SMS 598: Calibration and Validation for Ocean

Lecture 23 Primary Productivity

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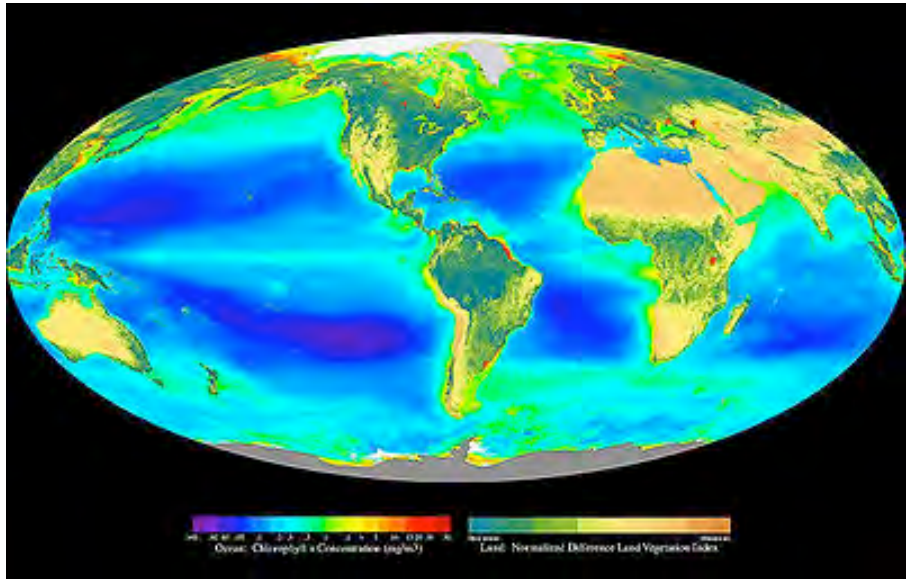
27 July 2011



Can we go from **biomass**
(in this case, mass Chl/area)
to
productivity
(mass carbon/area/**time**)?

What is primary productivity (PP)?

What is the best way to measure primary productivity?

Please answer these two questions – one sentence maximum

(no Proustian sentences)

"Their honour precarious, their liberty provisional, lasting only until the discovery of their crime; their position unstable, like that of the poet who one day was feasted at every table, applauded in every theatre in London, and on the next was driven from every lodging, unable to find a pillow upon which to lay his head, turning the mill like Samson and saying like him: "The two sexes shall die, each in a place apart!"; excluded even, save on the days of general disaster when the majority rally round the victim as the Jews rallied round Dreyfus, from the sympathy--at times from the society--of their fellows, in whom they inspire only disgust at seeing themselves as they are, portrayed in a mirror which, ceasing to flatter them, accentuates every blemish that they have refused to observe in themselves, and makes them understand that what they have been calling their love (a thing to which, playing upon the word, they have by association annexed all that poetry, painting, music, chivalry, asceticism have contrived to add to love) springs not from an ideal of beauty which they have chosen but from an incurable malady; like the Jews again (save some who will associate only with others of their race and have always on their lips ritual words and consecrated pleasantries), shunning one another, seeking out those who are most directly their opposite, who do not desire their company, pardoning their rebuffs, moved to ecstasy by their condescension; but also brought into the company of their own kind by the ostracism that strikes them, the opprobrium under which they have fallen, having finally been invested, by a persecution similar to that of Israel, with the physical and moral characteristics of a race, sometimes beautiful, often hideous, finding (in spite of all the mockery with which he who, more closely blended with, better assimilated to the opposing race, is relatively, in appearance, the least inverted, heaps upon him who has remained more so) a relief in frequenting the society of their kind, and even some corroboration of their own life, so much so that, while steadfastly denying that they are a race (the name of which is the vilest of insults), those who succeed in concealing the fact that they belong to it they readily unmask, with a view less to injuring them, though they have no scruple about that, than to excusing themselves; and, going in search (as a doctor seeks cases of appendicitis) of cases of inversion in history, taking pleasure in recalling that Socrates was one of themselves, as the Israelites claim that Jesus was one of them, without reflecting that there were no abnormals when homosexuality was the norm, no anti-Christians before Christ, that the disgrace alone makes the crime because it has allowed to survive only those who remained obdurate to every warning, to every example, to every punishment, by virtue of an innate disposition so peculiar that it is more repugnant to other men (even though it may be accompanied by exalted moral qualities) than certain other vices which exclude those qualities, such as theft, cruelty, breach of faith, vices better understood and so more readily excused by the generality of men; forming a freemasonry far more extensive, more powerful and less suspected than that of the Lodges, for it rests upon an identity of tastes, needs, habits, dangers, apprenticeship, knowledge, traffic, glossary, and one in which the members themselves, who intend not to know one another, recognise one another immediately by natural or conventional, involuntary or deliberate signs which indicate one of his congeners to the beggar in the street, in the great nobleman whose carriage door he is shutting, to the father in the suitor for his daughter's hand, to him who has sought healing, absolution, defence, in the doctor, the priest, the barrister to whom he has had recourse; all of them obliged to protect their own secret but having their part in a secret shared with the others, which the rest of humanity does not suspect and which means that to them the most wildly improbable tales of adventure seem true, for in this romantic, anachronistic life the ambassador is a bosom friend of the felon, the prince, with a certain independence of action with which his aristocratic breeding has furnished him, and which the trembling little cit would lack, on leaving the duchess's party goes off to confer in private with the hooligan; a reprobate part of the human whole, but an important part, suspected where it does not exist, flaunting itself, insolent and unpunished, where its existence is never guessed; numbering its adherents everywhere, among the people, in the army, in the church, in the prison, on the throne; living, in short, at least to a great extent, in a playful and perilous intimacy with the men of the other race, provoking them, playing with them by speaking of its vice as of something alien to it; a game that is rendered easy by the blindness or duplicity of the others, a game that may be kept up for years until the day of the scandal, on which these lion-tamers are devoured; until then, obliged to make a secret of their lives, to turn away their eyes from the things on which they would naturally fasten them, to fasten them upon those from which they would naturally turn away, to change the gender of many of the words in their vocabulary, a social constraint, slight in comparison with the inward constraint which their vice, or what is improperly so called, imposes upon them with regard not so much now to others as to themselves, and in such a way that to themselves it does not appear a vice."

What is primary productivity (PP)?

1) Need a common language – is my definition of primary productivity the same as your definition?

2) **Time** is of the essence – the time period of integration constrains the definition.

3) Satellites measure something related to biomass; need a **transfer function** to determine a rate from mass.

4) Ground truth-ing models – which productivity do you want? which productivity is (or, productivities are) used for validation? (*see next slide*)

Units of primary productivity (PP) – carbon centric

grams or mole C (m^{-2} or m^{-3} or globe) time^{-1}

mass typically C or O_2 in g or moles;
what is the advantage of moles?

area or volume: L or m^{-3} or m^{-2}(z) or basin/globe

time is typically hour, day, season, or year

Normalized rates: why normalize?

gram or mole C (cell^{-1}) time^{-1}

gram or mole C (gram chlorophyll *a* $^{-1}$) time^{-1}

gram or mole C ($a_{phyt}\{\lambda\}$ m $^{-1}$) time^{-1}

gram or mole C ($b_{bpt}\{\lambda\}$ m $^{-1}$) time^{-1} [$(C + \Delta C)/C$ ~ growth rate]

are there any other normalization terms?

There is more than one type of carbon productivity

1. **GPP:** gross PP, rate of phytoplankton fixation of carbon
2. **NPP:** net primary productivity, rate of phytoplankton fixation of carbon minus phytoplankton respiration
3. **NCP:** NPP, net minus heterotrophic consumption: (grazing by protoza and zooplankton; microbial respiration)
4. **EPP:** export production, need to boundary conditions – sinking of organics, zooplankton vertical transport, DOC subduction, resource harvesting {aside: in 2005, humans consumed 25% terrestrial PP}

NB: **Time period** for integrating makes a difference: NPP and NCP will be different if PP is integrated per hour vs. per day vs. per year. Or, at different seasons.

Outline for “What is primary productivity (PP)?"

Productivities – gross, net, community net, export {*previous slides*}

Photosynthesis

- **– the process and the products**
- – environmental controls on photosynthesis
  - * present: light and temperature
  - * history, expressed in physiology: light, nutrients, etc.
- – parameterization: P vs. E; quantum yield and absorption
  - (where does respiration come in?)
- – satellite models: source of input, availability of ground truth
- – how to measure in the ocean
  - * production of O_2, organic carbon
  - * consumption of CO_2 (DIC)
  - * fluorescence proxies
  - * time and space scales (bottles vs. *in situ*)

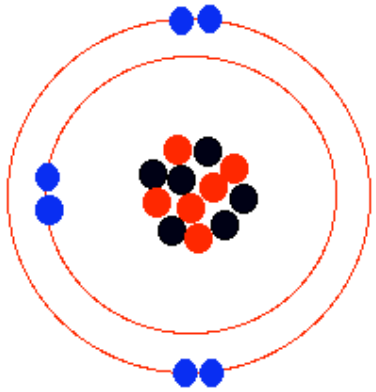
Primary productivity ⇔ rate of primary production
(both abbreviated as PP)

Photosynthesis
(in text books, all terms x 6):

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

Respiration is reverse

Life on earth is C based (atomic mass 12)



Even though O_2 is a product of photosynthesis, typically, we think of primary production as C centric: fixation of **CO_2** and production of **POC** and **DOC**.

Primary productivity is the **rate** (must have units of time).

Strong motivation for understanding Primary Productivity as carbon:

– ocean productivity (food web models use C as mass and energy)

– carrying capacity of the ocean (sustainability of marine food webs)

– global carbon cycle and sequestration of CO_2 (and global warming)

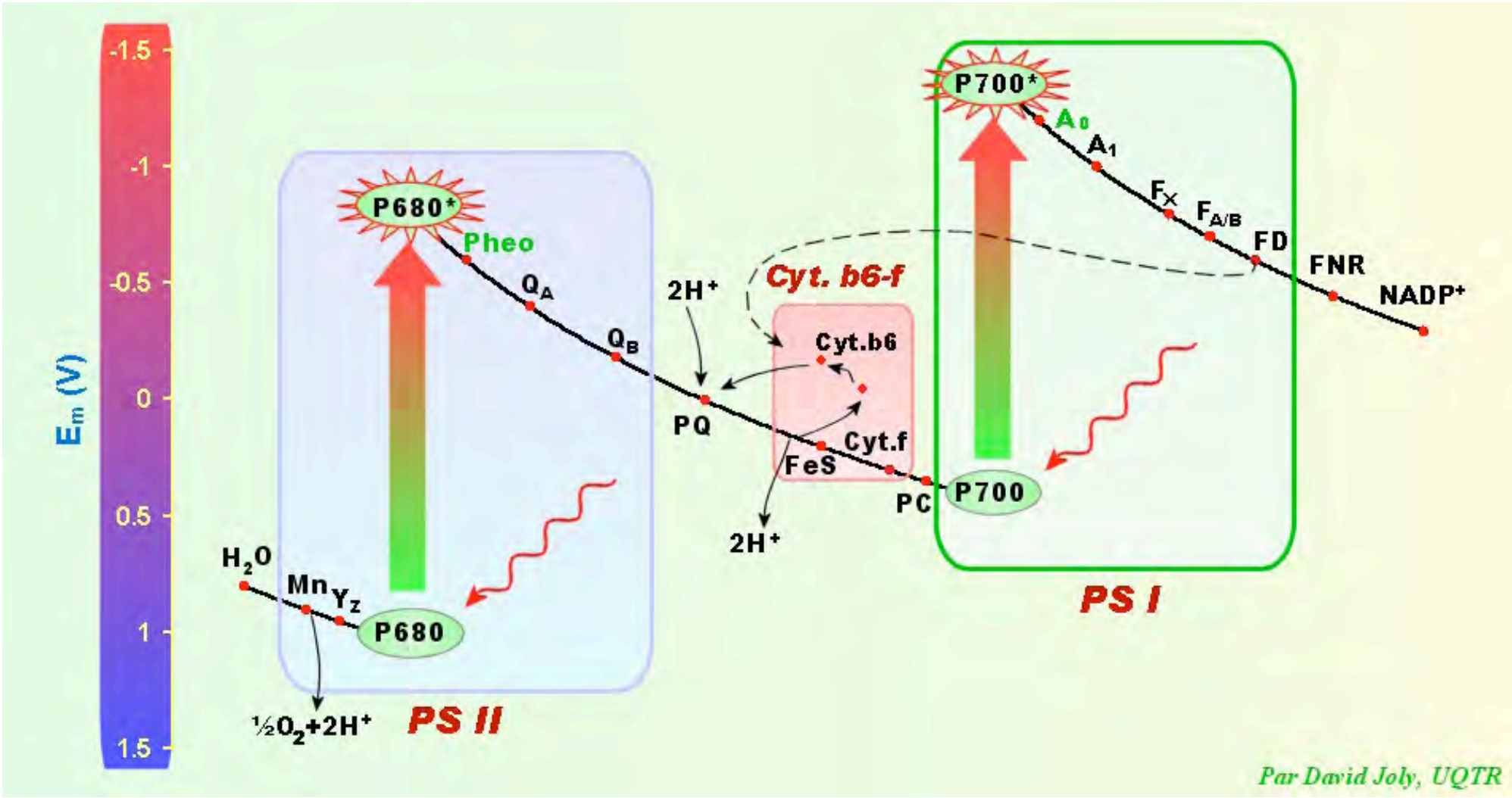
– environmental quality (too much PP can be bad ➔ "dead" zones)

Photosynthesis – process and products

1. photon absorption by LH chlorophyll & accessory pigments
2. exciton (energy) transfer from LH pigment to reaction center
3. PSII trans-membrane charge separation: high energy electron is transferred from P680 across membrane to plastoquinone (electron acceptor), leading to electron transport and production of **ATP**
4. PSI trans-membrane charge separation: high energy electron is transferred from P700 across membrane to pre-ferrodoxin (electron acceptor); leading to production of NADPH
5. split H_2O
   - replace electrons 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
6. electron transport from PSII replaces electrons lost by PSI ($P700^+$)
7. **ATP & NADPH** used to reduce **CO_2, NO_3^-, etc., biosynthetic energy**

➔ Should you expect stoichiometry between C and O ?

Photosynthesis – Z scheme with PS II and PS I



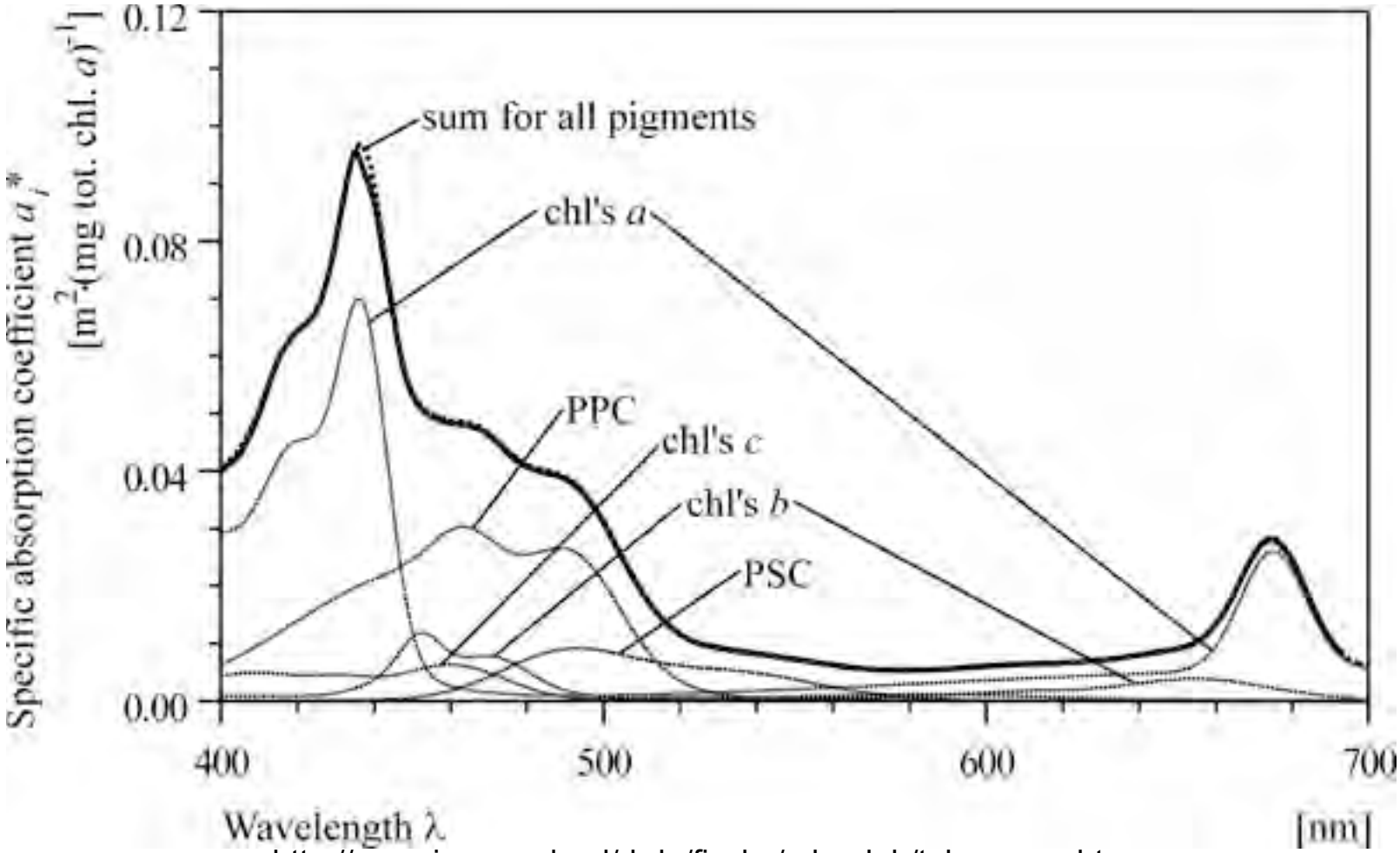
Products of photosynthesis: O_2, NADPH & ATP

