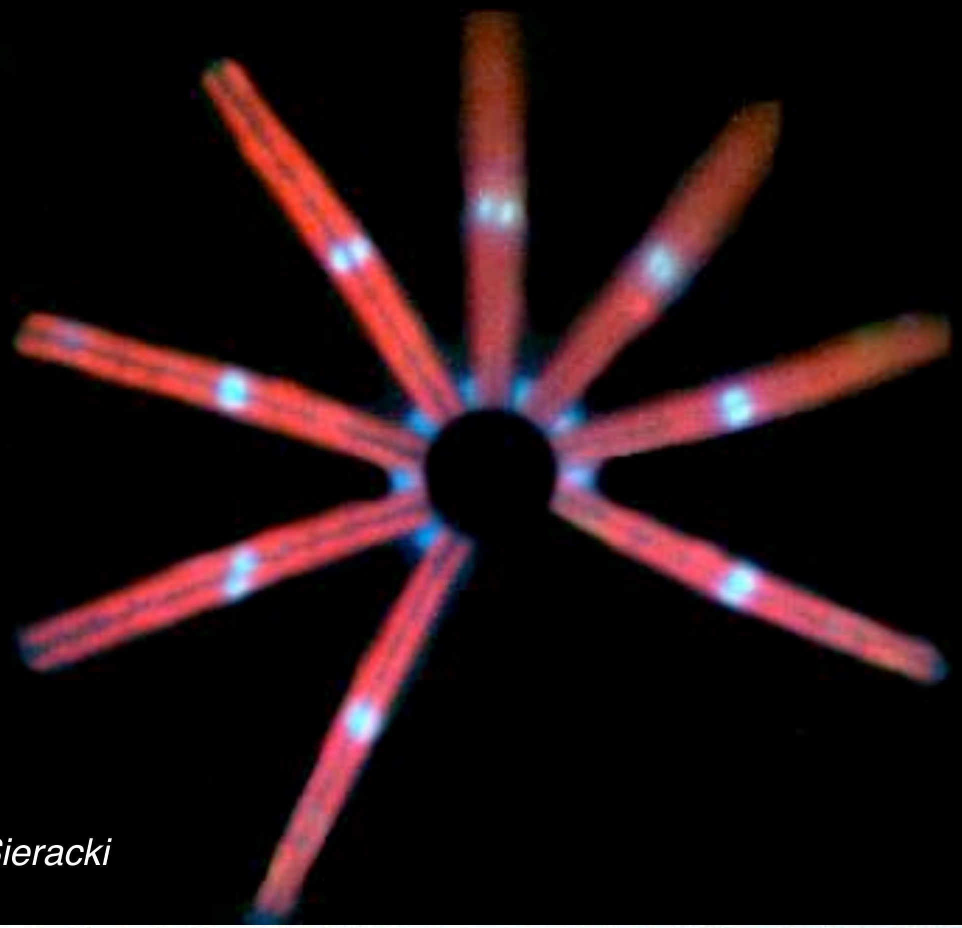
Measurement and interpretation of chlorophyll fluorescence: a most dangerous game



MIke Sieracki

John J. Cullen

with contributions from

Audrey B. Barnett

Adam Comeau

Susanne E. Craig

Richard F. Davis

Yannick Huot†

Christina Schallenberg

Dept. of Oceanography

Dalhousie University

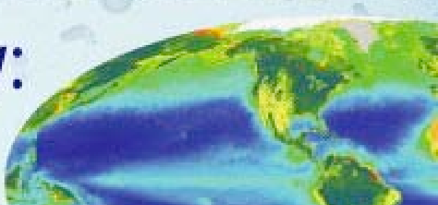
Halifax, Nova Scotia

Canada B3H 4J1

2008 HAWAI'I SUMMER COURSE ON MICROBIAL OCEANOGRAPHY

AGOURON INSTITUTE

Microbial Oceanography: Genomes to Biomes



Chlorophyll Fluorescence Simplified

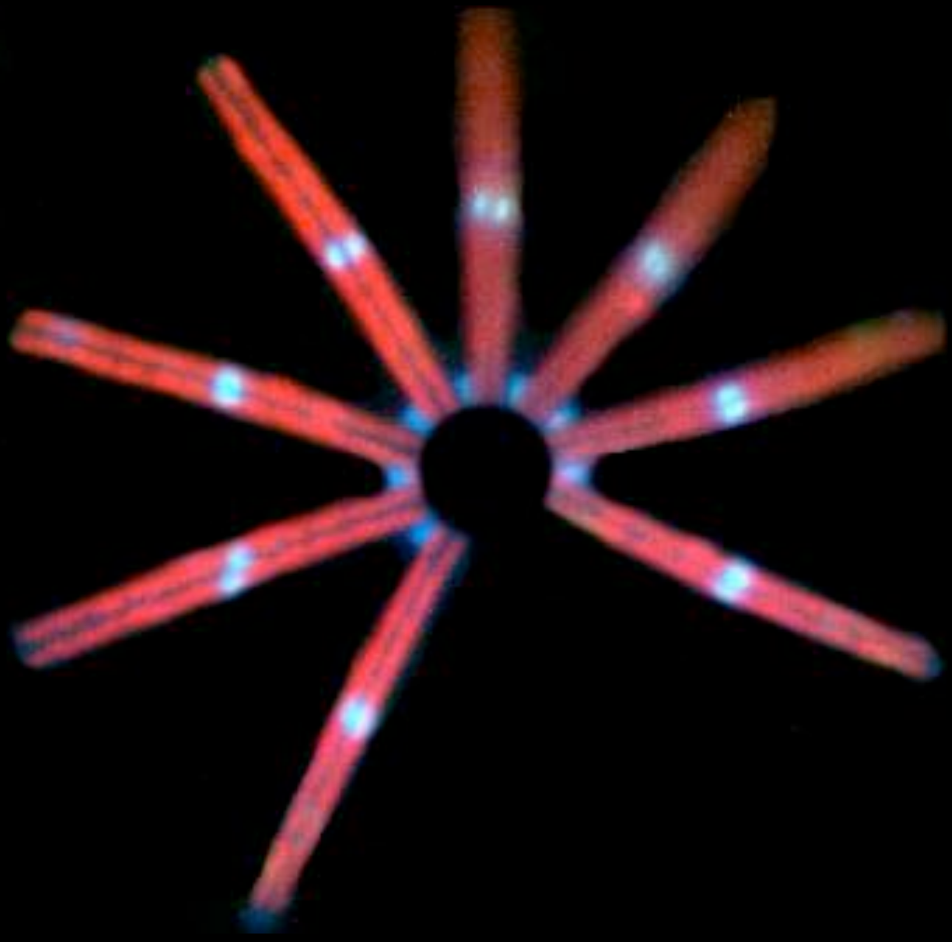
Equation	Equation number
$\frac{dA}{dt} = -\mathring{E}\,\sigma'_{PSII}\,A + \frac{B\,NADP}{\tau}$	3.41
$\frac{dB}{dt} = \mathring{E}\,\sigma'_{PSII}\,A - \frac{B\,NADP}{\tau} + K_{rep}\,C - \Psi_d\,\sigma'_{PSII}\,\mathring{E}\,B$	3.42
$\frac{dC}{dt} = -K_{rep}\,C + \Psi_d\,\sigma'_{PSII}\,\mathring{E}\,B$	3.43
$\frac{dk_{qE}}{dt} = \begin{cases} k_{ind}\left(k_{qE}^{st} - k_{qE}\right) & k_{qE}^{st} > k_{qE} \\ k_{rel}\left(k_{qE}^{st} - k_{qE}\right) & k_{qE}^{st} < k_{qE} \end{cases}$	3.28 and 3.29
$\frac{dNADP}{dt} = -\frac{B}{\tau} NADP + K_{Calvin} + k_{\text{sinks}}$	3.8
$k_{qE}^{st} = \gamma_d\,\mathring{E}\left(1 - \left[A + C\frac{\left(n_{Calvin}\,k_{Calvin}^{\max} - P_e^{RC}\right)}{n_{Calvin}\,k_{Calvin}^{\max}}\right]\right)$ and $\gamma_d = \gamma_o + \gamma_{NPQ}$	3.27
$\sigma'_{PSII} = \sigma_{PSII}^{O}\varphi_{pA} = \sigma_{PSII}^{O}\frac{k_p}{k_d + k_f + k_p + k_{qE}}$.	3.32
$K_{Calvin} = n_{Calvin}\frac{k_{Calvin}^{\max}\,NADPH}{NADPH_{1/2} + NADPH}$	3.9
$K_{rep}^{N} = \frac{k_{rep}^{\max}\,C}{C_{1/2} + C} N_{status}$	3.33 and 3.34
$P_e^{RC} = A\varphi_{pA}\,\sigma_{PSII}^{O}\,\mathring{E} = A\,\sigma'_{PSII}\,\mathring{E}$	3.36
$\varphi_f = A\frac{k_f}{k_d + k_f + k_p + k_{qE}} + B\frac{k_f}{k_d + k_f + k_{qE}} + C\frac{k_f}{k_d + k_f + k_I + k_{qE}}$	3.12
Acclimation	
$\frac{d\sigma_{PSII}^{O}}{dt} = \begin{cases} \kappa_{\sigma PSII}\,\sigma_{PSII}^{O}\left(\frac{A}{A+B}\left(\sigma_{PSII}^{O} / \sigma_{PSII}^{opt}\right)^x - 0.3\right) & \mathring{E} > 0 \\ 0 & \mathring{E} = 0 \end{cases}$	3.44

