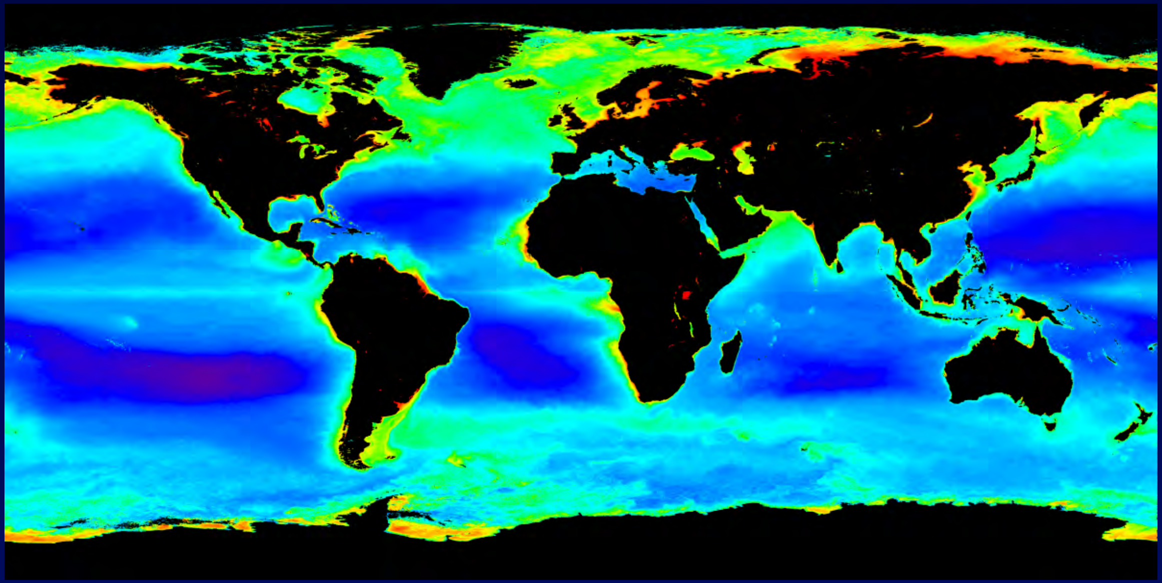
Measurements and Models of Primary Productivity



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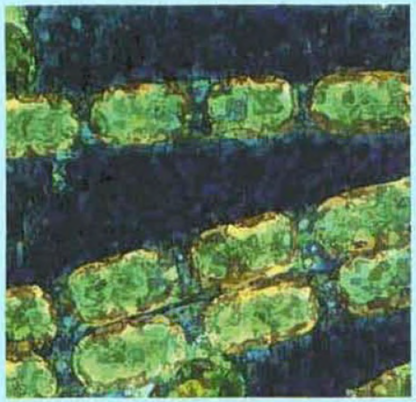
2014 C-MORE Summer Training Course
"Microbial Oceanography:
Genomes to Biomes"

Supported by NSERC including OTN

Provided by the SeaWiFS Project, NASA/Goddard Space Flight Center and ORBIMAGE

Source of some reading

http://www.ceotr.ca/publications/



CHAPTER 19

USING CULTURES TO INVESTIGATE THE PHYSIOLOGICAL ECOLOGY OF MICROALGAE

HUGH L. MACINTYRE
Dauphin Island Sea Lab

JOHN J. CULLEN
Centre for Marine Environmental Prediction, Department of Oceanography, Dalhousie University

MacIntyre and Cullen 2005

FLUORESCENCE-BASED MAXIMAL QUANTUM YIELD FOR PSII AS A DIAGNOSTIC OF NUTRIENT STRESS[1]

Parkhill et al. 2001

for reading lists, email
John.Cullen@Dal.CA

What is marine primary productivity?

Net Primary Productivity (Production)

Net rate of synthesis of organic material from inorganic compounds such as CO_2 and water

Chemosynthesis: chemical reducing power comes from reduced inorganic compounds such as H_2S and NH_3

Photosynthesis: reducing power comes from light energy

Photosynthetic primary production is usually measured and considered to dominate.

$g\ C\ m^{-3}\ h^{-1}$ $g\ C\ m^{-2}\ d^{-1}$

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More to it than that, of course

Table 2. Microbial metabolic processes

Term	*Energy source*	*e^- Donor*	*C source*
Photolithoautotroph	Light	H_2O, H_2S, H_2	CO_2
Photolithoheterotroph	Light	H_2O, H_2S, H_2	Org-C
Photoorganoautotroph	Light	Org-C	CO_2
Photoorganoheterotroph	Light	Org-C	Org-C
Chemolithoautotroph	Chemical	H_2S, $S_2O_3^{-2}$, NH_4^+/NO_2^-, H_2, red-Fe/Mn	CO_2
Chemolithoheterotroph	Chemical	H_2S, $S_2O_2^{-2}$, NH_4^+/NO_2^-, H_2, red-Fe/Mn	Org-C
Chemoorganoautotroph	Chemical	Org-C	CO_2
Chemoorganoheterotroph	Chemical	Org-C	Org-C
Mixotroph[1]	Light/Chemical	Red inorganic/ Org-C	CO_2/Org-C

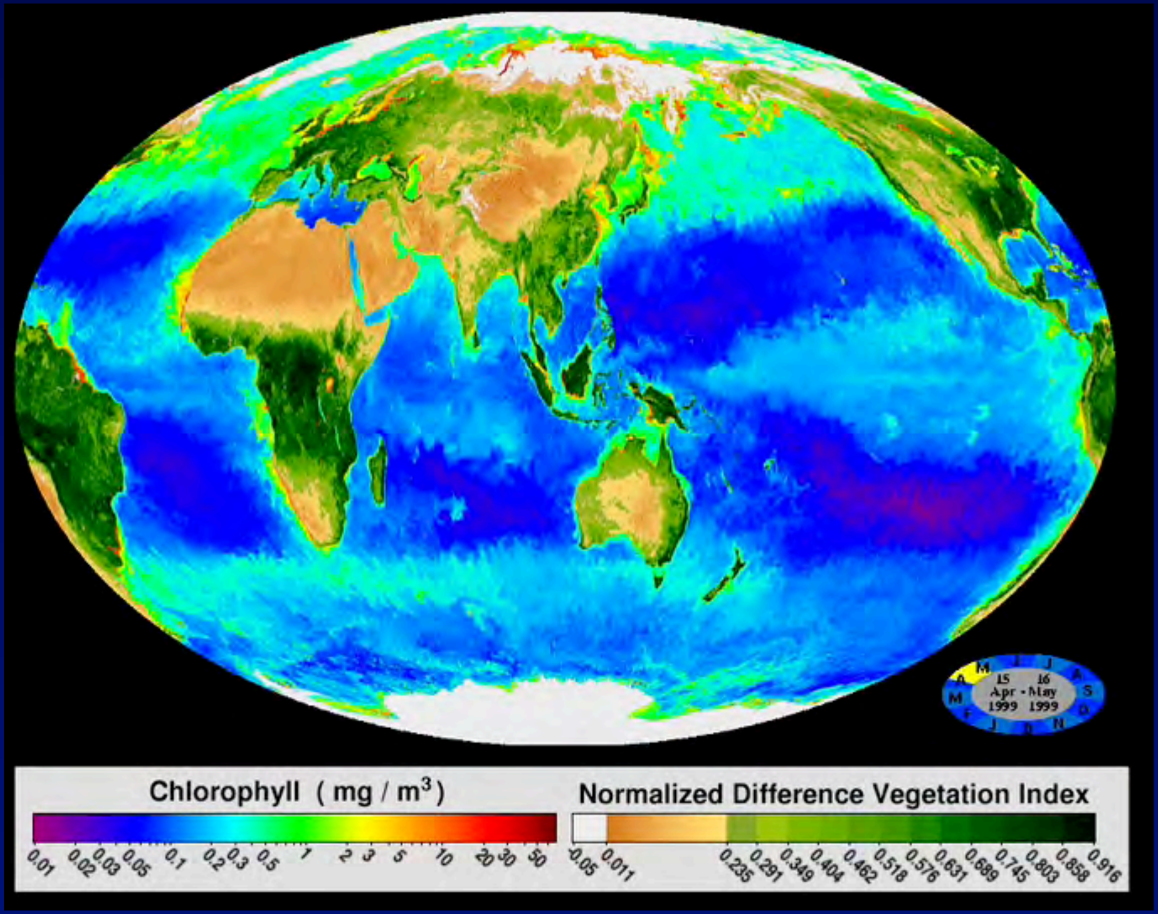
[1]Multiple possible use patterns of mixed energy sources, e^- donors and C-sources

Oceanic prokaryotic microorganisms use a diverse spectrum of metabolic processes to derive the energy and organic C required to support life, ranging from "pure" oxygenic photosynthesis (photolithoautotrophy) to classic heterotrophy (chemoorganoheterotrophy); recent work suggests that some of the intermediate pathways, such as photoorganoautotrophy and photoorganoheterotrophy, as well as mixotrophy, may play a much larger role in ocean ecology than previously thought

Doney, S. C.,et al. (2004), *Frontiers in Ecology and the Environment*, *2*(9), 457-466.

Biological oceanography and phytoplankton ecology

Describe the ***causes*** and ***consequences*** of variations in
primary productivity
(and food web structure)

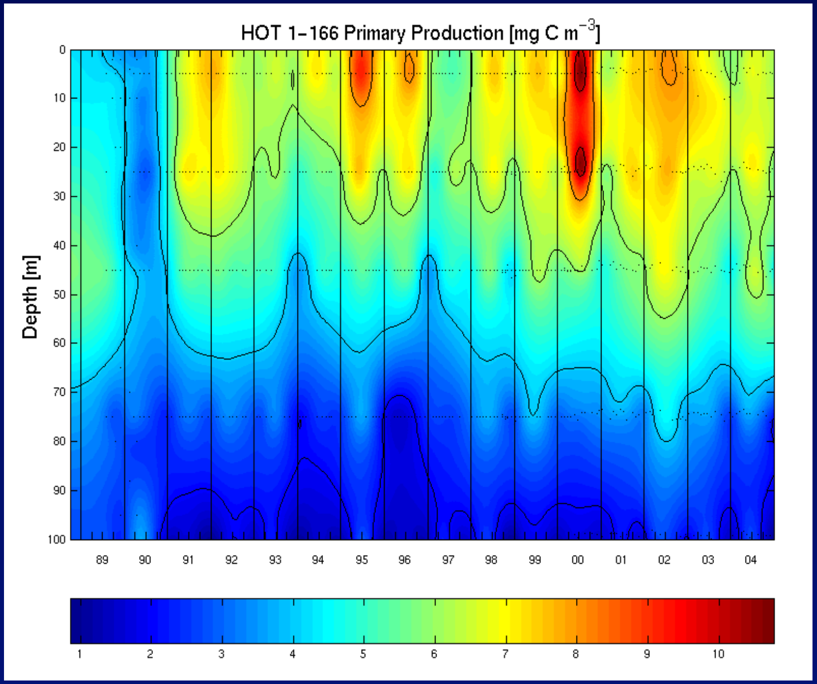


Why measure and model primary productivity?

Ecological prediction

Biogeochemical models

Climate change scenarios



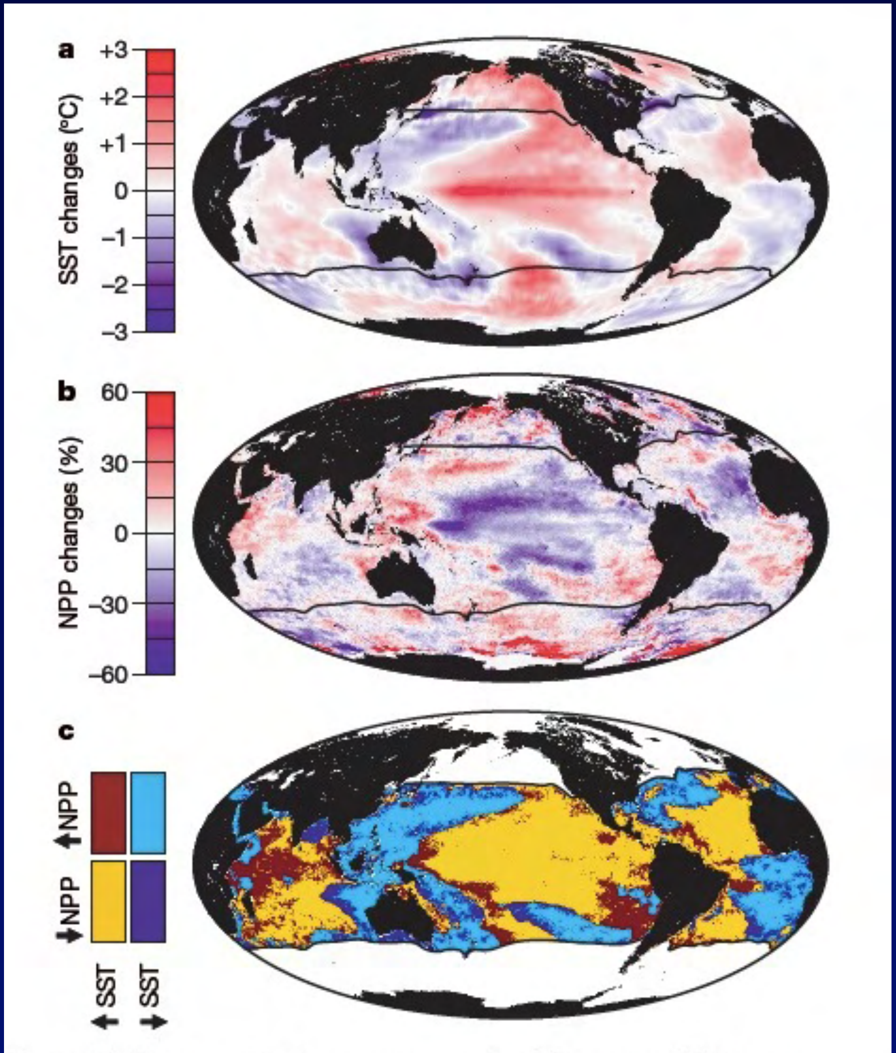


Figure 3 | Climate controls on ocean productivity cause NPP to vary inversely with changes in SST. Global changes in annual average SST (**a**) and

Behrenfeld et al. *Nature* 2006

Oxygenic Photosynthesis

$$CO_2 + 2H_2\overset{*}{O} \xrightarrow{\sim 8h\nu} (CH_2O) + H_2O + \overset{*}{O}_2$$

This process can be quantified directly by measuring the increase of oxygen, the decrease of CO_2, or the increase of organic carbon. Incubations can be conducted with ^{14}C, ^{13}C or $H_2{}^{18}O$ added as tracers.

The process has many chemical consequences that can be traced with measurements of the concentrations of oxygen and carbon, and their isotopic signatures

There are measurements and there are measurements…

What Is the Metabolic State of the Oligotrophic Ocean? A Debate

Hugh W. Ducklow[1] and Scott C. Doney[2]

The Oligotrophic Ocean Is Autotrophic*

Peter J. le B. Williams,[1] Paul D. Quay,[2] Toby K. Westberry,[3] and Michael J. Behrenfeld[3]

The Oligotrophic Ocean Is Heterotrophic*

Carlos M. Duarte,[1,2] Aurore Regaudie-de-Gioux,[1,4] Jesús M. Arrieta,[1] Antonio Delgado-Huertas,[5] and Susana Agustí[1,2,3]

Annual Review of Marine Science 2013

in vitro vs *in situ*

Table 1 Reported rates of net community production (NCP) for oligotrophic subtropical gyres of the open ocean

Study	Method(s)	Location	Biogeochemical zone(s)	NCP ± SE (mmol O_2 m^{-2} day^{-1})
		In vitro observations		
Gist et al. 2009	In vitro O_2 flux	—	NAST-E (Sp)	−3
Serret et al. 2001	In vitro O_2 flux	—	NAST-E (Su)	−111 ± 17
Serret et al. 2002	In vitro O_2 flux	—	NAST-E (Au)	−33 ± 14
Gist et al. 2009	In vitro O_2 flux	—	NAST-E (Au)	−15
González et al. 2002	In vitro O_2 flux	—	NAST-E (Sp, Au)	−77 ± 162
González et al. 2002	In vitro O_2 flux	—	SATL (Sp, Au)	−255 ± 167
Gist et al. 2009	In vitro O_2 flux	—	SATL (Au)	−14
Williams & Purdie 1991	In vitro O_2 flux	Station ALOHA	NPTG-E (Su, Au)	−0.9 ± 43
Williams et al. 2004	In vitro O_2 flux	Station ALOHA	NPTG-E (All)	−24 ± 5
		In situ observations		
Emerson et al. 1997	Surface O_2 budgets	Station ALOHA	NPTG-E (All)	5.5 ± 2.7
Benitez-Nelson et al. 2001	^{234}Th analysis	Station ALOHA	NPTG-E (All)	4.1 ± 2.2
Quay & Stutsman 2003	DIC and DIC δ^{13}	Station ALOHA	NPTG-E (All)	7.4 ± 3.8
Hamme & Emerson 2006	Ar/O_2 ratios	Station ALOHA	NPTG-E (All)	3.0 ± 1.4
Emerson et al. 2008	O_2 from moorings	Station ALOHA	NPTG-E (All)	11 ± 5.2
Quay et al. 2010	$^{17}O_2$ disequilibria	Station ALOHA	NPTG-E (All)	10 ± 2.7
Jenkins 1980	Tritium/^{3}He box model	Sargasso Sea	NAST-W	14
Musgrave 1990	Tritium/^{3}He box model	Sargasso Sea (32° N, 64° W)	NAST-W	6.8
Spitzer & Jenkins 1989	Upper-ocean O_2 balance	Sargasso Sea (32° N, 64° W)	NAST-W (All)	11 ± 3

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In situ estimates need calibration

JOURNAL OF GEOPHYSICAL RESEARCH, VOL. 117, C05012, doi:10.1029/2010JC006856, 2012

Evaluating triple oxygen isotope estimates of gross primary production at the Hawaii Ocean Time-series and Bermuda Atlantic Time-series Study sites

David P. Nicholson,[1] Rachel H. R. Stanley,[1] Eugeni Barkan,[2] David M. Karl,[3] Boaz Luz,[2] Paul D. Quay,[4] and Scott C. Doney[1]

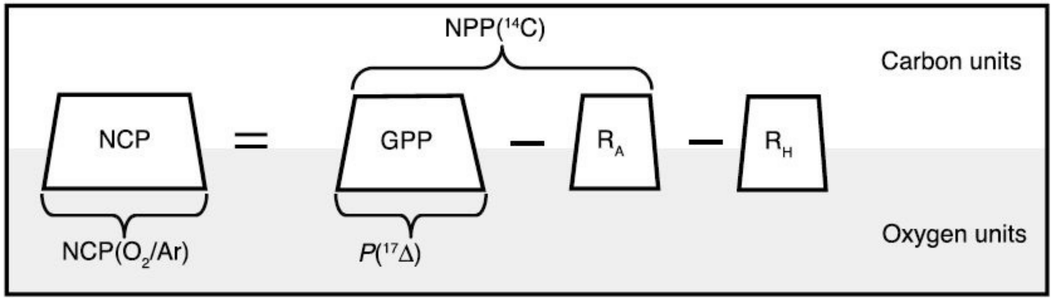
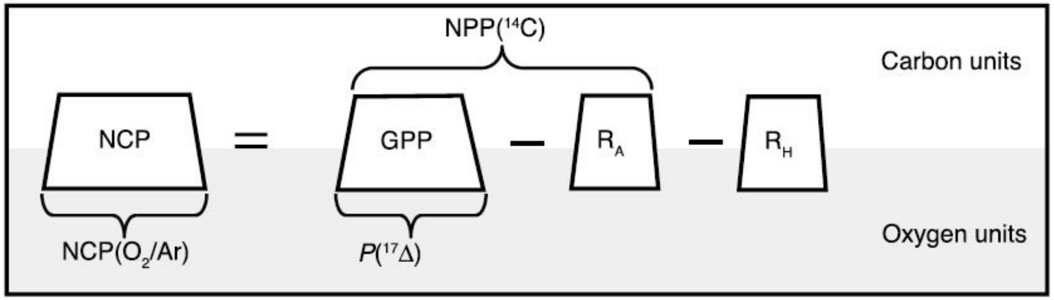


Figure 1. Schematic illustrating the relationships between different types of biological production and methods used for quantifying the rates of net community production (NCP), Gross primary production (GPP), net primary production (NPP), autotrophic respiration (R_A) and heterotrophic respiration (R_H). Rates are measured either in terms of production of oxygen, e.g., $P(^{17}\Delta)$) or production of organic carbon, e.g., (NPP(^{14}C)). Carbon and oxygen fluxes can be related by estimating the C:O_2 stoichiometry of each process.

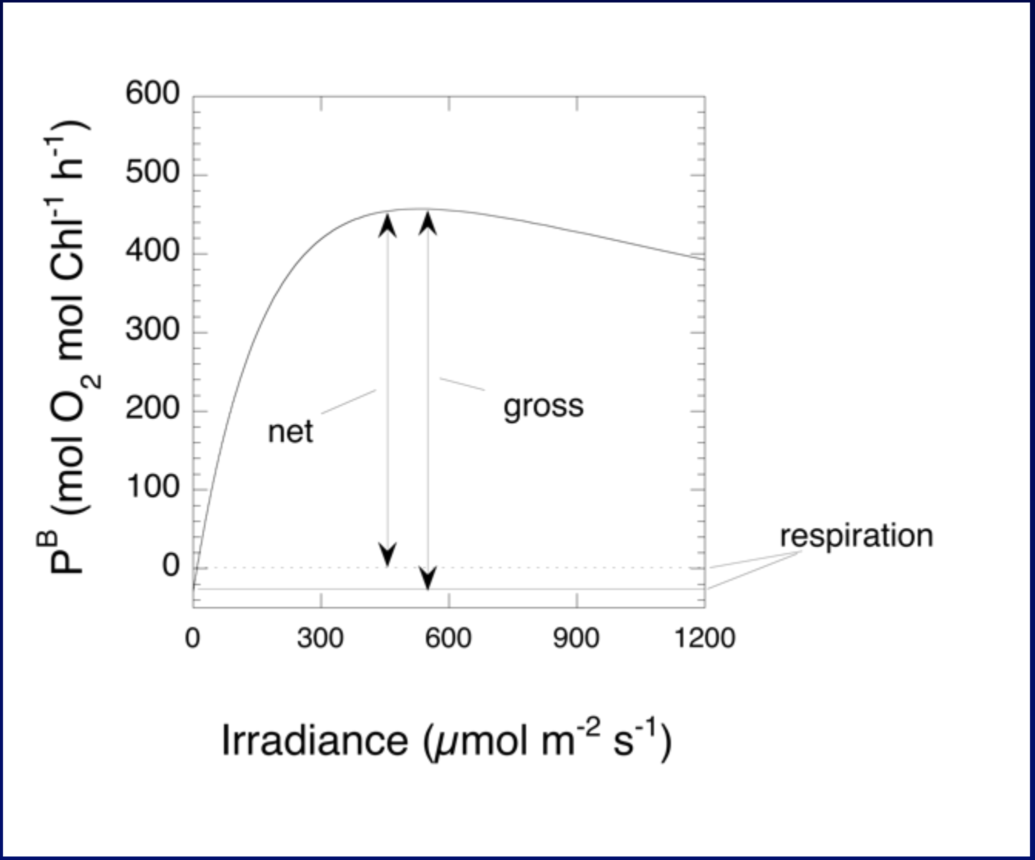


- **Gross primary production** (P_g) is the rate of photosynthesis, not reduced for losses to excretion or to respiration in its various forms
- **Net primary production** (P_n) is gross primary production less losses to respiration by phytoplankton
- **Net community production** (P_{nc}) is net primary production less losses to respiration by heterotrophic microorganisms and metazoans.

Cullen, J.J., 2001. Plankton: Primary production methods. In J. Steele, S. Thorpe, K. Turekian (Eds.), *Encyclopedia of Ocean Sciences* (pp. 2277-2284): Academic Press.

Effects of Light on Photosynthesis

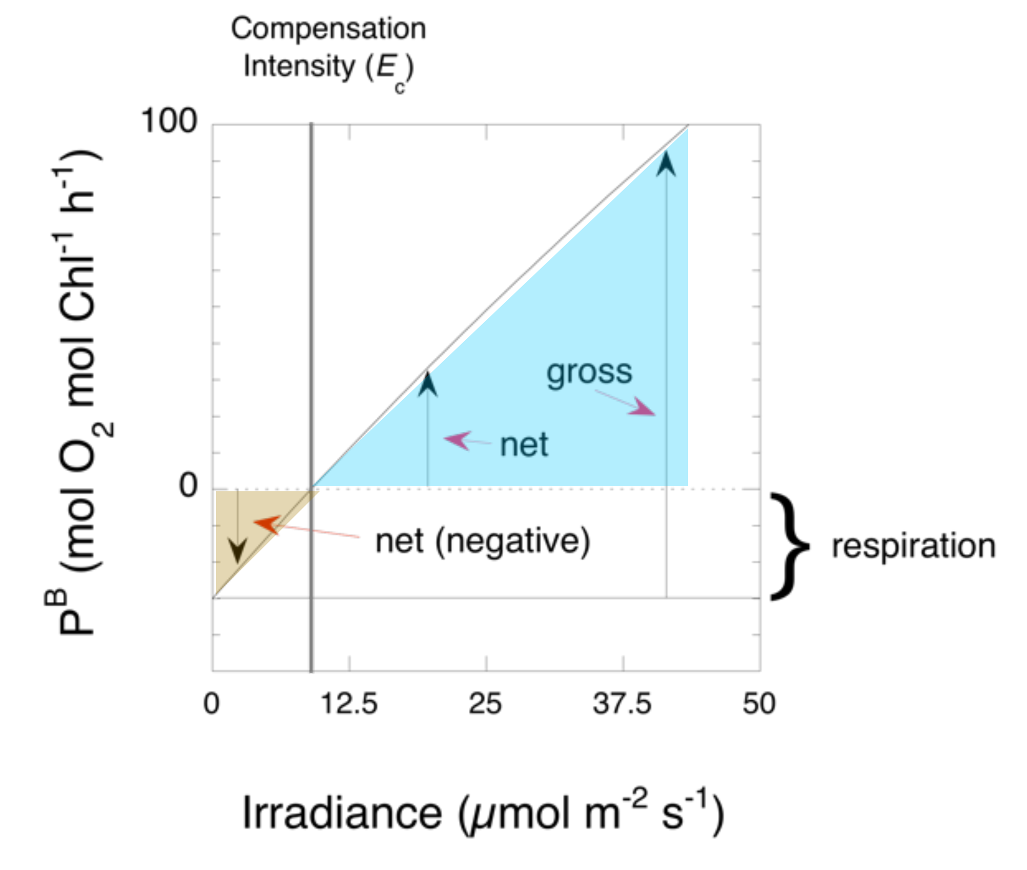
Net Photosynthesis = Gross Photosynthesis - Respiration



Respiration is measured directly only in the dark. The light-dependent component is much harder to measure (^{18}O-tracer can be used for that).

Effects of Light on Photosynthesis

Net Photosynthesis = Gross Photosynthesis - Respiration



Net photosynthesis is negative when irradiance is below the compensation irradiance.

Relating oxygen evolution to carbon assimilation with the photosynthetic quotient

Generalized reactions for growth on nitrate and ammonium

$$1.0\ NO_3^- + 5.7CO_2 + 5.4H_2O \longrightarrow (C_{5.7}H_{9.8}O_{2.3}N) + 8.5\ O_2 + 1.0\ OH^-$$

$$P.Q. = 1.49\,(O_2\ evolved\ /\ CO_2\ consumed)$$

$$1.0\ NH_4^+ + 5.7CO_2 + 3.4H_2O \longrightarrow (C_{5.7}H_{9.8}O_{2.3}N) + 6.25\ O_2 + 1.0\ H^+$$

$$P.Q. = 1.10$$

Note that more photosynthesis is required for growth on nitrate because the nitrate must be reduced.