{carton does not show ATP or use of reductants}

http://www.uqtr.ca/labcarpentier/eng/research.htm

1. photon absorption by LH chlorophyll & accessory pigments

Phytoplankton absorption is composite of absorption
by **chlorophyll and photosynthetic accessory pigments**
& non-photosynthetic, photoprotective pigments



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

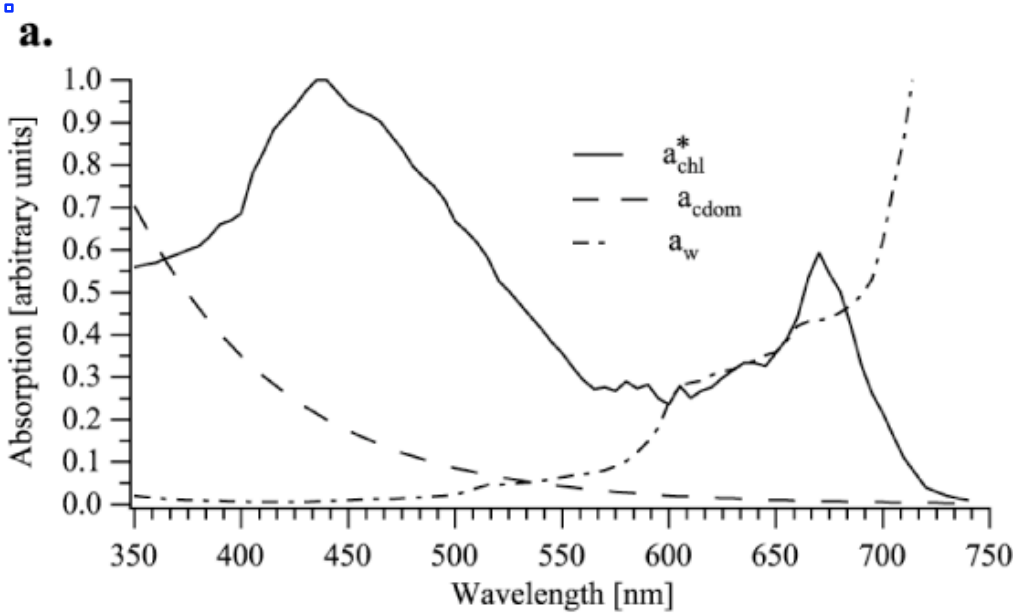
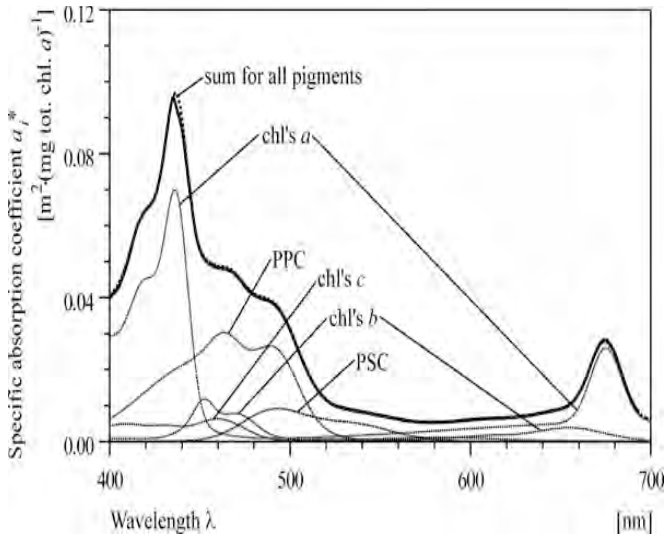
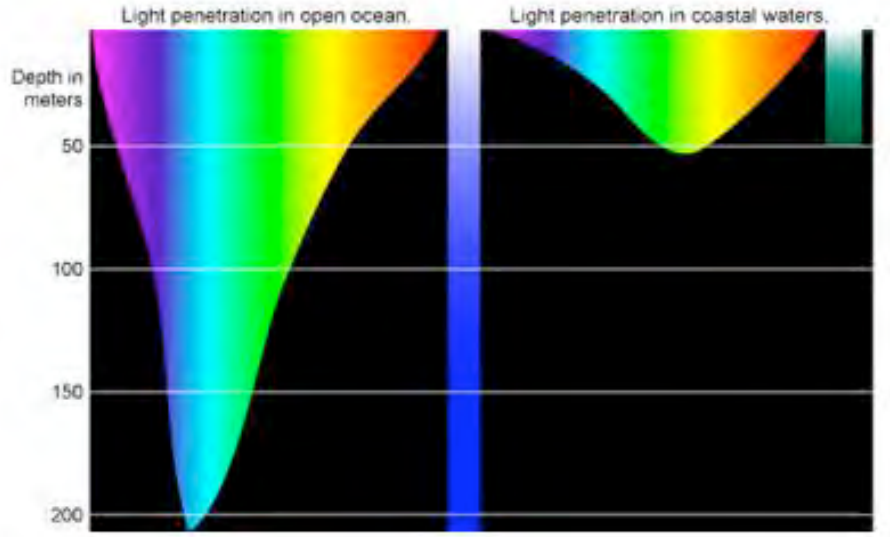


Fig. 1.1: Spectral variations of absorption in seawater. a: Qualitative comparison of the shapes of absorption spectra of pure water (Table 1.1), specific absorption by Chl (Prieur and Sathyendranath 1981), and CDOM as implemented in the HYDROLIGHT radiative transfer model (Mobley and Sundman 2000) described further by Morel and Maritorena (2001).

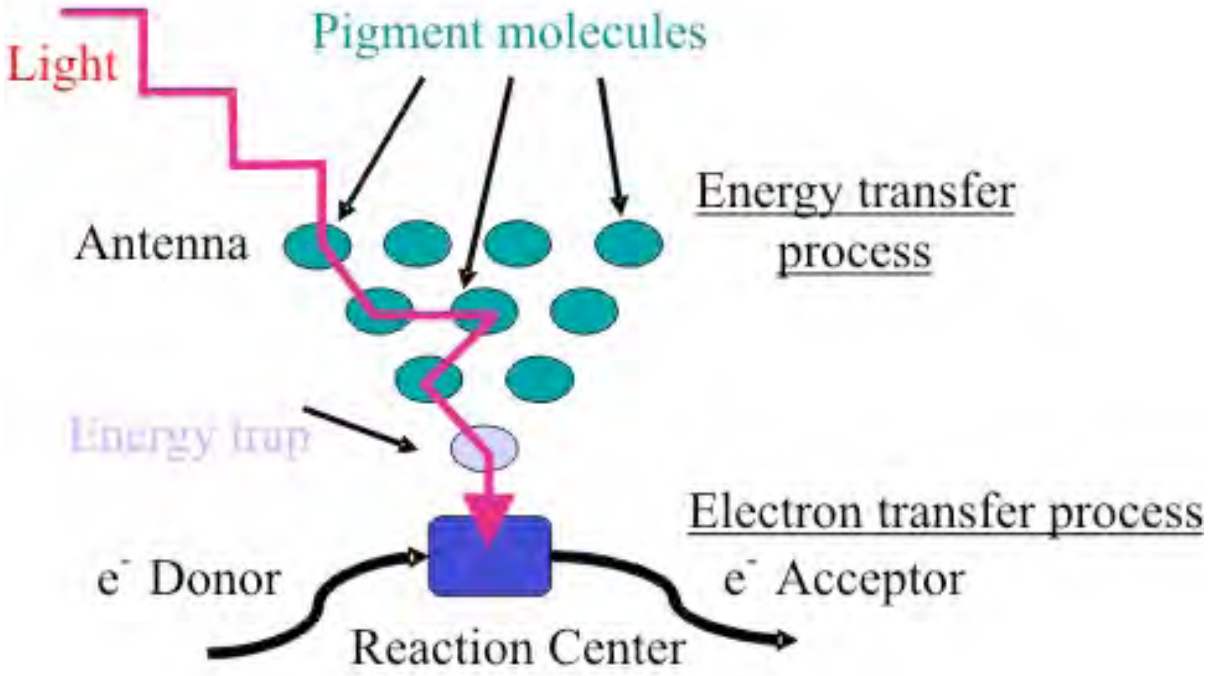
Photon absorption for photosynthesis requires a match between spectra of photosynthetic pigments ($a_{phyt}(\lambda)$) and spectra of underwater light field.

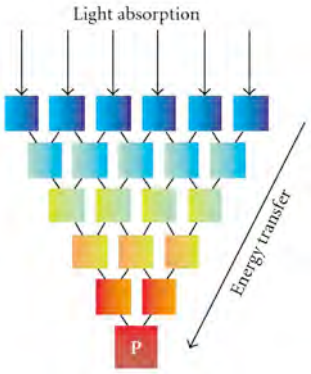
Water color is determined by absorption of water + CDOM + pigments.



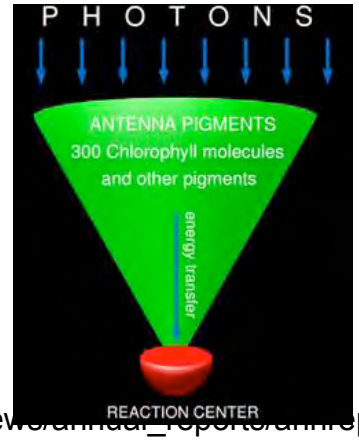


2. exciton (energy) transfer from excited pigment to reaction center





Energy transferred down gradient to reaction center

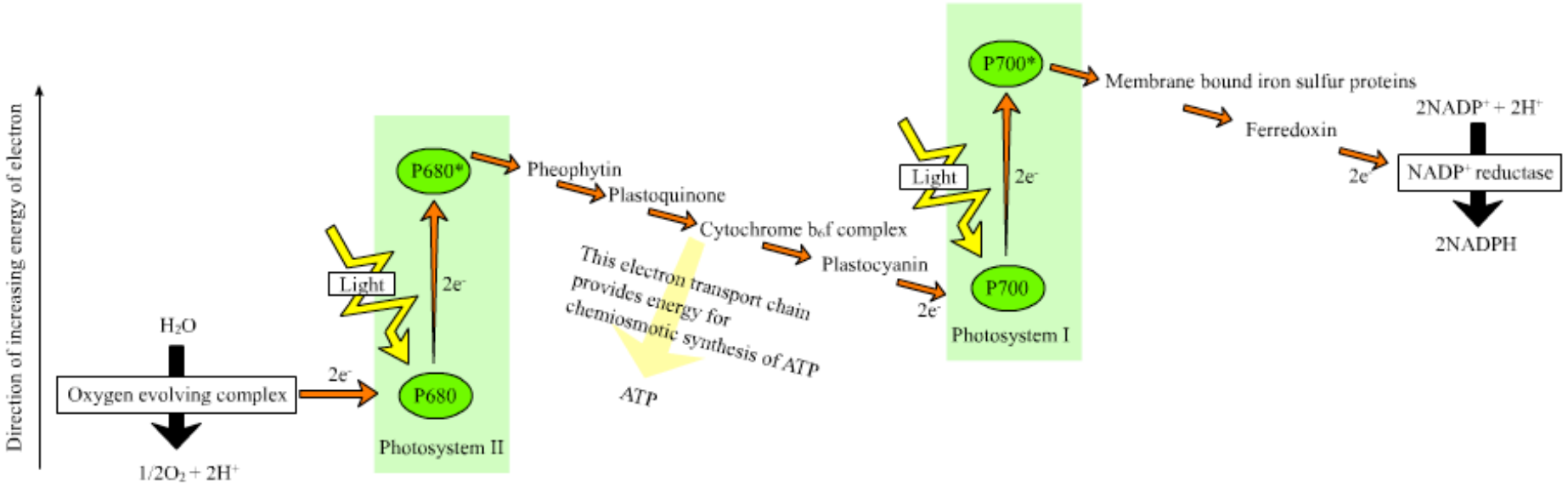


International Journal of Photoenergy, Volume 2009, Article ID 434897, 21 pages

http://www.nersc.gov/news/annual_reports/annrep04/html/adv-comp-sci/01-follow-the-energy.html

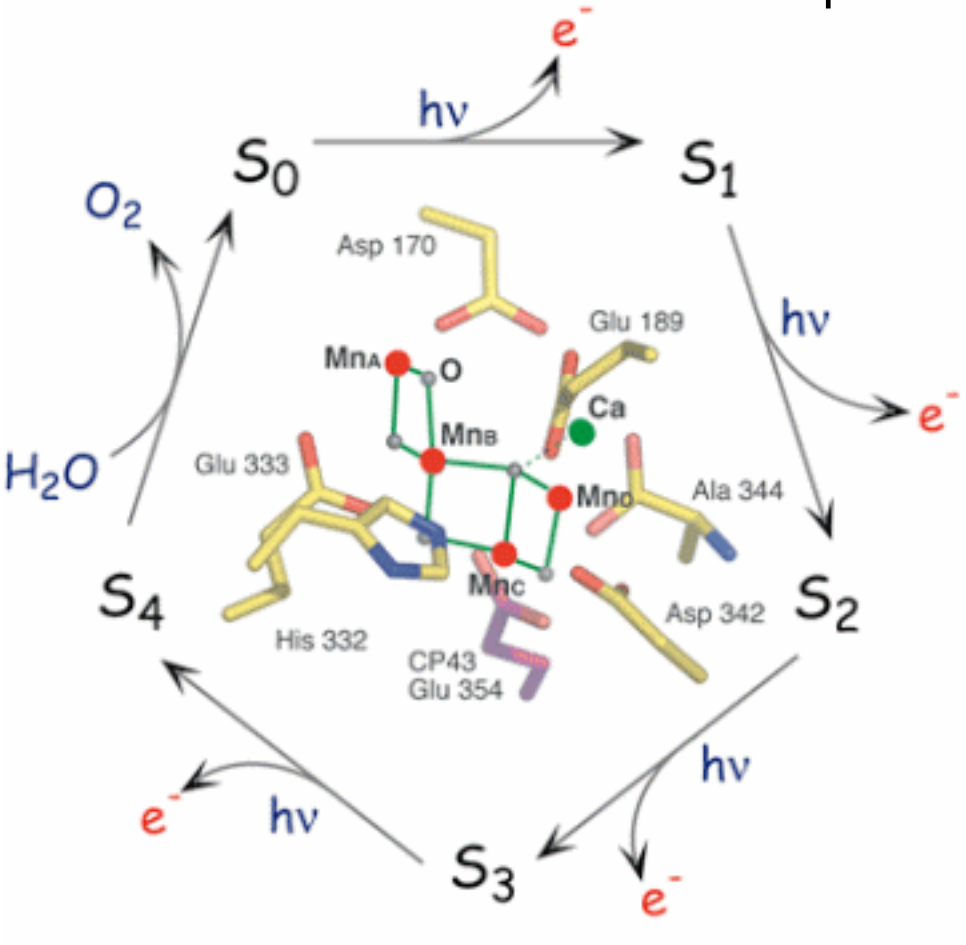
3 & 4. trans-membrane <u>charge separation:</u> high energy electron is stripped off P680 or P700 and transferred across membrane to electron acceptor (PSII plastoquinone for PSII; pre-ferrodoxin for PSI ➔**NADPH** production).

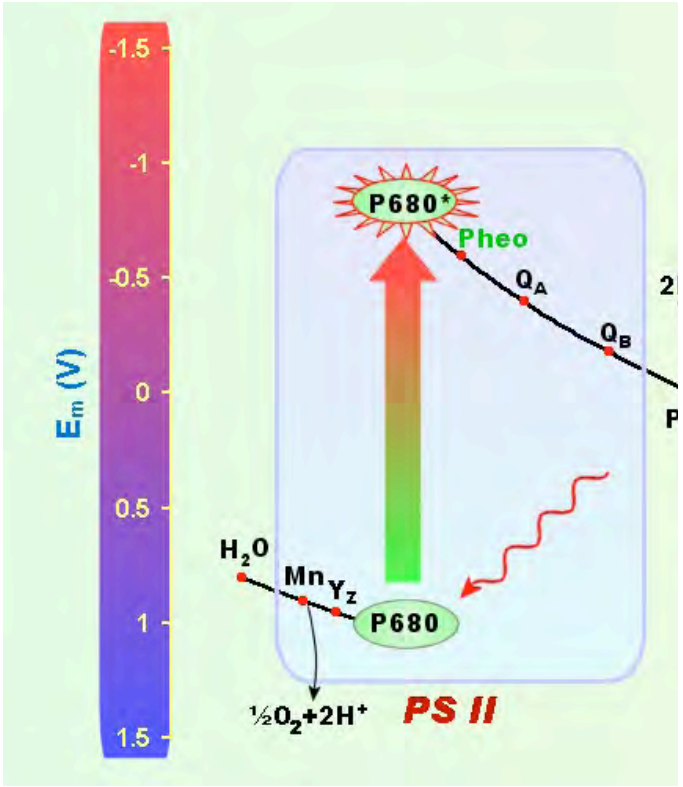
6. electron transport from PSII replaces electrons lost by PSI ($P700^+$), leads to production of **ATP,** and reduction of $P700^+$.