only kidding…

A Biological Property

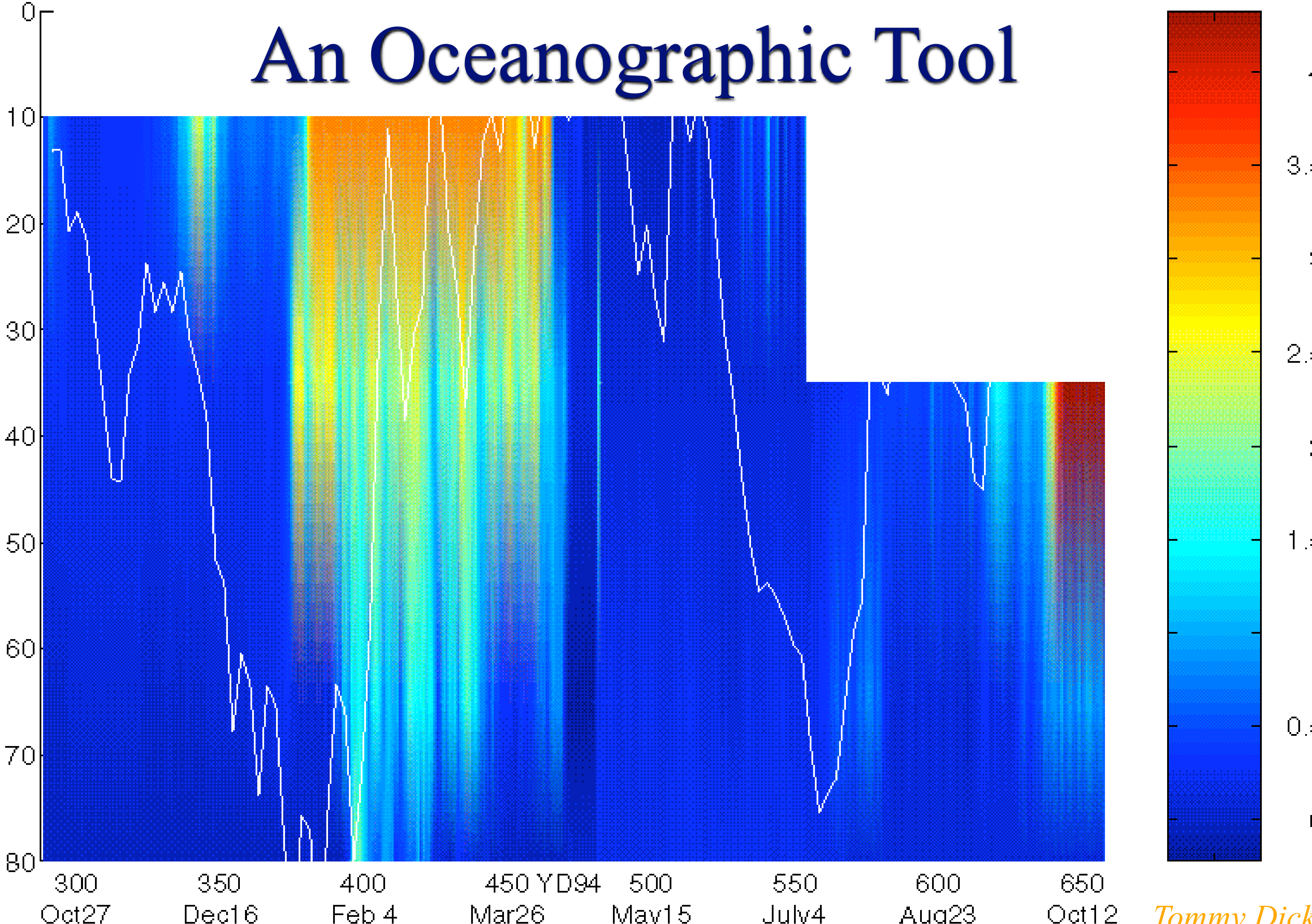
Sensitive to

- Physiology
- Acclimation
- Adaptation



MIke Sieracki

An Oceanographic Tool



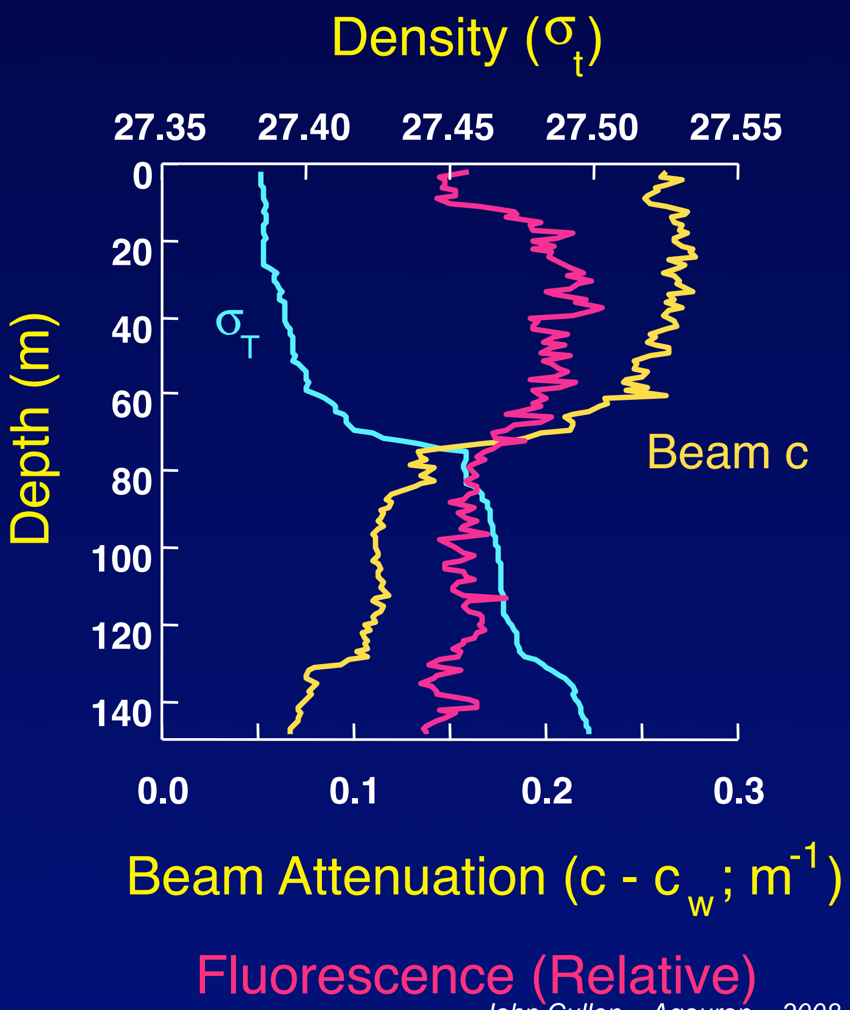
Tommy Dick

Figure 4.13 Chlorophyll a measured using stimulated fluorometers at 10,35,65,and 80m at the central moorin