Using Triple Isotopes of Dissolved Oxygen to Evaluate Global Marine Productivity

L.W. Juranek[1] and P.D. Quay[2]

[1]College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, Oregon 97331; email: ljuranek@coas.oregonstat

[2]School of Oceanography, University of Washir
email: pdquay@uw.edu

Annu. Rev. Mar. Sci. 2013. 5:503–24

Inevitable comparisons with satellite-based estimates (models)

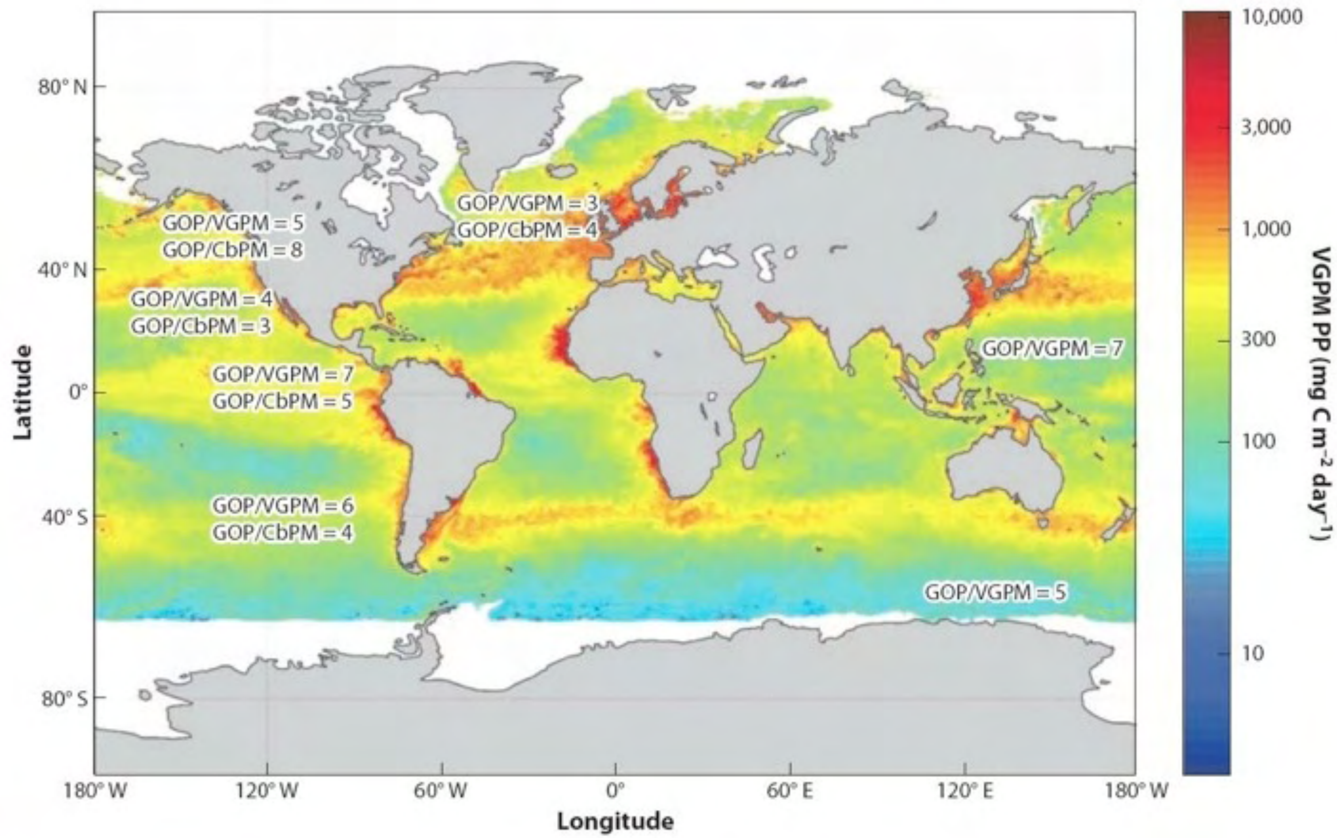
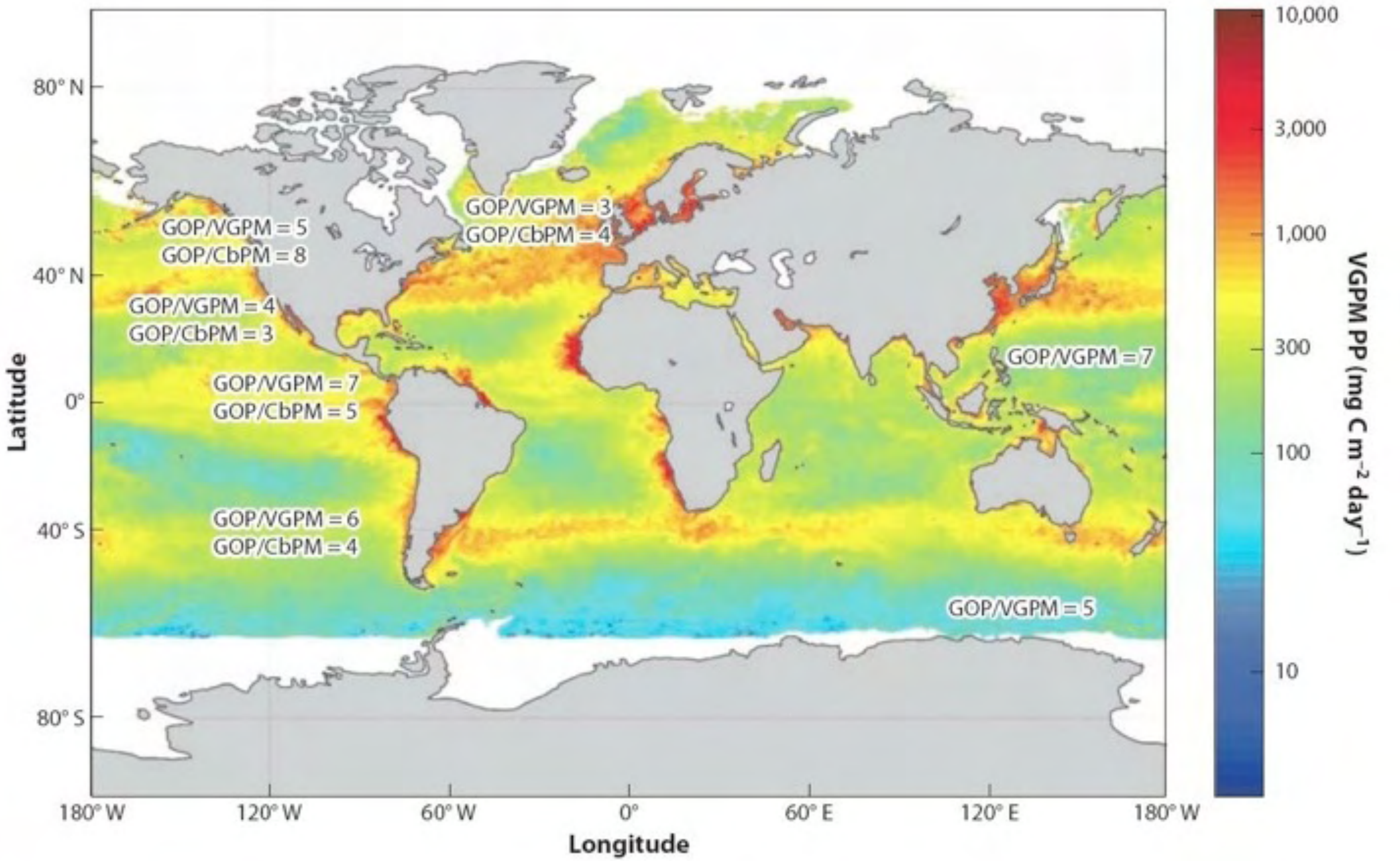


Figure 4

Map of satellite net primary production (NPP) estimated from the vertically generalized productivity model (VGPM) (Behrenfeld & Falkowski 1997), annotated with ratios of observed GOP/NPP (where GOP is gross O_2 production) for both the VGPM and C-based productivity model (CbPM) (Behrenfeld et al. 2005, Westberry et al. 2008) in several basin-scale studies.

What is behind this?



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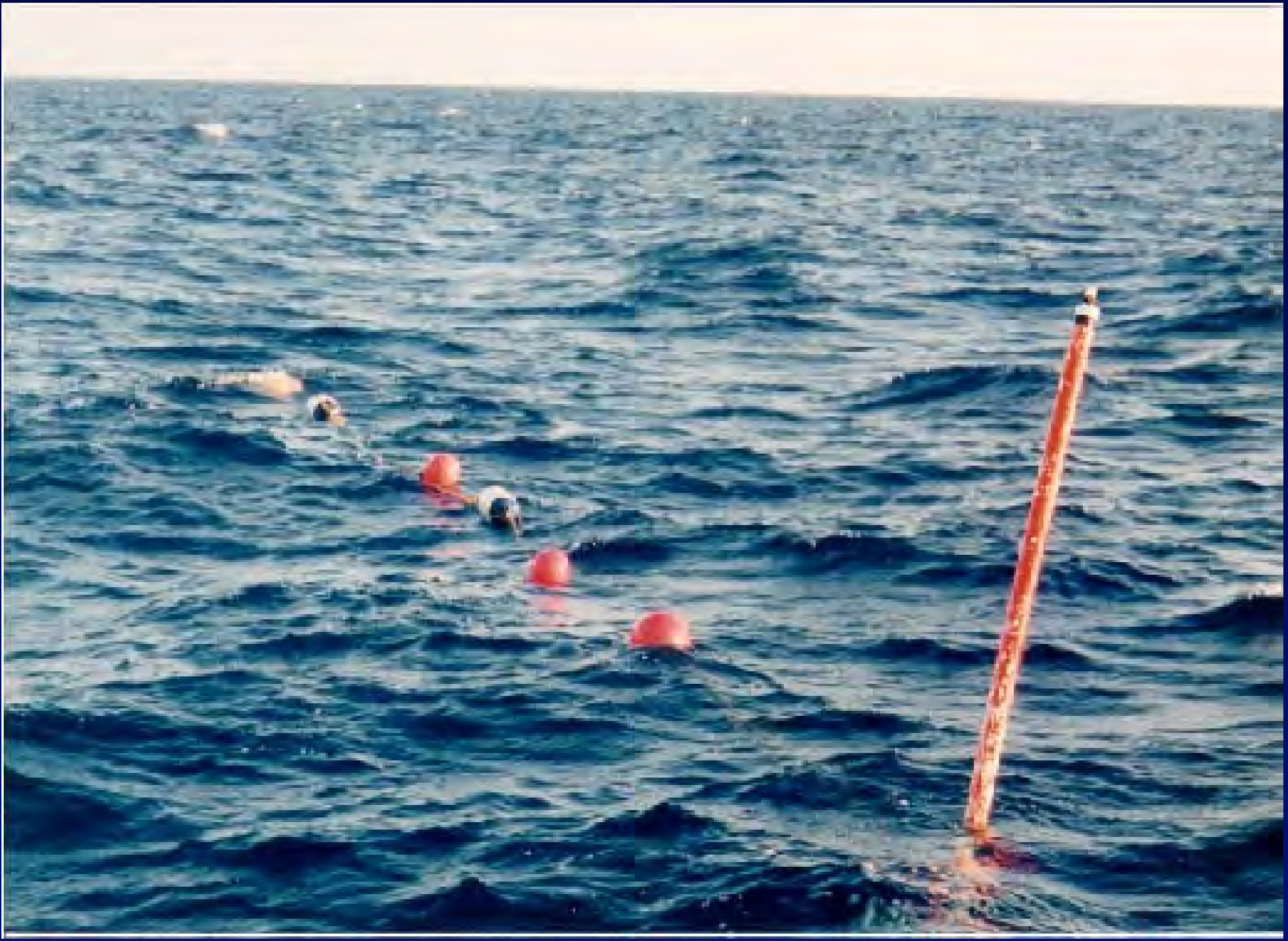
Still a benchmark: The ^{14}C method for measuring primary productivity



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HOT website

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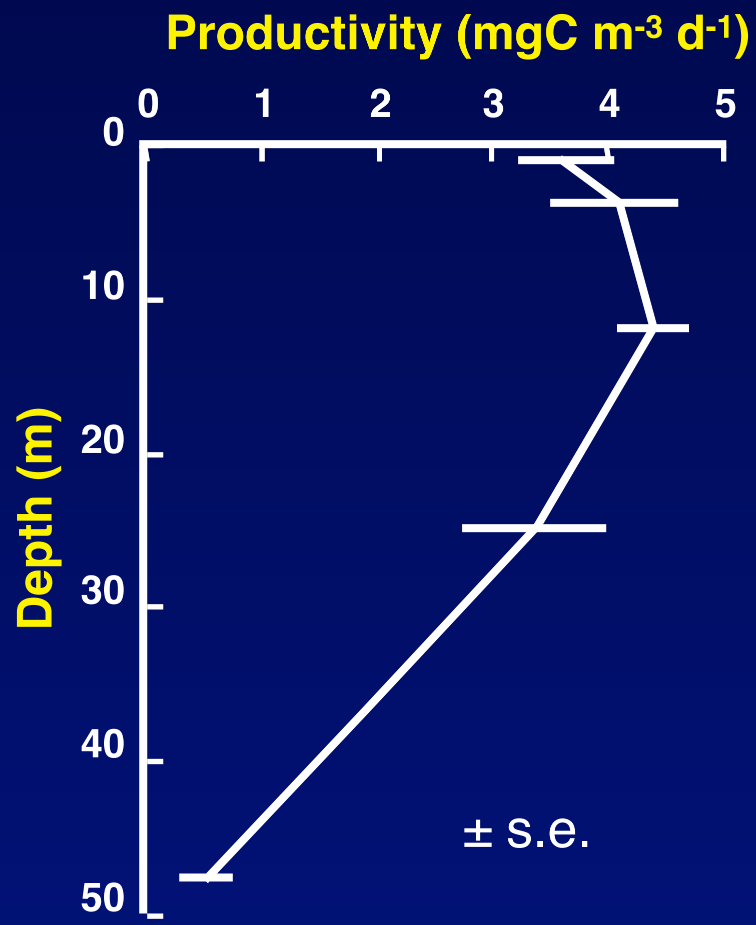
The ^{14}C method for measuring primary productivity



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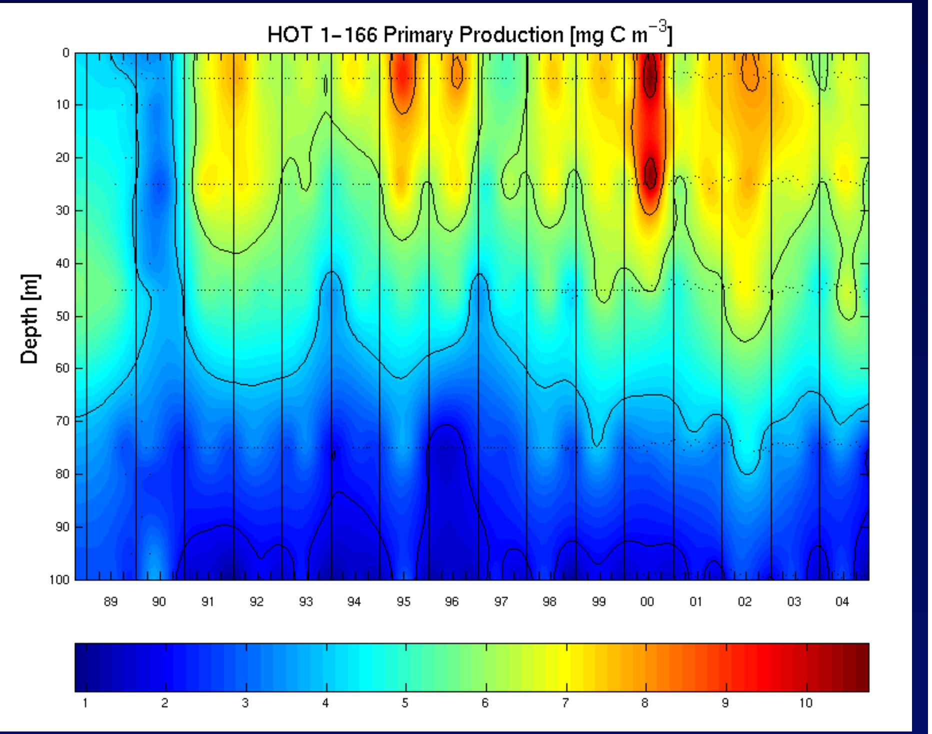
An incredibly useful tool for time series and process studies



HOT website

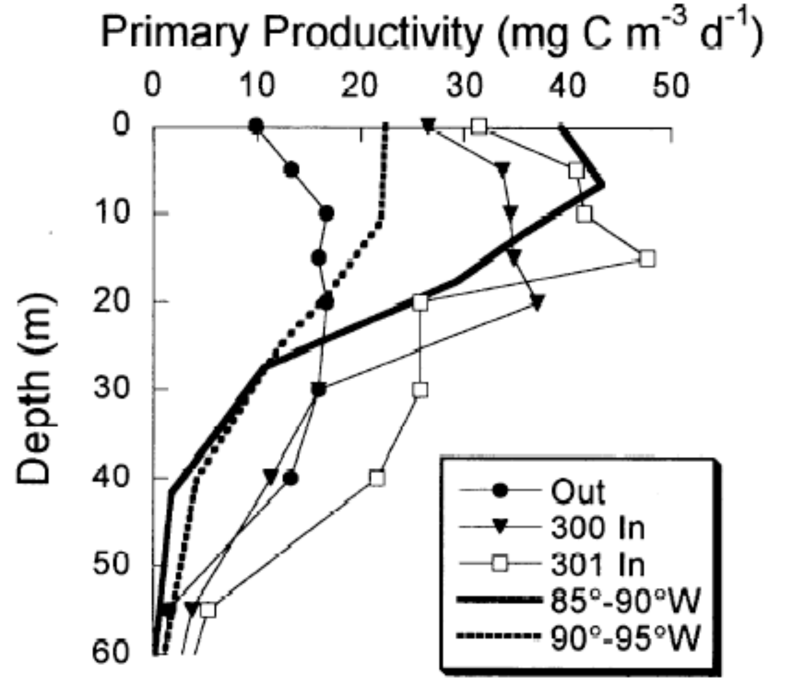
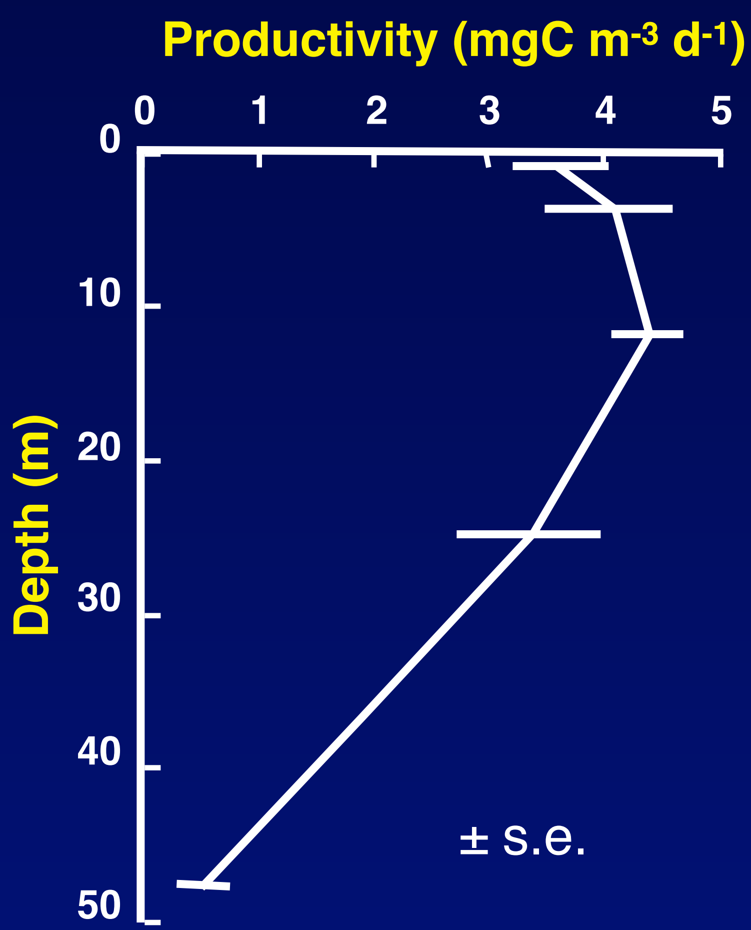
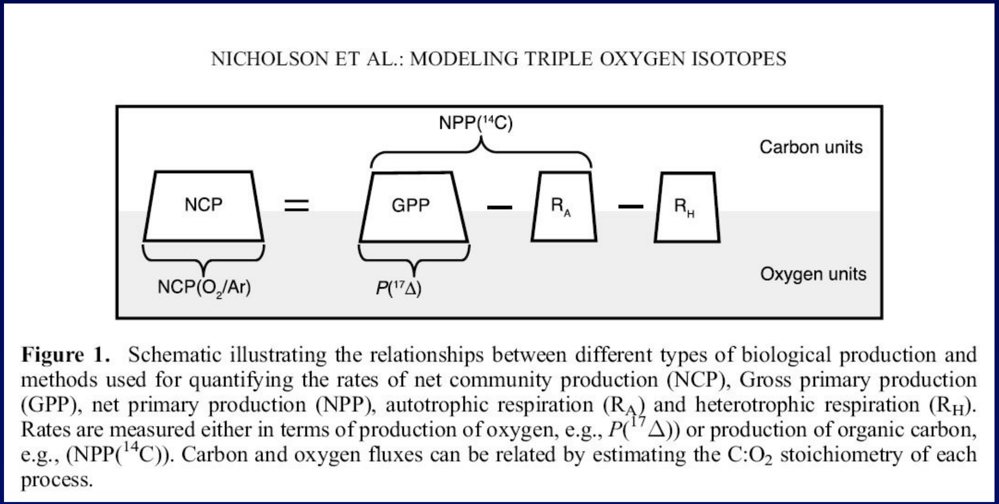


Fig. 1. Primary productivity at and near the site of the open-ocean enrichment experiment (near 5°S, 90°W). Profiles from out of the patch and in the patch 2 d (calendar day 300) and 3d (calendar day 301) after enrichment are from Martin et al. (1994). Profiles of historical averages east (4–6°S, 85–90°W; n = 10) and west of the site (4–6°S, 90–95°W; n = 11) are from R. Barber and F. Chavez as presented by Martin and Chisholm (1992). Error bars for the measurements during IronEx were presented by Martin et al. (1994) but not defined. For the average profiles, errors (presumed to be SE) were 16–22% ($\bar{x}$ = 18%) of the mean for 85–90°W and 7–22% ($\bar{x}$ = 13%) for 90–95°W.

Ideally, the ^{14}C method measures net primary productivity



12 - 24 h incubations



NICHOLSON ET AL.: MODELING TRIPLE OXYGEN ISOTOPES

Figure 1. Schematic illustrating the relationships between different types of biological production and methods used for quantifying the rates of net community production (NCP), Gross primary production (GPP), net primary production (NPP), autotrophic respiration (R_A) and heterotrophic respiration (R_H). Rates are measured either in terms of production of oxygen, e.g., $P(^{17}\Delta)$) or production of organic carbon, e.g., (NPP(^{14}C)). Carbon and oxygen fluxes can be related by estimating the C:O_2 stoichiometry of each process.

Sometimes, it does

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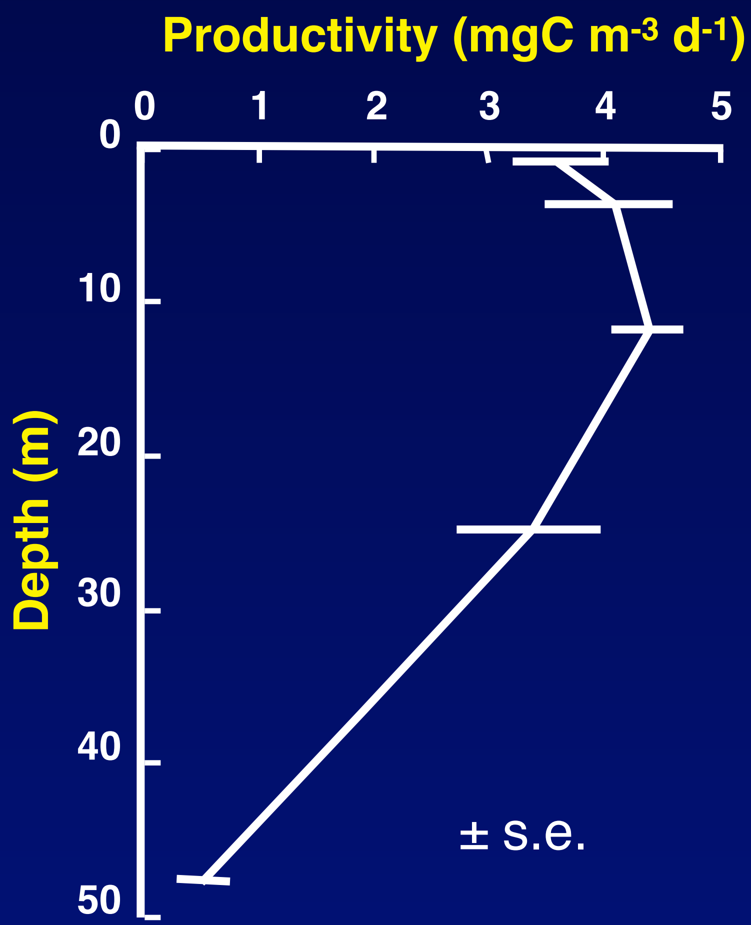
The measurement is subject to artifacts and biases



12 - 24 h incubations

Hypothesis: uncertainties inherent in the ^{14}C method are being forgotten with important consequences for the estimation of primary productivity using other methods.

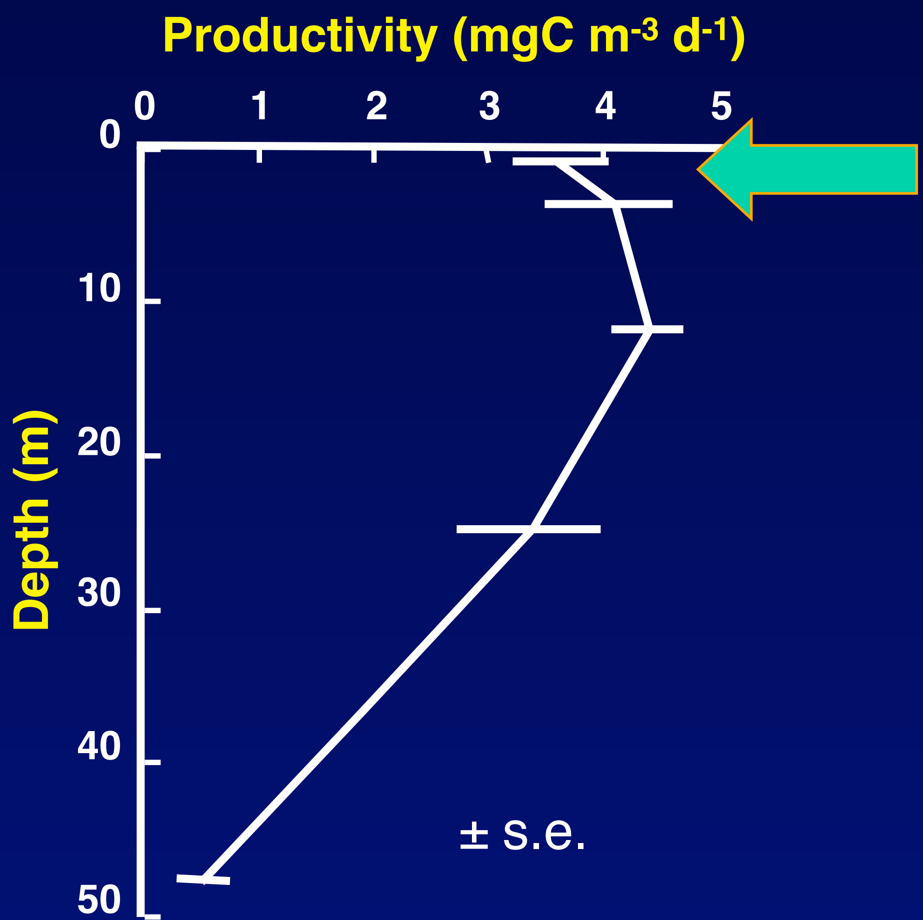
PRIMARY PRODUCTION METHODS

J. J. Cullen, Department of Oceanography, Halifax, Canada

doi:10.1006/rwos.2001.0203

Cullen, J.J., 2001. Plankton: Primary production methods. In J. Steele, S. Thorpe, K. Turekian (Eds.), *Encyclopedia of Ocean Sciences* (pp. 2277-2284): Academic Press.