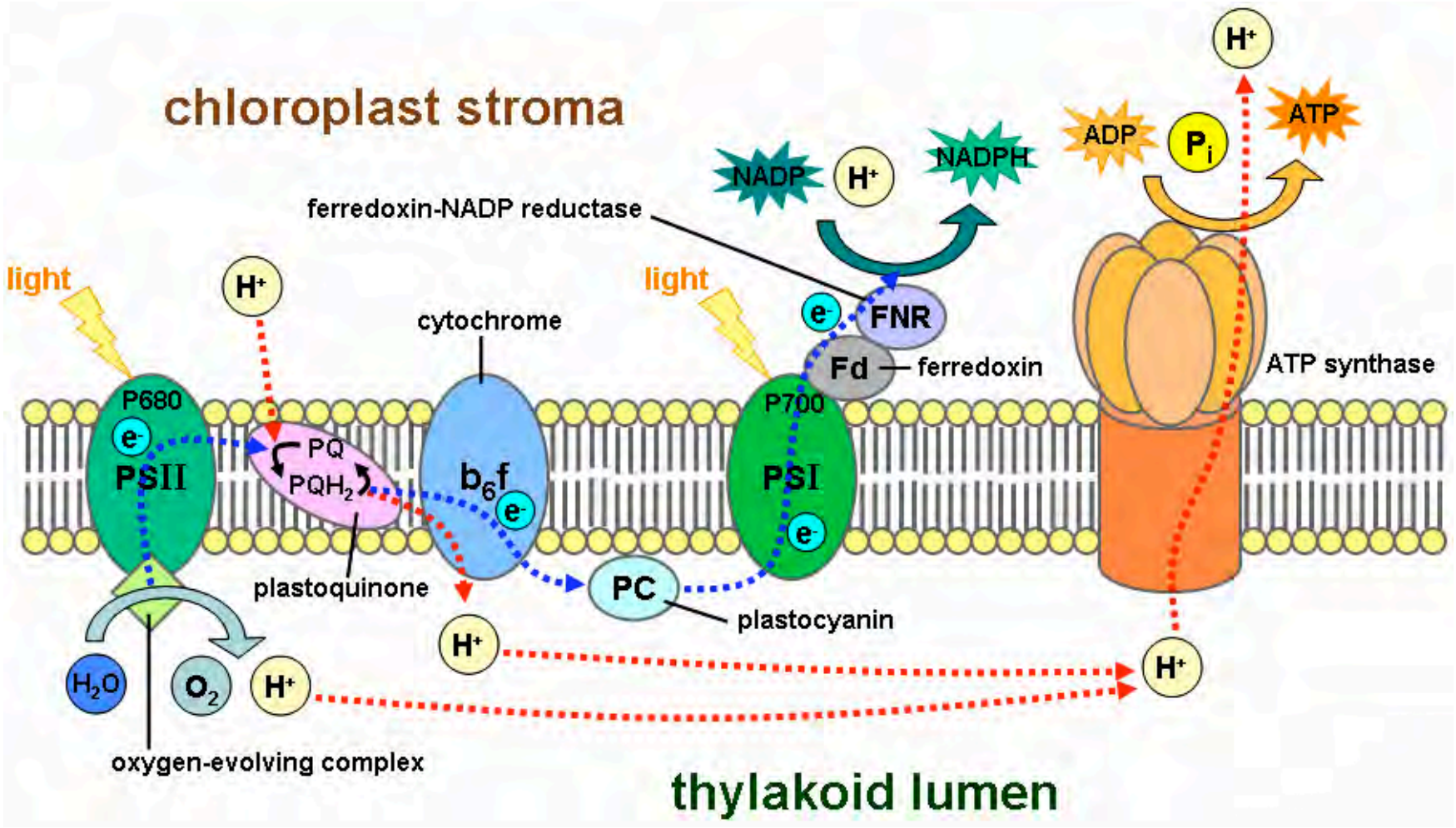
http://chemwiki.ucdavis.edu/Biological_Chemistry/Photosynthesis/Photosynthesis_overview/The_Light_Reactions

5. H_2O is split at PS
   - – 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





Putting it all together in the membrane

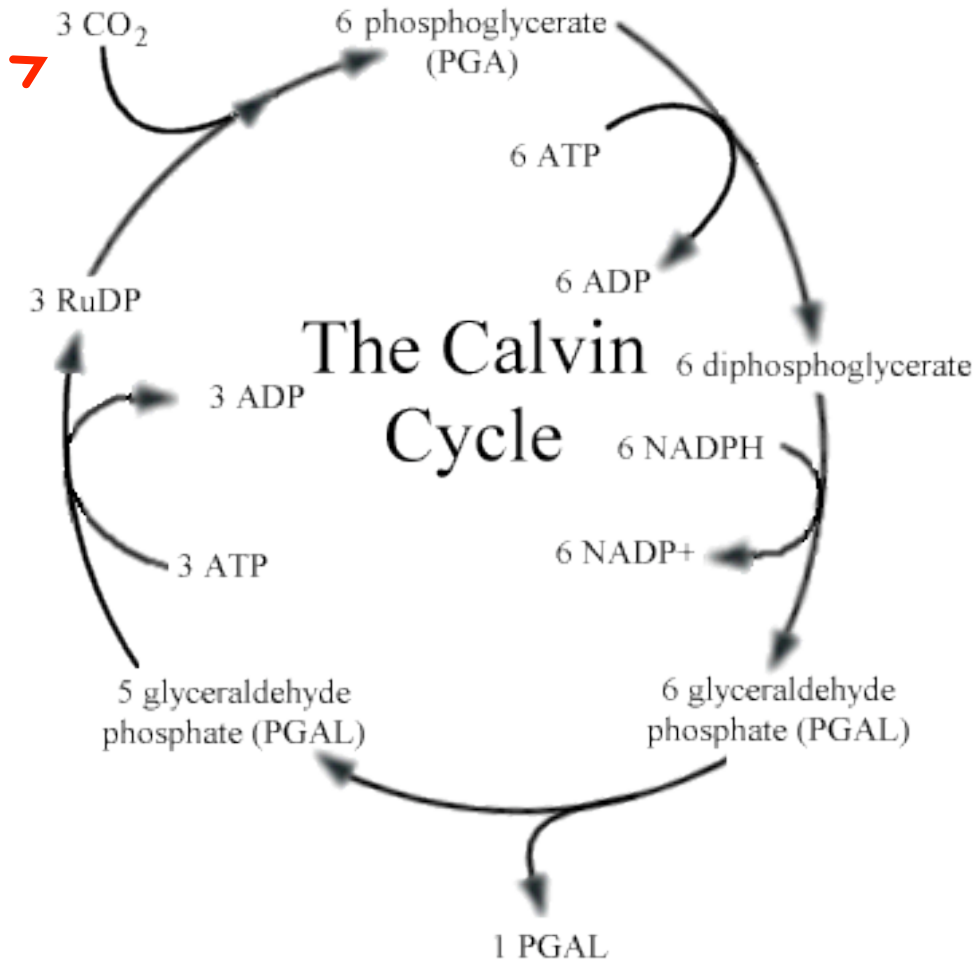


http://chemwiki.ucdavis.edu/Biological_Chemistry/Photosynthesis/Photosynthesis_overview/The_Light_Reactions

So where’s the carbon?

7. **ATP & NADPH** used to reduce **CO_2, NO_3^-** and provide energy for **biosynthesis of proteins, lipids, etc., etc.**

Here's the C



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: mol O_2 produced/mol photon absorbed;
Φ max ~ 0.125 at low light; Φ 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^-**, etc.

absorption of 10 photons to reduce CO_2 (**3 ATP, 2 NADPH**)

PS quantum yield: mol C produced/mol photon absorbed;
Φ max ~ 0.10; Φ lower at higher light;
lower if other uses for ATP and NADPH

Photosynthetic quotient: O_2 evolved to C fixed is >1; often 1.5

Outline for "What is primary productivity (PP)?"

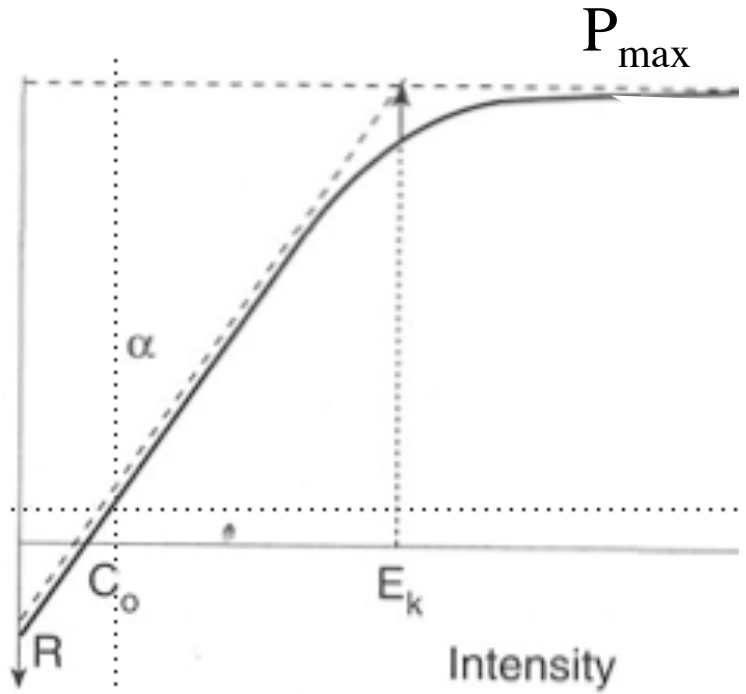
Productivities – gross, net, community net, export {*previous slides*}

Photosynthesis

- the process and the products
- **environmental controls on photosynthesis**
  - *** present: light and temperature**
  - *** history, expressed in physiology: light, nutrients, etc.**
- **parameterization: P vs. E; quantum yield and absorption (where does respiration come in?)**
- satellite models: source of input, availability of ground truth
- how to measure in the ocean
  - * production of O_2, organic carbon
  - * consumption of CO_2 (DIC)
  - * fluorescence proxies
  - * time and space scales (bottles vs. *in situ*)

Environmental regulation of photosynthetic rate:

1) function of instantaneous light (~linear and non-linear components) and temperature;
2) function of history of light, nutrients, etc. (various time scales)



β

$$P = P_{max}[1 - e^{-(E/Ek)}]$$

E

rate as C or O_2

P^b_{max}

α (slope)

$E_K = P_{max} / \alpha$

β

respiration

Slide for reference:
Units of photosynthetic parameters

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

P^B_{max} = maximal, light-saturated photosynthetic rate
typically **normalized** to chlorophyll concentration
units of g C (g chl)$^{-1}$ t^{-1}
(normalization makes parameters 'portable')
Upper measured limit: P^B_{max} is <25 g C/ g Chl/ h

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

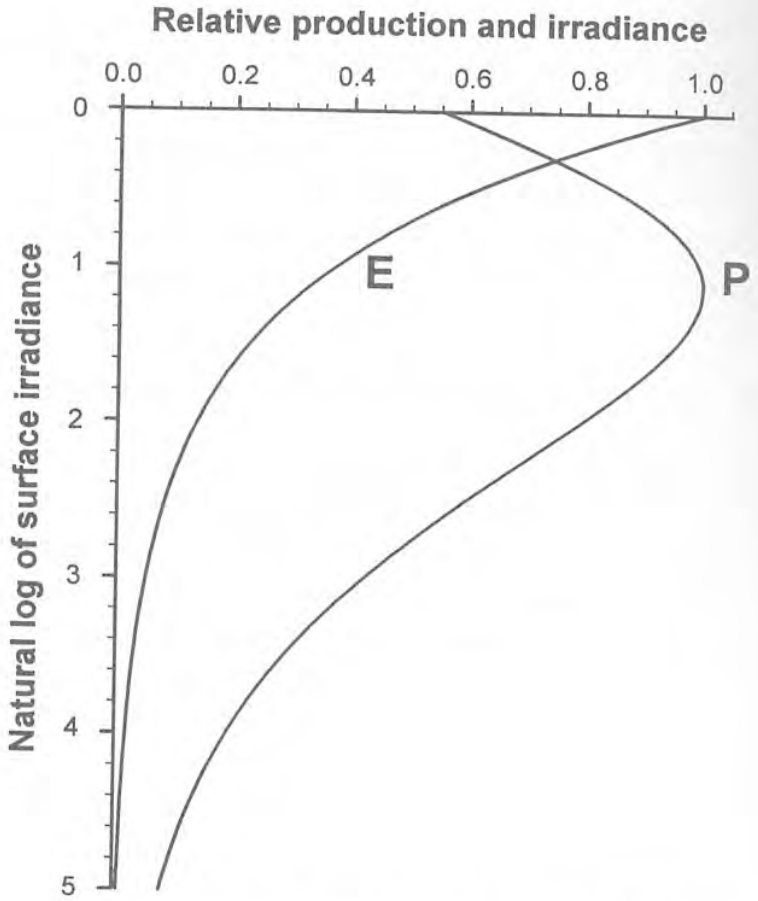


Figure 9.2 A schematic diagram showing the vertical profile of photosynthesis in a water column and the attenuation of irradiance. The vertical axis is presented as the natural logarithm of irradiance (i.e., the optical depth; see Eq 9.4). The position in the water column corresponding to 1% of the surface irradiance is at an ln of –4.6. It is assumed that the vertical distribution of photoautotrophic biomass is uniform throughout the water column.

E vs. z

PP vs. z

Photosynthetic quantum yield (Φ_{ps})

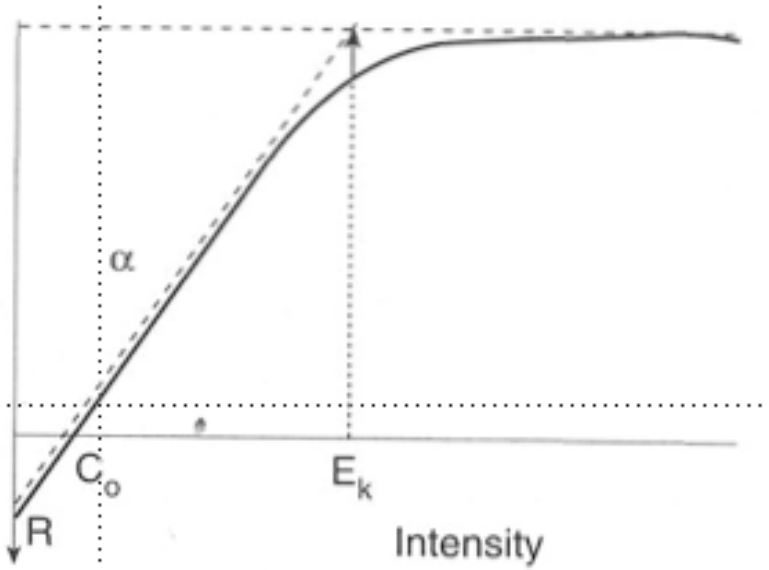
$$\Phi_{ps} = \frac{\text{moles product evolved *}}{\text{moles photons absorbed **}}$$

* product is C fixed, O_2 evolved, etc.