Fluorescence is measured to detect and quantify phytoplankton

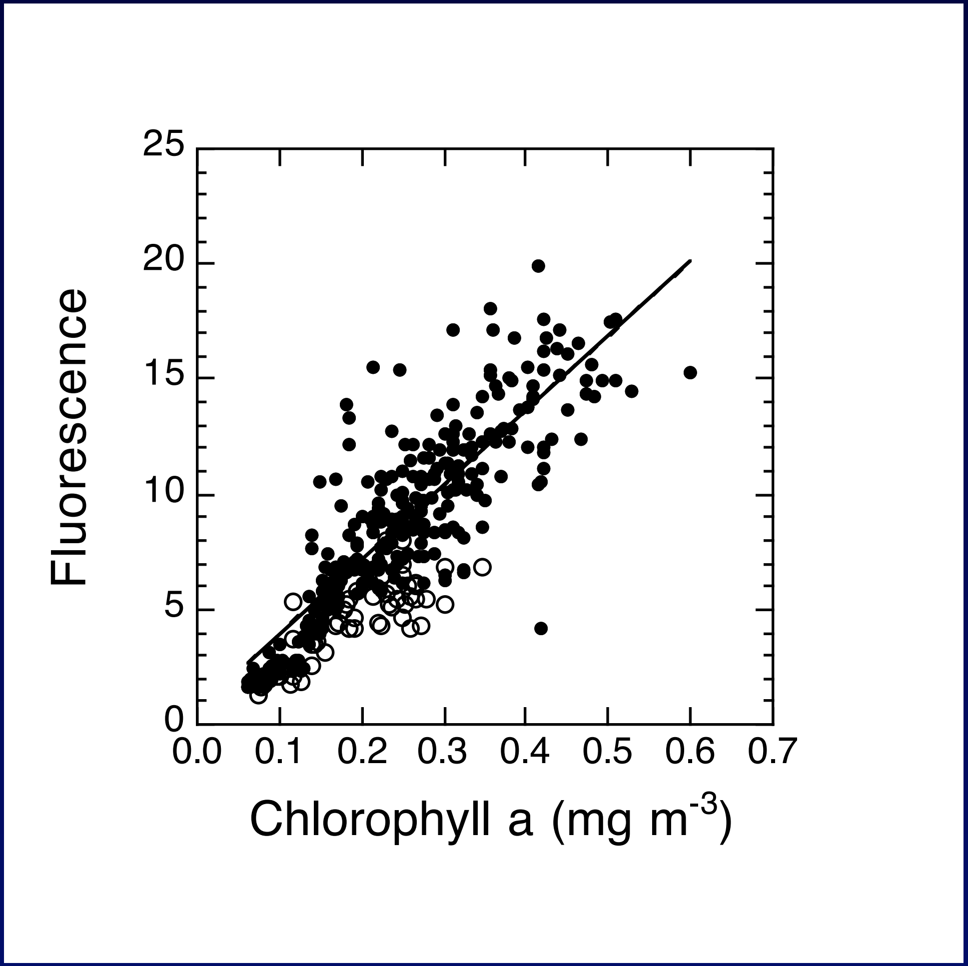
Bozone 1993: Wedell-Scotia Sea

Vertical Profiles



John Cullen – Agouron – 2008

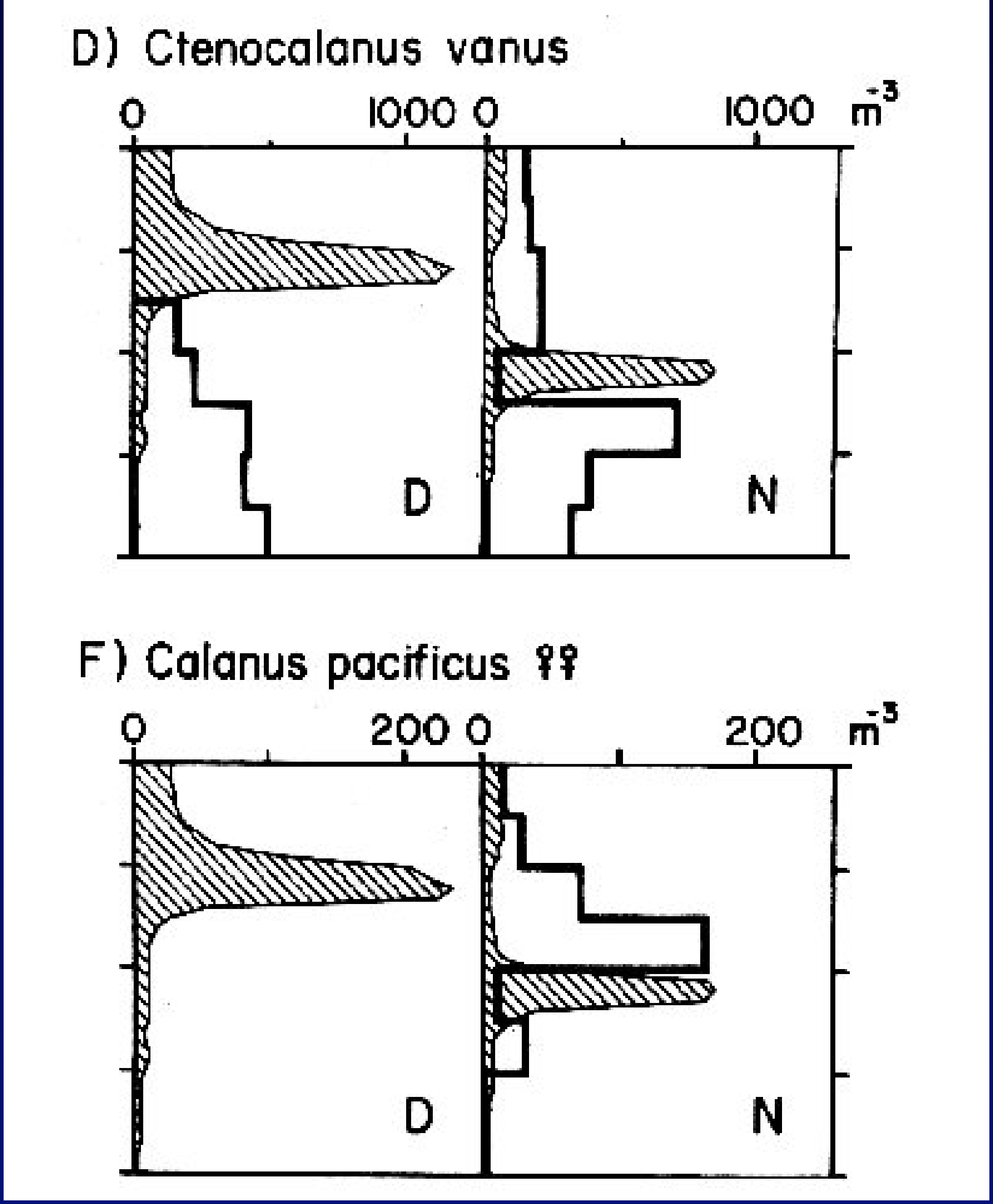
Specifically, fluorescence is measured to estimate chlorophyll



All phytoplankton have chlorophyll *a**

**Prochlorococcus* has divinyl Chl

…and chlorophyll is used as a measure of biomass



Fiedler PC (1982) Zooplankton avoidance and reduced grazing responses to *Gymnodinium splendens* (Dinophyceae). Limnology and Oceanography 27:961-965

However, the relationship between fluorescence and chlorophyll is variable

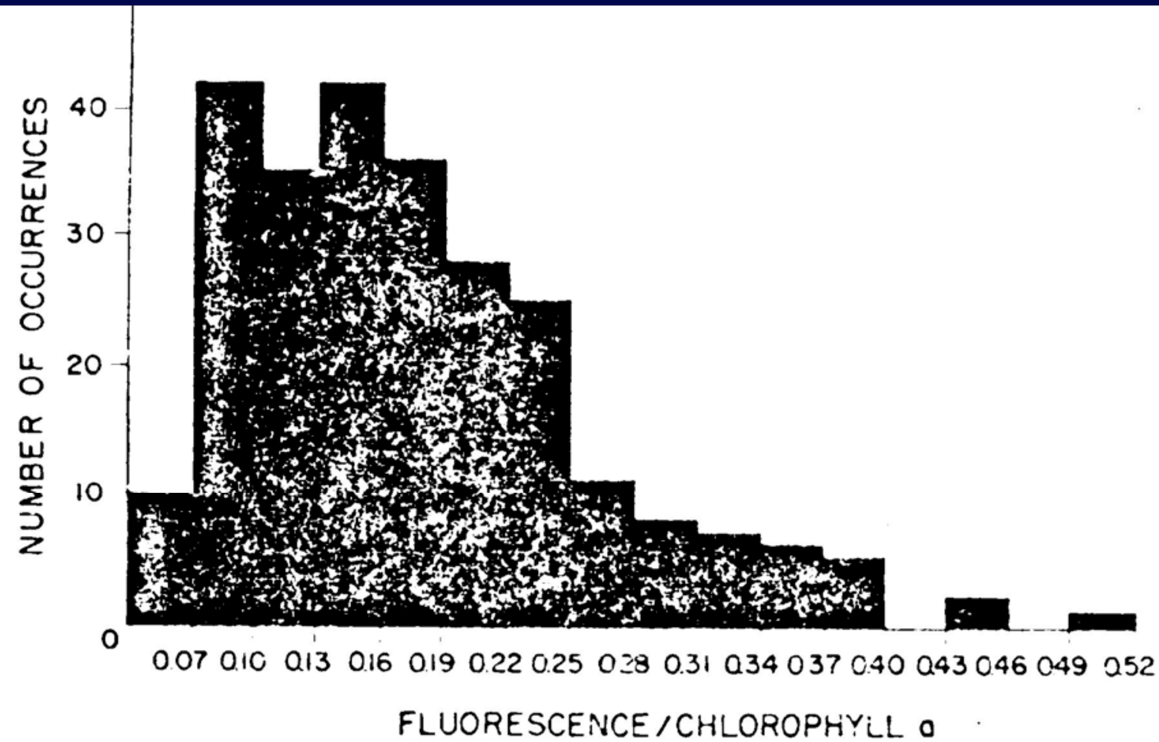


Fig. 1. Frequency polygon for all 250 measurements of fluorescence number made in coastal waters, Lake Tahoe, and Central North Pacific Gyre

Kiefer, Marine Biology, 1973a

As is the relationship between chlorophyll and biomass

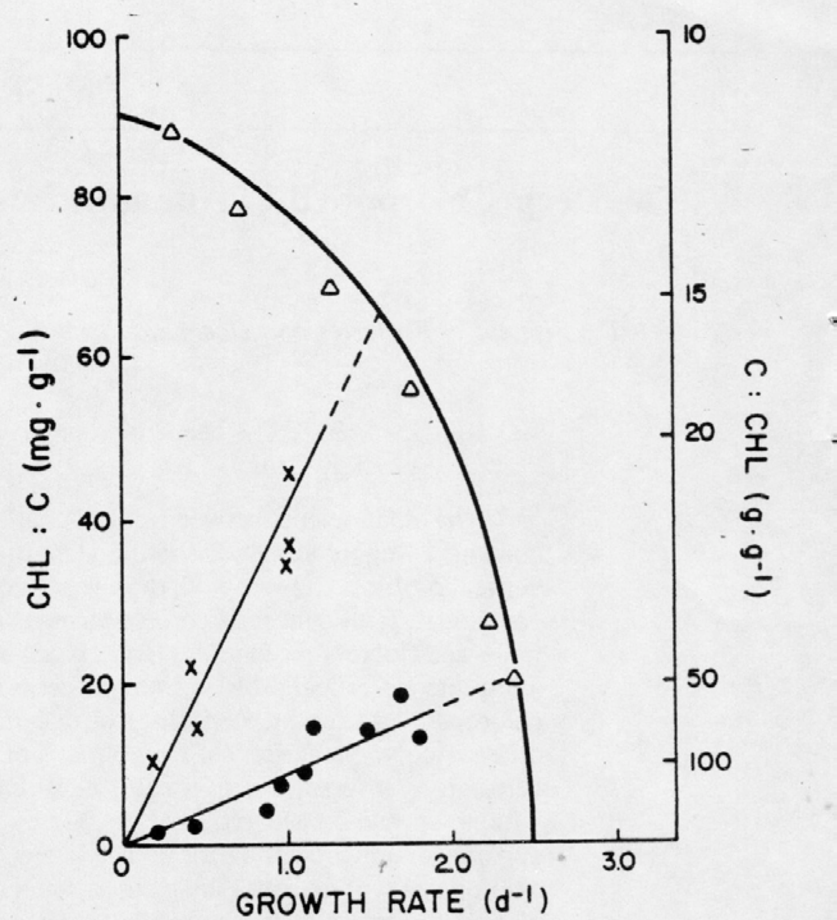


FIG. 1. The relationship between chlorophyll-to-carbon ratio (not C:Chl) and growth rate. Triangles, nutrient-saturated (light-limited) growth of *Chlorella pyrenoidosa* (Myers and Graham 1971); ×, nutrient-limited growth of *Thalassiosira pseudonana* at 0.07 $cal \cdot cm^{-2} \cdot min^{-1}$ and 12-h photoperiod (Eppley and Renger 1972; Perry 1976); circles, nitrate-limited growth of *T. pseudonana* at 0.1 $cal \cdot cm^{-2} \cdot min^{-1}$ continuous light (Caperon and Meyer 1972). In both light regimes, Chl:C is a linear function of nutrient-limited growth rate within the limits of precision, but at the lower irradiance the slope is steeper. The curve was calculated from a model presented by Bannister and Laws (1980), the source of this figure. C:Chl conversions are added for convenience.