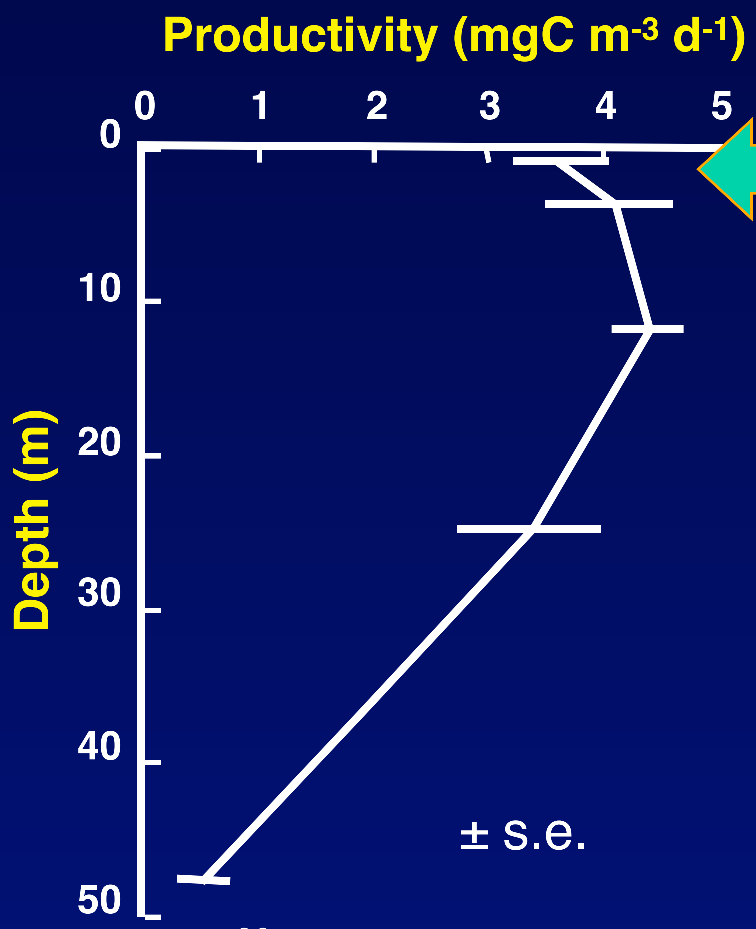
The measurement is subject to artifacts and biases



Overestimation due to exclusion of UV-B

12 - 24 h incubations

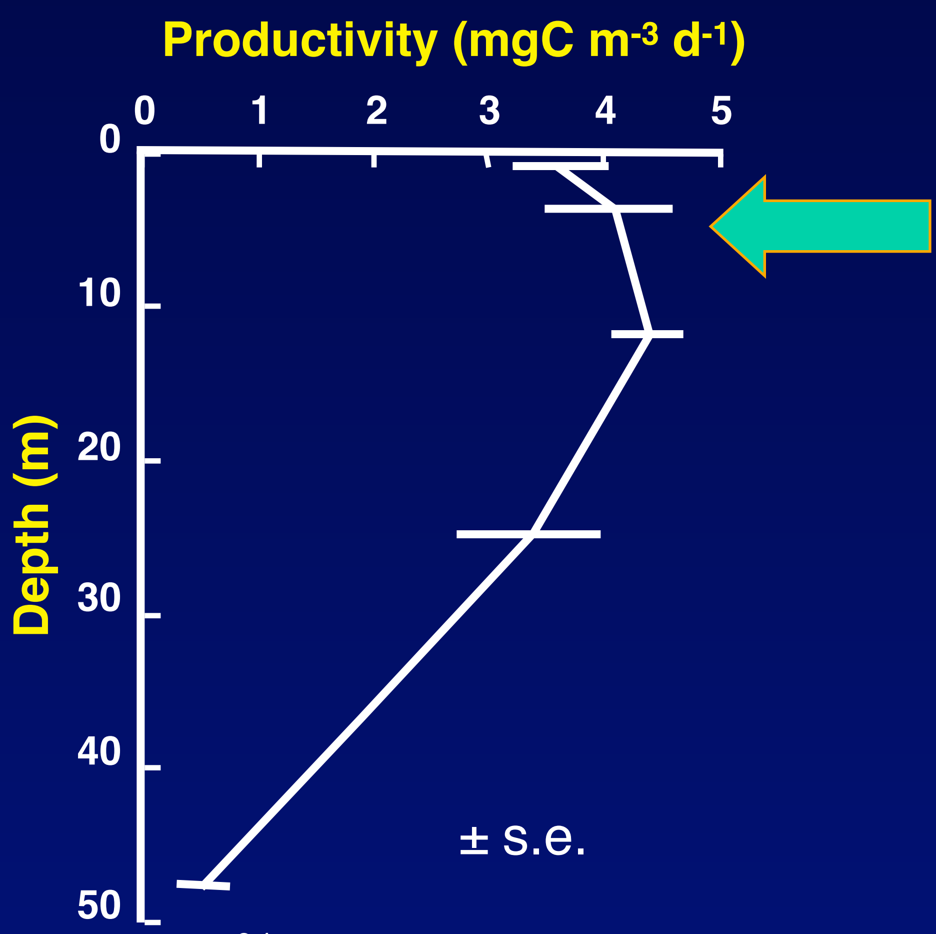
The measurement is subject to artifacts and biases



Underestimation due to static incubation at excessive irradiance

12 - 24 h incubations

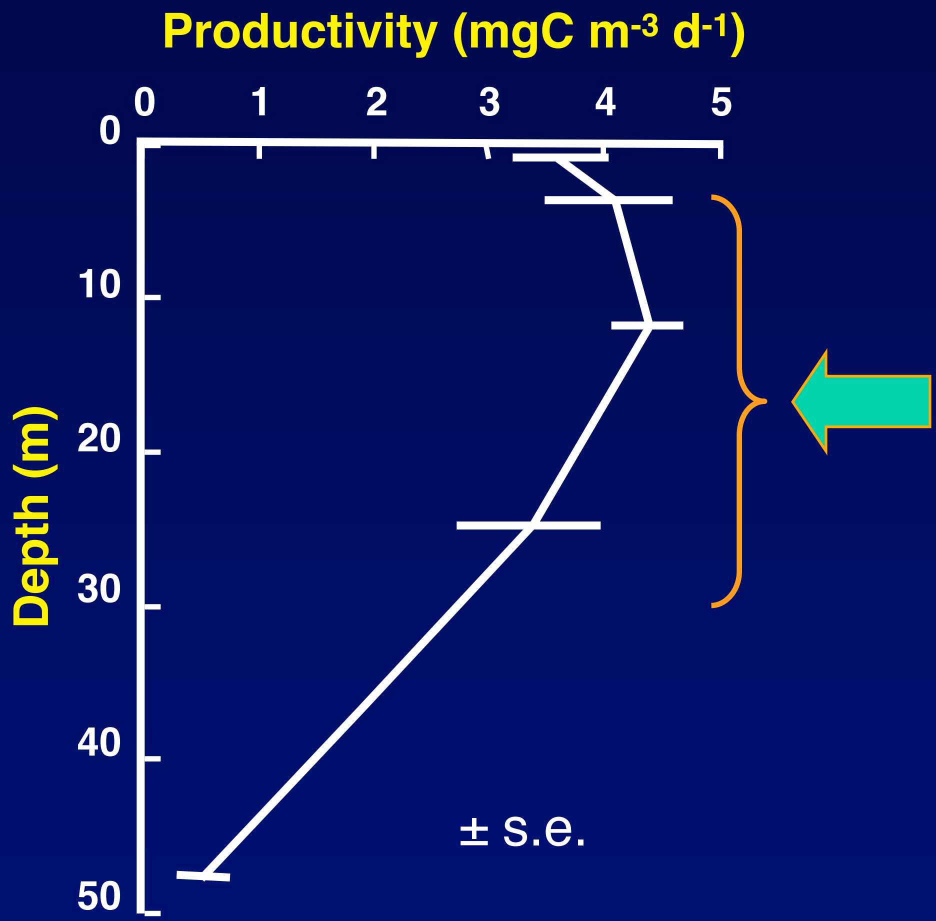
The measurement is subject to artifacts and biases



Underestimation due to dilution of intracellular DIC with respired cellular C

12 - 24 h incubations

The measurement is subject to artifacts and biases



12 - 24 h incubations

Overestimation due to unnatural accumulation of biomass (disruption or exclusion of grazers)

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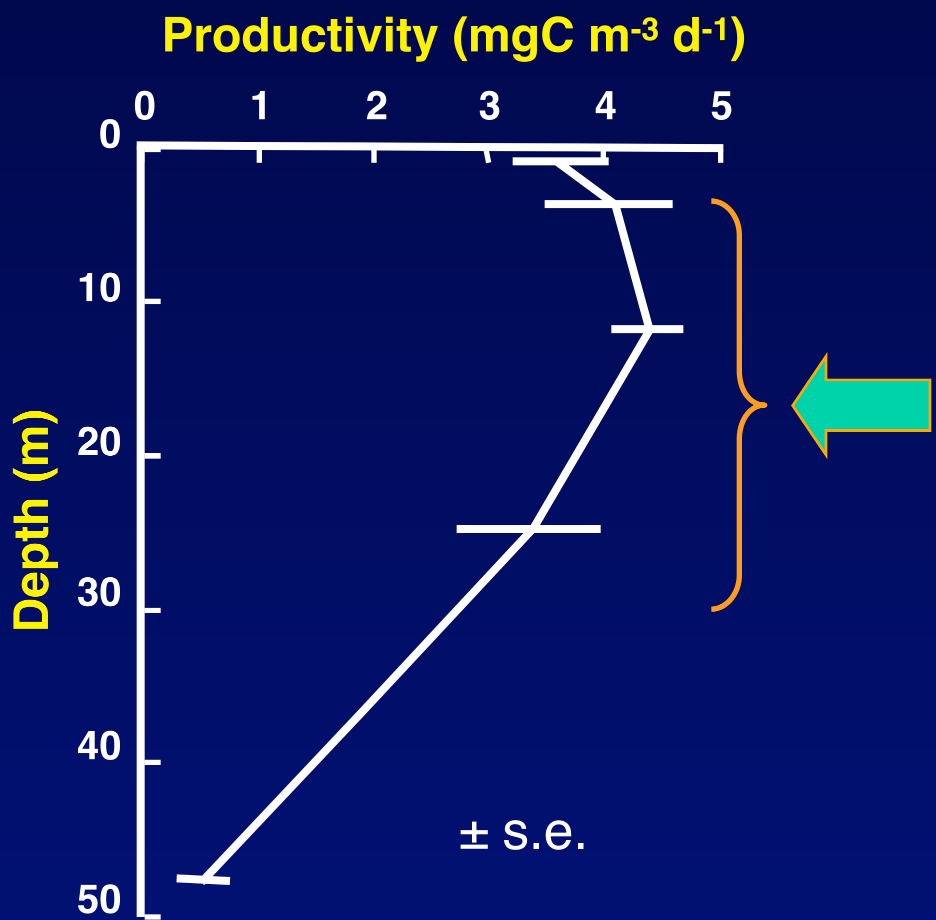
The measurement is subject to artifacts and biases



12 - 24 h incubations

Underestimation due to food-web cycling

(microbial respiration and excretion)

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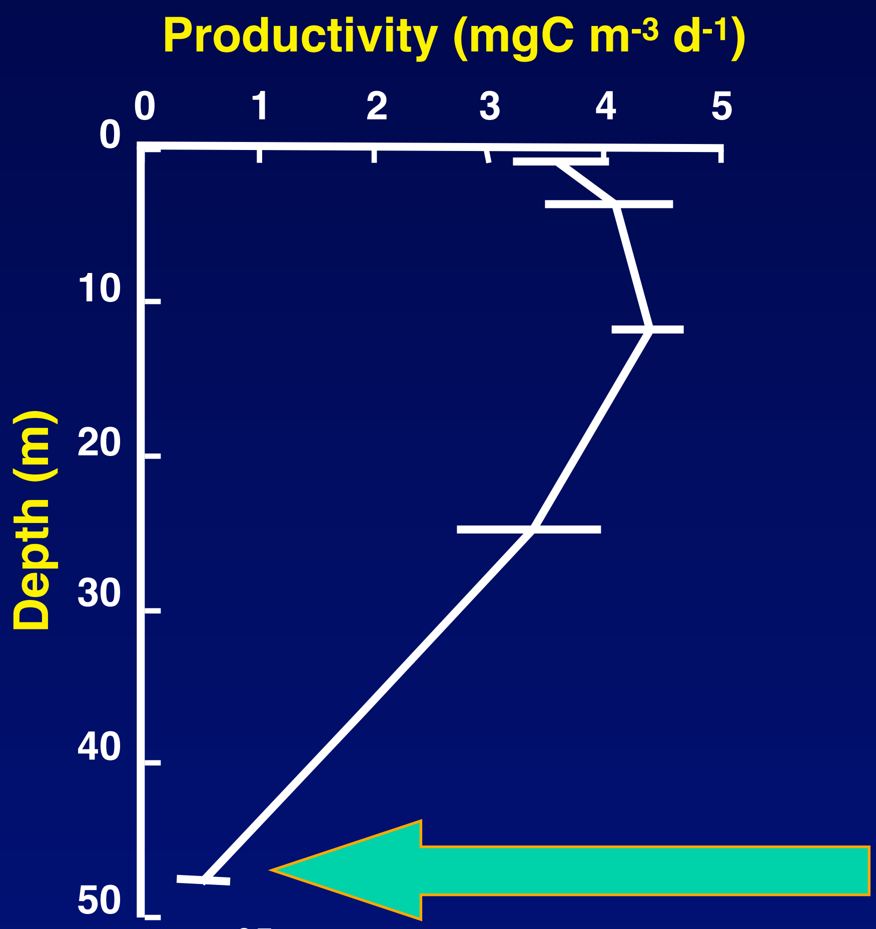
The measurement is subject to artifacts and biases



Overestimation due to inadequate time for respiration to be measured

12 - 24 h incubations

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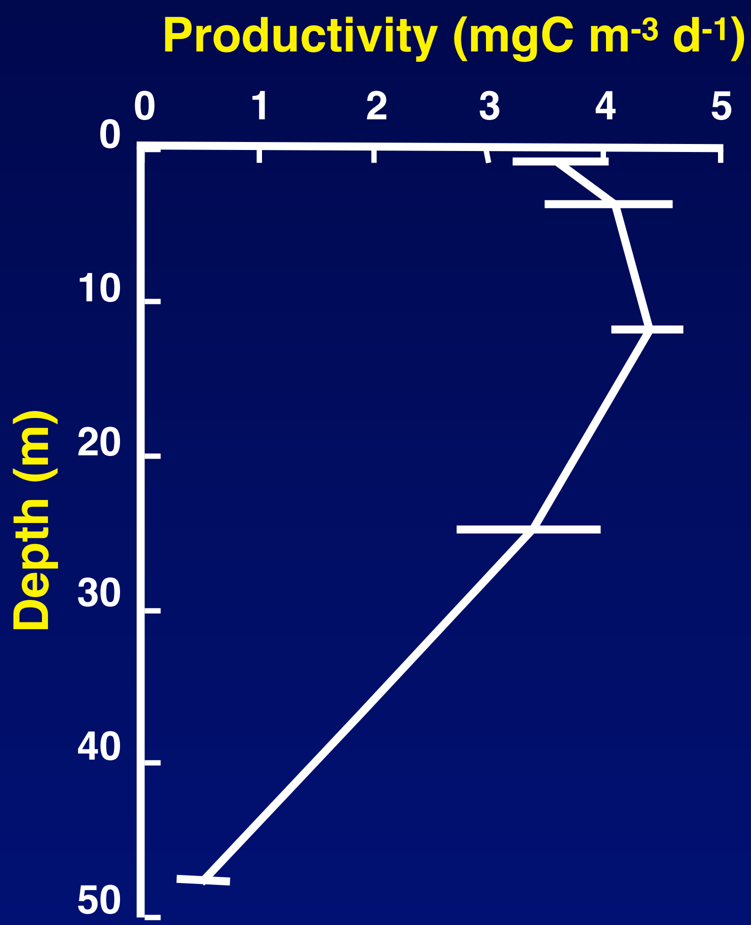
…and that's not all:



12 - 24 h incubations

Toxicity

Relief of iron limitation

Exposure to bright light

Disruption of fragile cells

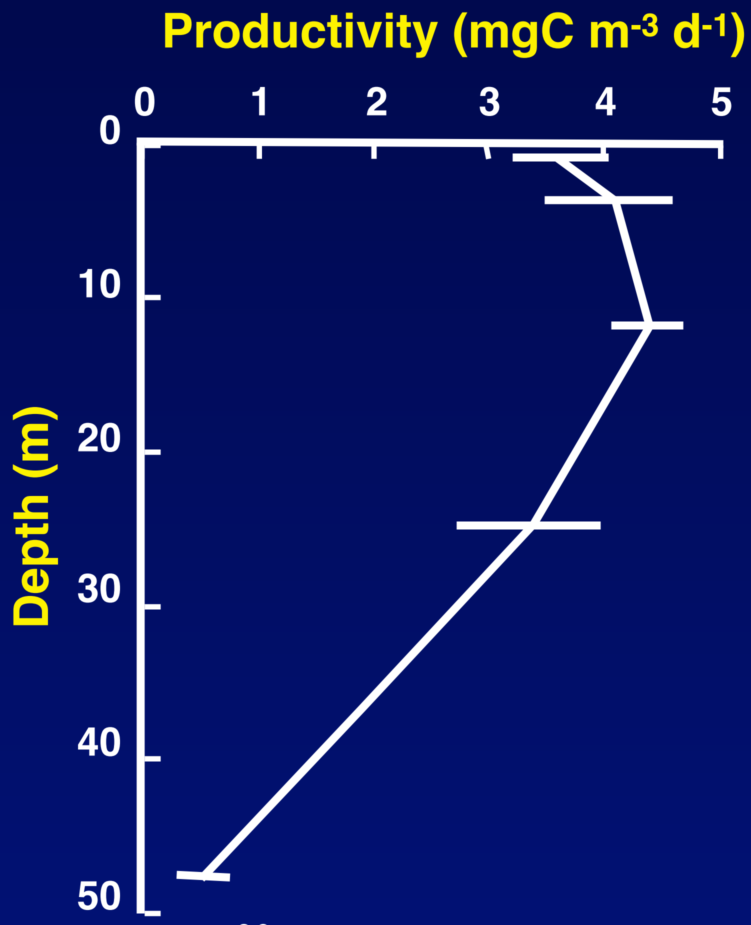
for Simulated in situ:

Poor match of irradiance

Inappropriate temperature

Possible diel bias

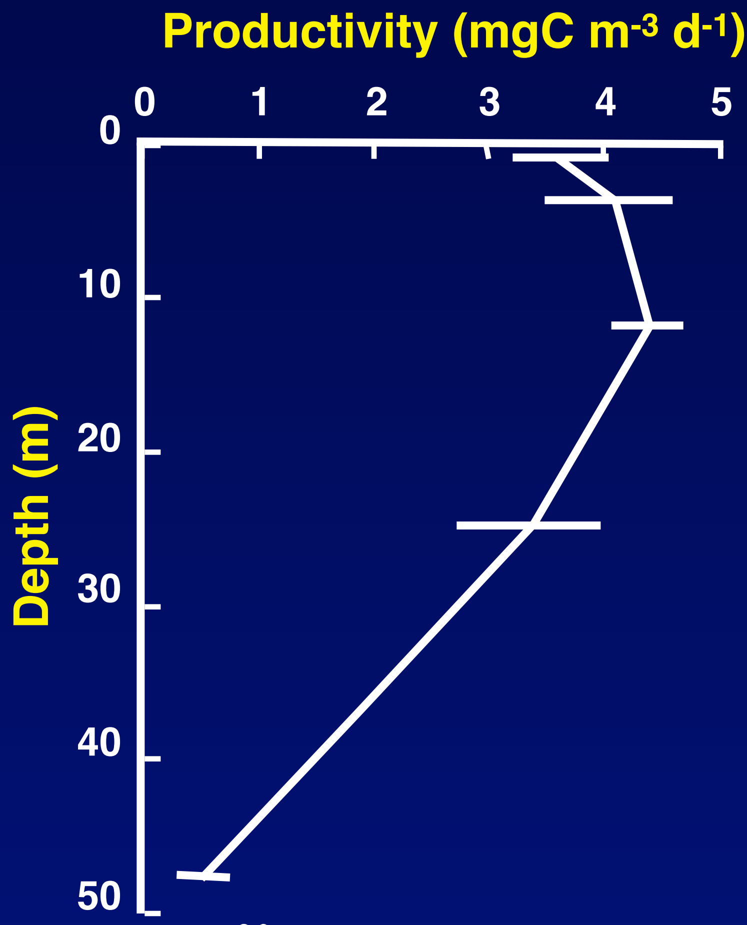
Productivity normalized to Chl is biased by:



12 - 24 h incubations

- Changes in Chl during incubations
- Inadequate extraction of Chl by 90% acetone
- Interference from Chl b (*fluorometric acid-ratio method*)

and in general…

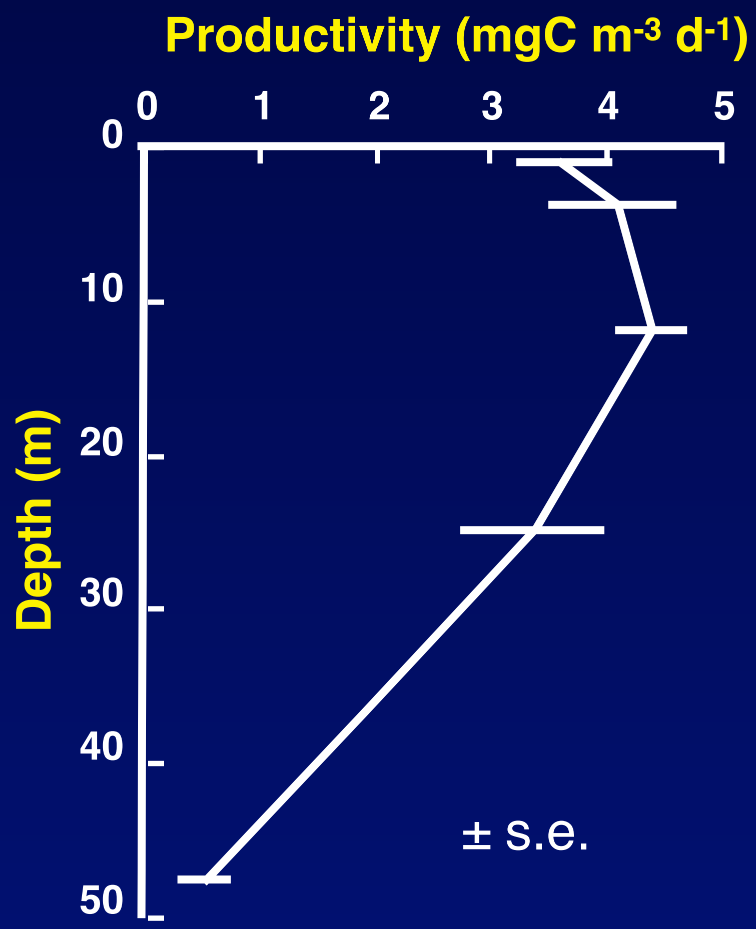


Irradiance is not controlled

Respiration is not accurately measured

12 - 24 h incubations

The measurement has its limitations



Net production?

Gross production?

Overestimate?

Underestimate?

A less skeptical view

Preprint, 2009
doi: 10.3354/ame01306

AQUATIC MICROBIAL ECOLOGY
Aquat Microb Ecol

Published online June 22, 2009

Contribution to AME Special 2: 'Progress and perspectives in aquatic primary productivity'

OPEN ACCESS

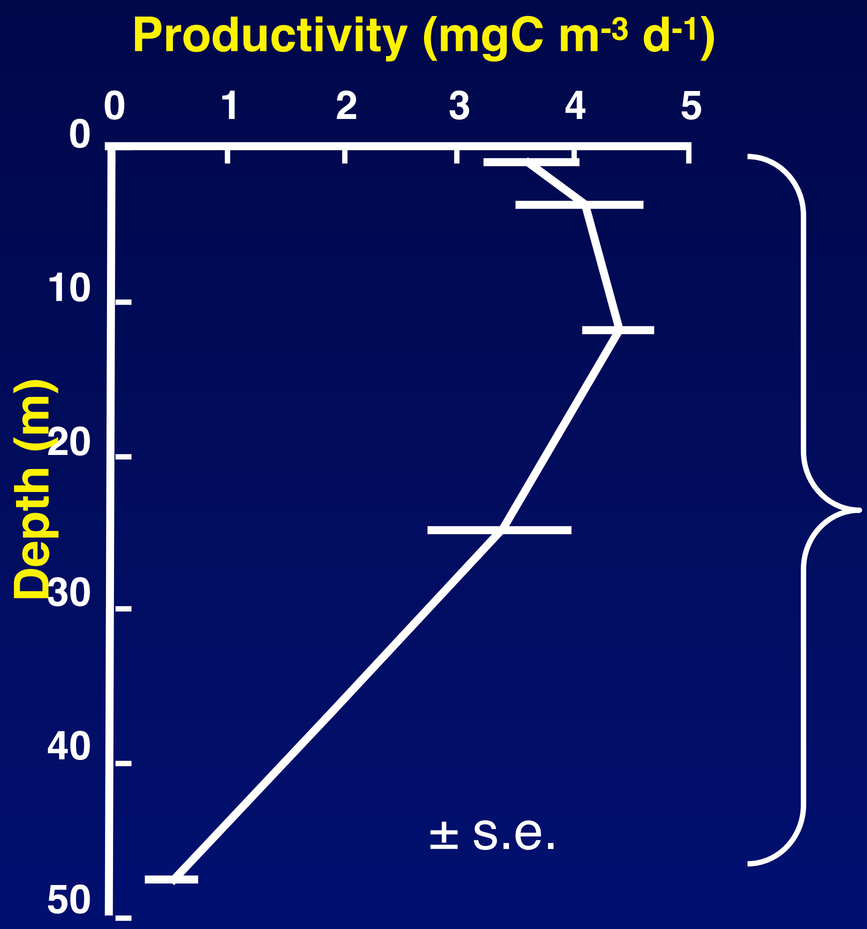
REVIEW

Net and gross productivity: weighing in with ^{14}C

John Marra*

Brooklyn College of the City University of New York, Brooklyn, New York 11210, USA

But we use it routinely



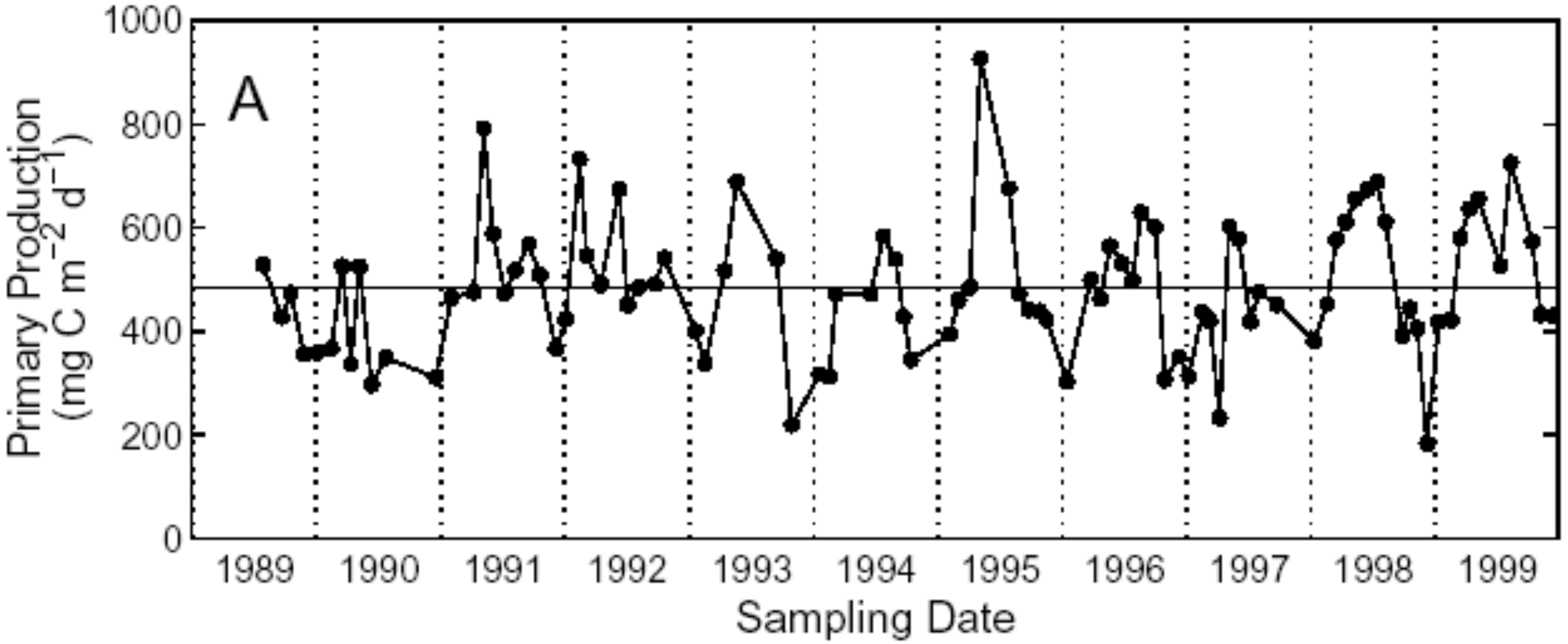
Water column integral is something like net primary production (photosynthesis less losses to respiration)

33

(*extent depends on temperature, light and maybe nutrients*)