** absorbed – only by PS pigments

(Φ is often not calculated correctly! because photoprotective pigments are included)

PS



Φ_{ps}

(draw functional response curve for Φ_{ps})

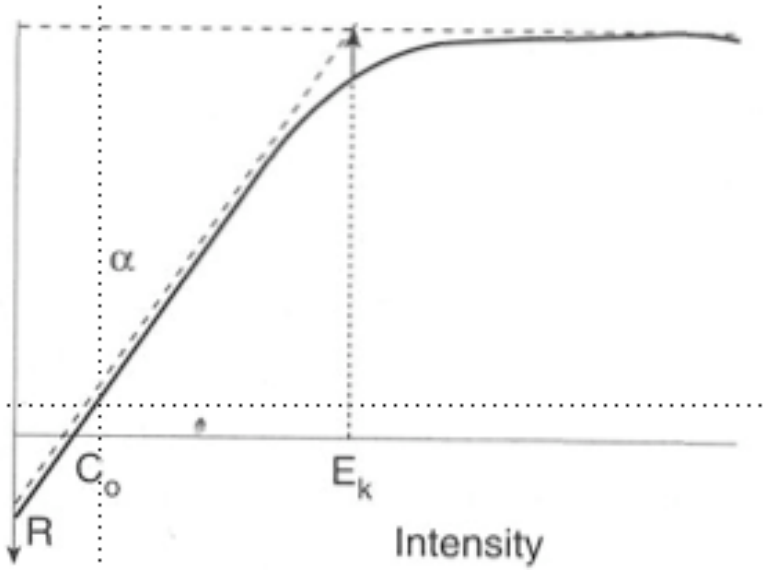
$$PS = E(\lambda) * a_{ps}(\lambda) * \Phi$$

Photosynthetic quantum yield (Φ_{ps})

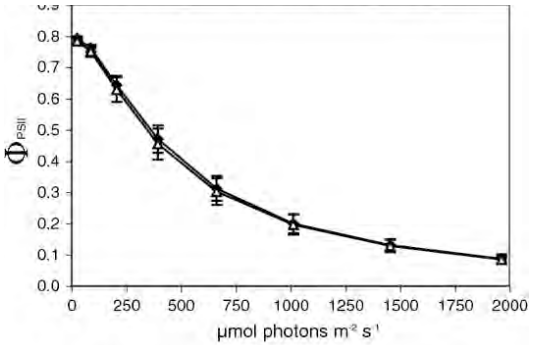
$$\Phi_{ps} = \frac{\text{moles product evolved}}{\text{moles photons absorbed}}$$

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

PS



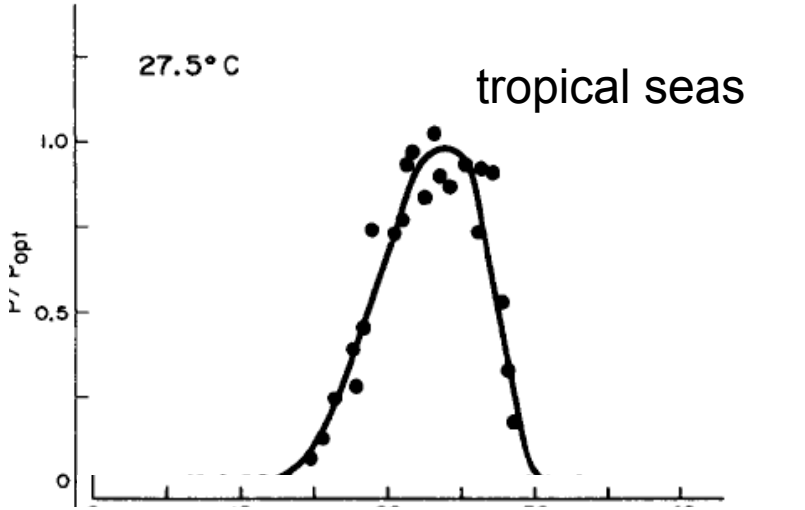
Φ_{ps}

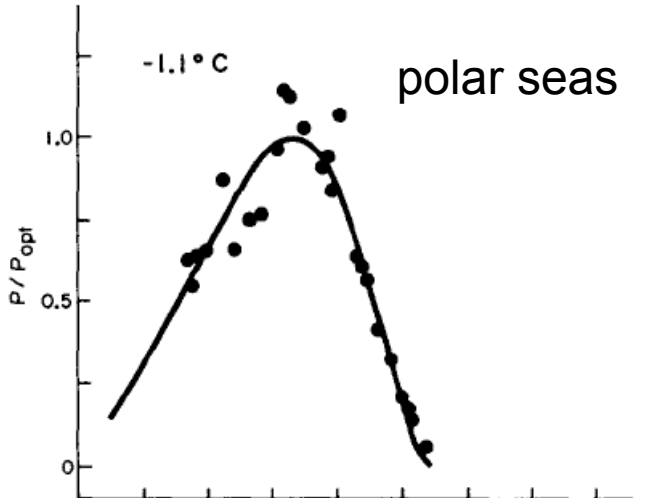


$$PS = E(\lambda) * a_{ps}(\lambda) * \Phi$$

upper limits Φ for C is 0.10

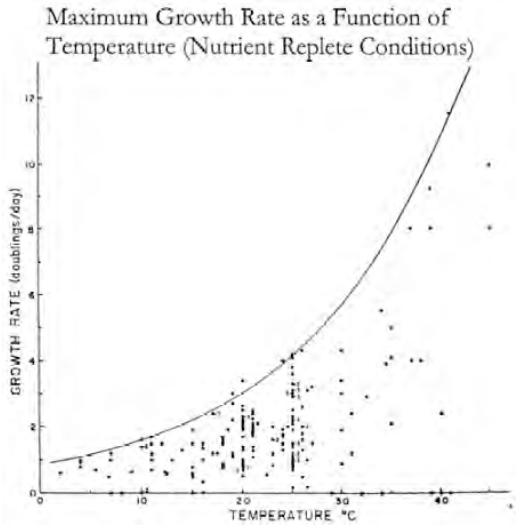
Environmental regulation by temperature: normalized maximal photosynthetic rate (^{14}C) as a function of temperature)





Li. 1985. DSR 32: 1381

Eppley, 1972
Growth rate vs.
temperature



Environmental history affects PS parameters (here light history):
More pigments at low light –> photosynthesis saturates at lower irradiances.

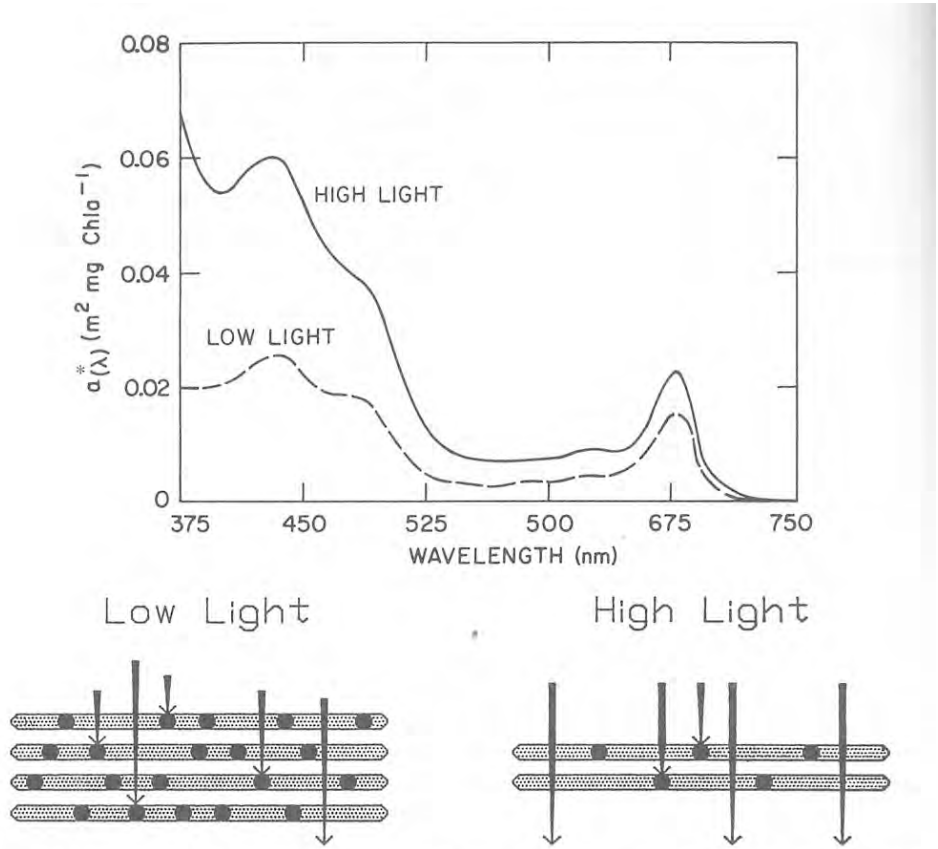
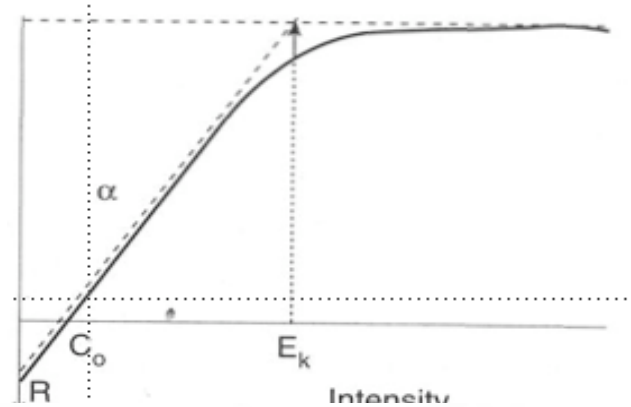
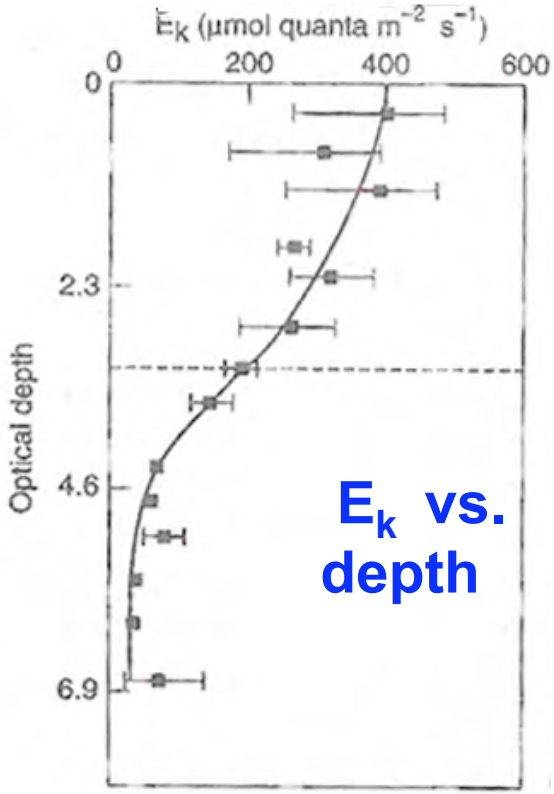


Figure 7.7 (Top) The effect of growth irradiance on the optical absorption cross-section normalized to chlorophyll *a*. Cells grown at high light have less cellular chlorophyll (see Fig 7.8) and generally have fewer thylakoid membranes or membrane stacks within the chloroplast. Hence, there is less chance of self-shading in cell (bottom). The optical consequences of these changes in chloroplast ultrastructure are an increased optical absorption cross-section for cells with lower chlorophyll content.





Outline for “What is primary productivity (PP)?"

Productivities – gross, net, community net, export {*previous slides*}

Photosynthesis

– the process and the products

– environmental controls on photosynthesis

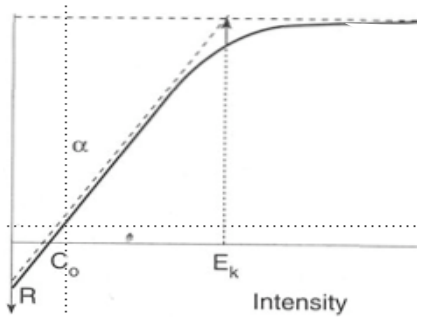
* present: light and temperature
* history, expressed in physiology: light, nutrients, etc.

– parameterization: P vs. E; quantum yield and absorption
(where does respiration come in?)

– **satellite models: source of input, data for ground truth?**

– how to measure in the ocean

* production of O_2, organic carbon
* consumption of CO_2 (DIC)
* fluorescence proxies
* time and space scales (bottles vs. *in situ*)



$$PS = E(\lambda) * a_{ps}(\lambda) * \Phi$$

$$P = P^{B}_{max}[1 - e^{-(E/Ek)}]$$

PP model: biomass (g) ➔ PP (rate, units of g/t)

Basic model variables: biomass, irradiance, and a transfer or yield function which incorporates the physiological response of the measured chlorophyll to light, nutrients, **temperature**, and other environmental variables.

Models vary with regard to:

degree of resolution in depth and irradiance
(wavelength- and depth-integrated; wavelength-integrated and depth-resolved; and wavelength- and depth-resolved) and

physiological transfer functions (quantum yield and P vs. E parameters)

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, α^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, α^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, σ	
Empirical		
dwcpe	initial slope, α^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}
α

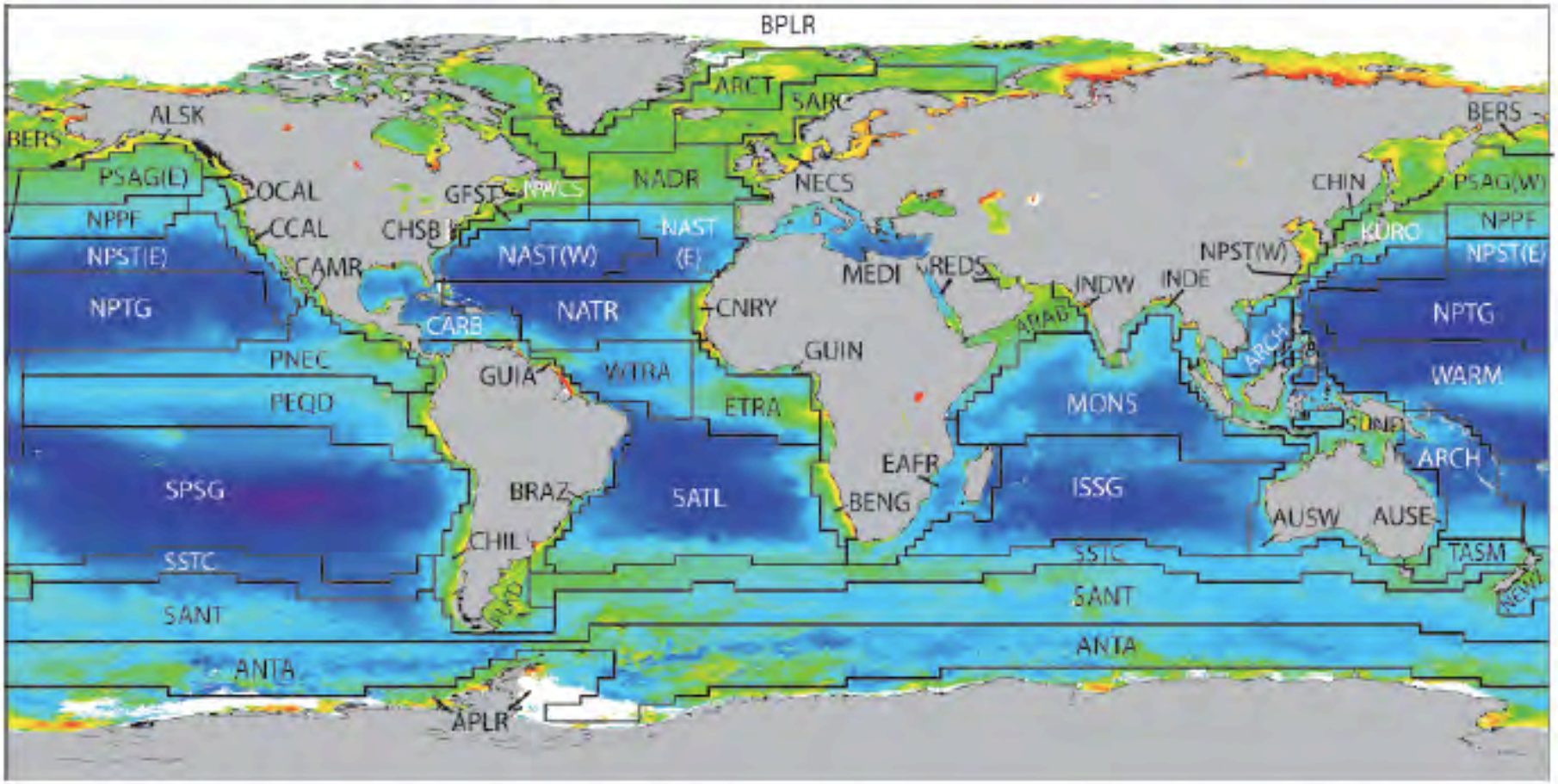
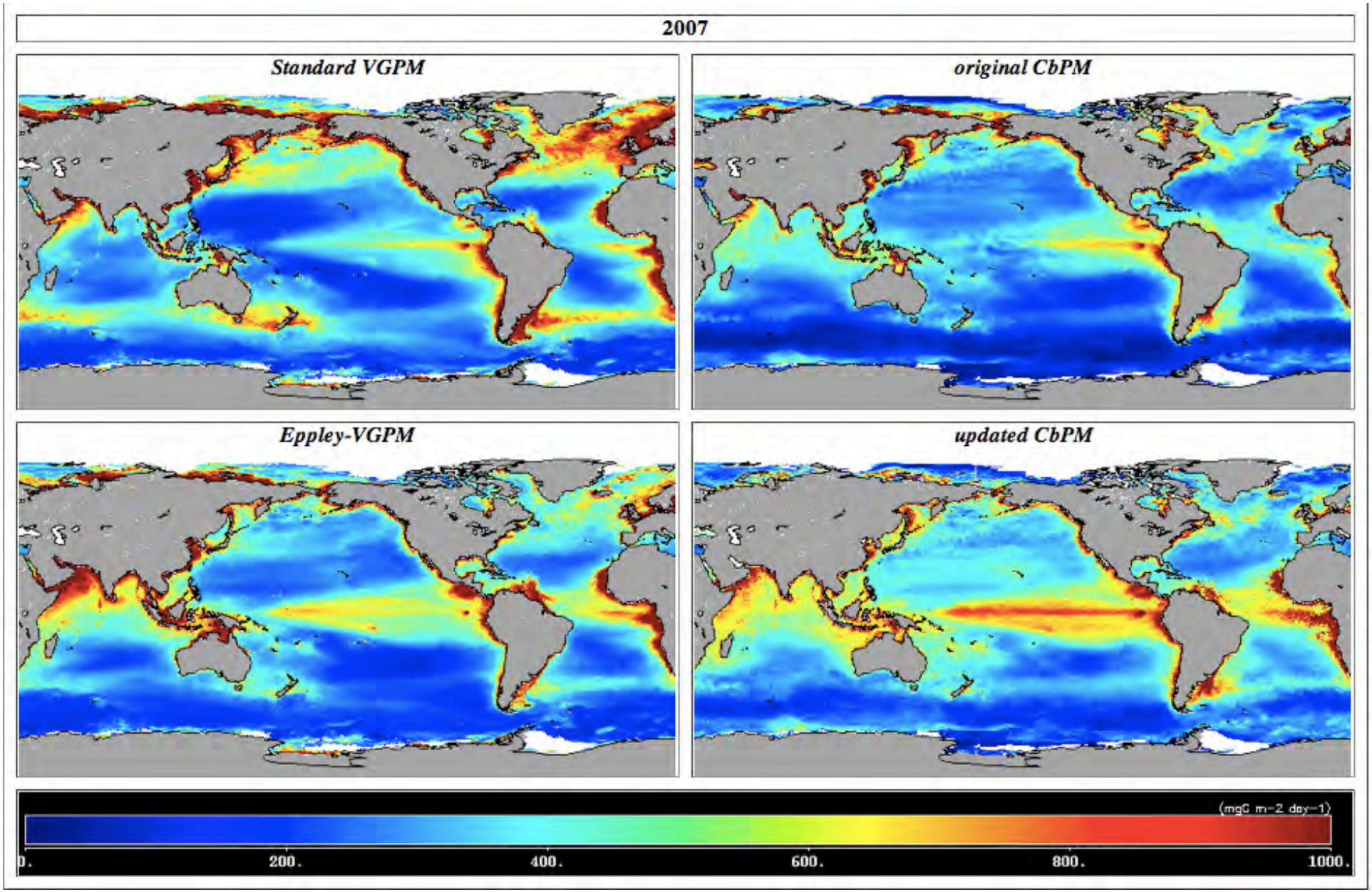