Bannister TT, Laws EA (1980) Modeling phytoplankton carbon metabolism. In: Falkowski PG (ed) Primary Productivity in the Sea. Plenum, New York, p 243-248

Variability of fluorescence can be related to environmental conditions, species and physiological condition

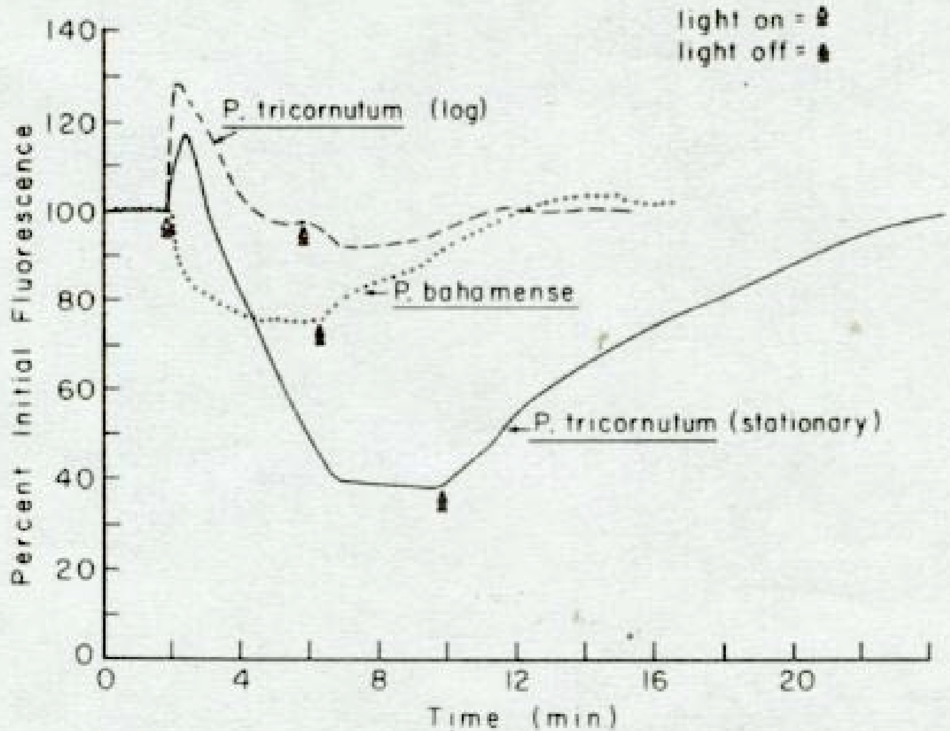
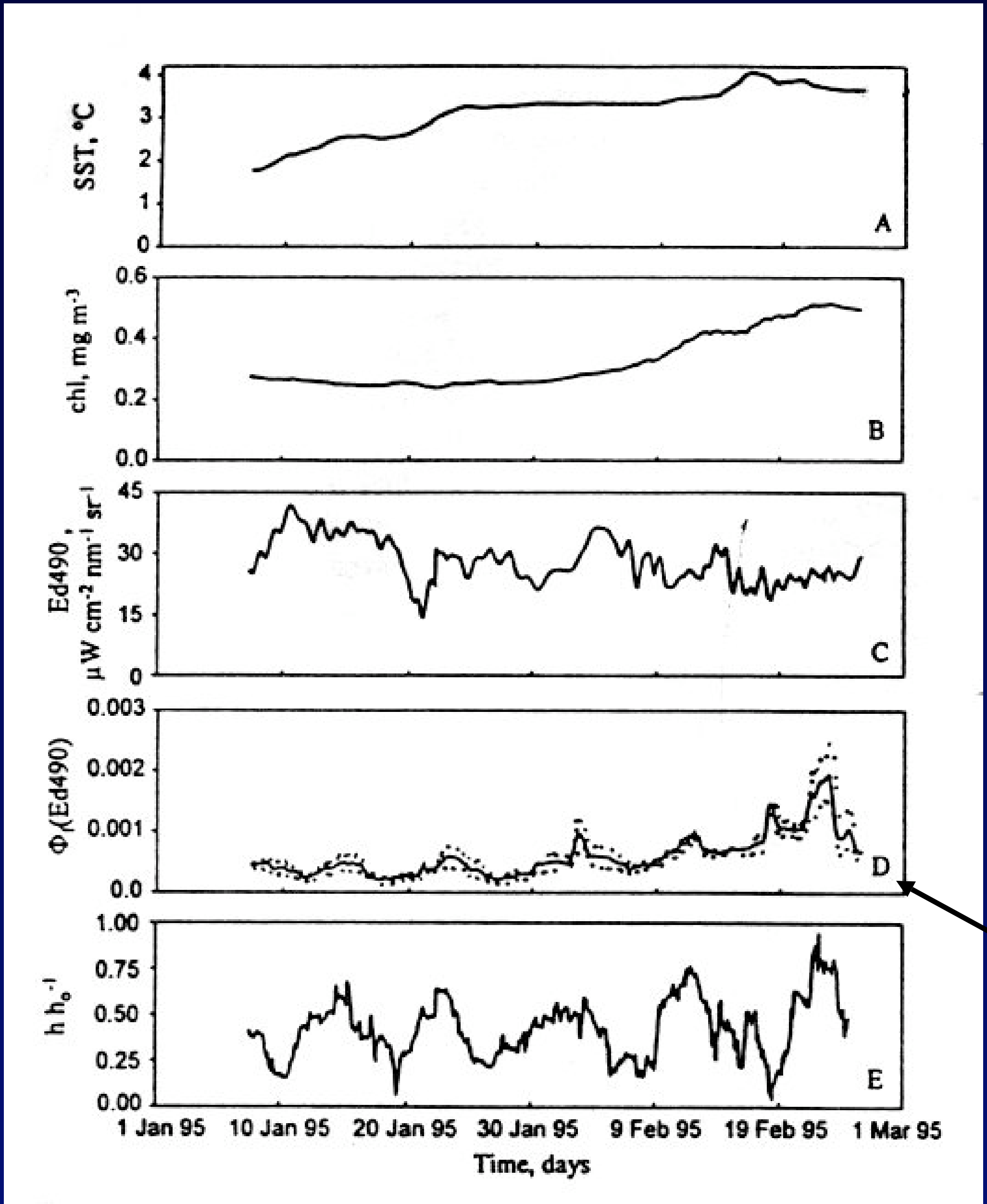


Fig. 4. The Kautsky induction effect elicited by conditions described in text for a natural population of *P. bahamense* and for *P. tricornutum* in log and stationary phase cultures.

Loftus ME, Seliger HH (1975) Some limitations of the *in vivo* fluorescence technique. Chesapeake Sci. 16:79-92

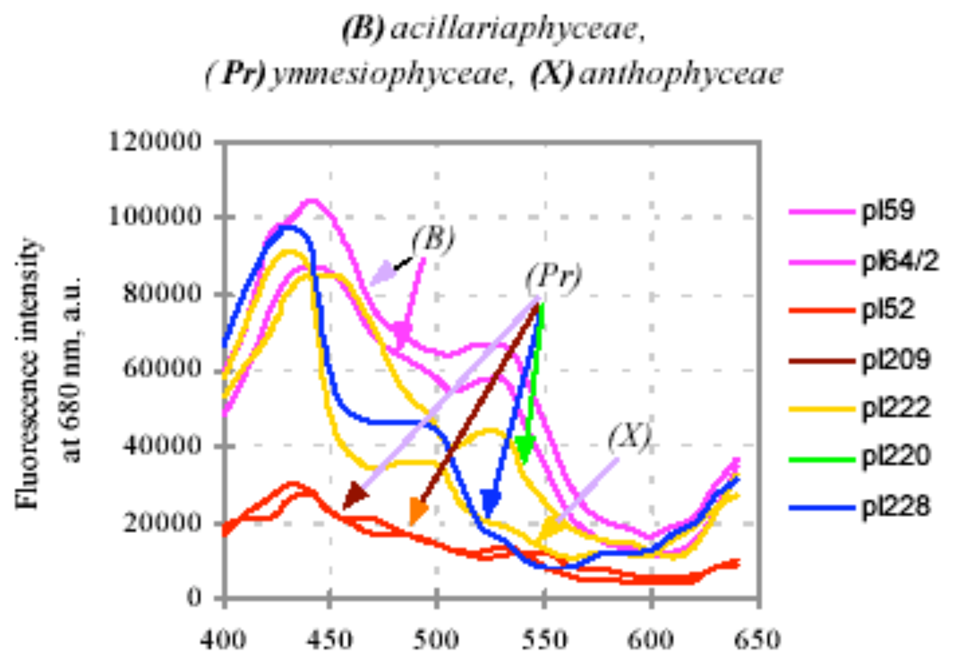


Information on physiological status is perhaps the ultimate reward

Fluorescence Yield

Letelier, R.M., Abbott MR, Karl DM (1996) Chlorophyll natural fluorescence response to upwelling events in the Southern Ocean. Geophysical Research Letters 24:409-412