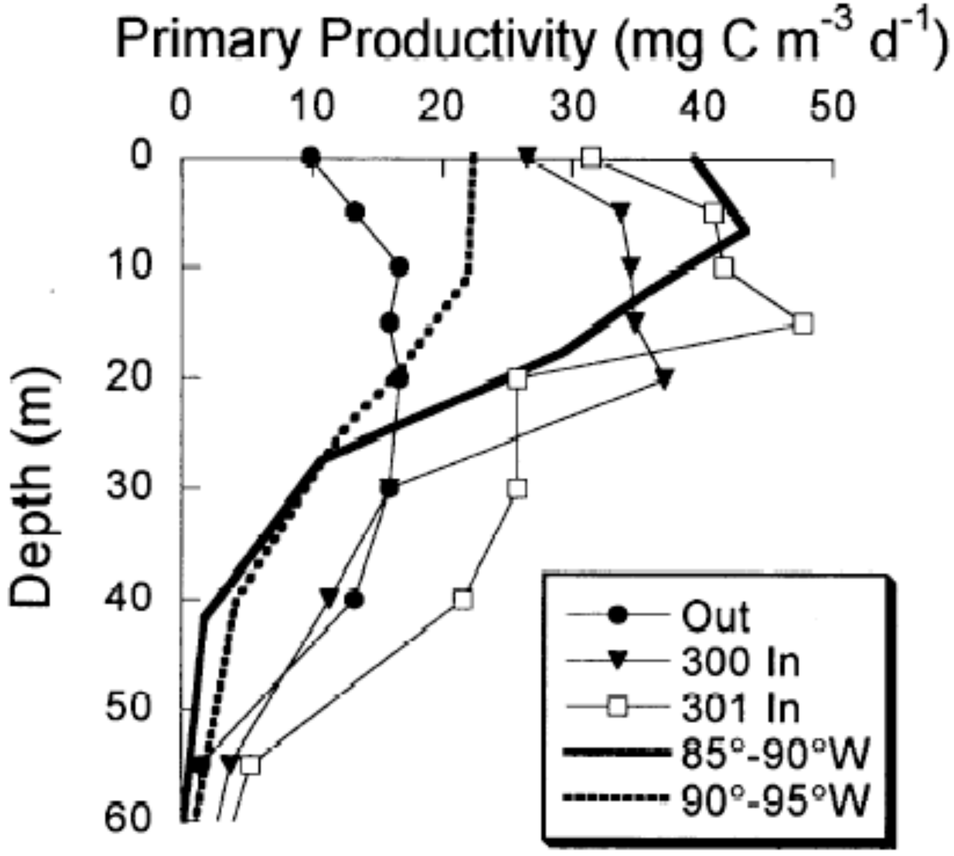
Regardless, it has served us very well

Time Series



Karl et al. in Williams et al. 2002

Process studies



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Solving mysteries

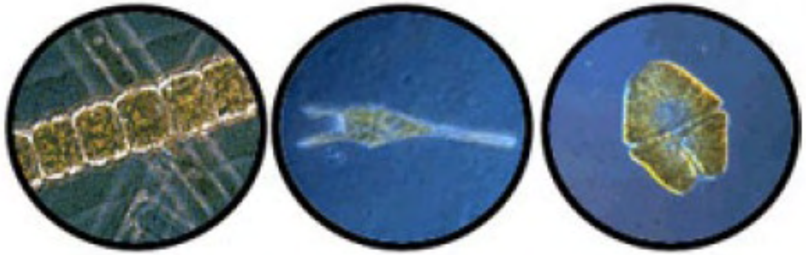
Vol 442|31 August 2006|doi:10.1038/nature05083 nature

Controls on tropical Pacific Ocean productivity revealed through nutrient stress diagnostics

Michael J. Behrenfeld[1], Kirby Worthington[2], Robert M. Sherrell[3], Francisco P. Chavez[4], Peter Strutton[5], Michael McPhaden[6] & Donald M. Shea[7]

PHYSORG.COM
SCIENCE : PHYSICS : TECH : NANO : NEWS

Study Solves Ocean Plant Mystery

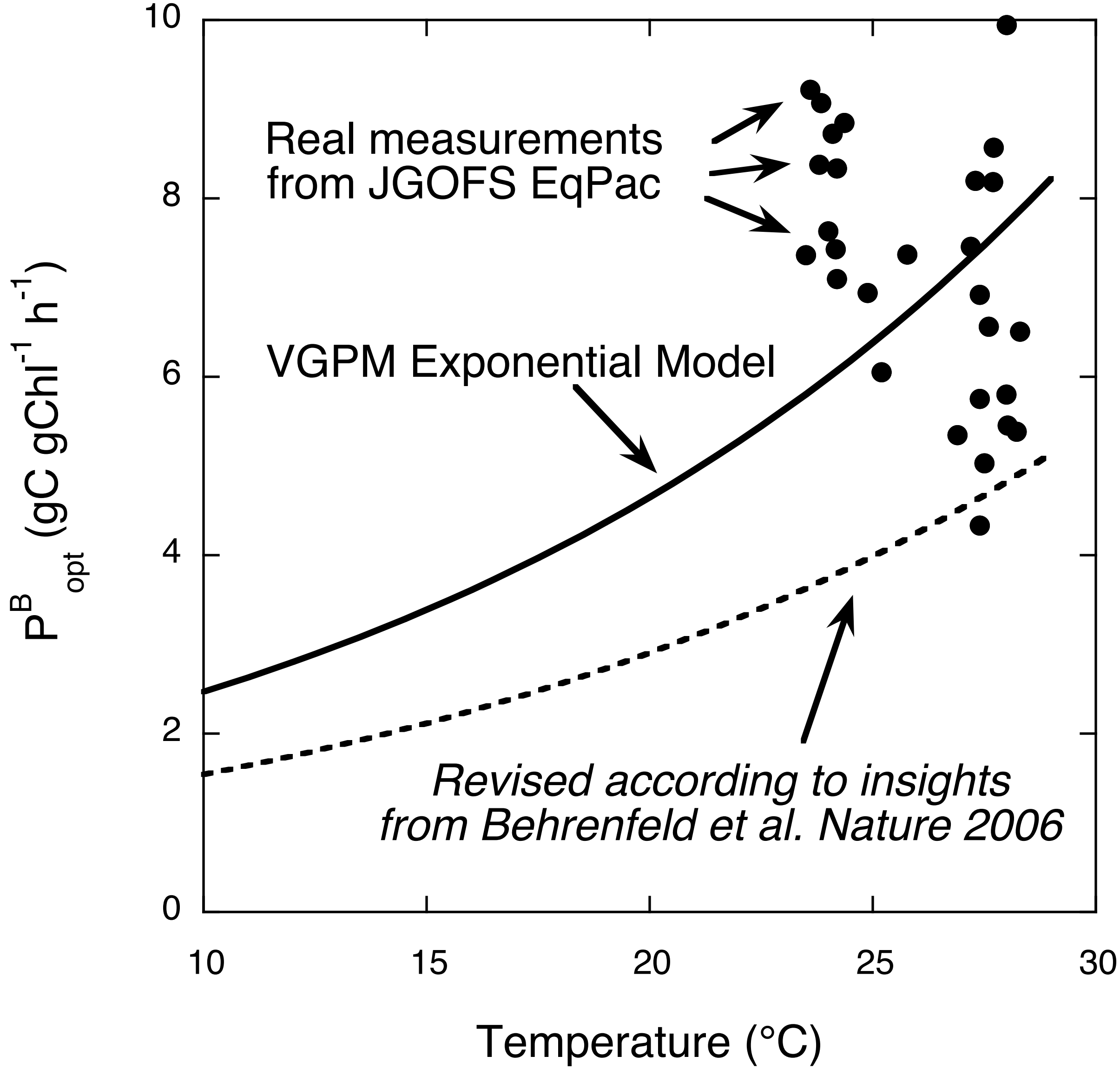


Different species of phytoplankton come in many different shapes and sizes. But they all get their green color from chlorophyll, the pigment they use during photosynthesis. Credit: (Left) NASA/SeaWiFS Project (Center and right): D.W. Coats

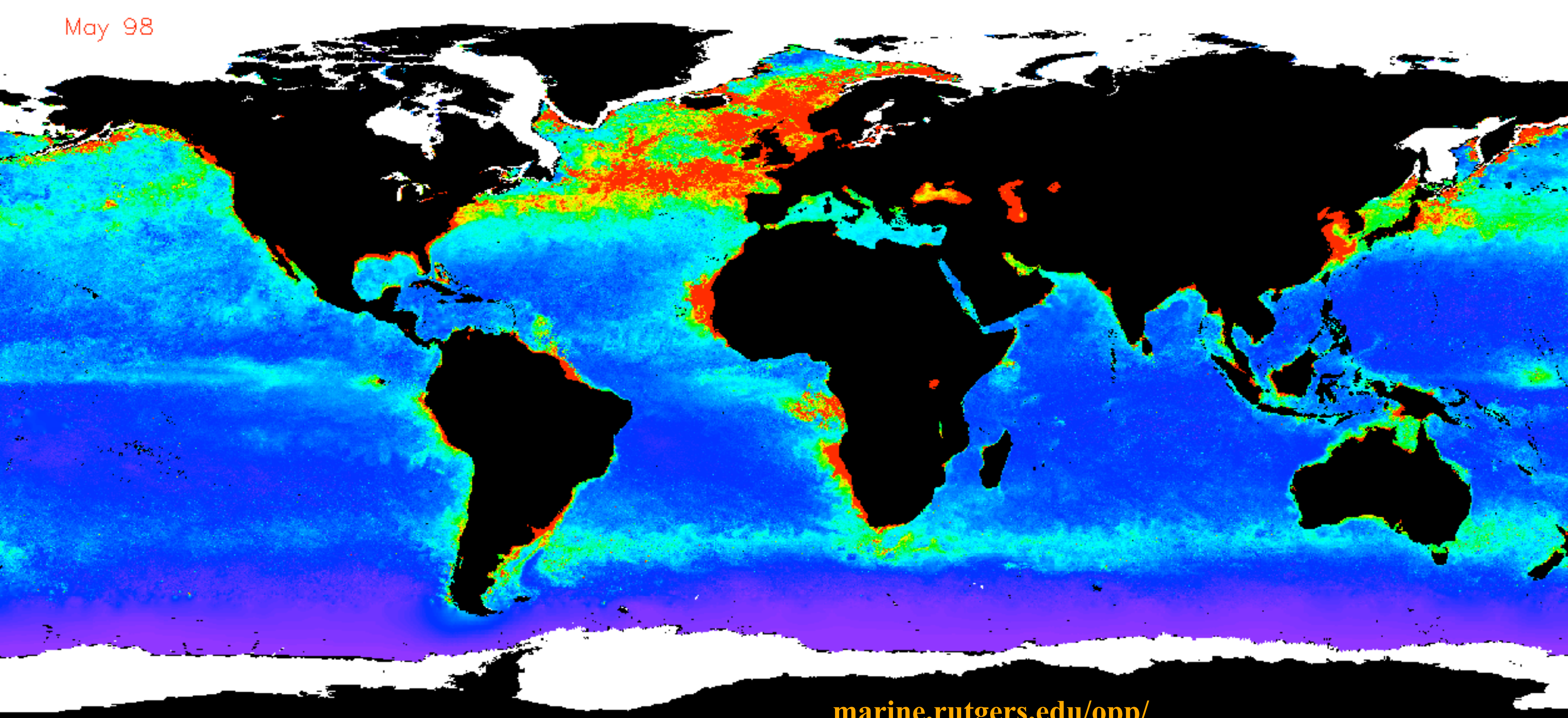
Equatorial Pacific – 140°W, 0° ± 2° – P^B_{opt}

Measurements vs Behrenfeld et al. Models

"Mystery Solved"

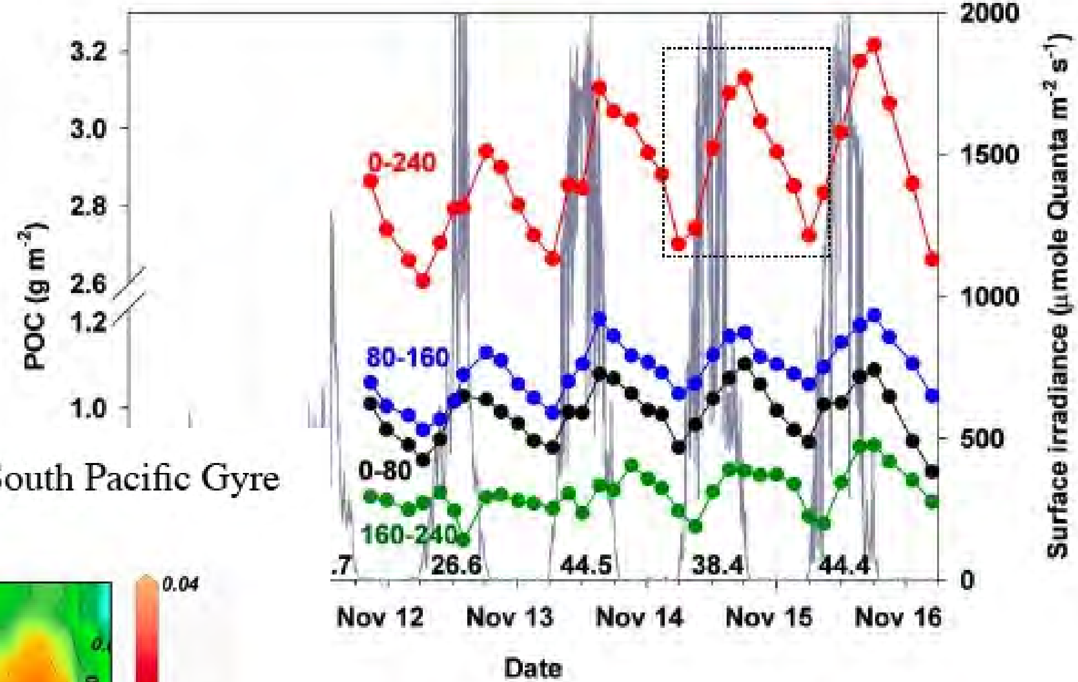


Direct Measurements will Never Provide Synoptic Estimates of Productivity

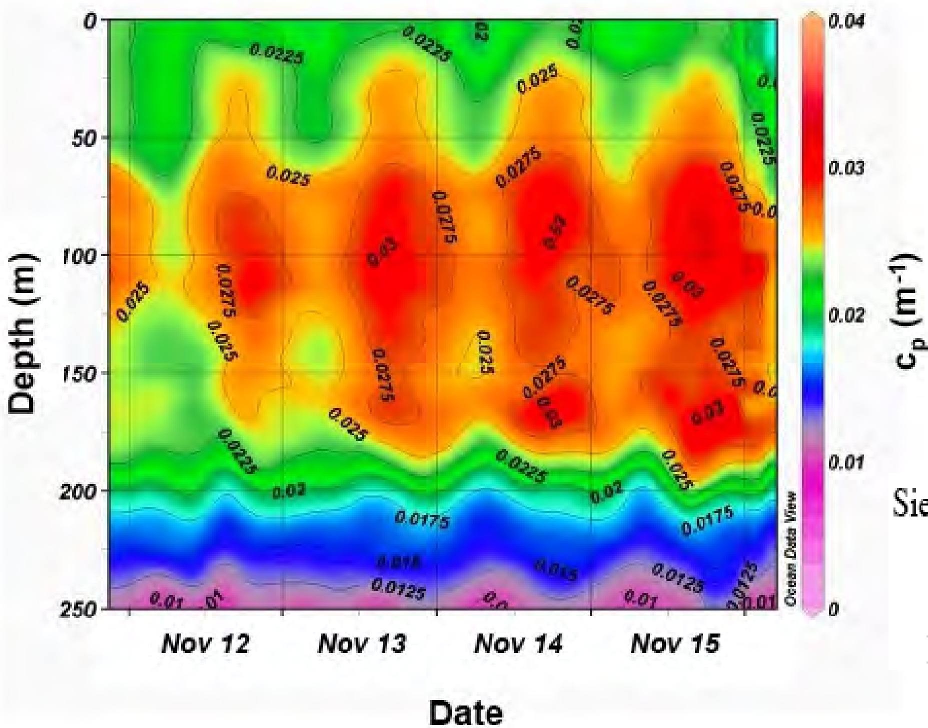


marine.rutgers.edu/opp/

Continuous measures of optics reveal rates



H. Claustre et al.: Metabolic balance in the South Pacific Gyre

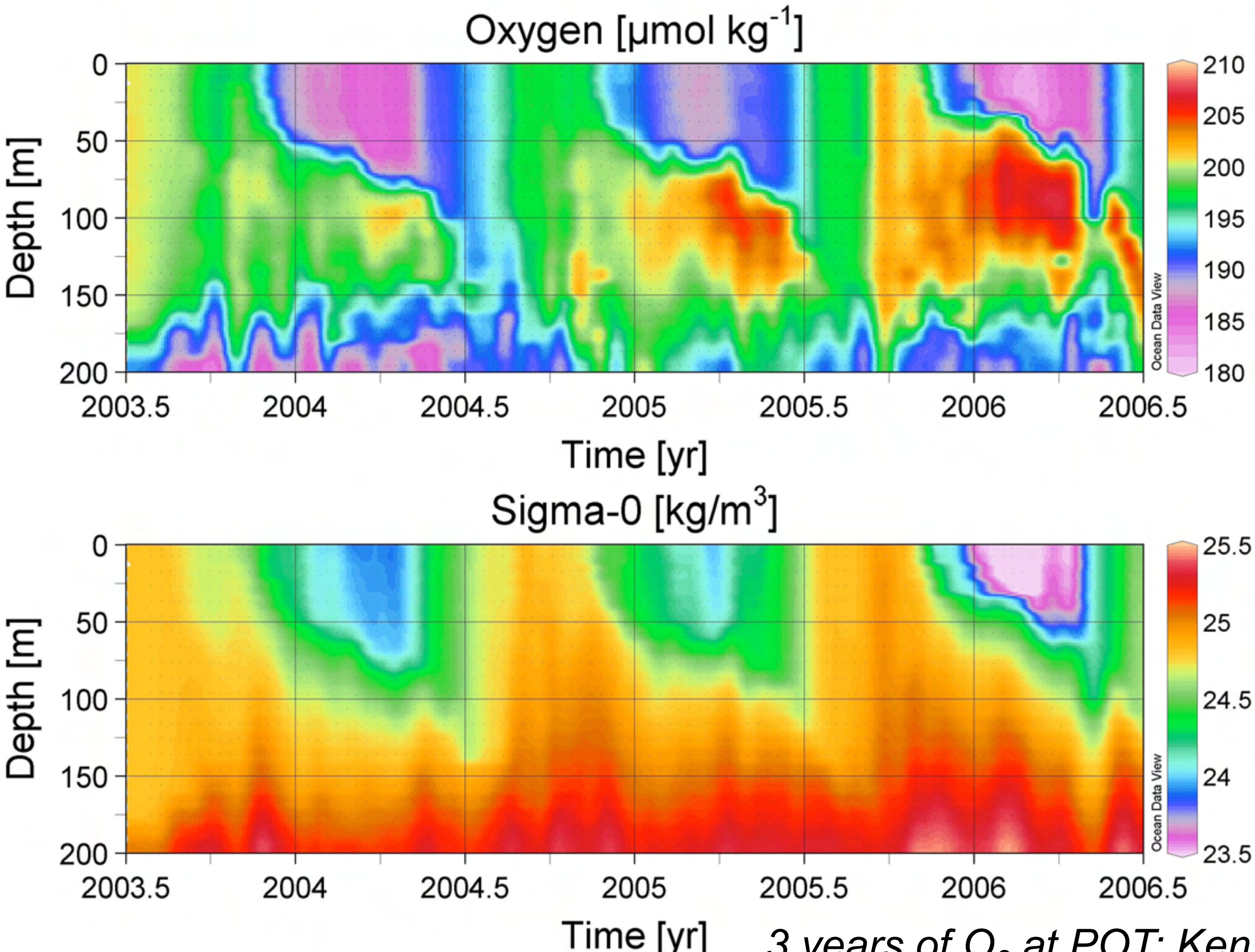


Biogeosciences, 5, 463–474, 2008

see

Siegel, D. A., Dickey, T. D., Washburn, L., Hamilton, M. K., and Mitchell, B. G.: Optical determination of particulate abundance and production variations in the oligotrophic ocean, Deep-Sea Res., 36, 211–222, 1989.

Ocean chemistry tells the tale — even in the most oligotrophic waters



3 years of O_2 at POT: Ken Johnson

Models are required for many applications

Productivity from ocean color

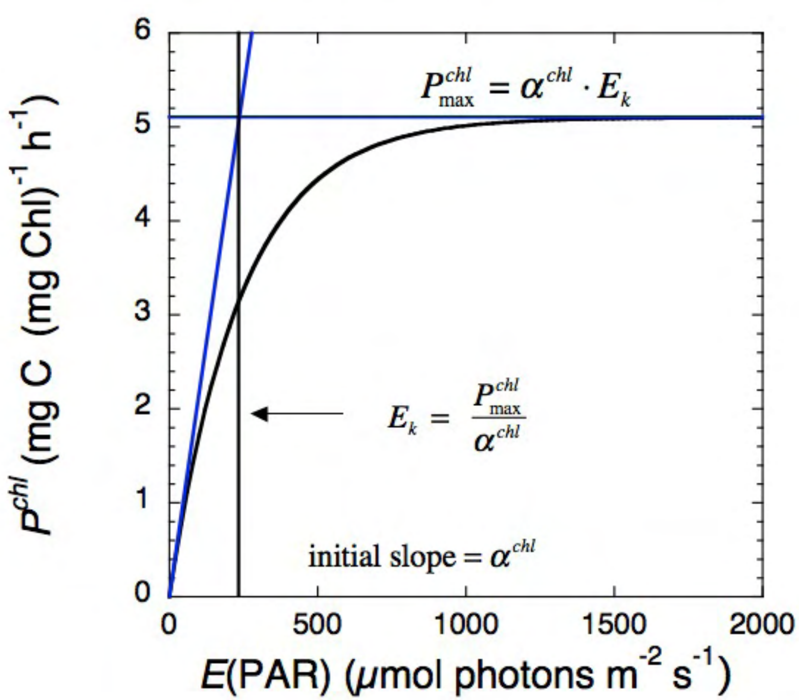
Ecological prediction

Biogeochemical models

Climate change scenarios

Photosynthesis normalized to chlorophyll is the foundation of productivity modeling

$$\underbrace{P^{chl}_{\max} \cdot \left(1 - \exp\left[{-(\alpha^{chl} \cdot E)}\Big/{P^{chl}_{\max}}\right]\right)}_{P^{chl} \text{ vs. } E \text{ relationship}}$$



Production from chlorophyll

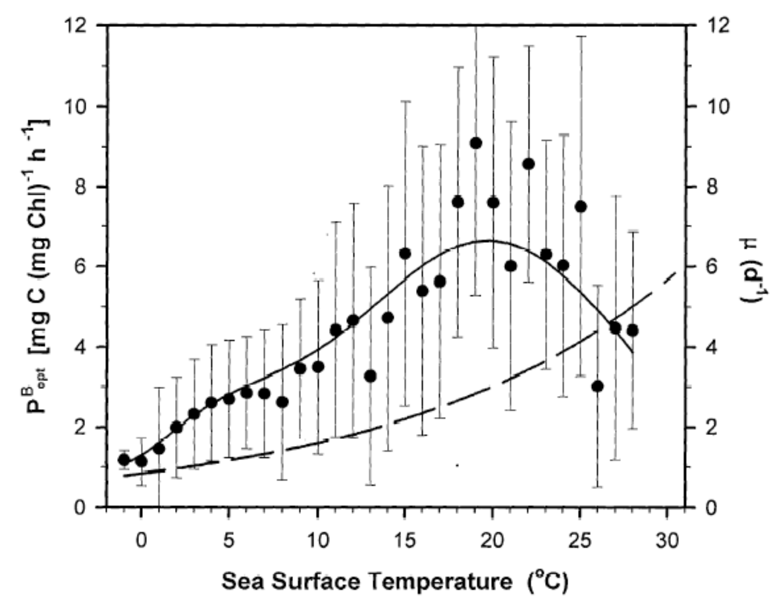
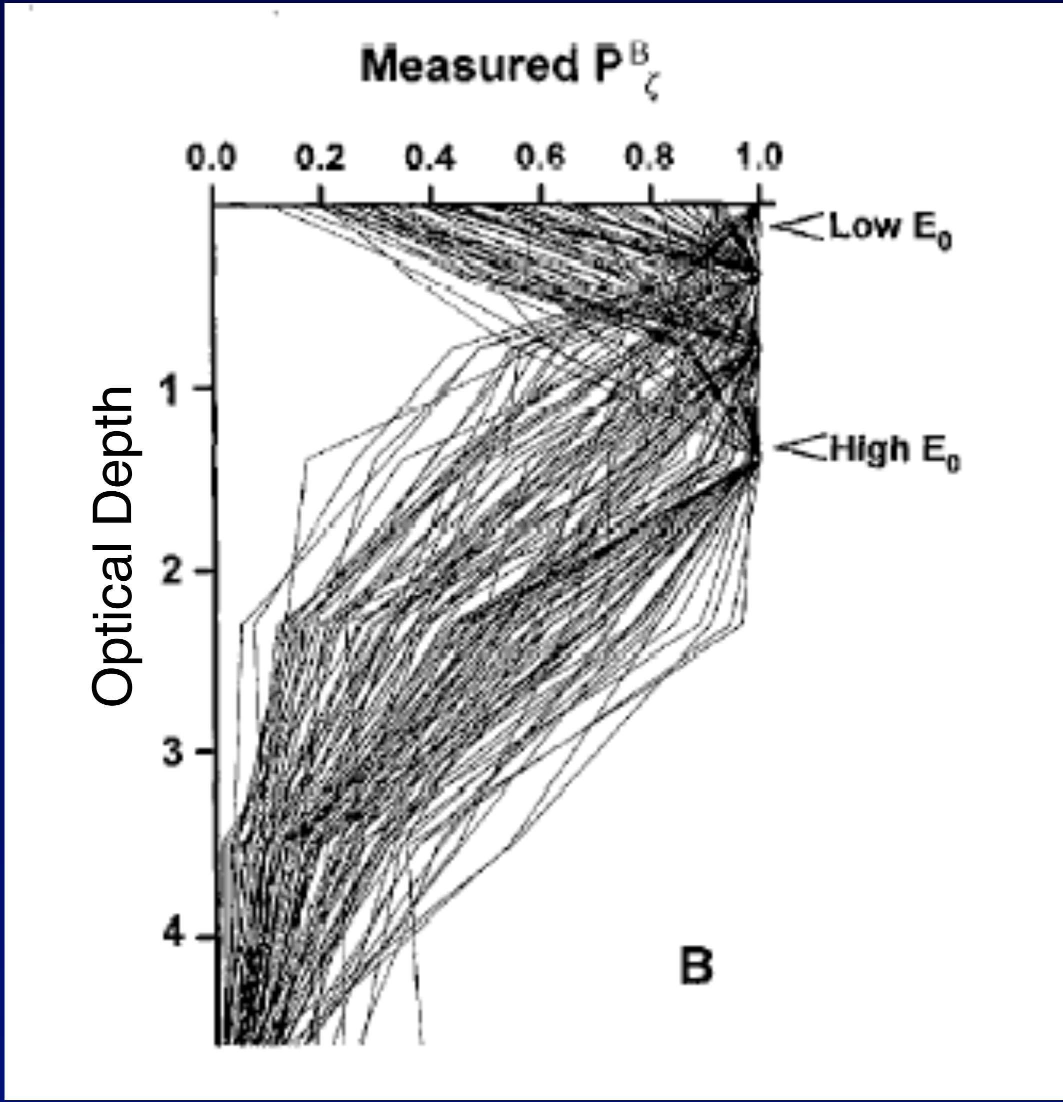


Fig. 7. Measured (●; ±SD) and modeled (——; Eq. 11) median value of the photoadaptive parameter, P^B_{opt}, as a function of sea surface temperature. Dashed curve indicates the theoretical maximum specific growth rate (μ; d^{-1}) of photoautotrophic unicellular algae described by Eppley (1972), which is used in a variety of productivity models (e.g. Balch and Byrne 1994; Antoine et al. 1996).