Figure 6.4 Distribution of the Longhurst oceanographic provinces adopted for the global ocean. Definition and acronyms of the provinces are detailed in Longhurst (1998; 2006).



http://orca.science.oregonstate.edu/npp.annual.comparison.php?year=2007

Variants of the VGPM

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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Deep-Sea Research II 53 (2006) 741–770

DEEP-SEA RESEARCH
PART II

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A comparison of global estimates of marine primary production from ocean color

Mary-Elena Carr[a,*], Marjorie A.M. Friedrichs[b,bb], Marjorie Schmeltz[a], Maki Noguchi Aita[c], David Antoine[d], Kevin R. Arrigo[e], Ichio Asanuma[f], Olivier Aumont[g], Richard Barber[h], Michael Behrenfeld[i], Robert Bidigare[j], Erik T. Buitenhuis[k], Janet Campbell[l], Aurea Ciotti[m], Heidi Dierssen[n], Mark Dowell[o], John Dunne[p], Wayne Esaias[q], Bernard Gentili[d], Watson Gregg[q], Steve Groom[r], Nicolas Hoepffner[o], Joji Ishizaka[s], Takahiko Kameda[t], Corinne Le Quéré[k,u], Steven Lohrenz[v], John Marra[w], Frédéric Mélin[o], Keith Moore[x], André Morel[d], Tasha E. Reddy[e], John Ryan[y], Michele Scardi[z], Tim Smyth[r], Kevin Turpie[q], Gavin Tilstone[r], Kirk Waters[aa], Yasuhiro Yamanaka[c]

The third primary production algorithm round robin (PPARR3) compares output from 24 models that estimate depth-integrated primary production from satellite measurements of ocean color, as well as seven general circulation models (GCMs) coupled with ecosystem or biogeochemical models. Here we compare the global primary production fields corresponding to eight months of 1998 and 1999 as estimated from common input fields of photosynthetically-available radiation (PAR), sea-surface temperature (SST), mixed-layer depth, and chlorophyll concentration. We also quantify the sensitivity of the ocean-color-based models to perturbations in their input variables. The pair-wise correlation between ocean-color models was used to cluster them into groups or related output, which reflect the regions and environmental conditions under which they respond differently. The groups do not follow model complexity with regards to wavelength or depth dependence, though they are related to the manner in which temperature is used to parameterize photosynthesis. Global average PP varies by a factor of two between models. The models diverged the most for the Southern Ocean, SST under 10 °C, and chlorophyll concentration exceeding 1 mg Chl m^{-3}. Based on the conditions under which the model results diverge most, we conclude that current ocean-color-based models are challenged by high-nutrient low-chlorophyll conditions, and extreme temperatures or chlorophyll concentrations. The GCM-based models predict comparable primary production to those based on ocean color: they estimate higher values in the Southern Ocean, at low SST, and in the equatorial band, while they estimate lower values in eutrophic regions (probably because the area of high chlorophyll concentrations is smaller in the GCMs). Further progress in primary production modeling requires improved understanding of the effect of temperature on photosynthesis and better parameterization of the maximum photosynthetic rate.

Assessing the uncertainties of model estimates of primary productivity in the tropical Pacific Ocean

Original Research Article
Journal of Marine Systems, Volume 76, Issues 1-2, 20 February 2009, Pages 113-133
Marjorie A.M. Friedrichs, Mary-Elena Carr, Richard T. Barber, Michele Scardi, David Antoine, Robert A. Armstrong, Ichio Asanuma, Michael J. Behrenfeld, Erik T. Buitenhuis, Fei Chai, James R. Christian, Aurea M. Ciotti, Scott C. Doney, Mark Dowell, John Dunne, Bernard Gentili, Watson Gregg, Nicolas Hoepffner, Joji Ishizaka, Takahiko Kameda *et al.* View Abstract

Depth-integrated primary productivity (PP) estimates obtained from satellite ocean color-based models (SatPPMs) and those generated from biogeochemical ocean general circulation models (BOGCMs) represent a key resource for biogeochemical and ecological studies at global as well as regional scales. Calibration and validation of these PP models are not straightforward, however, and comparative studies show large differences between model estimates. The goal of this paper is to compare PP estimates obtained from 30 different models (21 SatPPMs and 9 BOGCMs) to a tropical Pacific PP database consisting of $\sim$ 1000 ^{14}C measurements spanning more than a decade (1983–1996). Primary findings include: skill varied significantly between models, but performance was not a function of model complexity or type (i.e. SatPPM vs. BOGCM); nearly all models underestimated the observed variance of PP, specifically yielding too few low PP (< 0.2 g C m^{-2} d^{-1}) values; more than half of the total root-mean-squared model–data differences associated with the satellite-based PP models might be accounted for by uncertainties in the input variables and/or the PP data; and the tropical Pacific database captures a broad scale shift from low biomass-normalized productivity in the 1980s to higher biomass-normalized productivity in the 1990s, which was not successfully captured by any of the models. This latter result suggests that interdecadal and global changes will be a significant challenge for both SatPPMs and BOGCMs. Finally, average root-mean-squared differences between in situ PP data on the equator at 140°W and PP estimates from the satellite-based productivity models were 58% lower than analogous values computed in a previous PP model comparison 6 years ago. The success of these types of comparison exercises is illustrated by the continual modification and improvement of the participating models and the resulting increase in model skill.

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 surface chlorophyll-*a* and sea surface temperature, nor in high-nitrate low-chlorophyll waters. Water column depth was the primary influence on ocean color model performance such that average skill was significantly higher at depths greater than 250 m, suggesting that ocean color models are more challenged in Case-2 waters (coastal) than in Case-1 (pelagic) waters. Given that in situ chlorophyll-*a* data was used as input data, algorithm improvement is required to eliminate the poor performance of ocean color NPP models in Case-2 waters that are close to coastlines. Finally, ocean color chlorophyll-*a* algorithms are challenged by optically complex Case-2 waters, thus using satellite-derived chlorophyll-*a* to estimate NPP in coastal areas would likely further reduce the skill of ocean color models.

Correspondence to: V. S. Saba (vsaba@princeton.edu)

Outline for “What is primary productivity (PP)?"

Productivities – gross, net, community net, export {*previous slides*}

Photosynthesis

- the process and the products
- environmental controls on photosynthesis
  - * present: light and temperature
  - * history, expressed in physiology: light, nutrients, etc.
- parameterization: P vs. E; quantum yield and absorption (where does respiration come in?)
- satellite models: source of input, data for ground truth?
- **how to measure in the ocean? → model input & validation**
  - * time and space scales matter (bottles vs. *in situ*)
  - * production of O_2, organic carbon
  - * consumption of CO_2 (DIC)
  - * fluorescence proxies

Model input and validation – which 'P' is used?

1. **GPP:** gross PP, rate of phytoplankton fixation of carbon
2. **NPP:** net primary productivity, rate of phytoplankton fixation of carbon minus phytoplankton respiration
3. **NCP:** NPP, net minus heterotrophic consumption: (grazing by protoza and zooplankton; microbial respiration)
4. **EPP:** export production, need to boundary conditions – sinking of organics, zooplankton vertical transport, DOC subduction, resource harvesting {aside: in 2005, humans consumed 25% terrestrial PP}

NB: **Time period** for integrating makes a difference: NPP and NCP will be different if PP is integrated per hour vs. per day vs. per year. Or, at different seasons.

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 (AKA BOD) – changes in oxygen, pH, biomass

2) **Direct observations in environment** – days to weeks
   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 (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

Incubations – short time scales (typically 1 hour to 1 day)
Duration of incubations will partly determine if measurement is GPP, NPP, or between NPP and NCP

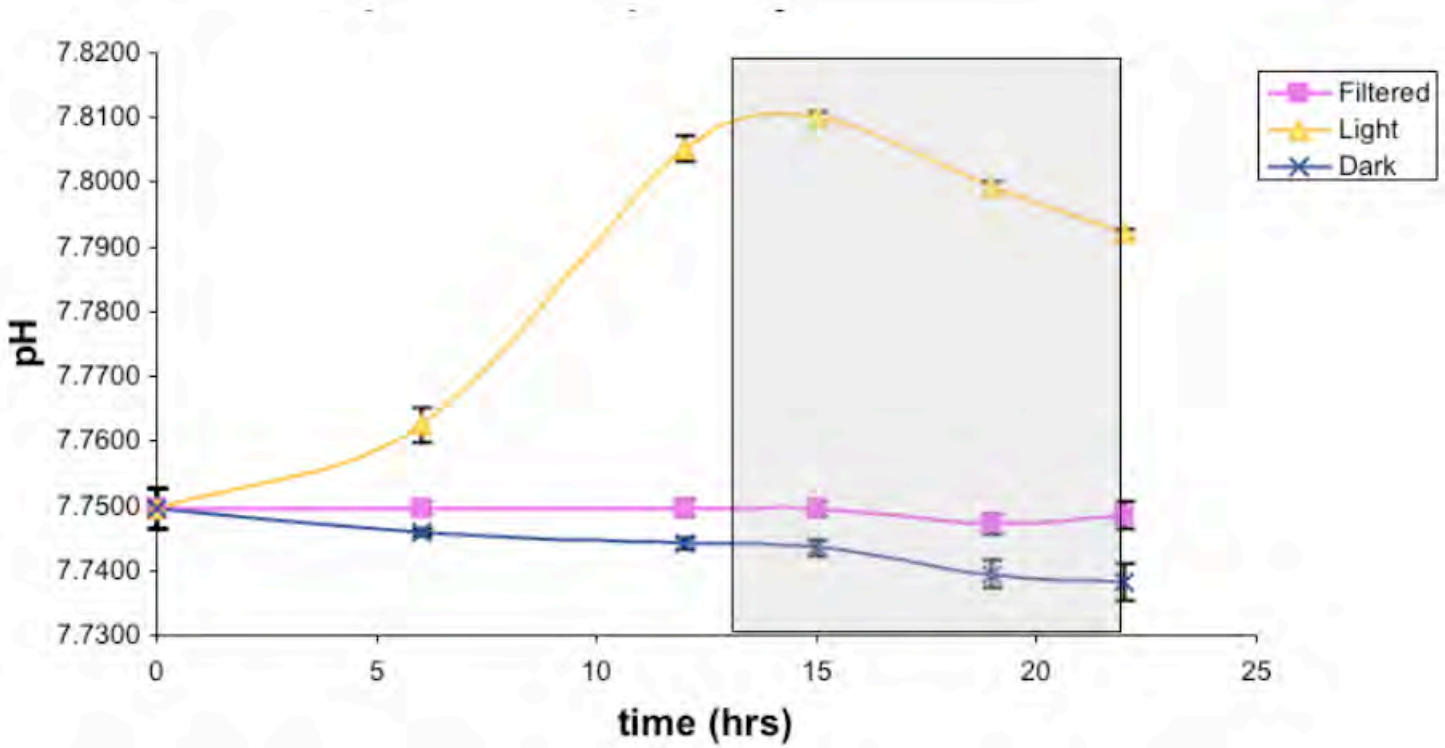
Light (production)/dark (respiration) bottles and tracers

1. CO_2 - pH sensitive dye, Hassuk (1888);
   not adapted for seawater until 1910's
   reintroduced by Clayton and Byrne (1993)
   (current interest - acidification; PS & respiration)
2. O_2 - Winkler (1888) method
   changes in light and dark bottles
3. ^{14}C method - 1952 Steeman Nielsen
4. ^{18}O method – Michael Bender and others

Normalize rates to biomass (primarily Chl), so rates are "transportable" – apply to other data sets, use in models.

1. Changes in CO_2 system; here as change in pH

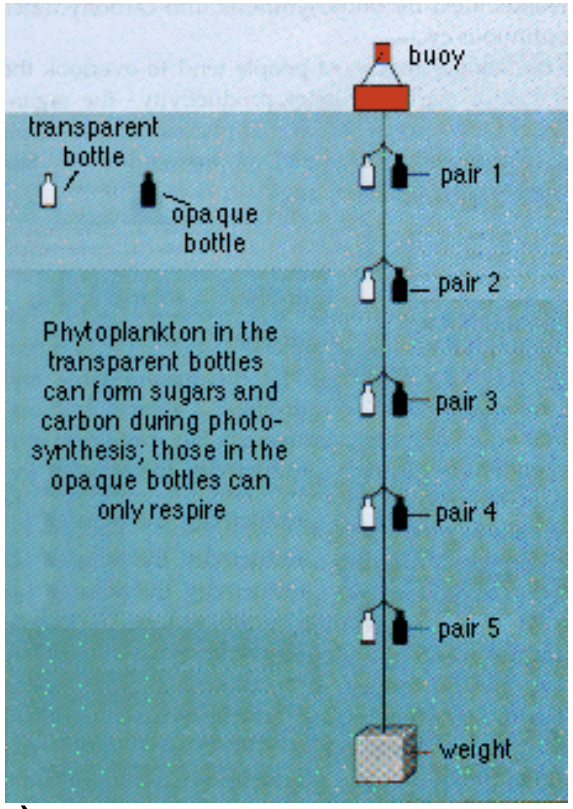
(could be other measure of DIC system)



Perry and E. Kallin, Damariscotta River Estuary;
Chlorophyll concentration ~ 3 μg L^{-1}

2. Changes in O_2 in light/dark bottles

(1916, Gran); used today 'BOD'



ΔO_2 in light = PS - respiration

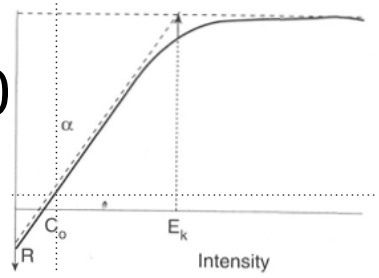
ΔO_2 in dark = respiration

PS = light – dark

(add the assumed respiratory loss of O_2; assumes dark respiration = light respiration)

For low biomass, need long incubations, (newer methods more sensitive). Oxygen isotopes.

Original P vs. E curve – Penelope Jenkins, ~1930 culture of diatoms as different depths (light)



3. Tracer incubation methods – ^{14}C or ^{18}O

Radiolabeled ^{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.'

$$CO_2 + H_2O \quad \text{---}> \quad -(CH_2O)- + O_2$$

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

$^{12}HCO_3^-$ ^{12}C in new biomass

^{18}O-labeled water vs. ^{14}C-labelled DIC

^{18}O is 1.5 to 2-fold higher than ^{14}C due to photorespiration, biosynthesis, DO^{14}C recycling, nitrate reduction.