Fluorescence can yield information on species composition

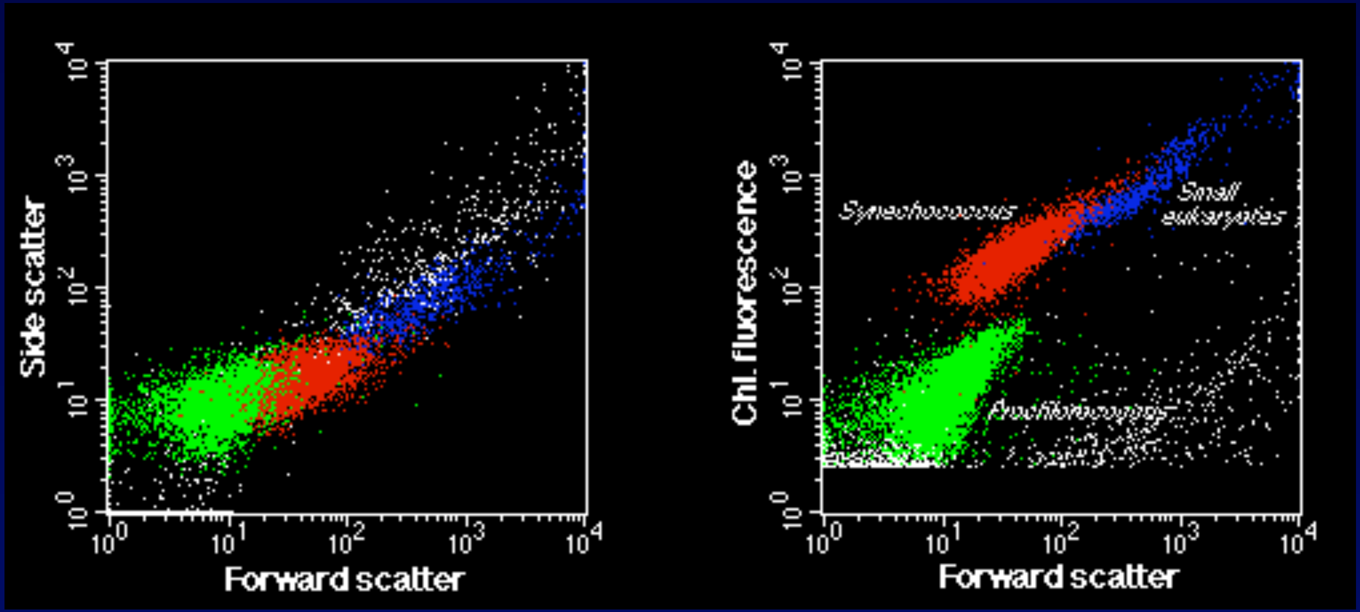


ANALYSIS OF PHYTOPLANKTON PIGMENTS BY EXCITATION SPECTRA OF FLUORESCENCE

Larisa Poryvkina, Sergey Babichenko and Aina Leeben

Institute of Ecology / LDI, Tallinn, Estonia

Flow Cytometry



www.bigelow.org/cytometry/Examples.html#GB

- Identification
- Physiological properties

Active Fluorescence

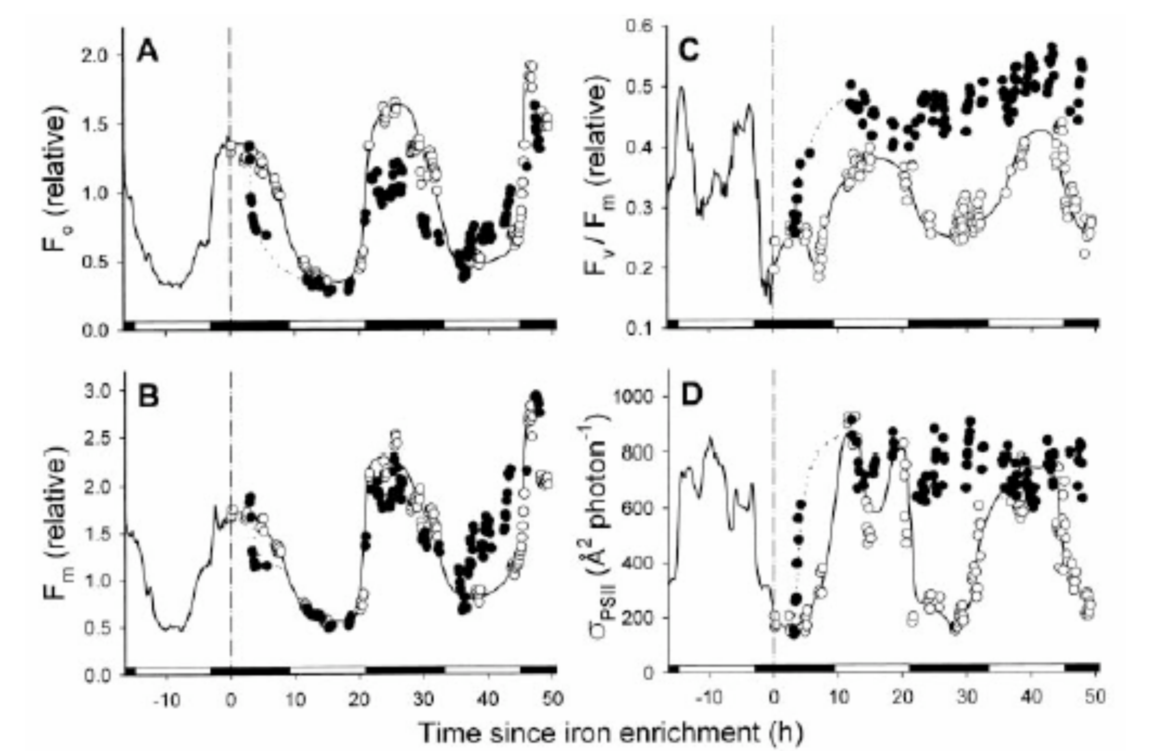


Fig. 2. Effects of in situ iron enrichment (2 nM iron) on diel fluorescence patterns in the South Pacific. (**A**) Initial fluorescence (F_O), (**B**) maximal fluorescence (F_m), (**C**) photochemical quantum efficiencies (F_v/F_m), (**D**) functional absorption cross sections of PSII (σ_{PSII}). Vertical dash-dot line indicates end of iron enrichment. Solid circles, fluorescence data collected inside the iron enrichment area; open circles, fluorescence data collected outside the enrichment area. Fluorescence patterns from the final day of the transect study (Fig. 1) are shown to the left of the vertical dash-dot line (negative time on *x* axis). Solid and open bars indicate night and day. Methods are described in (*5, 7*).

Behrenfeld and Kolber 1999, Science

- FRRF
- PAM
- FIRe
- Benchtop
- Submersible
- Physiology
- Controversies
- Technical issues

…and the rate of photosynthesis

$$f(t) = F_o + (F_m - F_o)\left(C(t)\frac{1-p}{1-C(t)p}\right)$$

$$\frac{\partial C(t)}{\partial I} = \sigma_{PS\,II}\frac{1-C(t)}{1-C(t)p}.$$

$$\frac{dC(t)}{dt} = \sigma_{PS\,II}\frac{dI}{dt}\frac{1-C(t)}{1-C(t)p} = \sigma_{PS\,II}\, i(t)\frac{1-C(t)}{1-C(t)p}$$

$$C(t) = \int_0^t \sigma_{PS\,II}\, i(\upsilon)\frac{1-C(\upsilon)}{1-C(\upsilon)p}d\upsilon,$$

$$C(t) = \int_0^t \sigma_{PS\,II}\, i(\upsilon)\frac{1-C(\upsilon)}{1-C(\upsilon)p}g(t-\upsilon)d\upsilon$$

$$g(t-\upsilon) = g(\Delta t) = \alpha_1\exp(-\Delta t/\tau_1)$$

$$+\alpha_2\exp(-\Delta t/\tau_2) + \alpha_3\exp(-\Delta t/\tau_3).$$

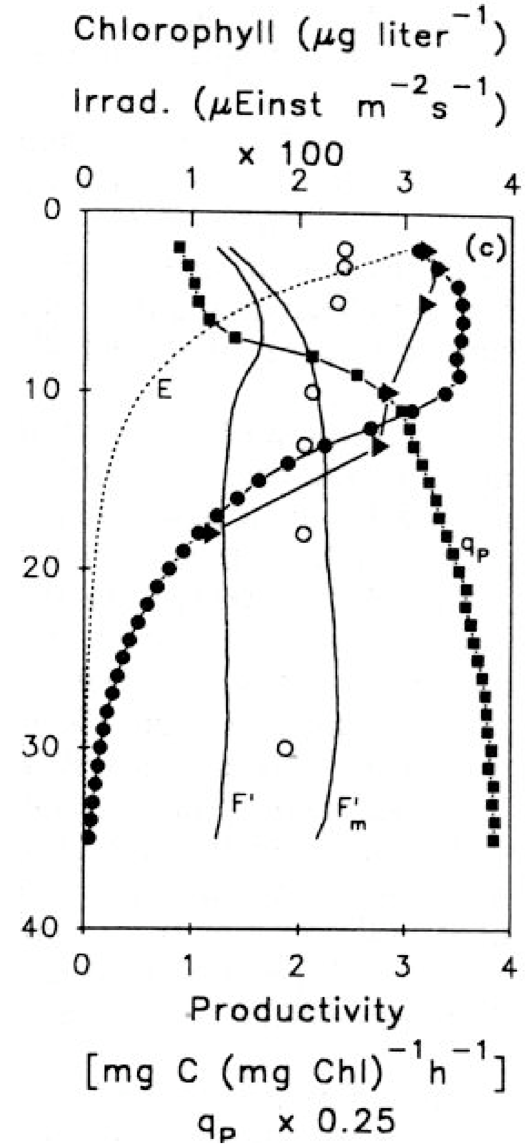
$$f_n = F_o + (F_m - F_o)C_n\frac{1-p}{1-C_n p}$$

$$C_n - C_{n-1}\sum_{k=1}^{m}A_{n,k} + I_n\sigma_{PS\,II}\frac{1-\left(C_{n-1}\sum_{k=1}^{m}A_{n,k}\right)}{1-p\left(C_{n-1}\sum_{k=1}^{m}A_{n,k}\right)}$$

$$A_{n,k} = (A_{n-1,k} + C_{n-1}\alpha_k/\sigma_{PS\,II})\exp(-\Delta t/\tau_k).$$

$$C(t) = \sigma_{PS\,II}\int_0^t i(\upsilon)\frac{F_m - f(\upsilon)}{F_m - F_o}d\upsilon = \sigma_{PS\,II}\int_0^t [i(\upsilon)q_p(\upsilon)]d\upsilon.$$

