ | 65% | 1 °C | 20% | 40% |

Ocean color model performance was highly limited by the accuracy of input variables. Roughly half of the model-data misfit could be attributed to uncertainty in the four input variables, with the largest contributor being uncertainties in Chl-*a*. Moreover, another 22% of misfit could be attributed to uncertainties in the NPP measurements. These results suggest that ocean color models are capable of accurately estimating NPP if errors in measurements of input data and NPP are considered. Therefore, studies that use ocean color models to estimate NPP should note the degree of error in their estimates based on both the input data they use and the region where NPP is being estimated.

Refresher

Photosynthetic coefficients are normalized to phytoplankton biomass, are a function of light, and incorporate physiology (photo-adapatation, nutrient limitation, etc.)

$$P = P_{max}(1 - e^{-(E/Ek)})\, e^{-(E/E\beta)}$$




E (light)

$P^b_{max}$ (normalized rate – usually to Chl); product is C or $O_2$

α (slope)

$E_K = P_{max} / \alpha$

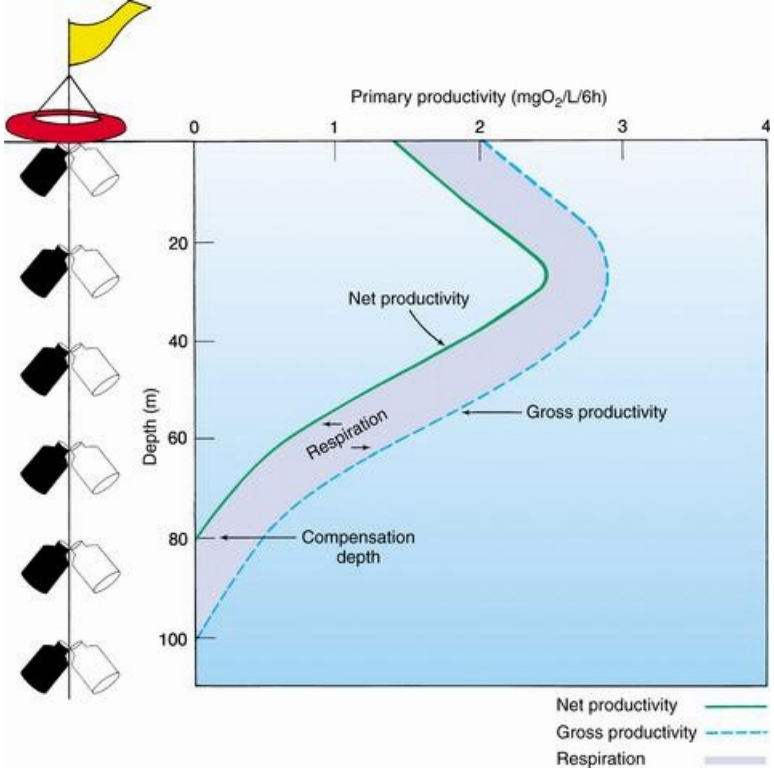
β (light inhibition)

$E_\beta = P_{max} / \beta$

R = respiration

Refresher

# Typical units of photosynthetic parameters and photosynthesis vs. depth




E = irradiance in photons (not energy)
units of μmole photon $m^{-2}$ $s^{-1}$

$P^B_{max}$ = maximal, light-saturated photosynthetic rate
typically **normalized** to chlorophyll concentration
units of g C (g chl)$^{-1}$ $s^{-1}$
(normalization makes parameters 'portable')
Upper measured limit: $P^B_{max}$ is <25 g C/ g Chl/ h

$\alpha$ = slope of the P vs E cure
units of g C (g chl)$^{-1}$ $s^{-1}$ (μmole photon $m^{-2}$ $s^{-1}$)$^{-1}$ [ugly !]