^{18}O ~ GPP; ^{14}C ~ between GPP and NPP but really depends on length of incubation

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^{18}O ~ GPP; ^{14}C ~ between GPP and NPP but really depends on length of incubation

Incubations - P vs. E *or*
at depth (or simulated depth)

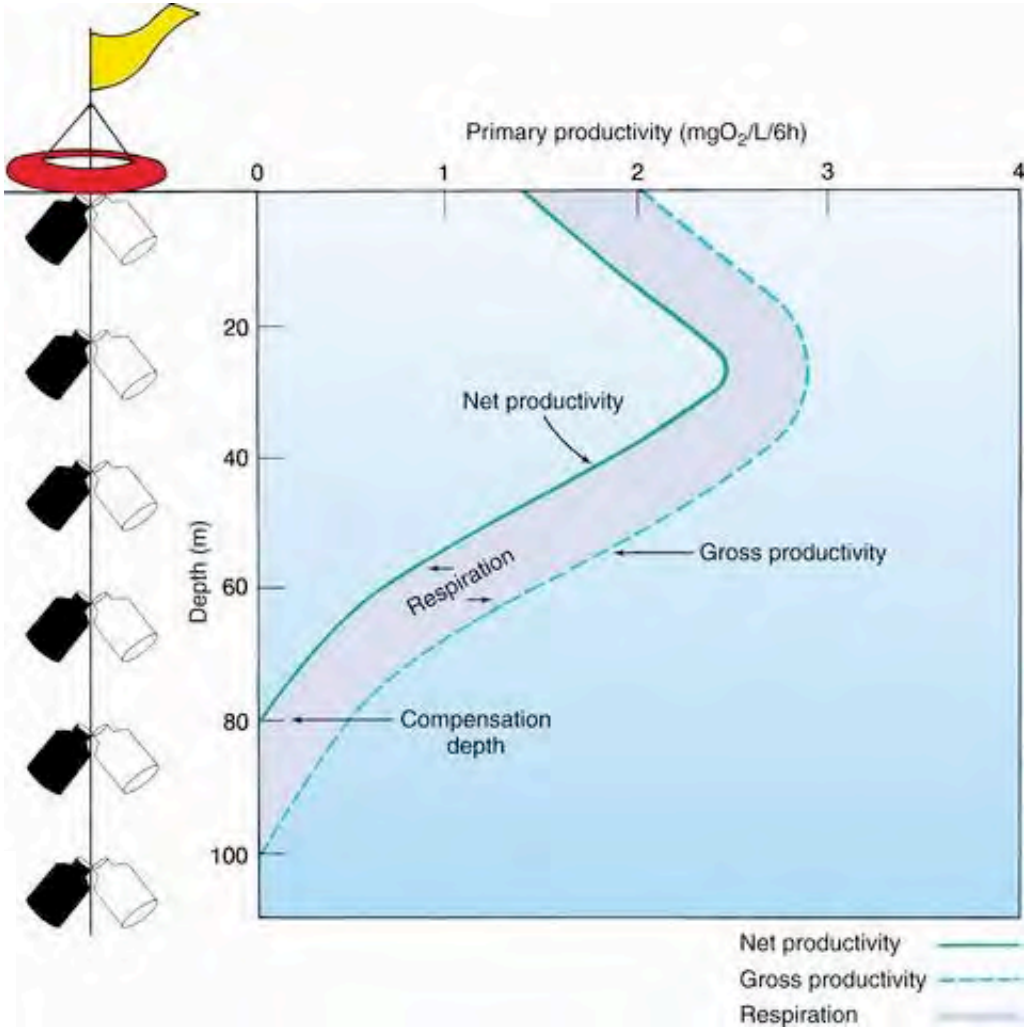
Patterns:

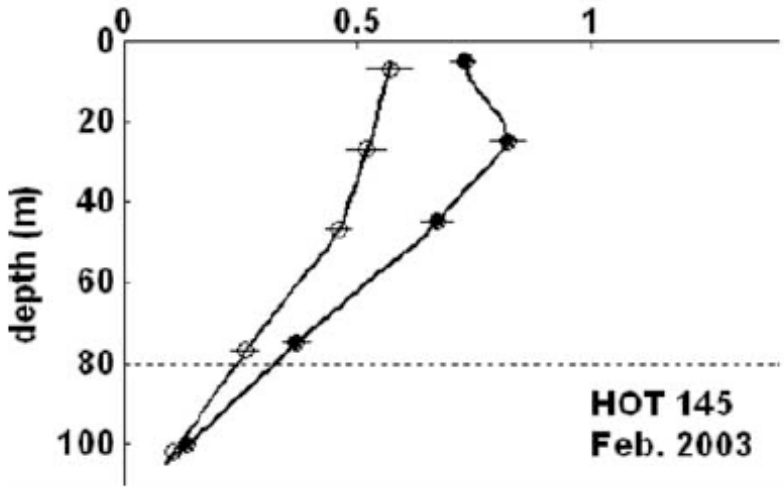
Surface photo inhibition

Note variability in rates
normalized to Chl

Respiration (net PP)

Compensation depth





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

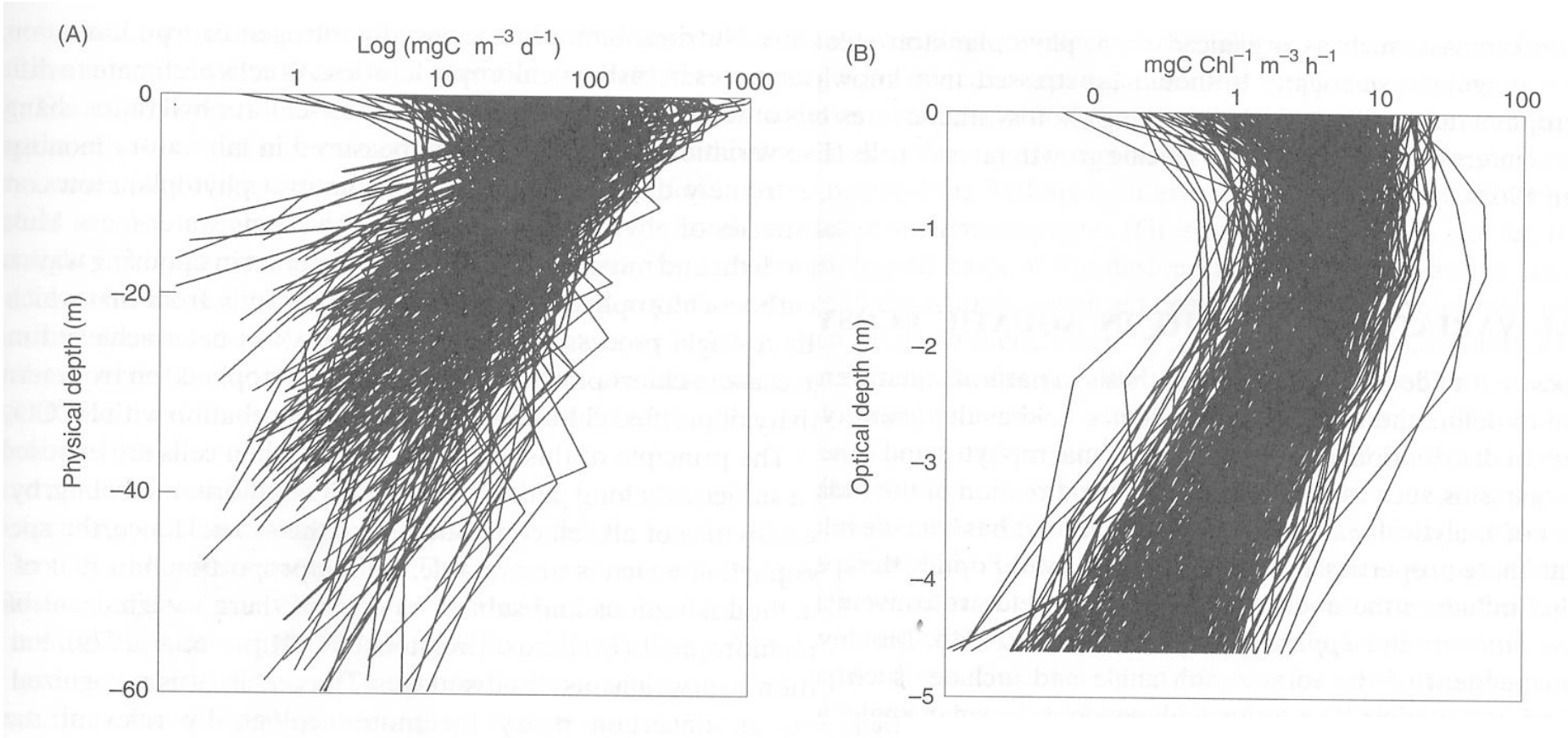
Juranek & Quay (2005) BGC 19,GB3009.

^{18}O is also tracer method

Example of data from ^{14}C measurements

log C vs Z

log C vs. log E



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   i. change in product over time (**O_2** evolution and **phytoplankton concentration)** – is that NCP?
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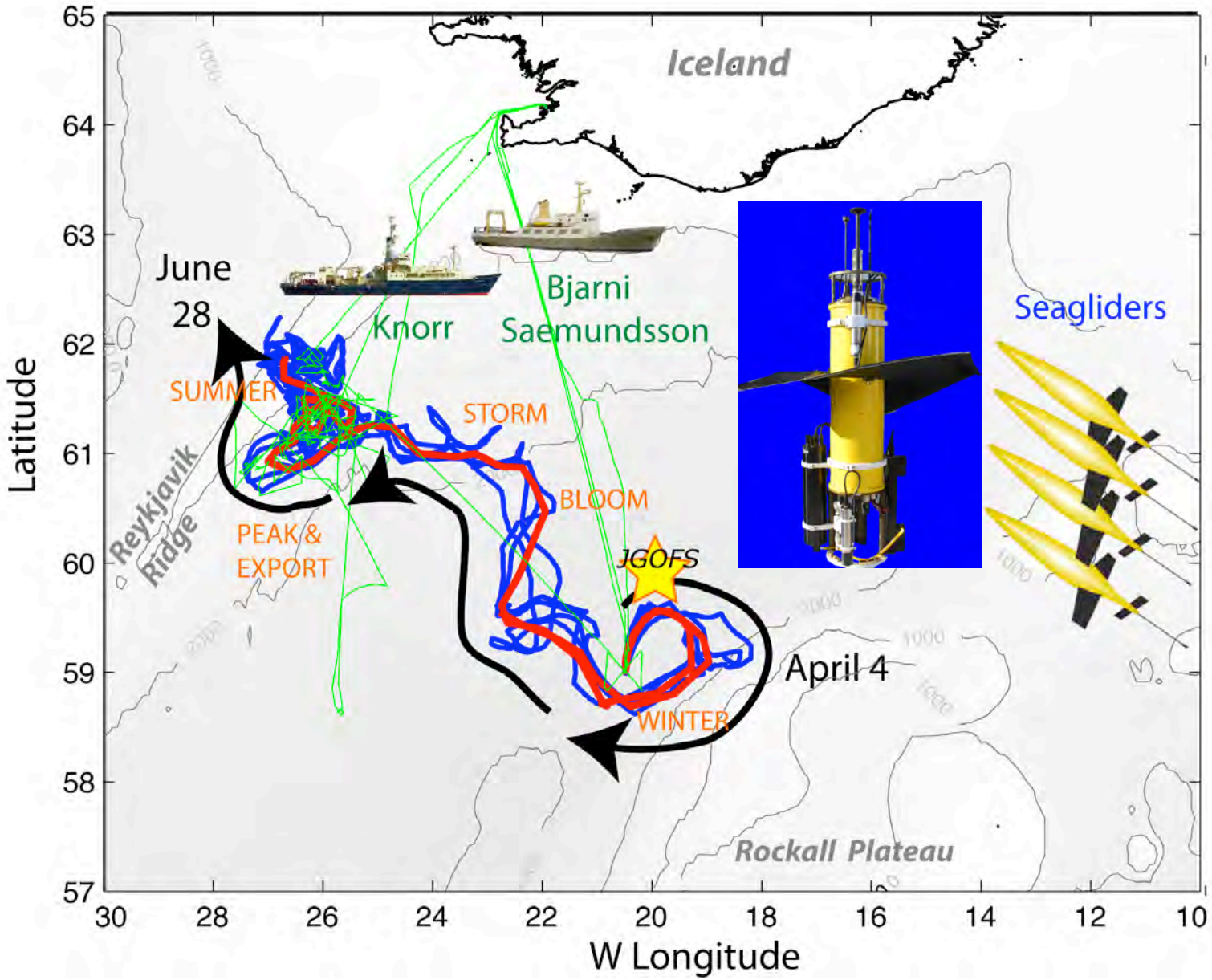
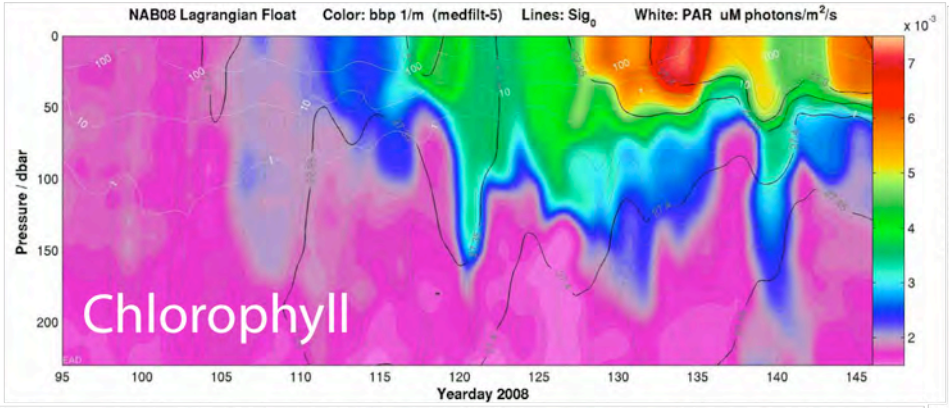
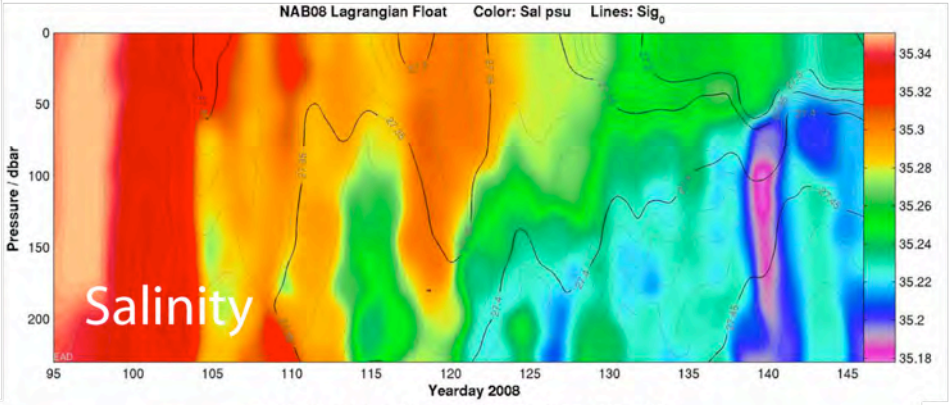
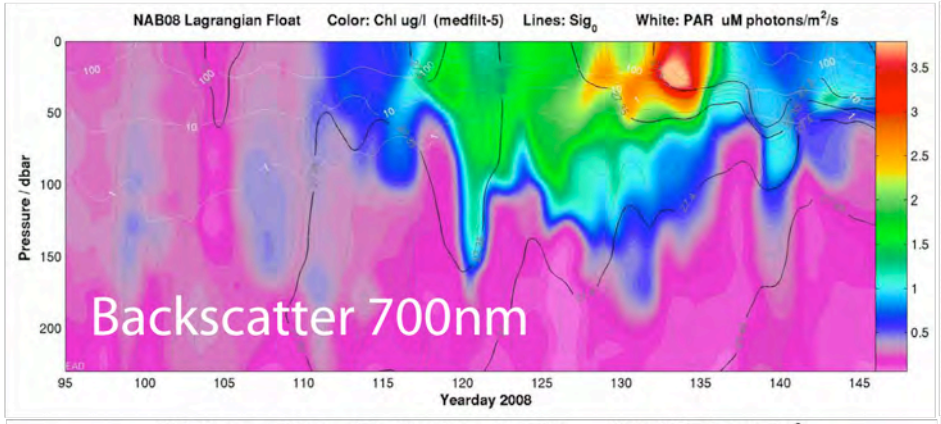
3) Variants of probe fluorometry (pump and probe, PAM, FRRF) – provides terms for PS electron flow models