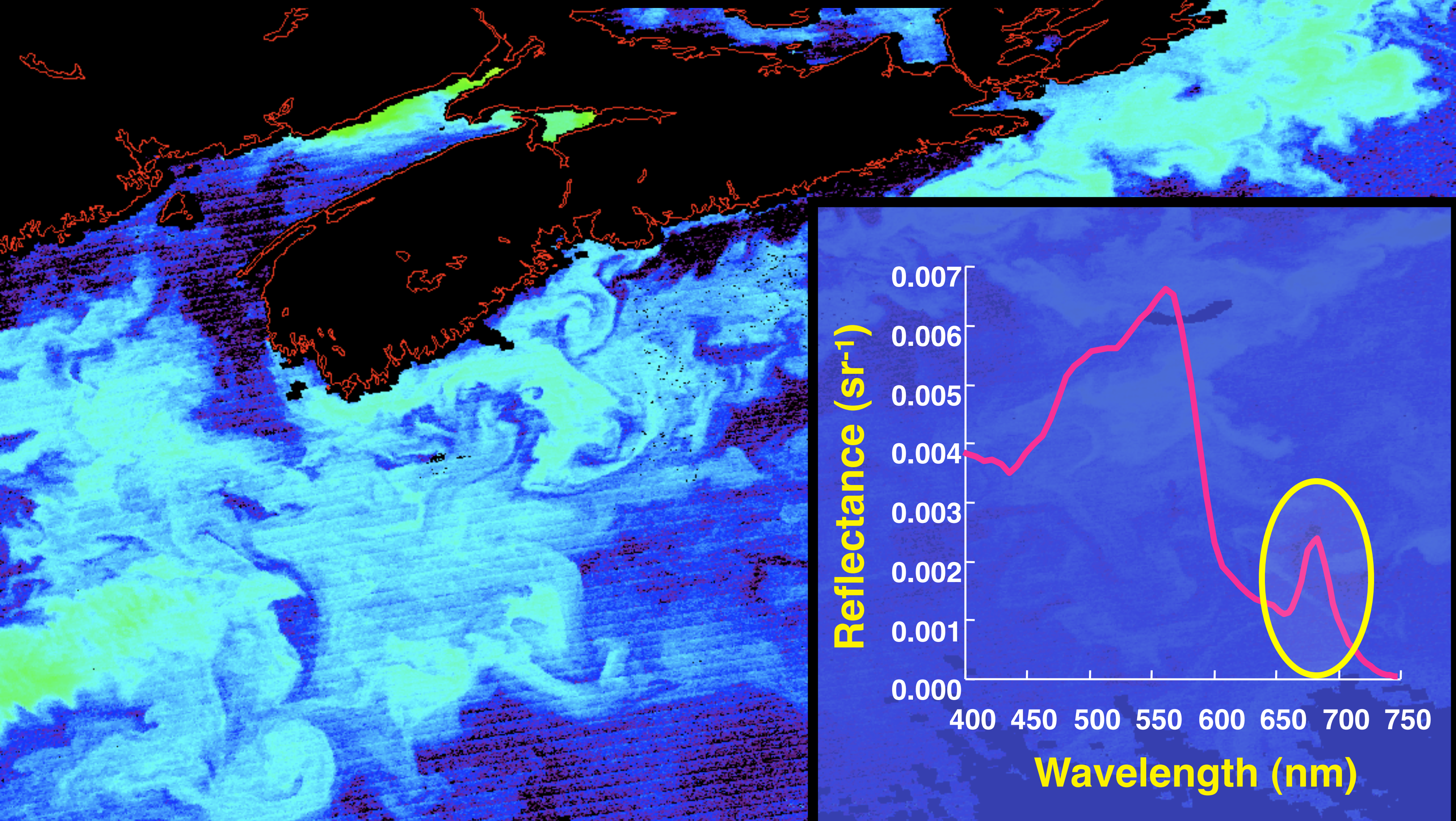
$$\sigma_{PS\,II} = \left[\int_0^\infty [i(\upsilon)q_p(\upsilon)]d\upsilon\right]^{-1}$$



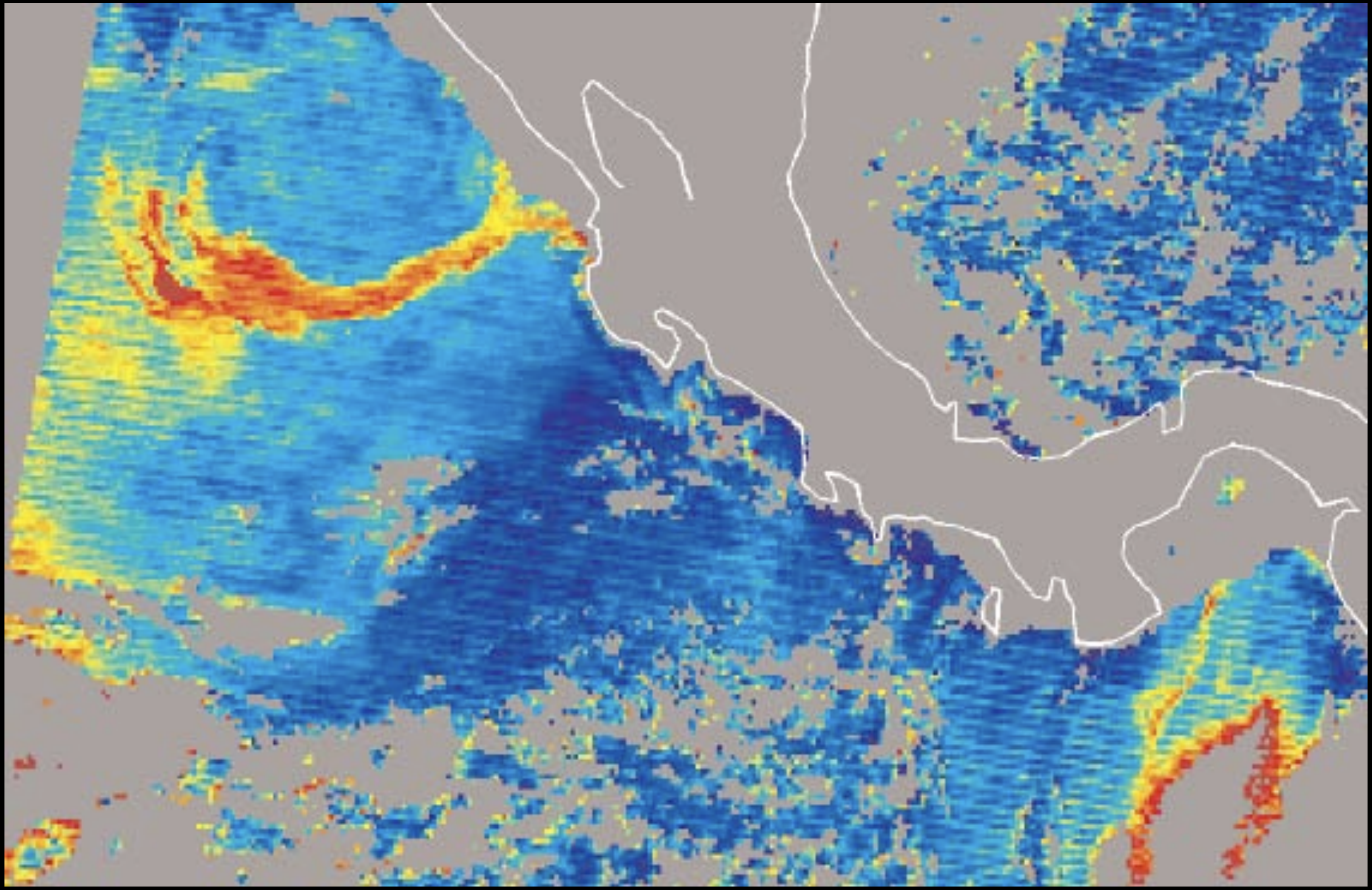
Kolber Z, Falkowski PG (1993) Use of active fluorescence to estimate phytoplankton photosynthesis in situ. Limnology and Oceanography 38:1646-1665

Sun Induced Chlorophyll Fluorescence:

The only signal emitted from the ocean and detectable from space that can be unambiguously ascribed to phytoplankton



The big goal:
Interpreting natural variability of φ_f as detected from space



What does an oceanographer need to know?

What does an oceanographer need to know?

- Principles of measurement

What does an oceanographer need to know?

- Principles of measurement
- Physiological processes

What does an oceanographer need to know?

- Principles of measurement
- Physiological processes
- Environmental influences

What does an oceanographer need to know?

- Principles of measurement
- Physiological processes
- Environmental influences
- Taxonomic variability

What does an oceanographer need to know?