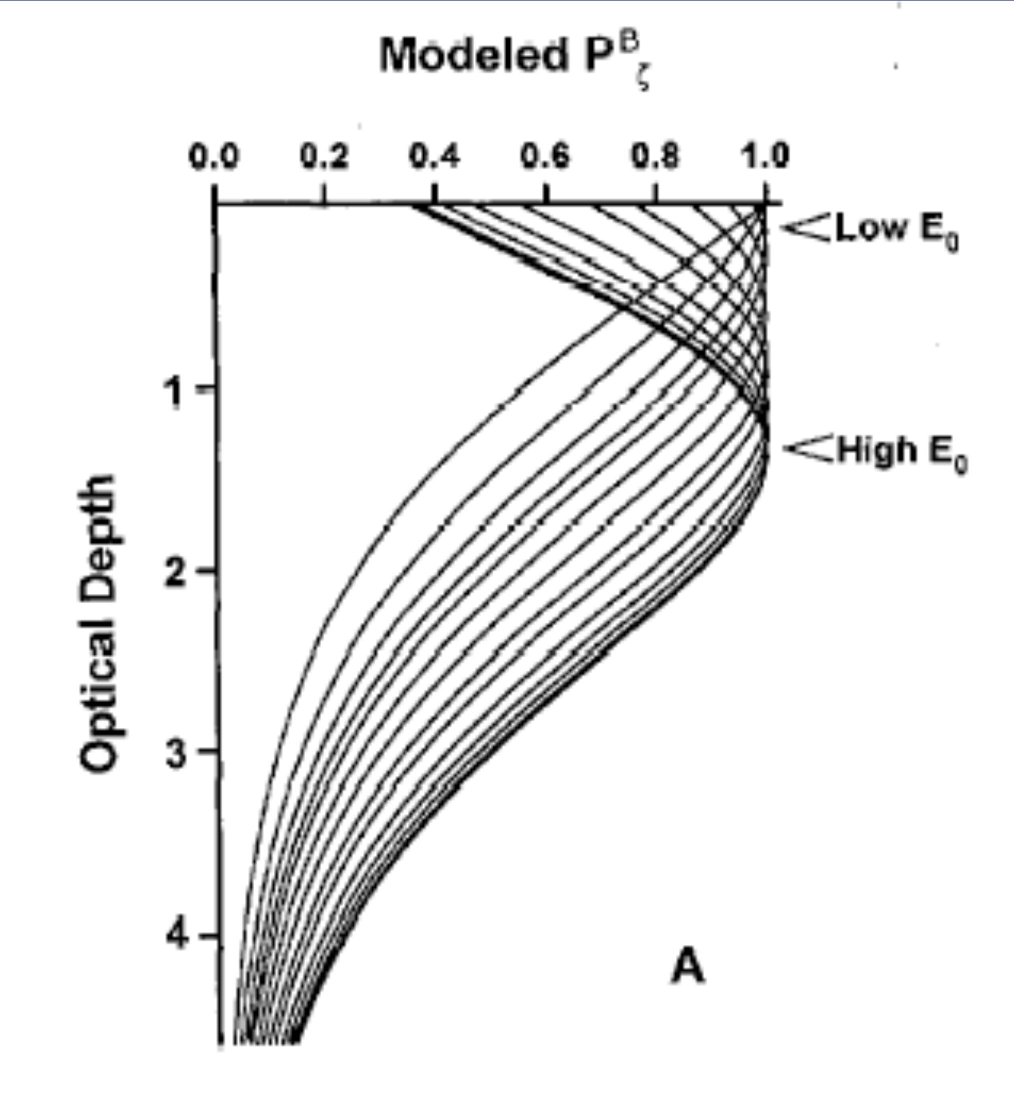
Behrenfeld and Falkowski L&O 1997

One approach: model the measurements



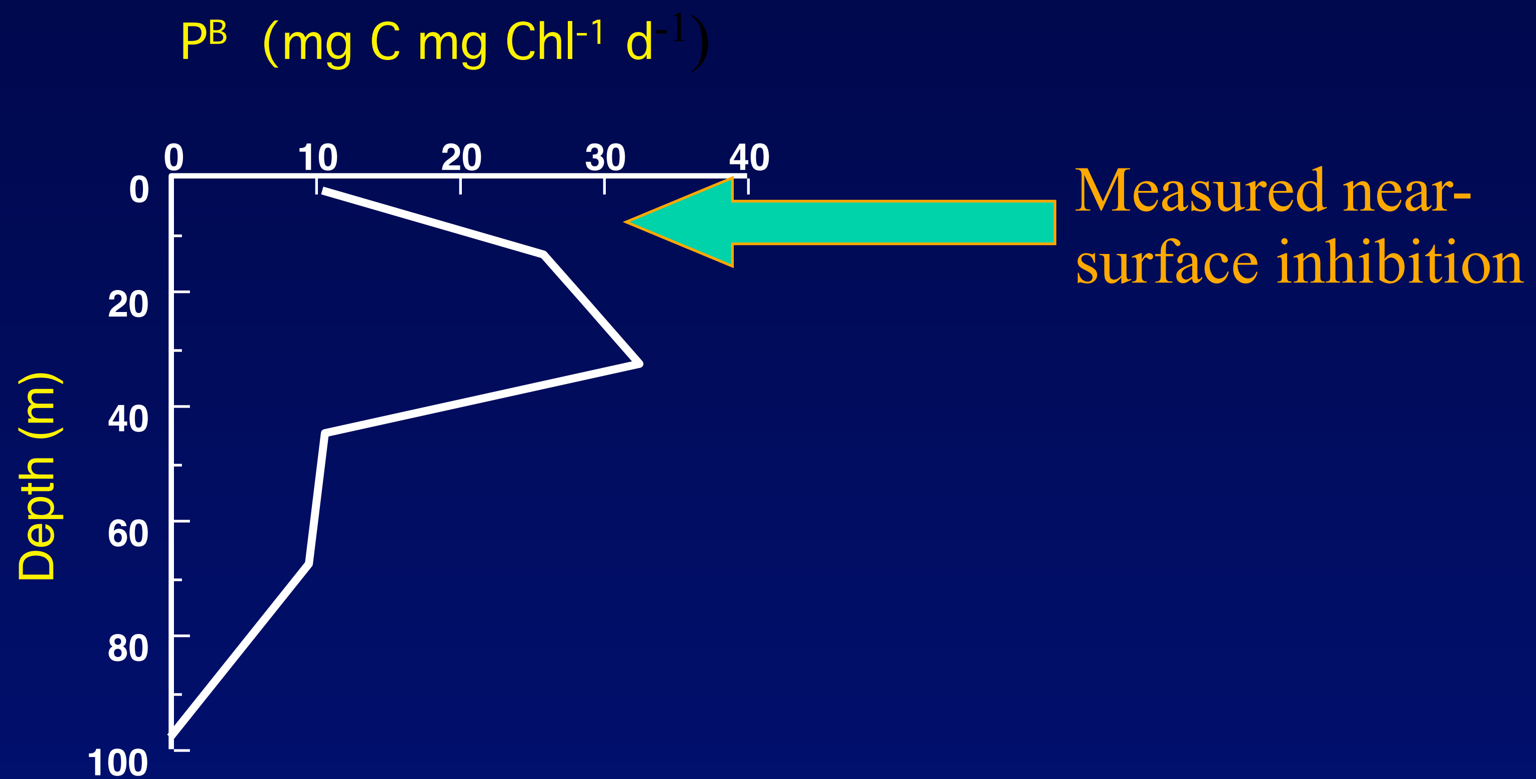
Behrenfeld and Falkowski 1997a L&O

Simplified functions describe major patterns

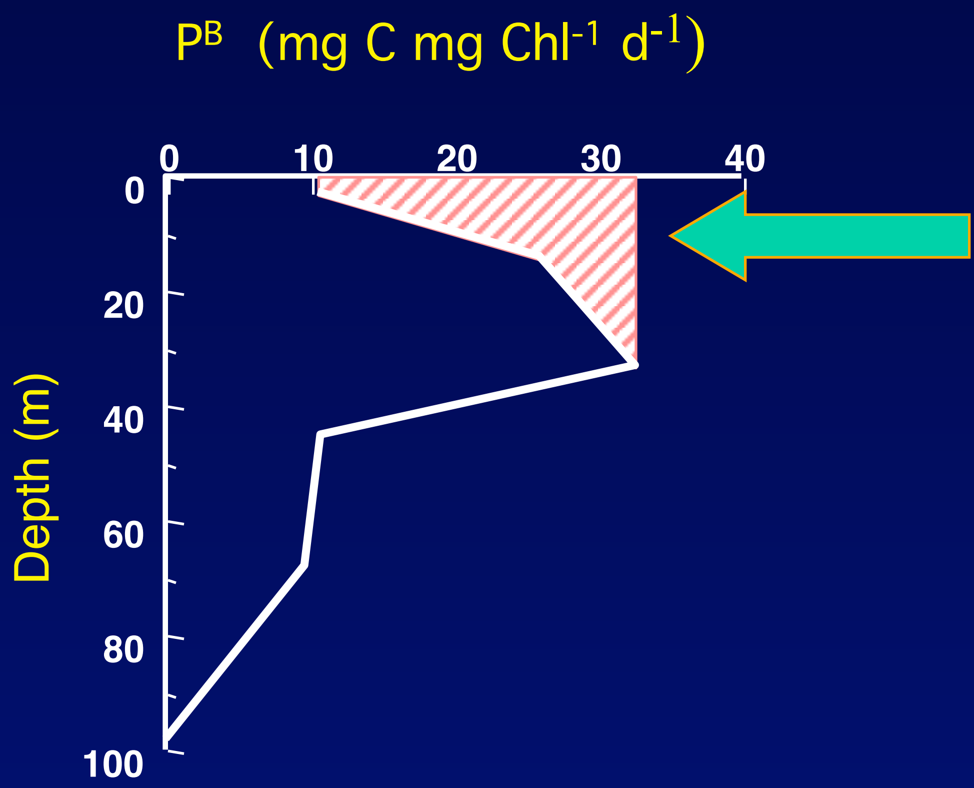


Behrenfeld and Falkowski 1997a L&O

Is the measured/modeled pattern real?

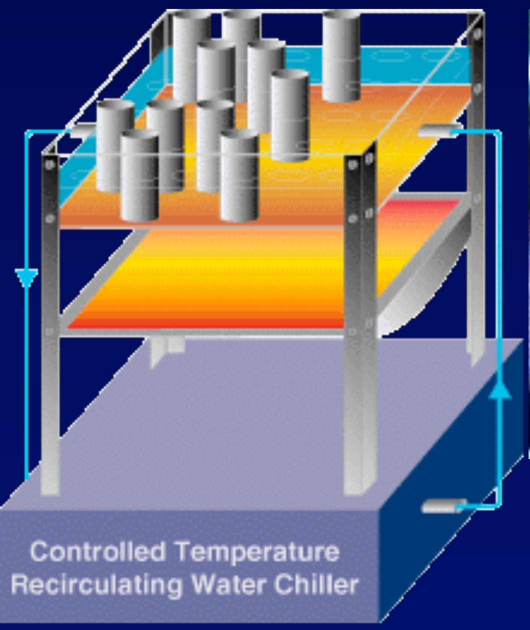


Is the measured/modeled pattern real?



or an artifact of fixed-depth incubation?

Measurements must be made on a shorter time scale



Photosynthetron: Controlled
laboratory incubation
(Lewis and Smith 1983)

A comprehensive approach

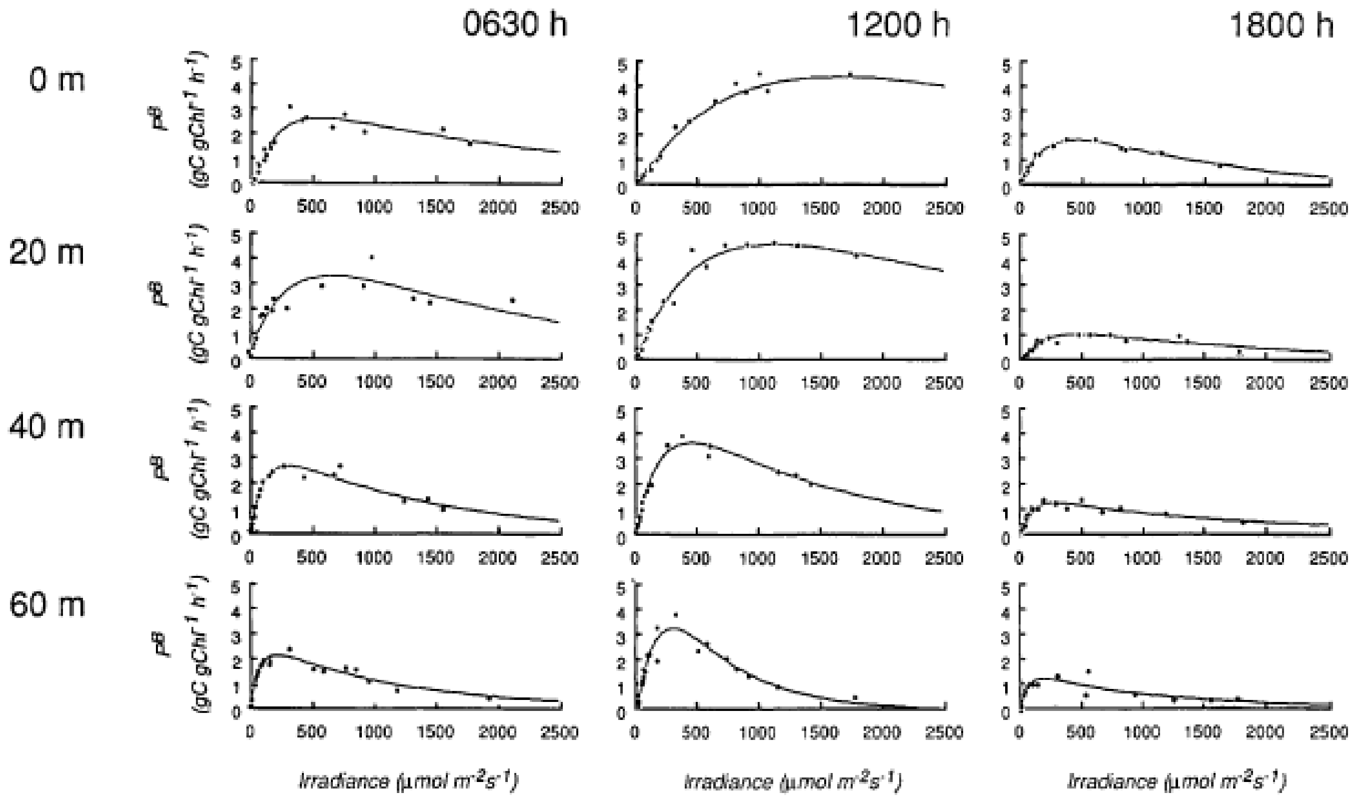
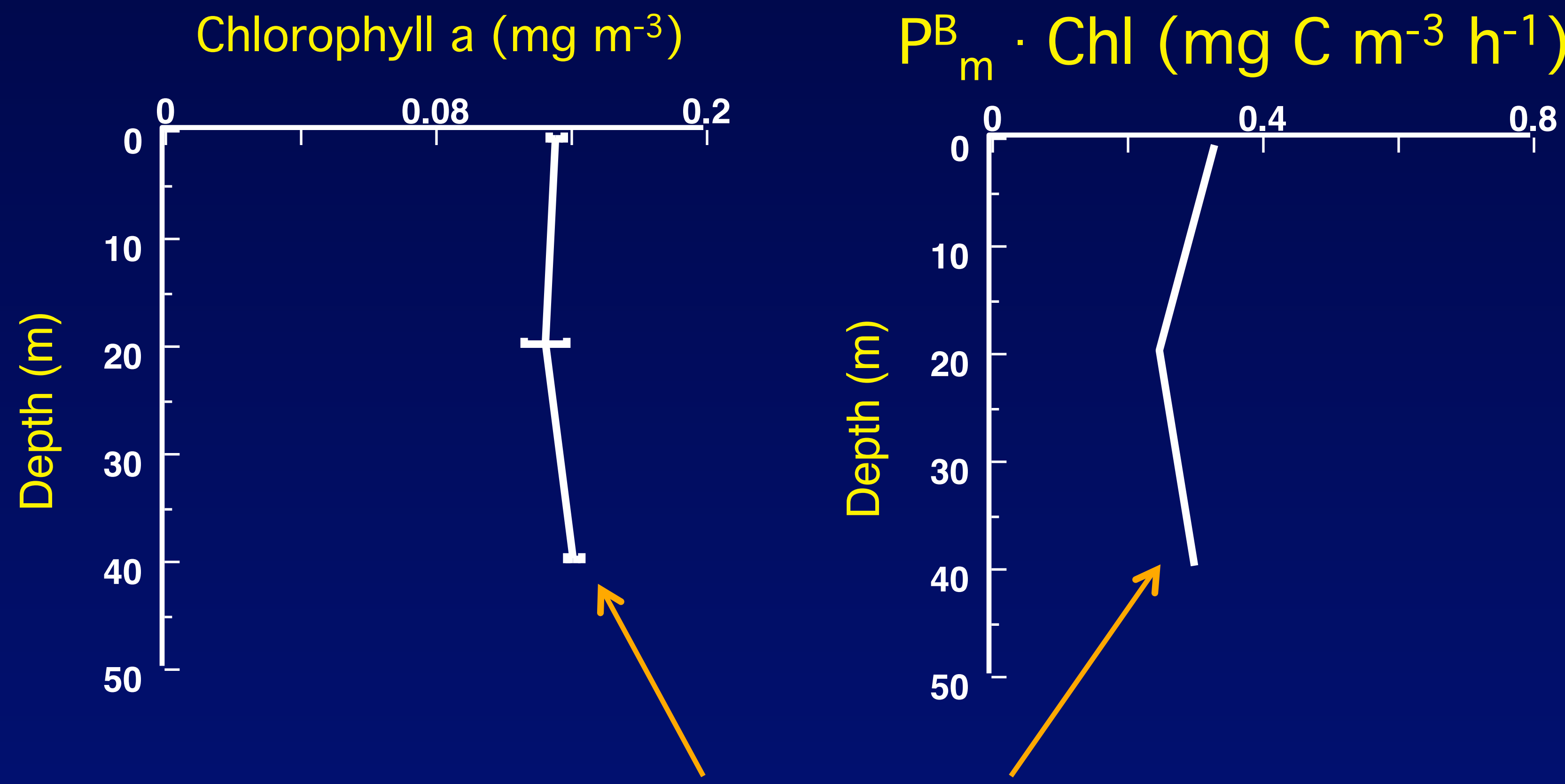


Fig. 2. Measurements of photosynthesis versus irradiance at the equator, 150°W, March 4, 1988. Lines are best fits to equation (1).

Cullen, J. J., M. R. Lewis, C. O. Davis, and R. T. Barber. 1992. Photosynthetic characteristics and estimated growth rates indicate grazing is the proximate control of primary production in the equatorial Pacific. Journal of Geophysical Research 97: 639-654.

Approach introduced by Jitts, H. R., A. Morel, and Y. Saijo. 1976. The relation of oceanic primary production to available photosynthetic irradiance. Aust. J. Mar. Freshwater Res. 27: 441-454.

Short-term measurements can detect near surface inhibition



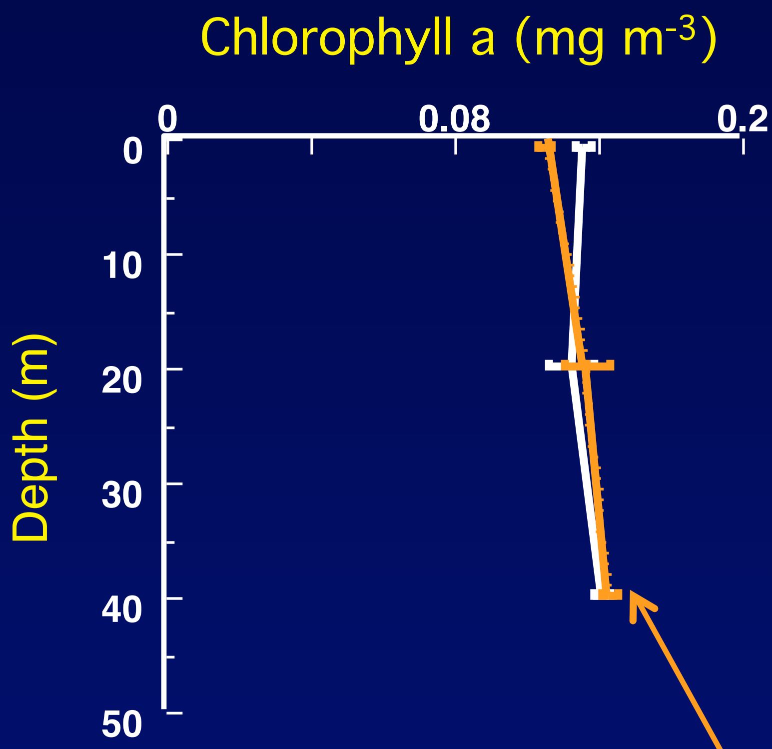
MORNING

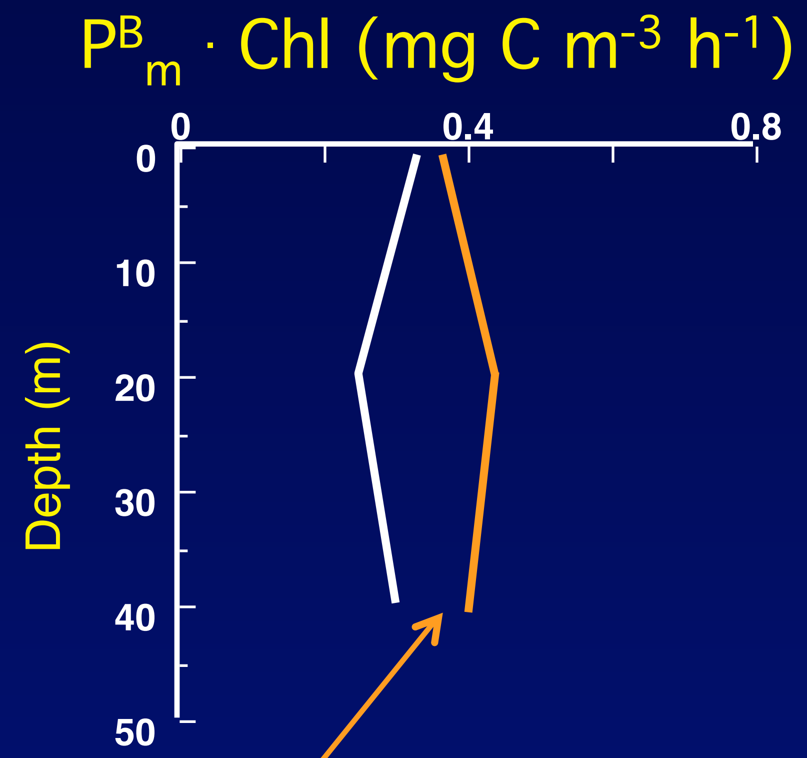
0630 h: Chlorophyll and P_{max}
are nearly uniform in the 50-m mixed layer

Principles described by Marra, Harris, Yentsch -- all prior to 1980

Is measured near-surface inhibition real?

Assessment with short-term P vs E

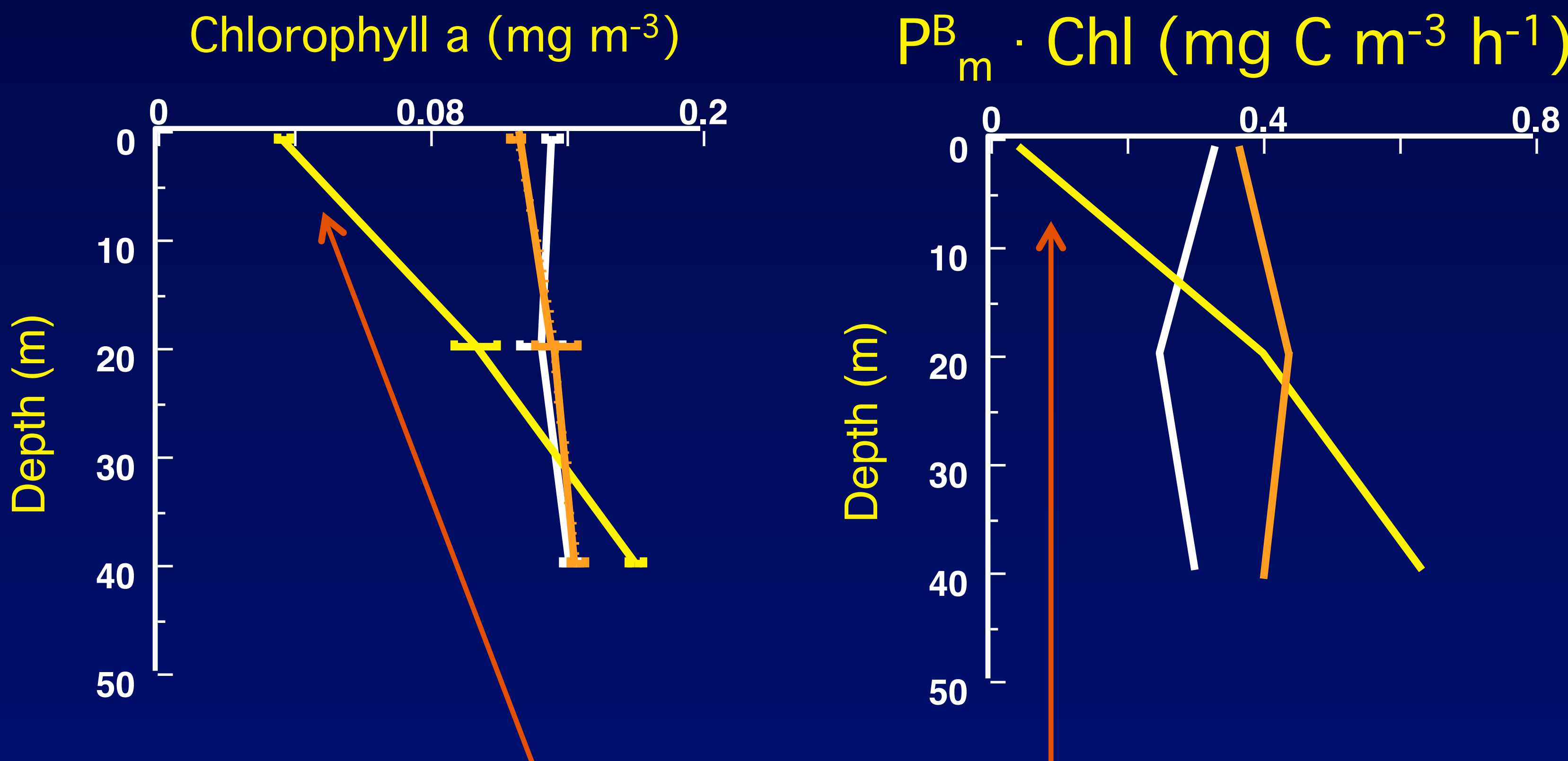




MIDDAY

1215 h: Chlorophyll and Potential Productivity are still nearly uniform in the 50-m mixed layer

Surface incubation led to artifact

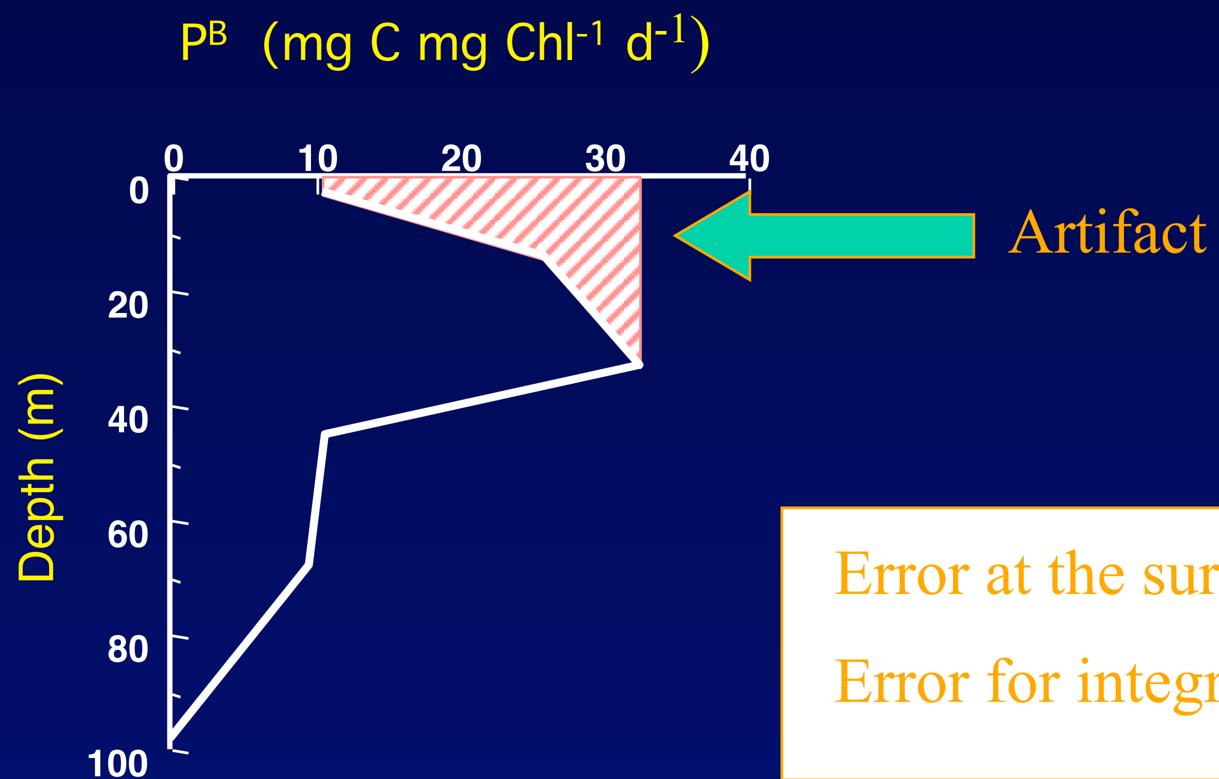


INCUBATED

1530 h: Fixed-depth incubations at the surface are "fried" — an artifact of sustained exposure
35% underestimation of ML productivity