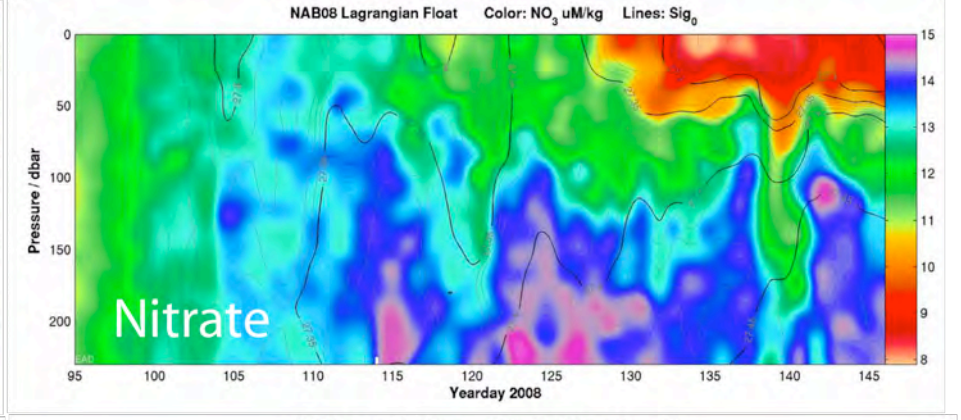
Follow a patch

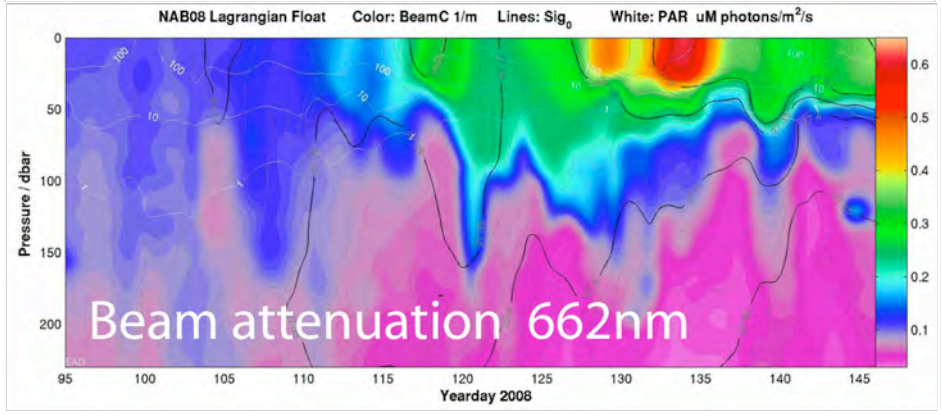


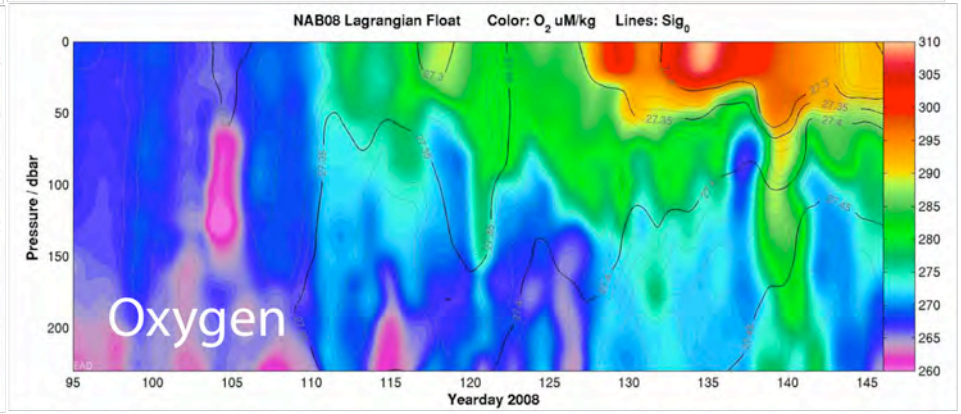




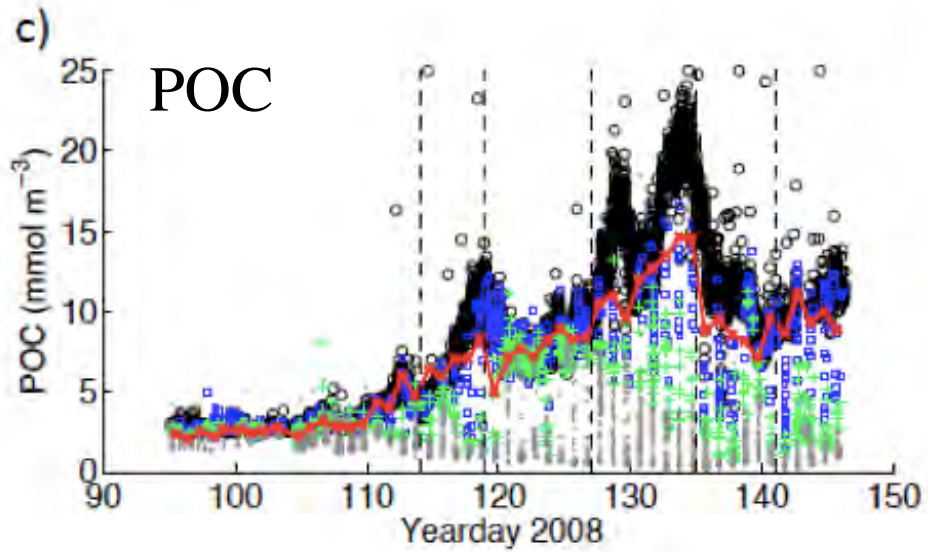


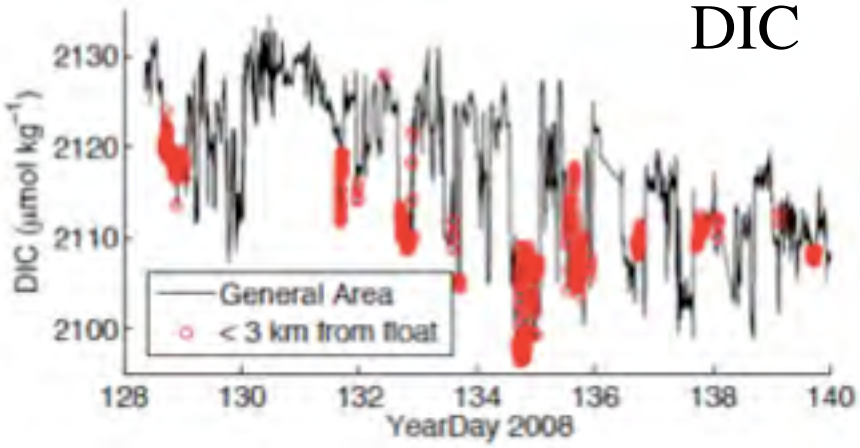


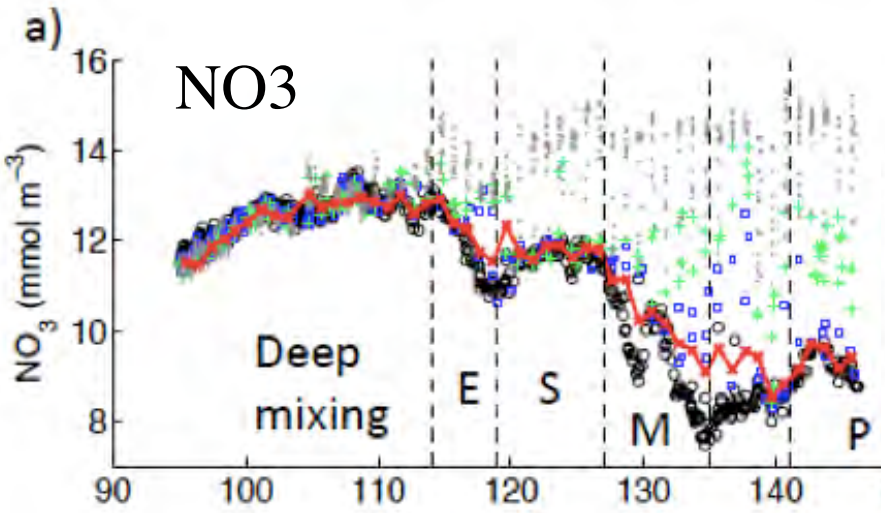


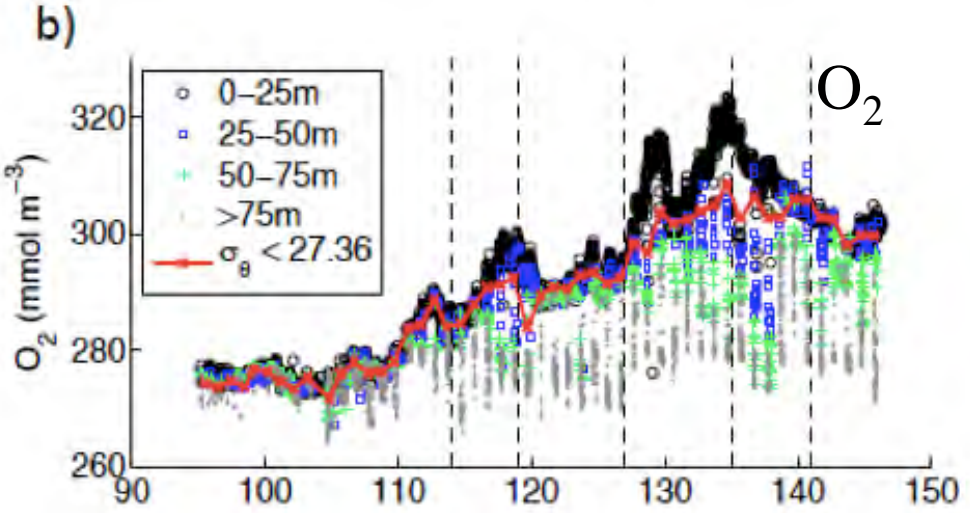


Float data, Alkire et al., sub.



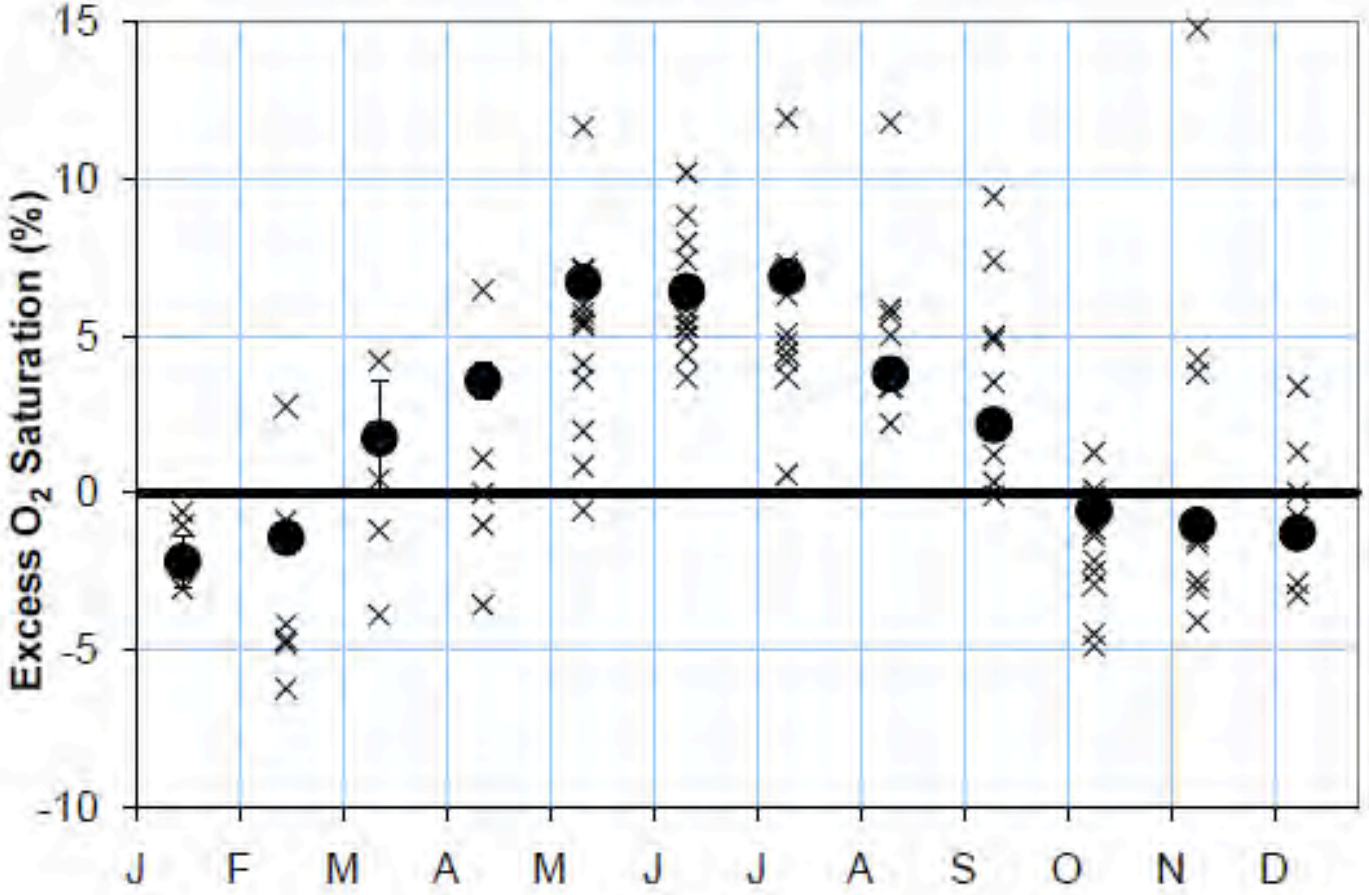






POC from nitrate & O2, Redfield conversion
does not equal POC biomass

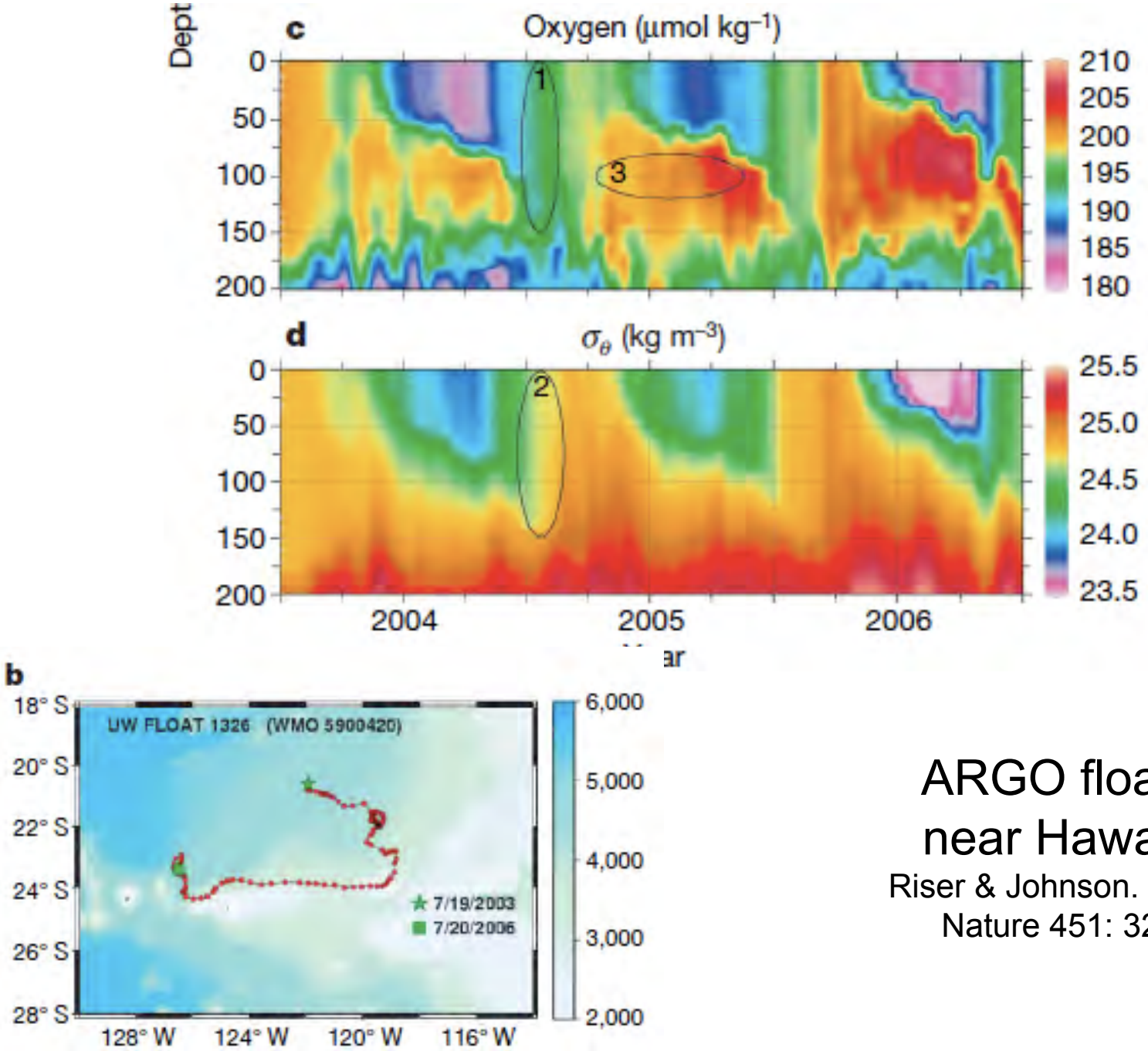
Float data, Alkire et al., sub.