- Principles of measurement
- Physiological processes
- Environmental influences
- Taxonomic variability

…and interactions among all of these

Measurement of Fluorescence

History: 1966

In the beginning…

Deep-Sea Research, 1966, Vol. 13, pp. 223 to 227. Pergamon Press Ltd. Printed in Great Britain.

A method for the continuous measurement of *in vivo* chlorophyll concentration*

CARL J. LORENZEN†

(*Received* 7 *December* 1965)

Abstract—*In vivo* chlorophyll, like many other organic molecules, possesses the ability to fluoresce. This fluorescence was measured continuously with a modified model III Turner fluorometer at sea. Reliable readings were obtained over the range of 0·04–2·0 mg chlorophyll *a* m^{-3} while on a 21-day cruise off the coast of Baja California. Since the relationship between fluorescence and chlorophyll was linear on all scales, it should be possible to continuously monitor chlorophyll from 0·04 to between 10 and 15 mg m^{-3}, a range adequate for all open ocean studies.

Benchtop Fluorometer

- Blue Excitation
- Red emission
- Discrete samples
- Flow-through
- Low excitation
- High sensitivity

Turner, Turner Designs (brown), Turner Designs (black)
(watch out for lamp changes)

Pandora's Box

John Cullen -

cmep
Centre for Marine Environmental Prediction

Lorenzen covered the bases

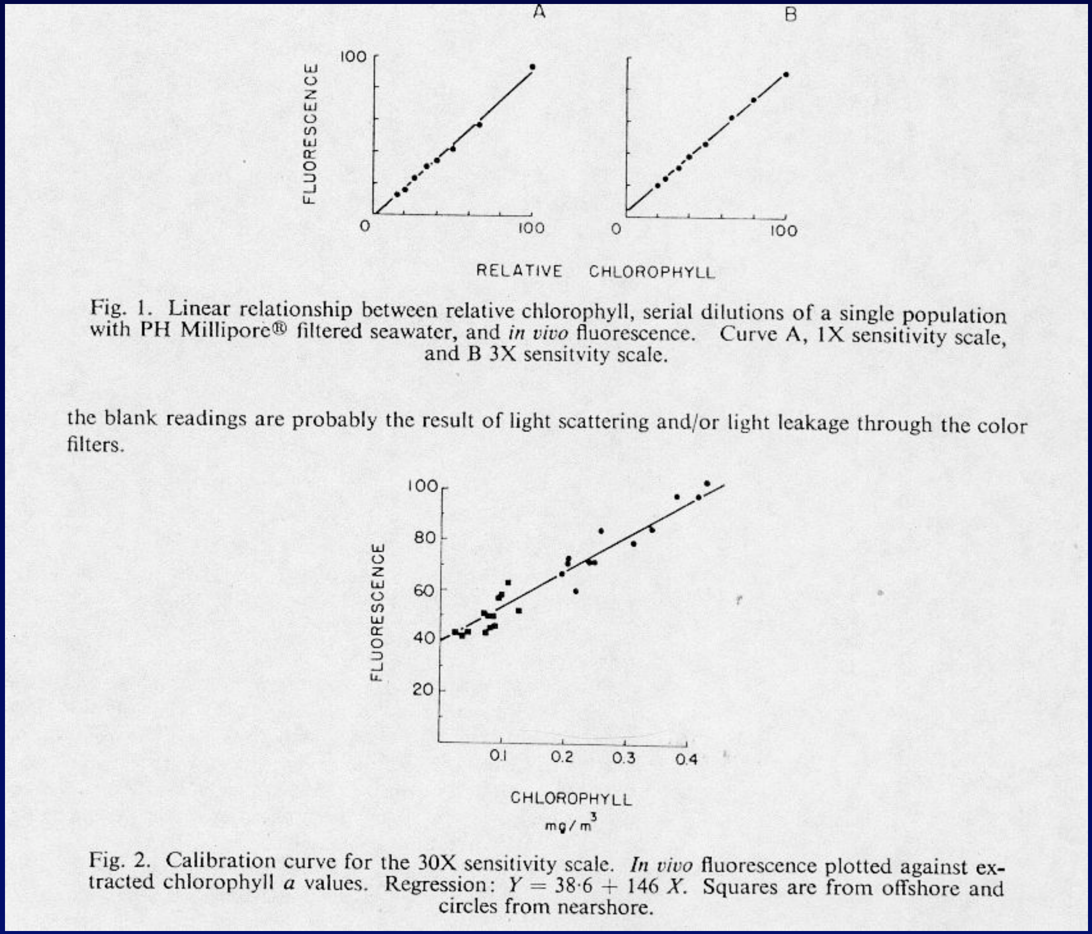


Fig. 1. Linear relationship between relative chlorophyll, serial dilutions of a single population with PH Millipore® filtered seawater, and *in vivo* fluorescence. Curve A, 1X sensitivity scale, and B 3X sensitvity scale.

the blank readings are probably the result of light scattering and/or light leakage through the color filters.

Fig. 2. Calibration curve for the 30X sensitivity scale. *In vivo* fluorescence plotted against extracted chlorophyll *a* values. Regression: $Y = 38{\cdot}6 + 146\ X$. Squares are from offshore and circles from nearshore.

Calibration, linearity, possible interference

Lorenzen 1966

Early application:
Transects of Chlorophyll

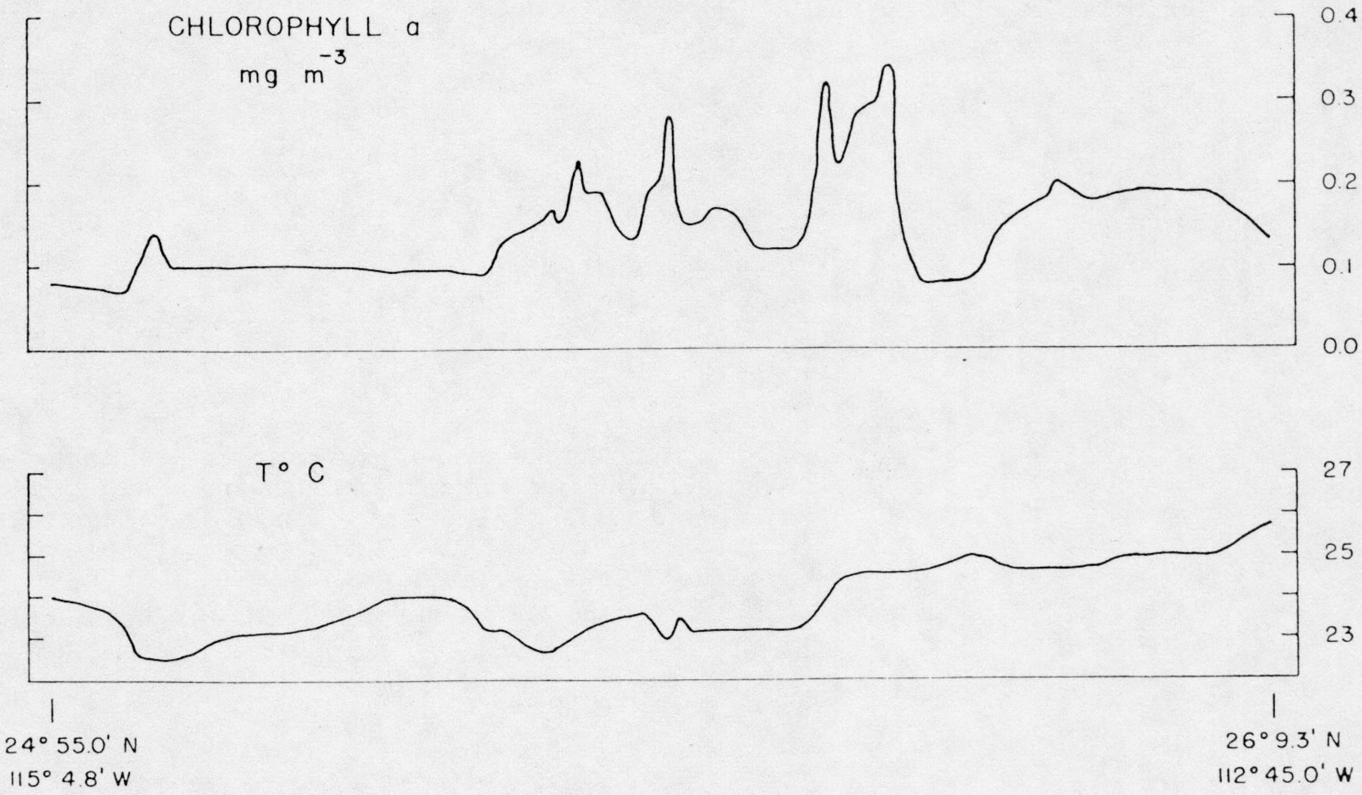
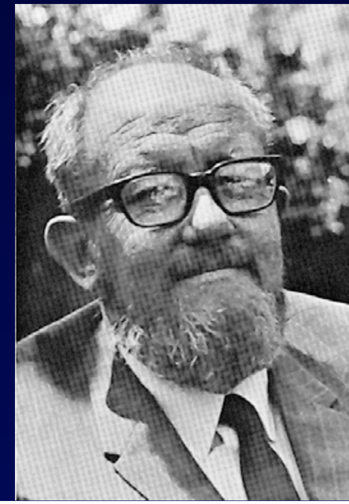