Cullen C-MORE 2014

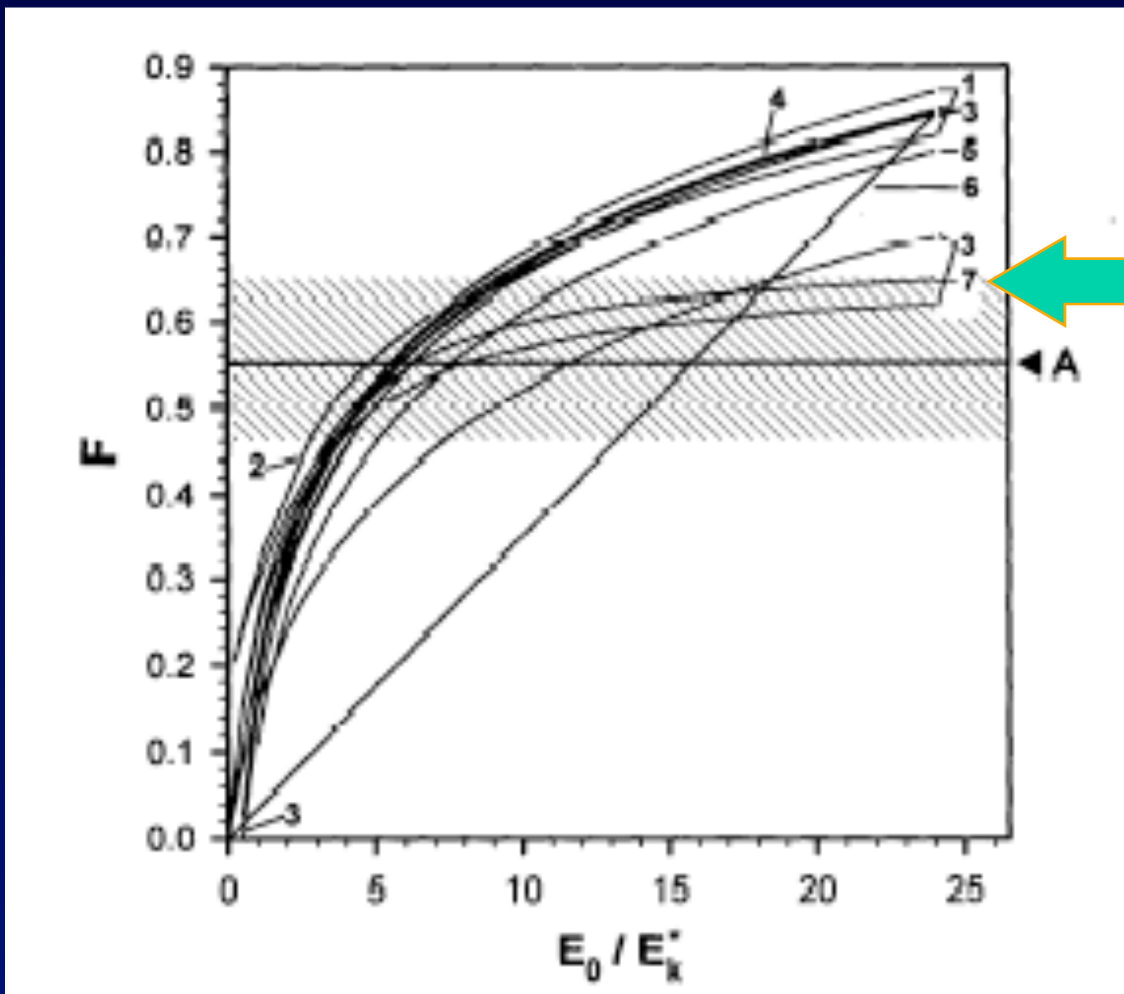
Conventional ^{14}C:
Near-surface inhibition is <u>over</u>estimated



Error at the surface: big

Error for integral: 8%

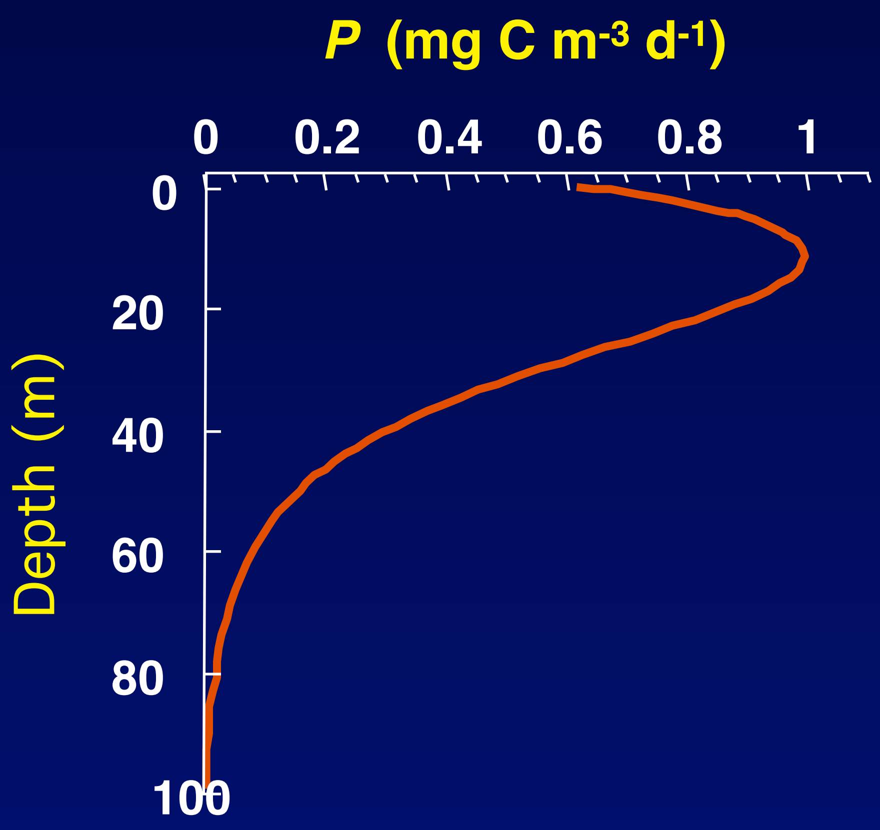
Consequences for a model: minor except for irradiance dependence of ΣP at higher daily irradiance



Parameterization of an Artifact?

Behrenfeld and Falkowski Consumer's Guide: L&O 1997

Many models calculate *P* from measured relationships



From

P^B vs E

and

E vs depth

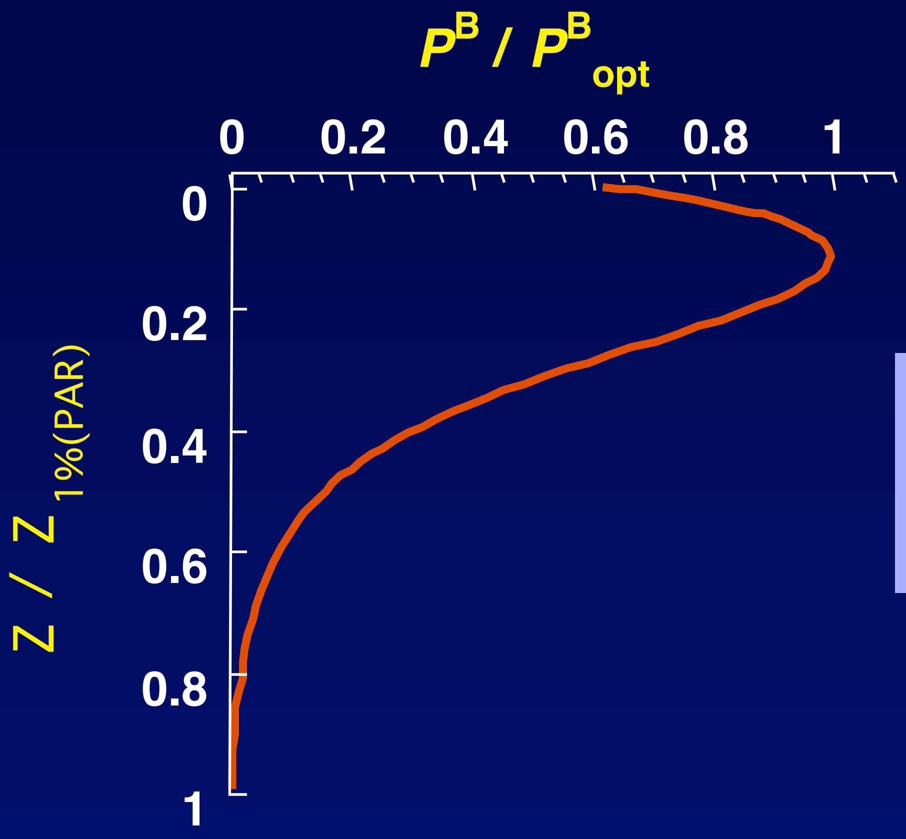
and

Chl

to

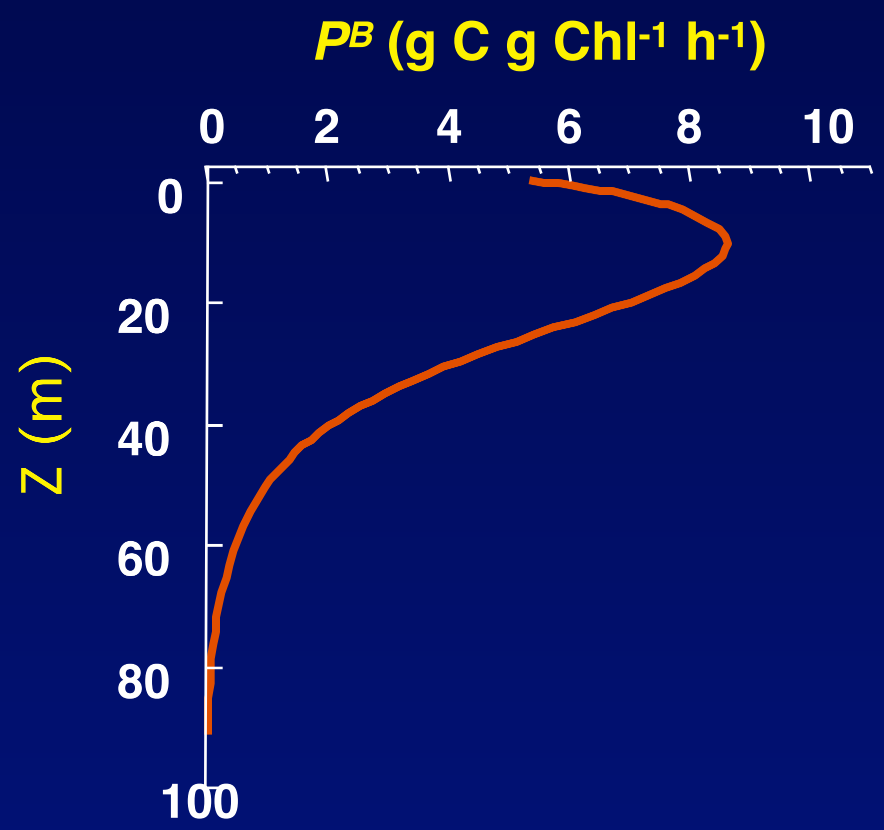
daily water column net primary productivity

Results can be generalized



$$P_Z = \frac{P^{B}_{opt} \cdot B}{K_{PAR}} \cdot f\left(E_{PAR}(0) \big/ E_k \right)$$

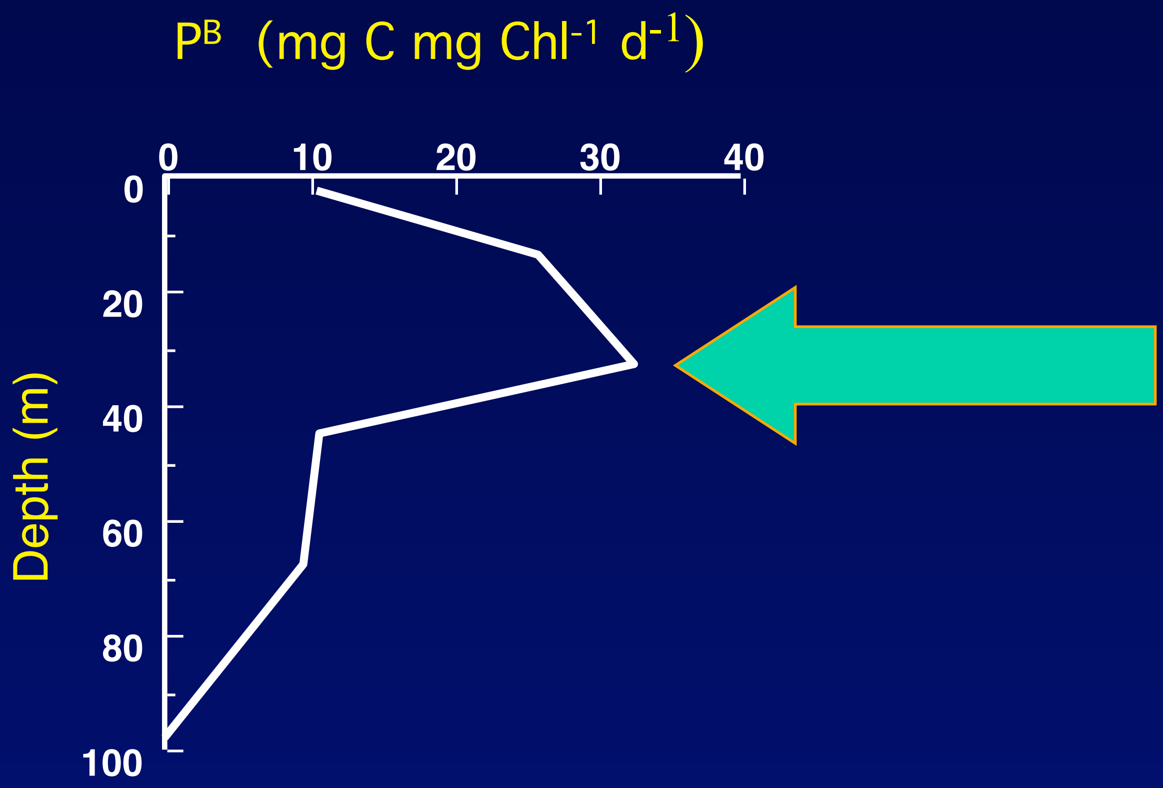
Maximum P^B is still a key parameter for most models



Even the spectral ones — even the quantum-yield models

Cullen C-MORE 2014

Compared to other measures, P^B_{opt} is relatively insensitive to artifact



Global assessment of primary productivity requires global assessment of maximum P^B

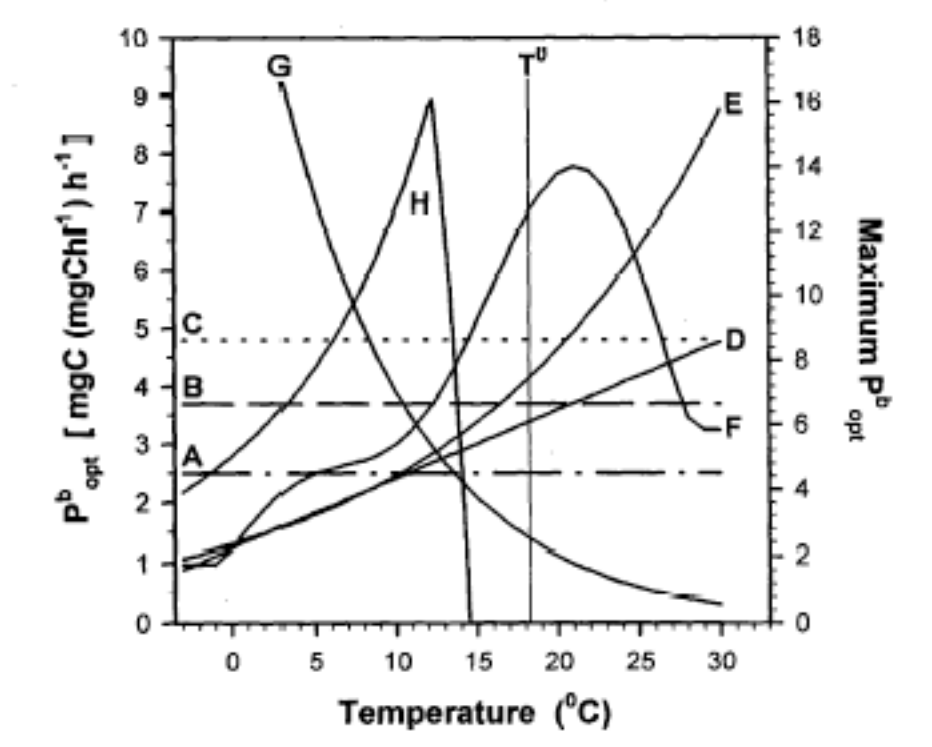


Fig. 4. Summary of published models for estimating the maximum chlorophyll-specific carbon fixation rate within a water column (P^b_{opt}).

Behrenfeld and Falkowski 1997b L&O

P^B_{opt} modelled as a function of temperature

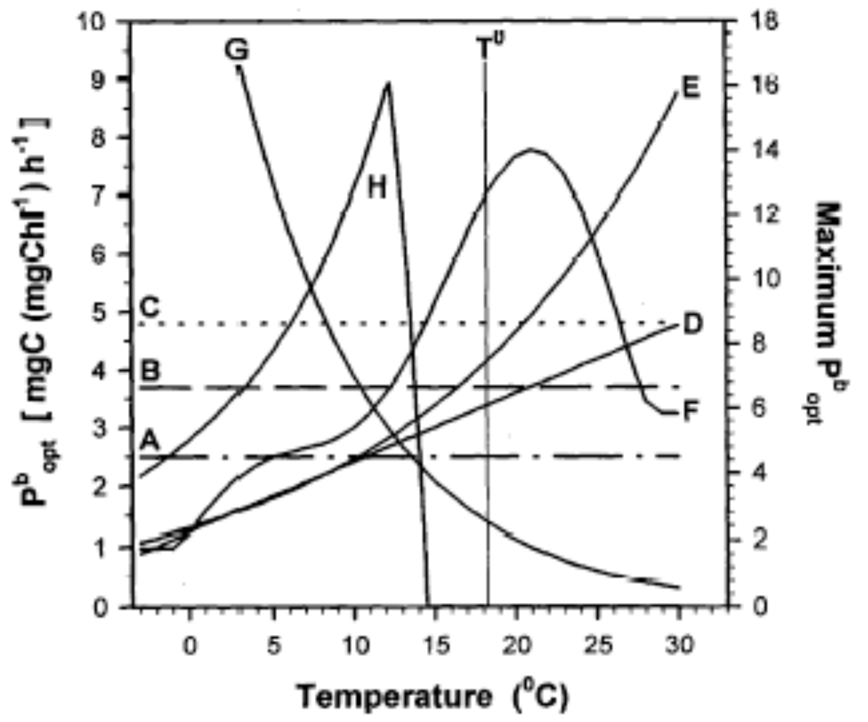
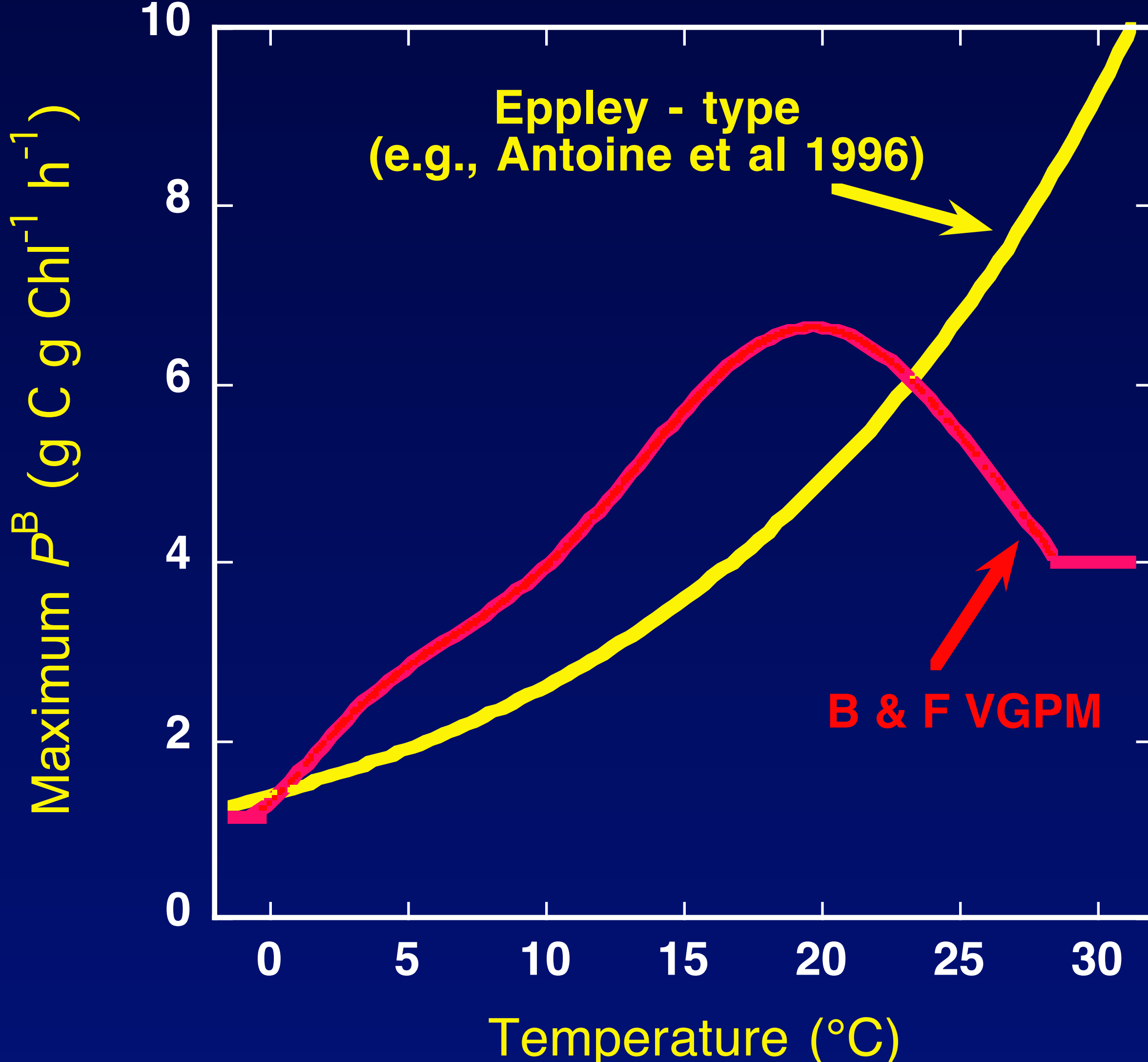


Fig. 4. Summary of published models for estimating the maximum chlorophyll-specific carbon fixation rate within a water column (P^b_{opt}).

Behrenfeld and Falkowski 1997b L&O

Two commonly used functions



Behrenfeld and Falkowski 1997b L&O

You may have seen the figure

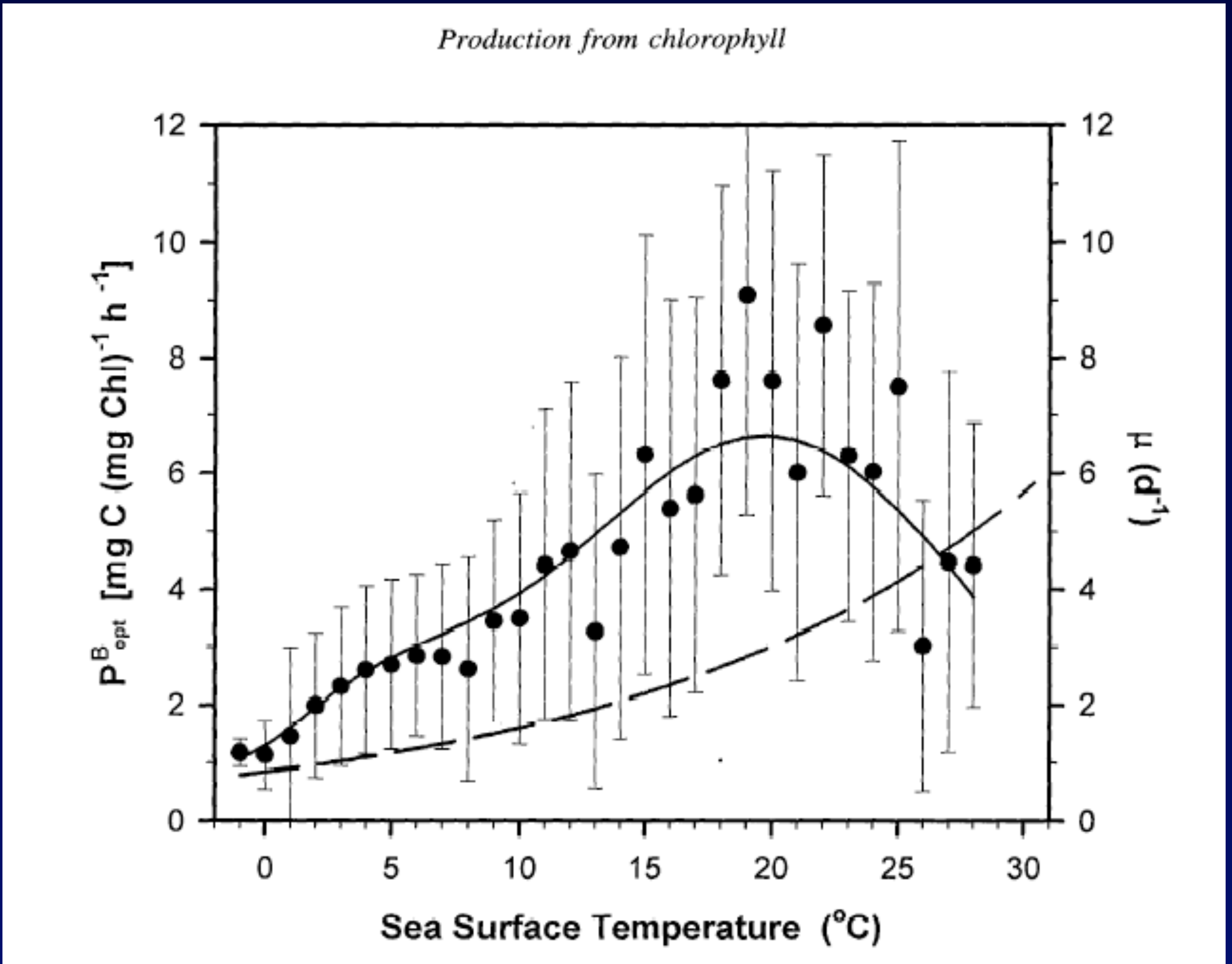
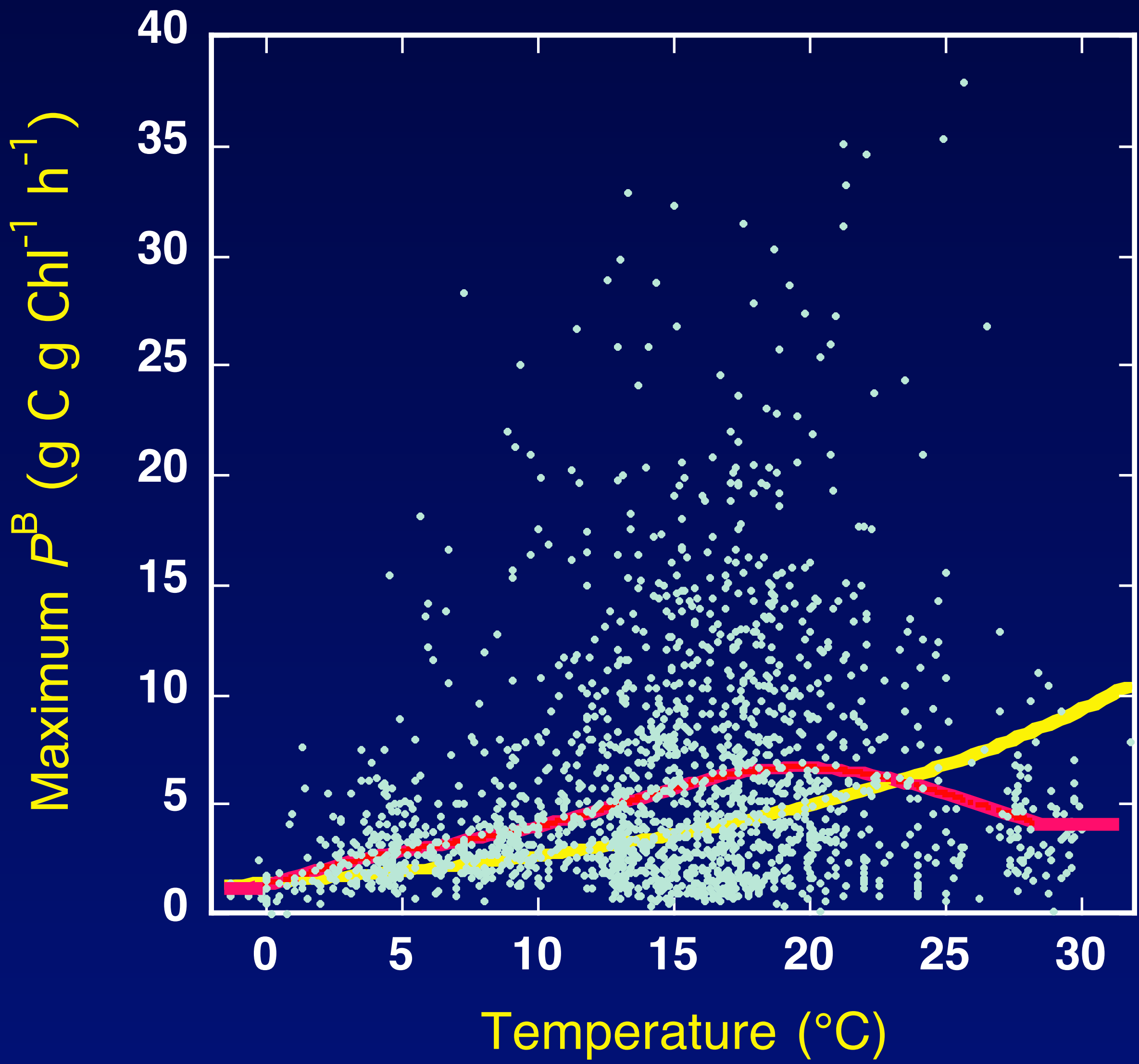


Fig. 7. Measured (●; ±SD) and modeled (——; Eq. 11) median value of the photoadaptive parameter, P^B_{opt}, as a function of sea surface temperature. Dashed curve indicates the theoretical maximum specific growth rate (μ; d^{-1}) of photoautotrophic unicellular algae described by Eppley (1972), which is used in a variety of productivity models (e.g. Balch and Byrne 1994; Antoine et al. 1996).