Pool data from lots of ships in the same place (correct for air/sea flux)

Fig. 9. The monthly average O_2 saturation excess (%, where saturation with air is 0%) in surface layer of the subpolar N. Atlantic (40°- 65°N, 10°-60°W) for each year between 1991 and 2005 (X) based on ~90 cruises and ~5000 measurements during the CARINA program [*Stendardo et al.*, 2009]. The mean monthly average for the 15 year interval (●) with error bars that represent the SEM at 95% confidence level (most often within the symbol size).

Quay, in review



ARGO floats near Hawaii.

Riser & Johnson. 2008. Nature 451: 323

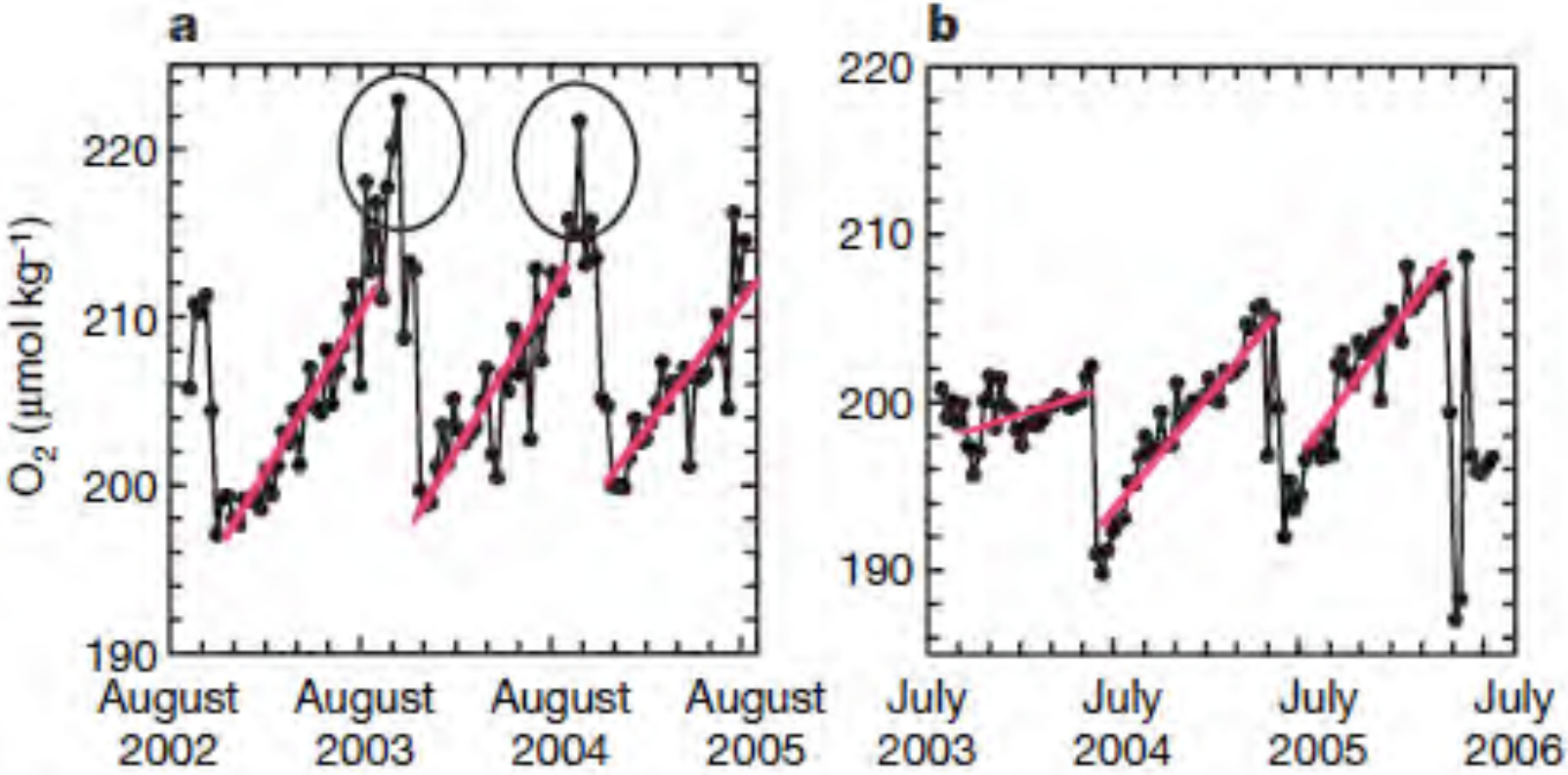
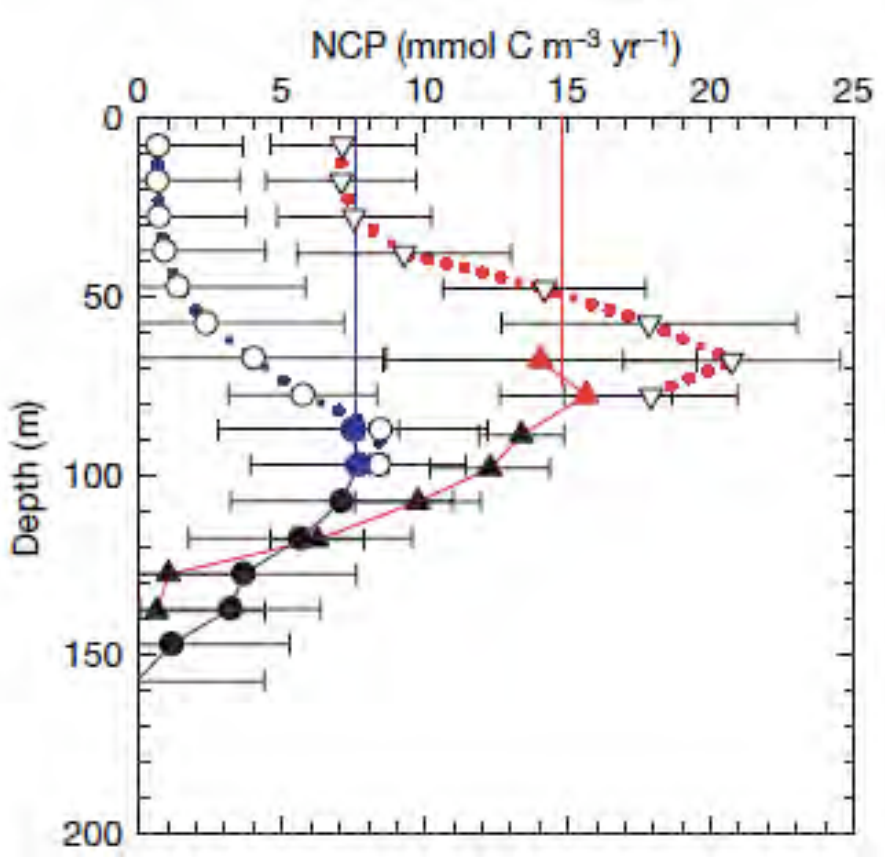


Figure 3 | Oxygen concentrations in the SOM versus time. Oxygen concentrations at 78 m for float 0894 (**a**) and 87 m for float 1326 (**b**) are shown. Black lines and solid circles are oxygen concentrations measured by the float at each depth. Pink lines are fitted to the oxygen data each year by least squares to estimate the rate of oxygen production. Large black ovals in **a** identify late summer blooms that increase oxygen concentration in the SOM significantly above the trend line predicted from data earlier in each year.

* NCP versus depth. Triangles - float 0894, circles - float 1326.
* Filled symbols calculated from slope of oxygen vs. time (below ML).
* Open symbols calculated from slope of oxygen anomaly (oxygen – oxygen solubility) in ML.
* Vertical solid lines are extrapolation to surface of 2 highest rates (symbols colored in red or blue) based on slope of oxygen vs. time.
* Vertically integrated NCP is area to left of lines connecting solid points and solid lines to surface.
* Oxygen production converted to carbon w/ modified Redfield ratio.
* Error bars (61 s.d.) were computed from rate of oxygen change for each of the three years for which floats operated.



Upper ocean is net autotrophic

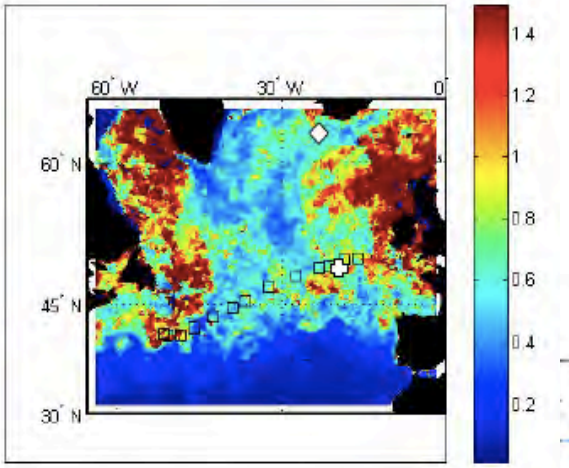
Riser & Johnson. 2008. Nature 451: 323

Triple oxygen isotope: 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).

Therefore, 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), can estimate gross photosynthesis.

Dissolved oxygen/argon (O_2/Ar) ratios in mixed layer are indicative of net community production (NCP) because O_2 and Ar share similar physical solubility properties, but only O_2 is biologically produced and consumed. Ar corrects for disequilibrium of dissolved O_2 in mixed layer associated with heat fluxes, bubble injections, and variations in atmospheric pressure. Biological oxygen is supersaturated (undersaturated) within the mixed layer if community photosynthesis/respiration is greater (less) than 1.

Container ship N. Atlantic, triple O isotope PP, compared with satellite model of NPP



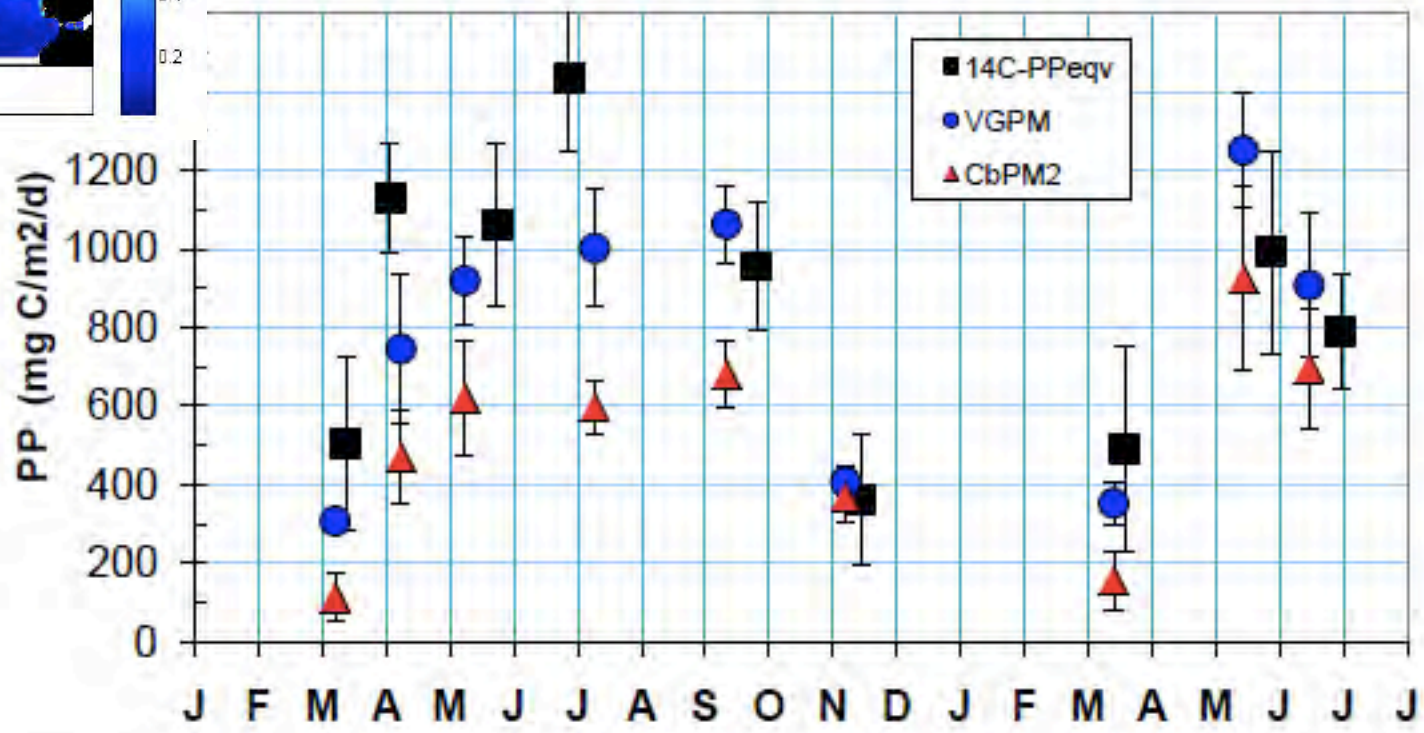
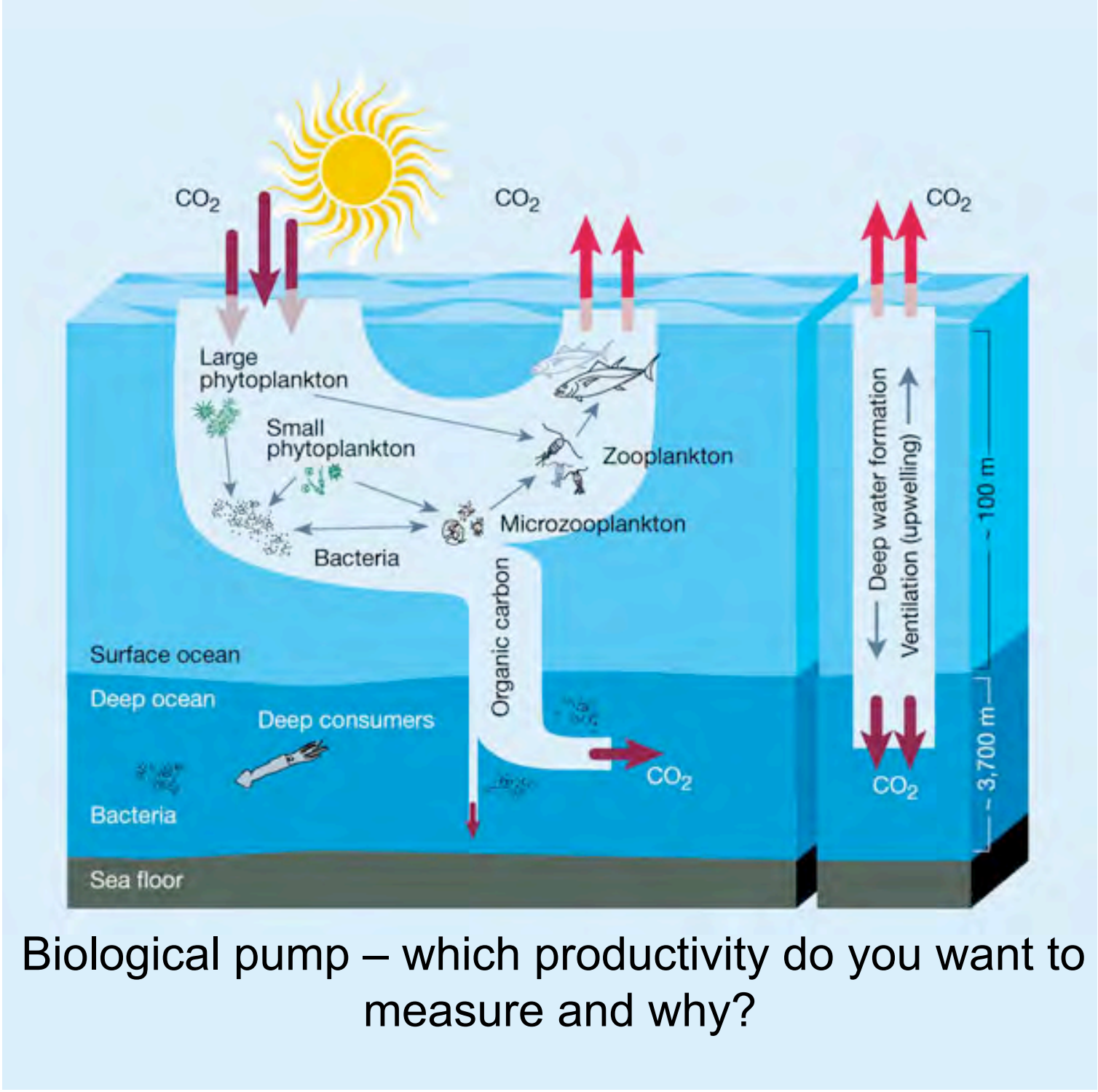


Fig. 8. The mean basin-wide of ^{14}C-PP$_{eqv}$ (■) estimated from $^{17}\Delta$-GOP for each cruise compared to the concurrent PP rates estimated using satellite algorithms VGPM (O) (Behrenfeld and Falkowski, 1997) and CbPM2 (Δ) (Westbury et al., 2008). The error bars represent ±SEM at 95% confidence level.

Quay, in review



Biological pump – which productivity do you want to measure and why?