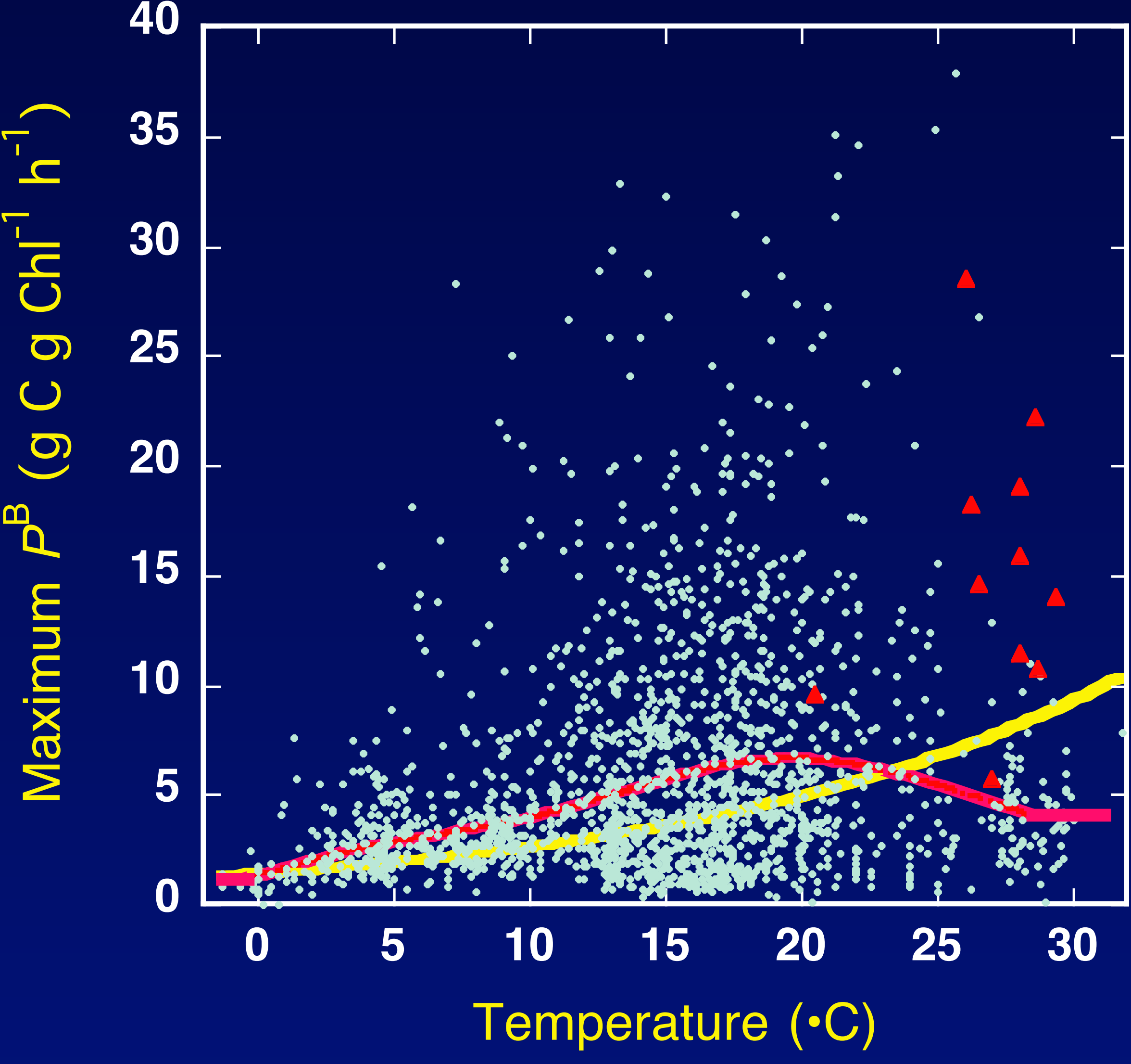
Behrenfeld and Falkowski 1997b L&O

Here are the measurements



Rutgers OPP Study Data Base

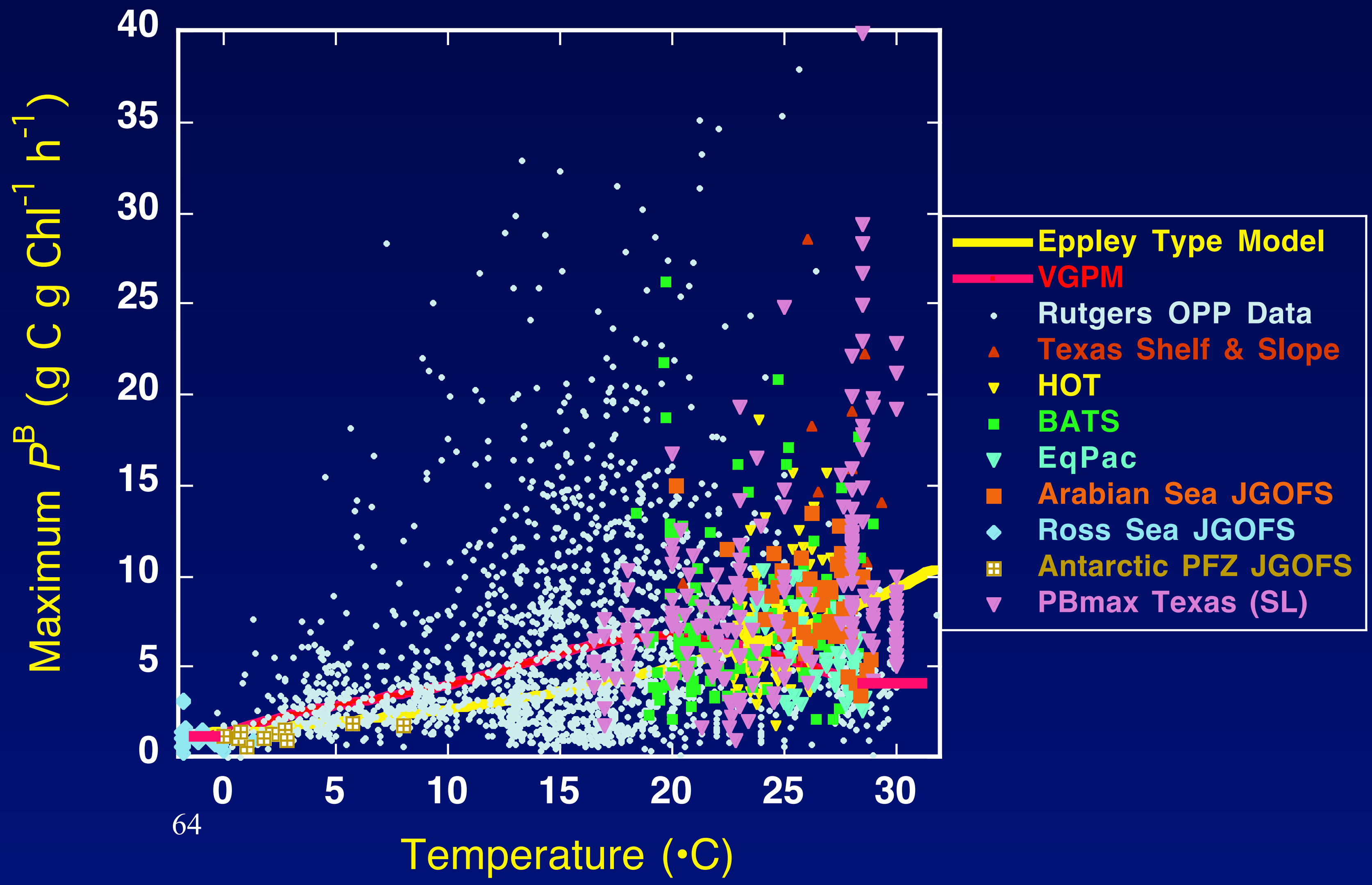
Compared with more measurements



Texas Shelf

Cullen C-MORE 2014

and more measurements!



Cullen C-MORE 2014

The foundations of VGPM

Published Statistical Fit

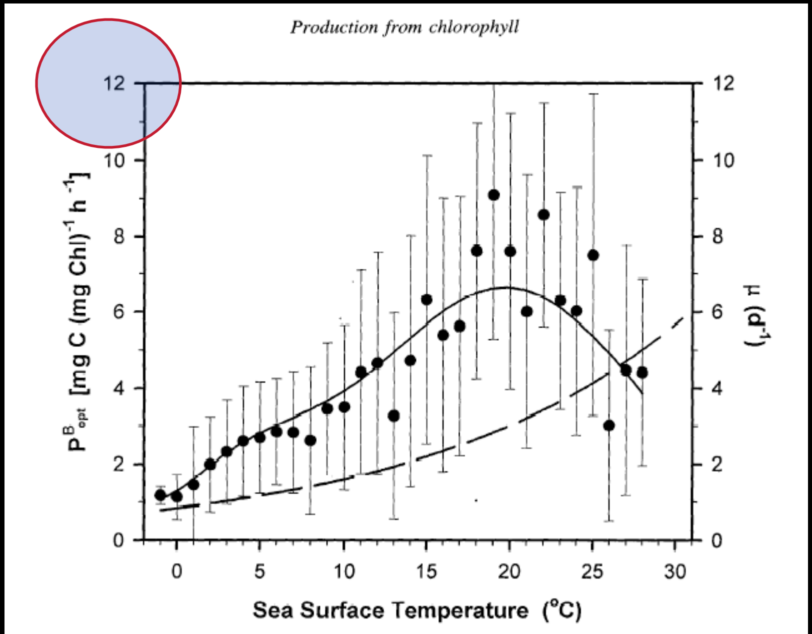
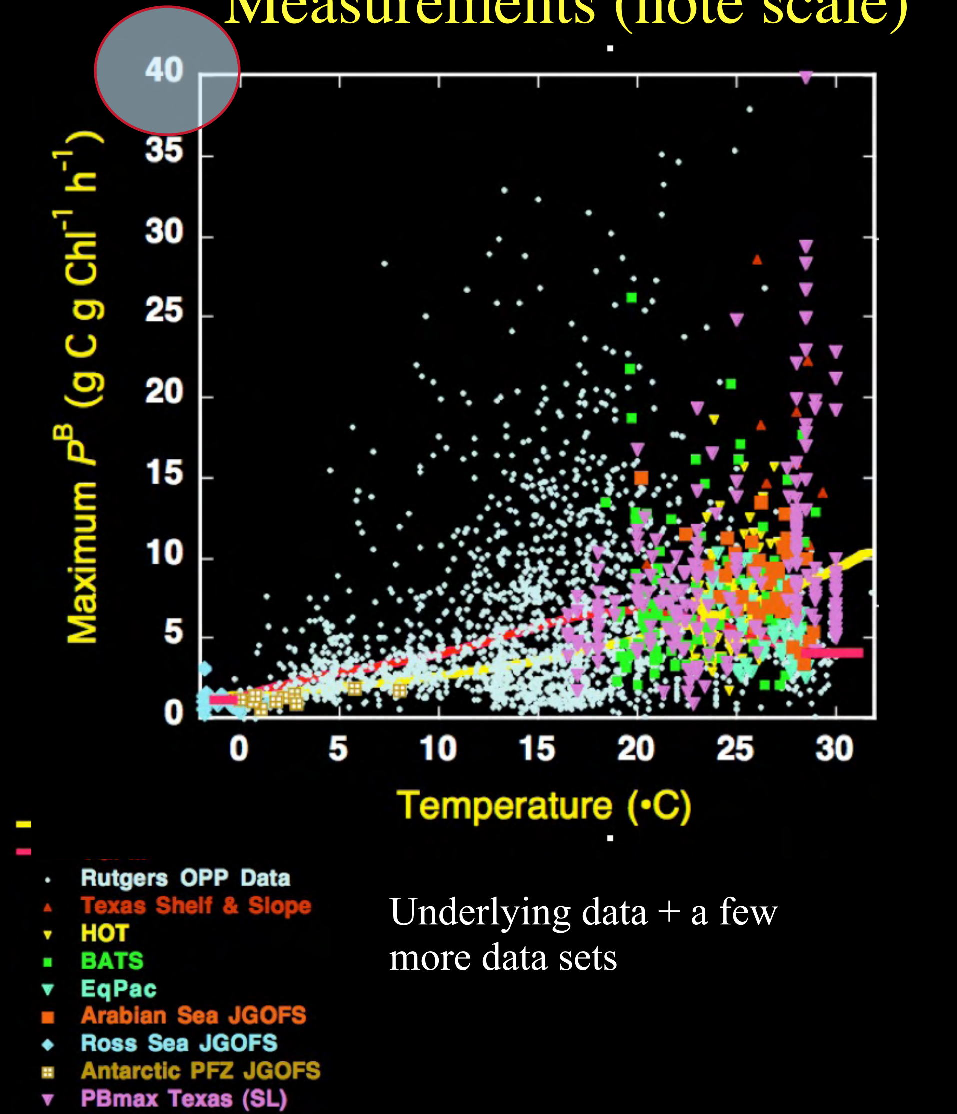


Fig. 7. Measured (●; ±SD) and modeled (——; Eq. 11) median value of the photoadaptive parameter, P^B_{opt}, as a function of sea surface temperature. Dashed curve indicates the theoretical maximum specific growth rate (μ; d^{-1}) of photoautotrophic unicellular algae described by Eppley (1972), which is used in a variety of productivity models (e.g. Balch and Byrne 1994; Antoine et al. 1996).

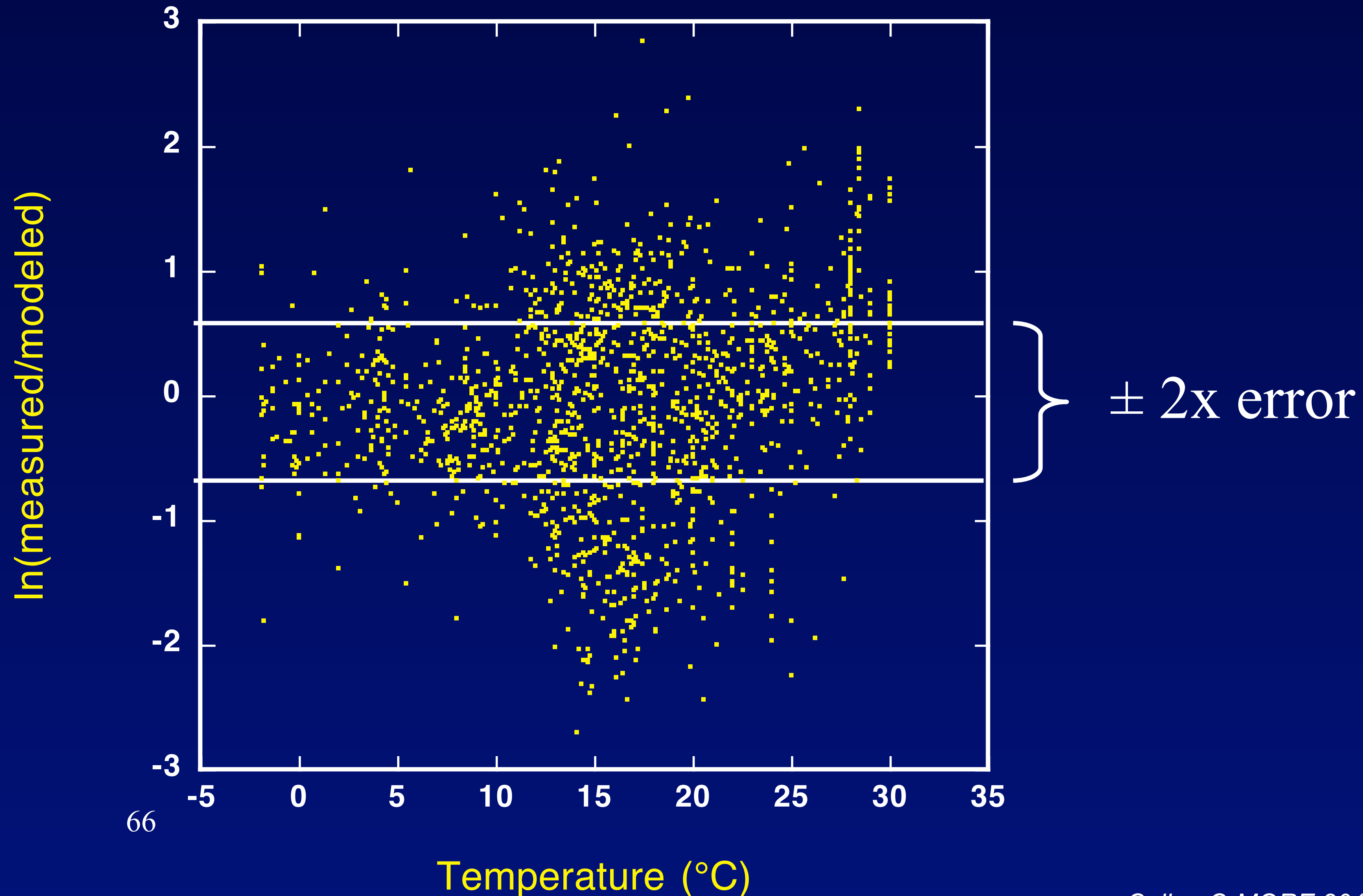
Behrenfeld and Falkowski 1997 L&O

Measurements (note scale)



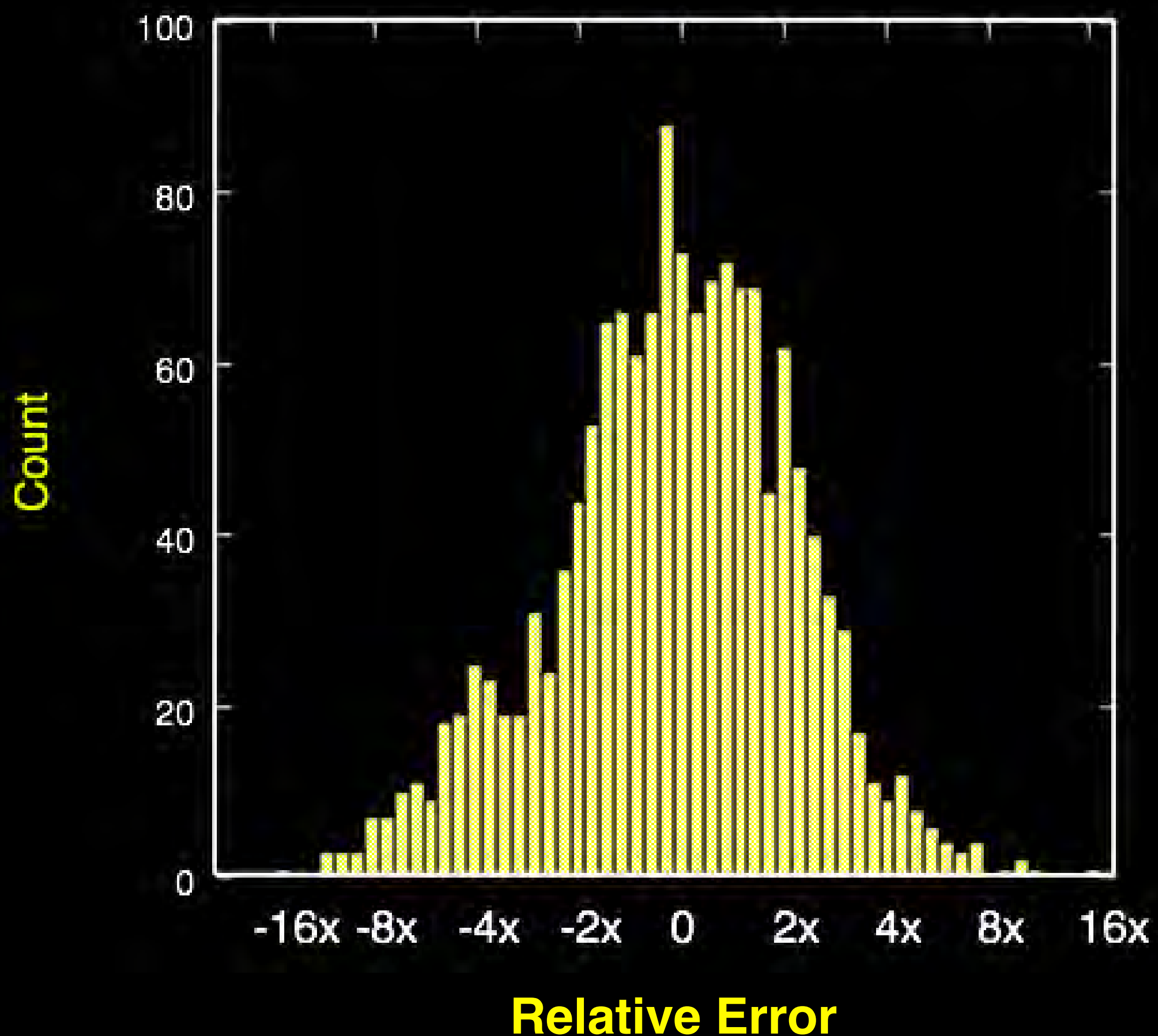
Underlying data + a few more data sets

General functions of T cannot capture major causes of variability in water column productivity

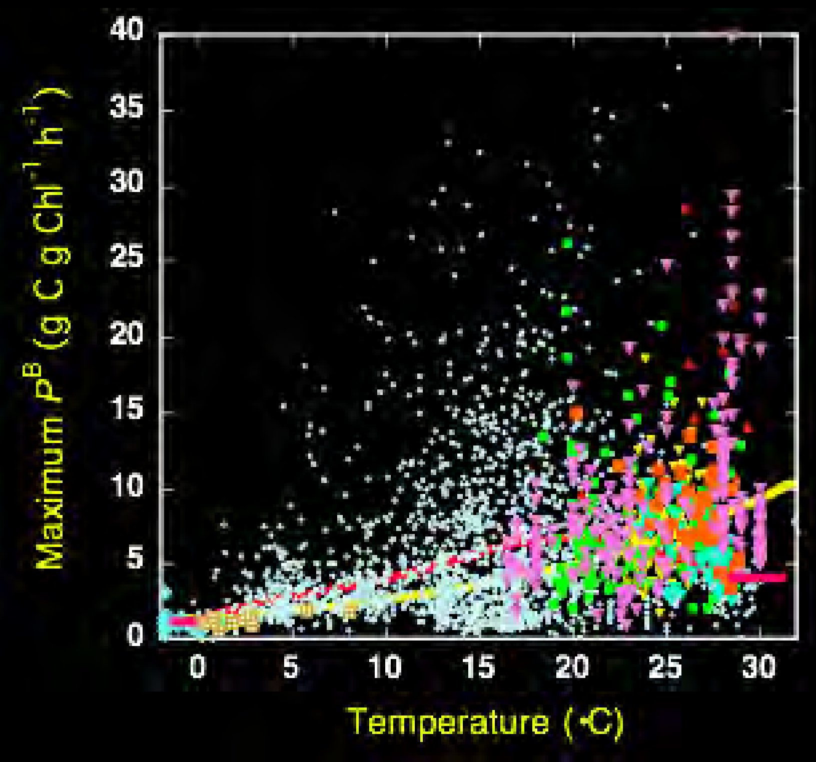


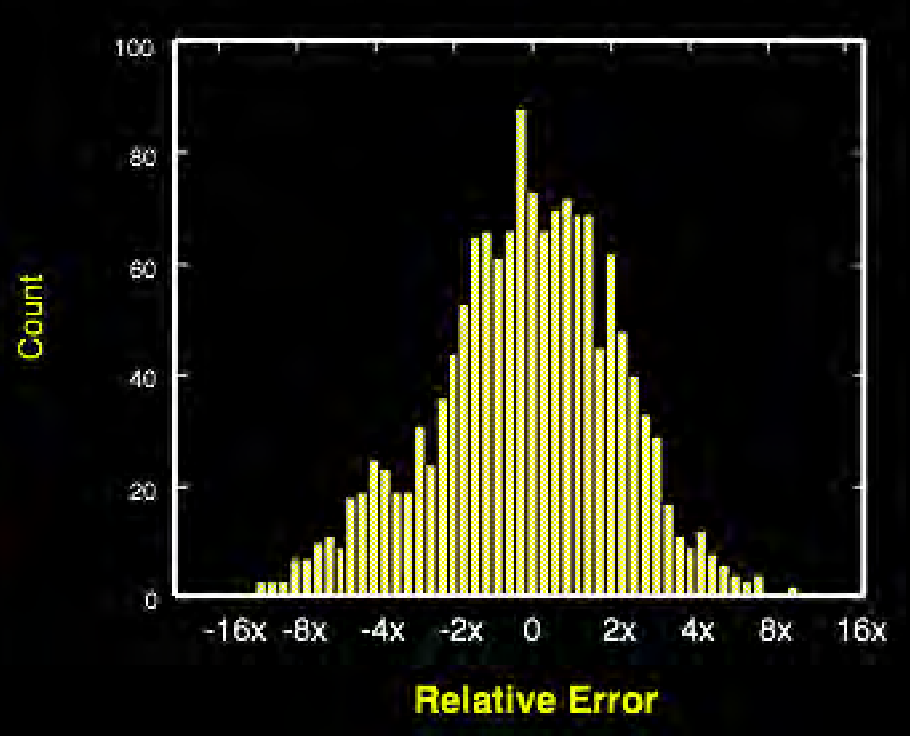
Cullen C-MORE 2014

Conclusion: General functions of T cannot capture major causes of variability in water column productivity



We must appreciate the implications of this unexplained variability





…and implications of a carbon-based model that isn't

GLOBAL BIOGEOCHEMICAL CYCLES, VOL. 19, GB1006, doi:10.1029/2004GB002299, 2005

Carbon-based ocean productivity and phytoplankton physiology from space

Michael J. Behrenfeld,[1,2] Emmanuel Boss,[3] David A. Siegel,[4] and Donald M. Shea[5]

$$\mathrm{NPP} = \mathrm{C} \times \mu \times \mathrm{Z}_{\mathrm{eu}} \times h(\mathrm{I}_0), \qquad (5)$$

$$\mu = 2 \times \mathrm{Chl:C_{sat}} / \left[0.022 + (0.045 - 0.022)\exp^{-3\mathrm{Ig}}\right] \times \left(1 - \exp^{-3\mathrm{Ig}}\right). \qquad (4)$$

Carbon cancels out!

How much confidence should we have?

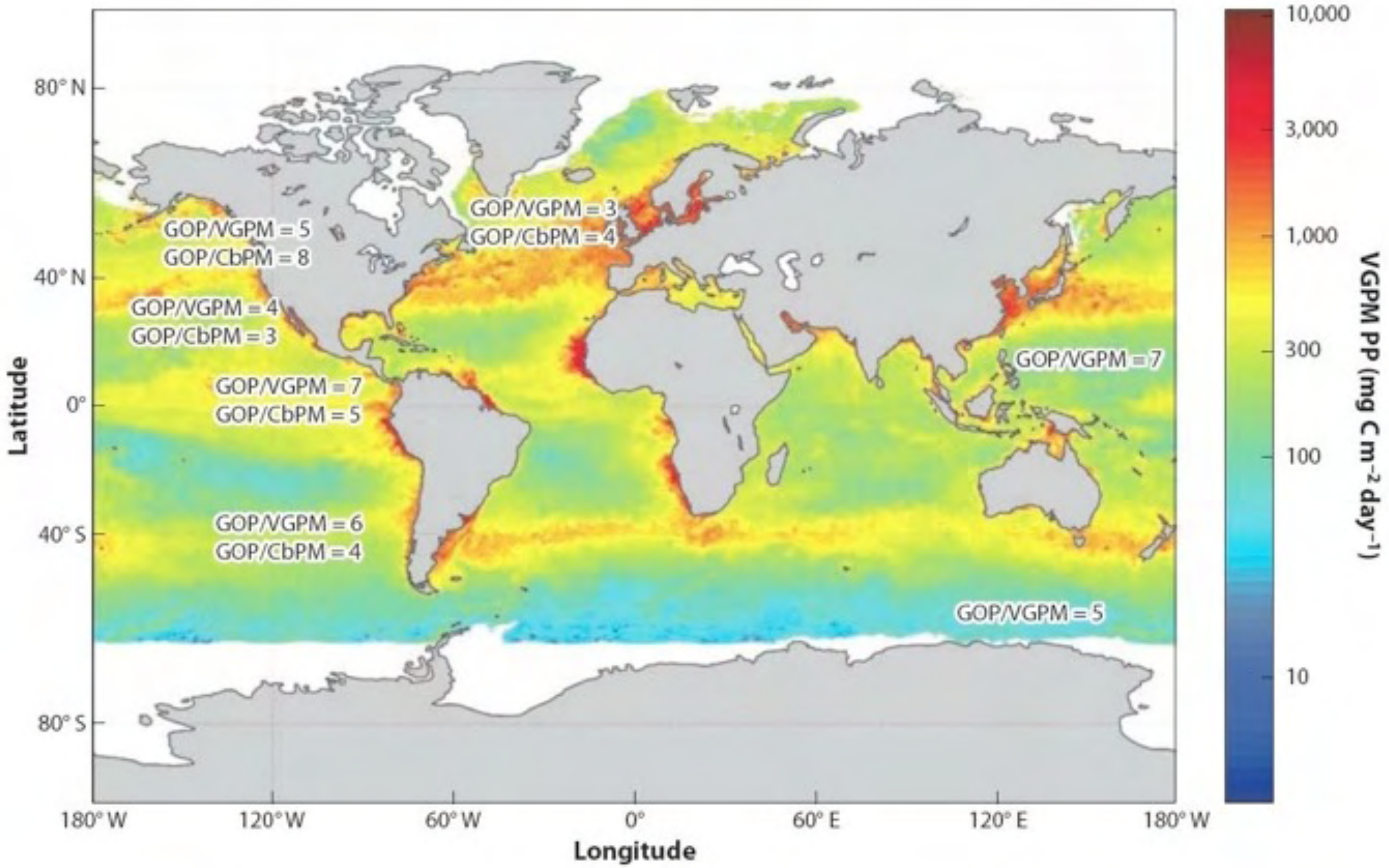


Figure 4

Map of satellite net primary production (NPP) estimated from the vertically generalized productivity model (VGPM) (Behrenfeld & Falkowski 1997), annotated with ratios of observed GOP/NPP (where GOP is gross O_2 production) for both the VGPM and C-based productivity model (CbPM) (Behrenfeld et al. 2005, Westberry et al. 2008) in several basin-scale studies.

Juranek and Quay 2013 Ann Rev Mar Sci

Estimates like these (NPP) do not yet account for variable physiology beyond central tendencies

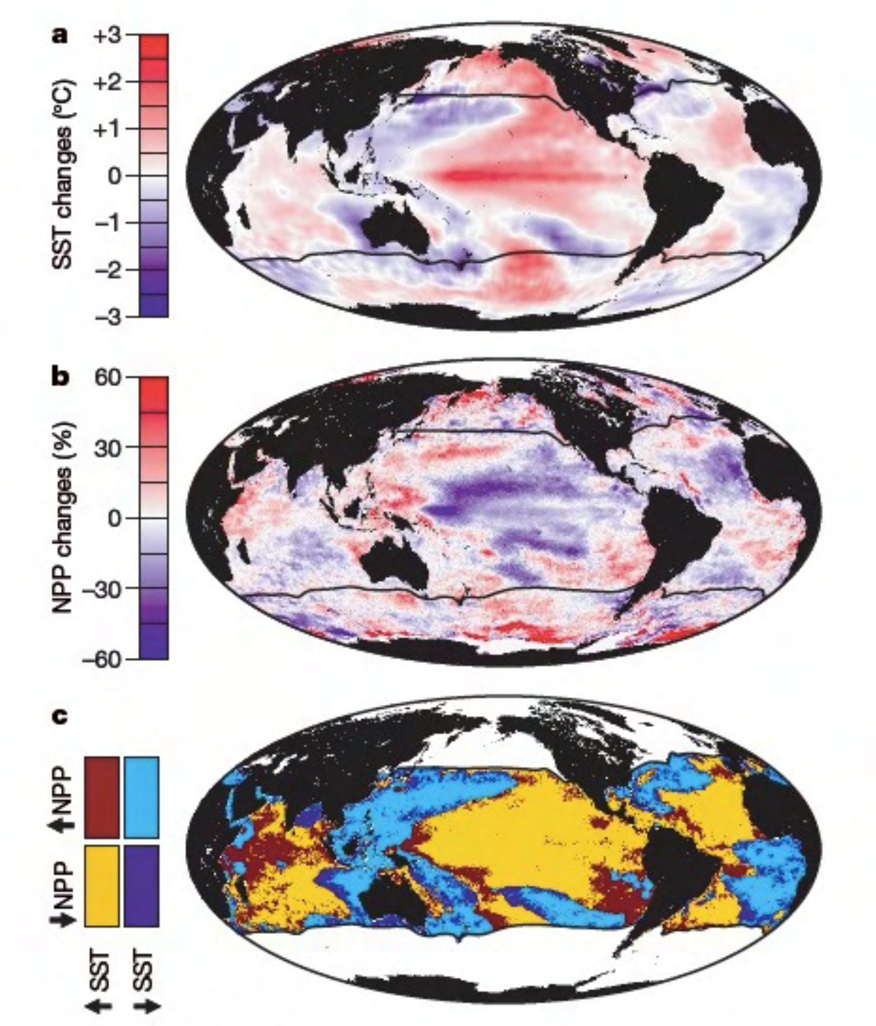
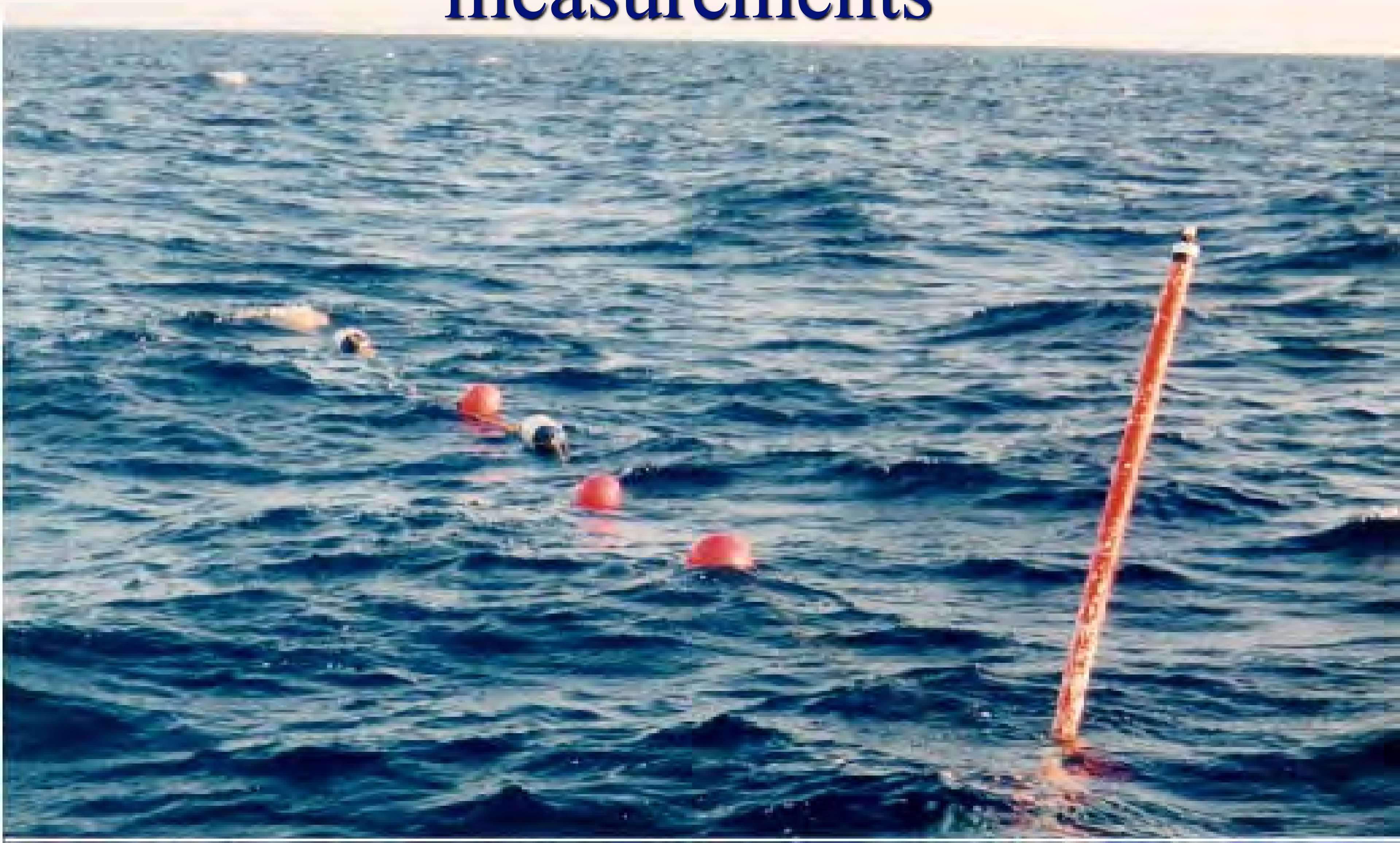


Figure 3 | Climate controls on ocean productivity cause NPP to vary inversely with changes in SST. Global changes in annual average SST (**a**) and

Behrenfeld et al. *Nature* 2006

The need to compare models with measurements



Validation is important

Journal of Marine Systems 76 (2009) 113–133

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journal homepage: www.elsevier.com/locate/jmarsys

JOURNAL OF MARINE SYSTEMS

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

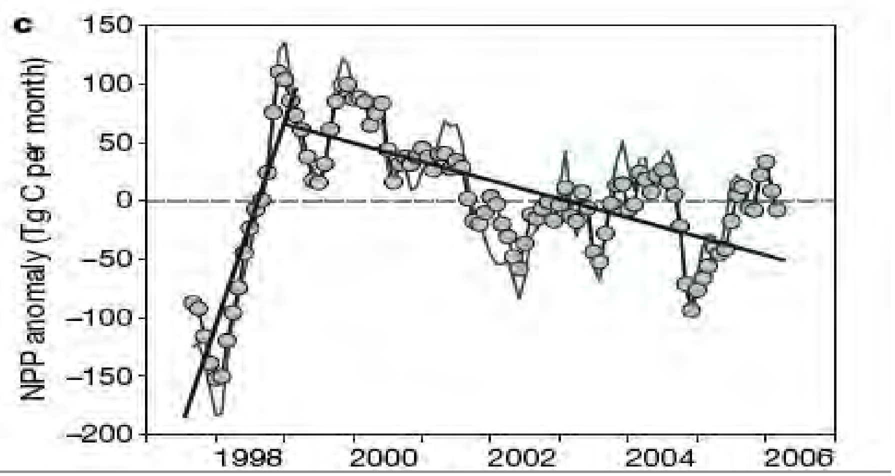
Marjorie A.M. Friedrichs[a,*], Mary-Elena Carr[b,1], Richard T. Barber[c], Michele Scardi[d], David Antoine[e], Robert A. Armstrong[f], Ichio Asanuma[g], Michael J. Behrenfeld[h], Erik T. Buitenhuis[i], Fei Chai[j], James R. Christian[k], Aurea M. Ciotti[l], Scott C. Doney[m], Mark Dowell[n], John Dunne[o], Bernard Gentili[e], Watson Gregg[p], Nicolas Hoepffner[n], Joji Ishizaka[q], Takahiko Kameda[r], Ivan Lima[m], John Marra[s], Frédéric Mélin[n], J. Keith Moore[t], André Morel[e], Robert T. O'Malley[h], Jay O'Reilly[u], Vincent S. Saba[a], Marjorie Schmeltz[b], Tim J. Smyth[v], Jerry Tjiputra[w], Kirk Waters[x], Toby K. Westberry[h], Arne Winguth[y]

Model

nature Vol 444|7 December 2006|doi:10.1038/nature05317

Climate-driven trends in contemporary ocean productivity

Michael J. Behrenfeld[1], Robert T. O'Malley[1], David A. Siegel[3], Charles R. McClain[4], Jorge L. Sarmiento[5], Gene C. Feldman[4], Allen J. Milligan[1], Paul G. Falkowski[6], Ricardo M. Letelier[2] & Emmanuel S. Boss[7]

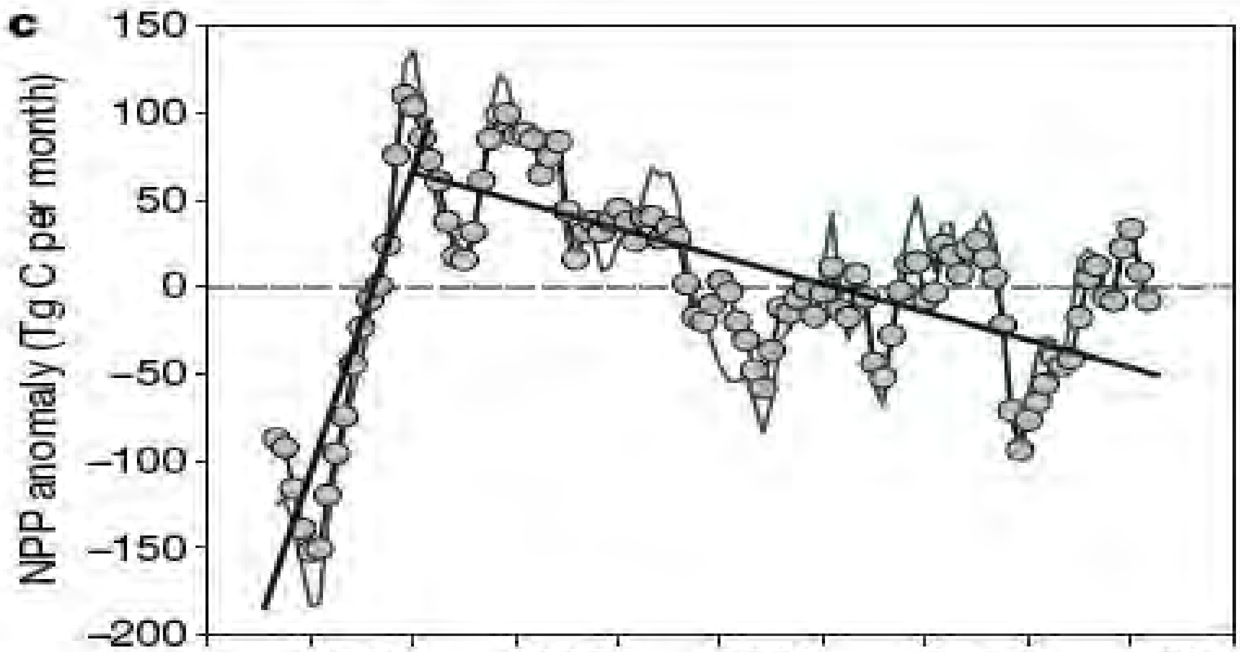


Headline

OCEAN SCIENCE ALERT:
WARMER SEAS WILL WIPE OUT PHYTOPLANKTON, SOURCE OF OCEAN LIFE
By Steve Connor, Science Editor
The Independent UK
19 January 2006

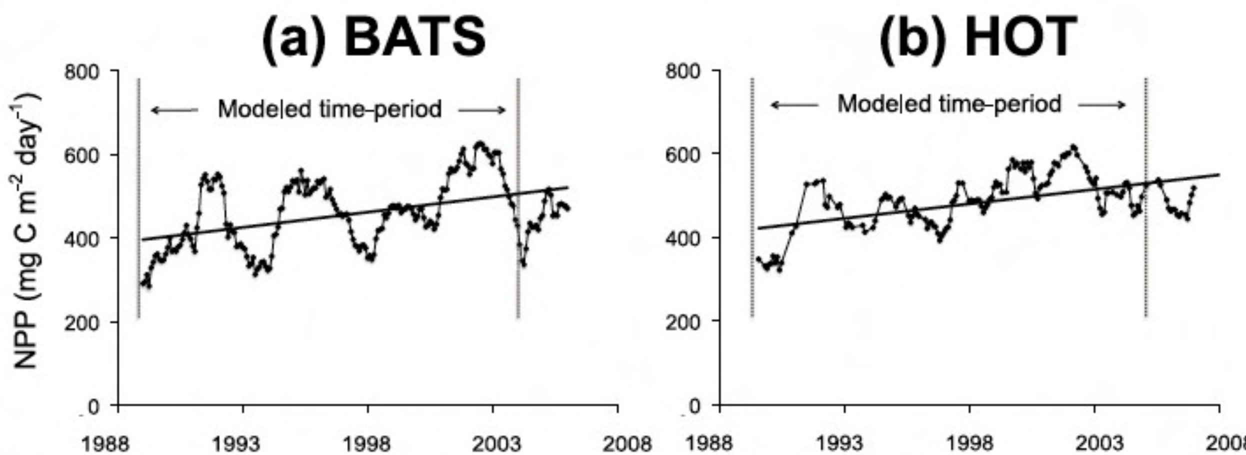
The microscopic plants that underpin all life in the oceans are likely to be destroyed by global warming.

Published model result

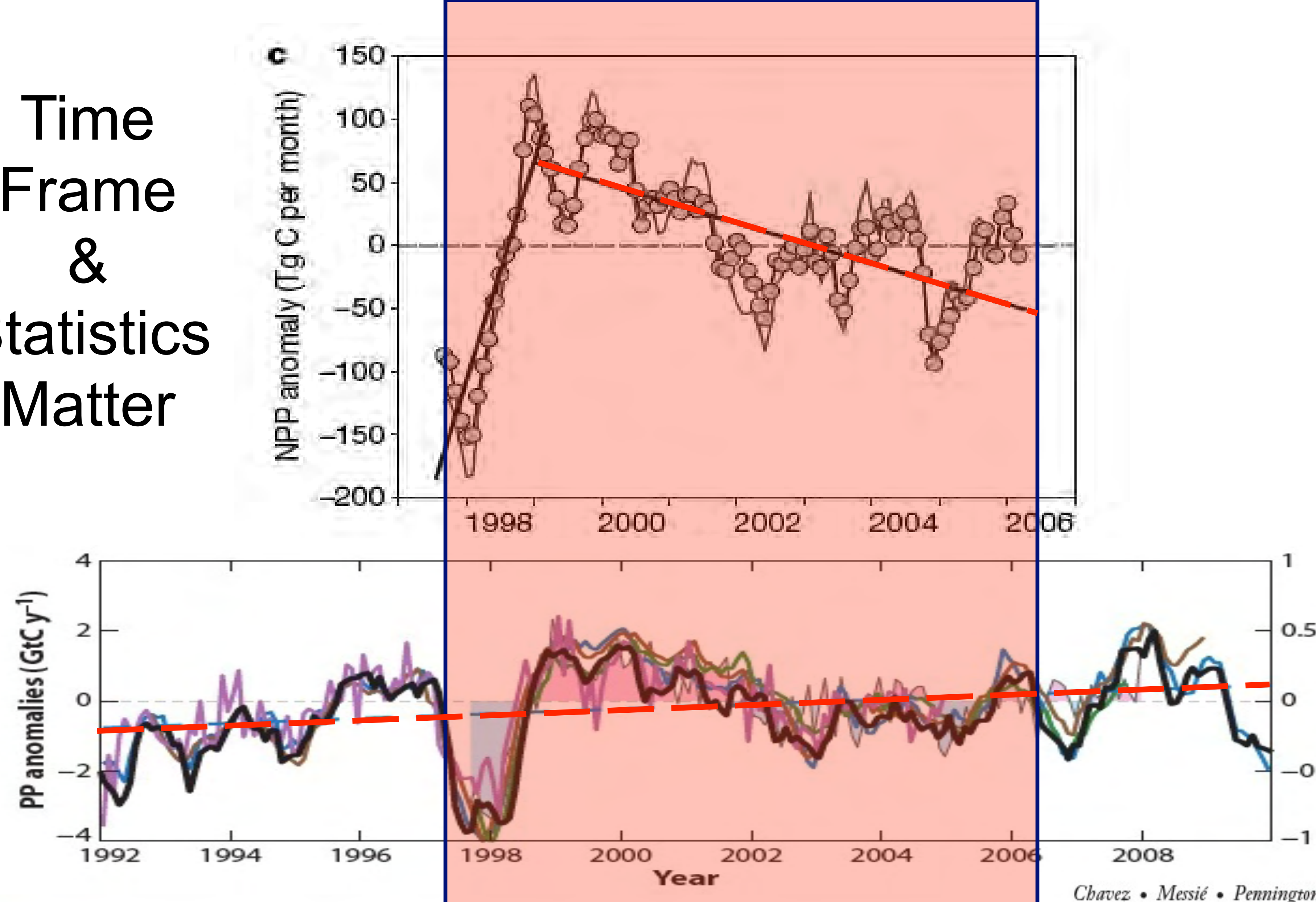


SABA ET AL.: MODELING MARINE PRIMARY PRODUCTIVITY

Measurements show the opposite trend



Time Frame & Statistics Matter



Chavez • Messié • Penningtor

gure 6

lobal primary production anomaly (PPA) and first empirical orthogonal function (EOF) modes
rface temperature (SST), sea level anomaly (SLA), sea level pressure (SLP), chlorophyll (logCh
ormalized Multivariate ENSO Index (MEI). PP anomalies were calculated as the global VGPM

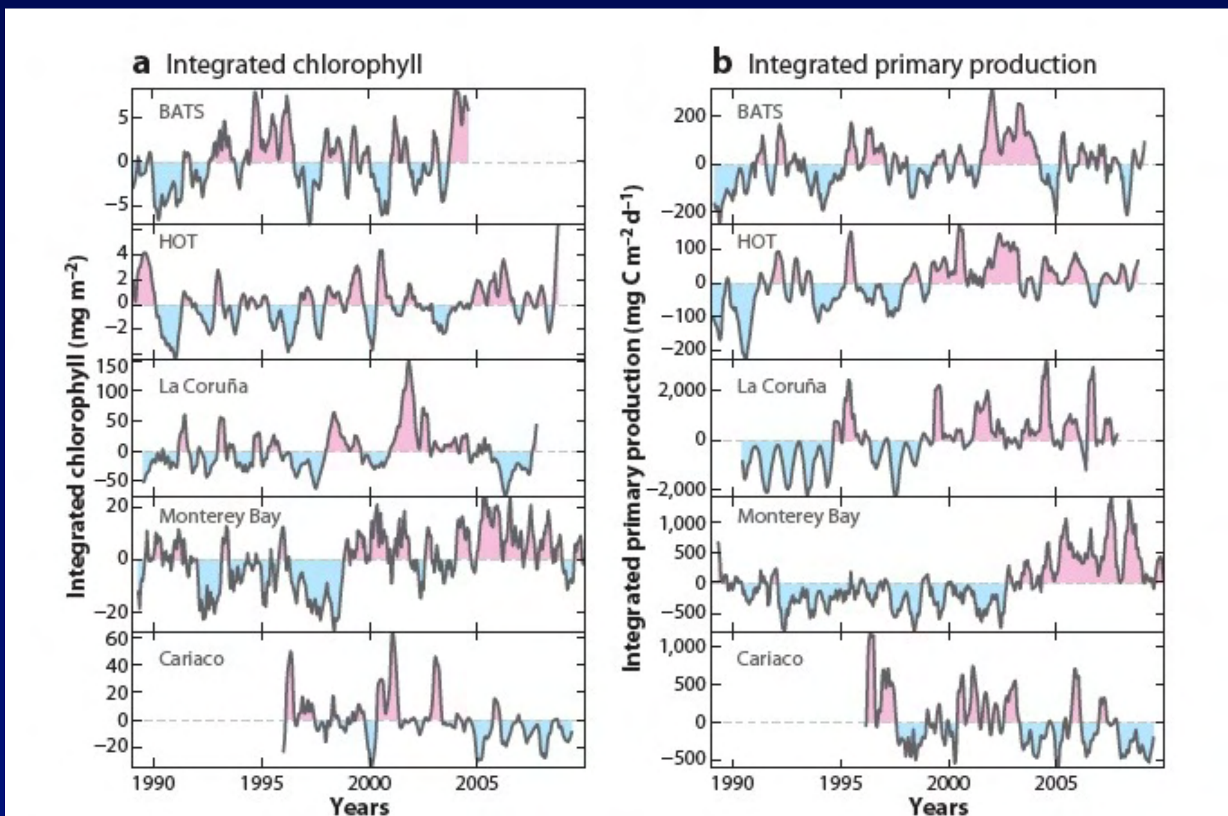
Measurements

(no headlines)

Marine Primary Production in Relation to Climate Variability and Change

Francisco P. Chavez, Monique Messié, and J. Timothy Pennington

Monterey Bay Aquarium Research Institute, Moss Landing, California 95039; email: chfr@mbari.org



Annu. Rev. Mar. Sci. 2011. 3:227–60

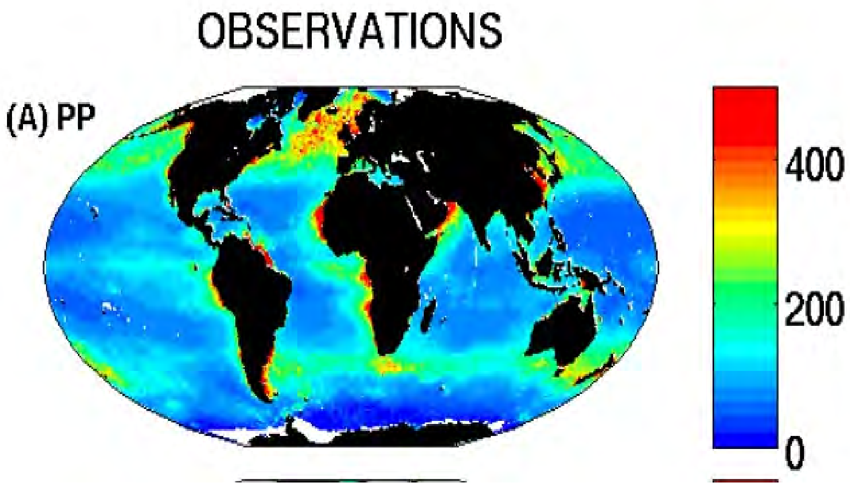
First published online as a Review in Advance on October 27, 2010

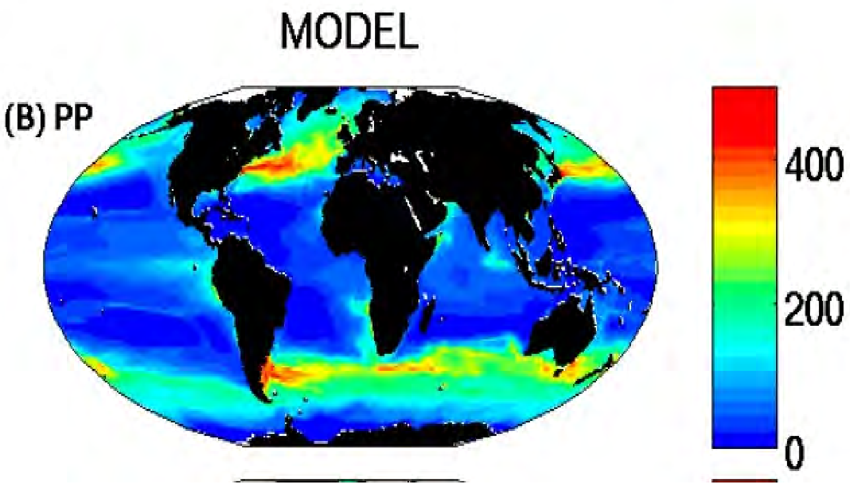
The *Annual Review of Marine Science* is online at marine.annualreviews.org

This article's doi:
10.1146/annurev.marine.010908.163917

1941-1405/11/0115-0227$20.00

It is also useful to remember the distinction between models and observations





VGPM model

Follows et al. Model

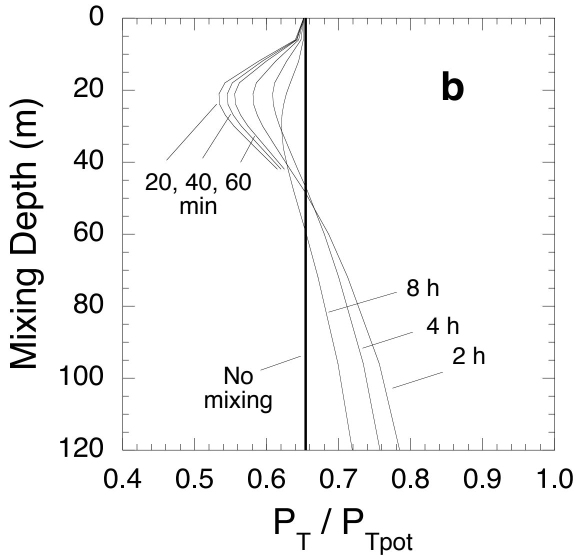
No one is immune!

Many models cannot be directly verified

Interactive effects of ozone depletion and vertical mixing on photosynthesis of Antarctic phytoplankton

Patrick J. Neale*, Richard F. Davis† & John J. Cullen†

NATURE | VOL 392 | 9 APRIL 1998



Conclusions

- Models of primary productivity are a fundamental requirement for describing and explaining ecosystem dynamics and biogeochemical cycling in the sea
- The models are based on measurements:
  - The measurements are not perfect
  - The models are not perfect
- Capabilities and limitations of models should always be considered when they are applied
    - Effects of underlying assumptions
    - Comparison with real measurements when available
- Know your model!