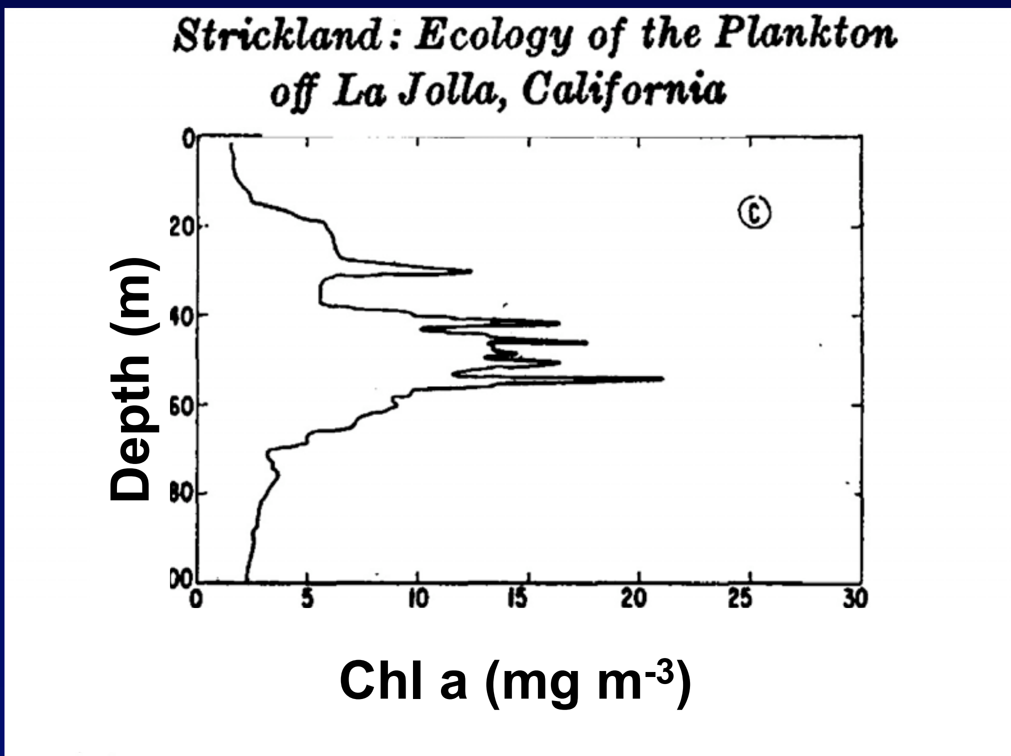
Fig. 3. A portion of the trace obtained on cruise TO–65–1 showing variations in chlorophyll *a* concentrations and temperature as the ship proceeded from 24° 55·0N′–115° 04·8′W to 26° 09·3′N 112° 45·0′W.

Lorenzen 1966

Continuous vertical profiles



John Strickland
and the
Food Chain
Research Group
1967 Red Tide Study



Fluorescence

Carl Lorenzen

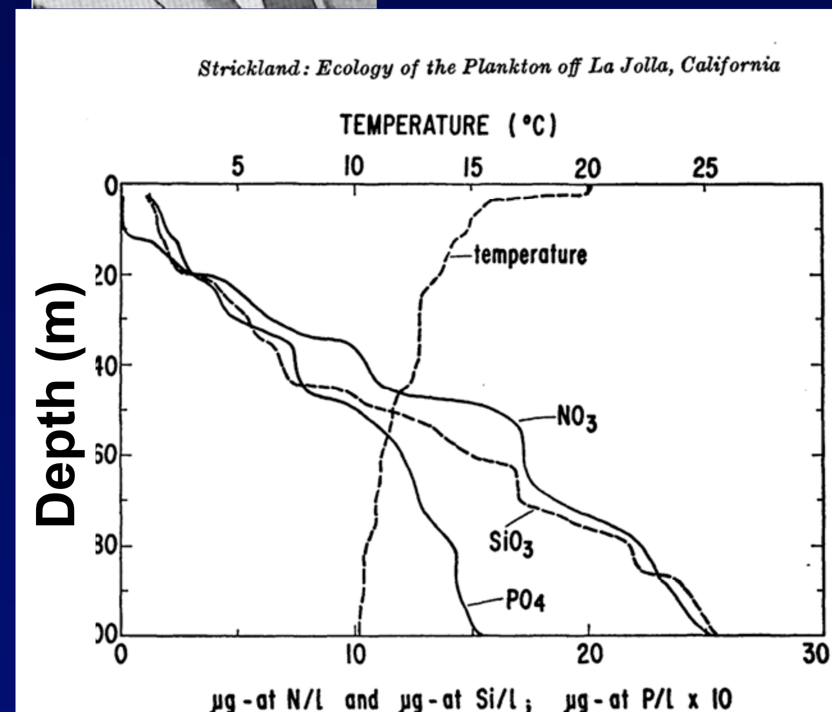


Fig. I-8. Profile of phosphate, nitrate, and silicate concentrations and temperature at station 3, 19 July 1967.

Nutrients, too!

John Cullen – Agouron – 2008

Lorenzen described the measurement of blanks

Volume 12 (2) June 2003

Pages 29–35

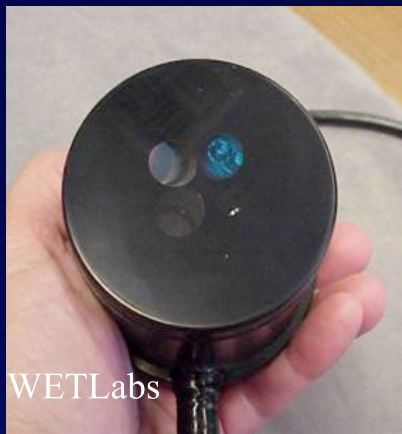
LIMNOLOGY AND OCEANOGRAPHY
BULLETIN

Published by the American Society of Limnology and Oceanography

THE BLANK CAN MAKE A BIG DIFFERENCE IN OCEANOGRAPHIC MEASUREMENTS

John J. Cullen and Richard F. Davis, Department of Oceanography, Dalhousie University, Halifax, NS B3H 4J1 Canada; john.cullen@dal.ca, richard.davis@dal.ca

In situ Fluorometer

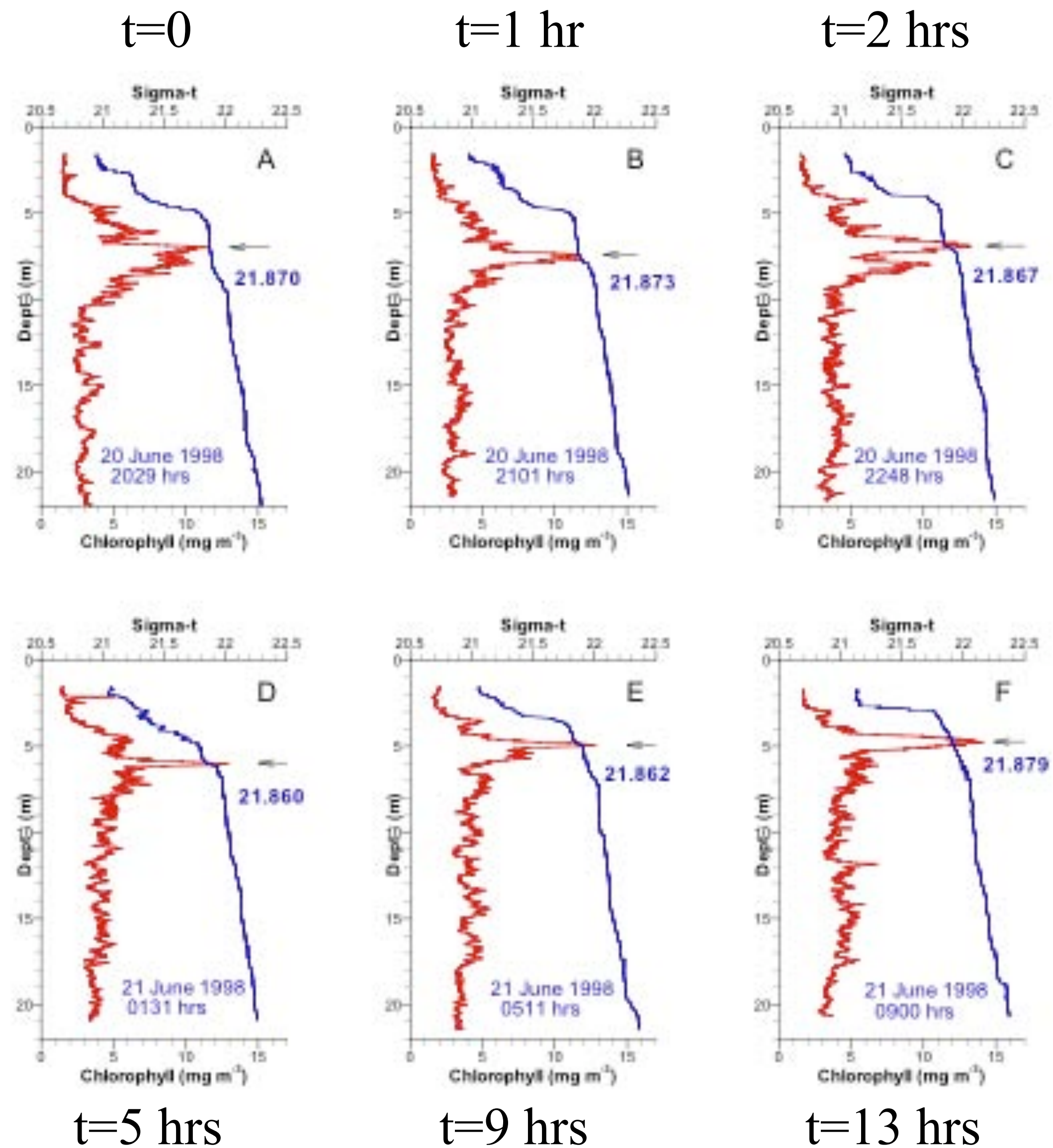


- Profilers
- Moorings
- Pulsed
- High sensitivity
- Ambient irradiance influences fluorescence yield

Frequency, intensity and spectral quality of excitation varies with manufacturer.

Now an indispensable tool

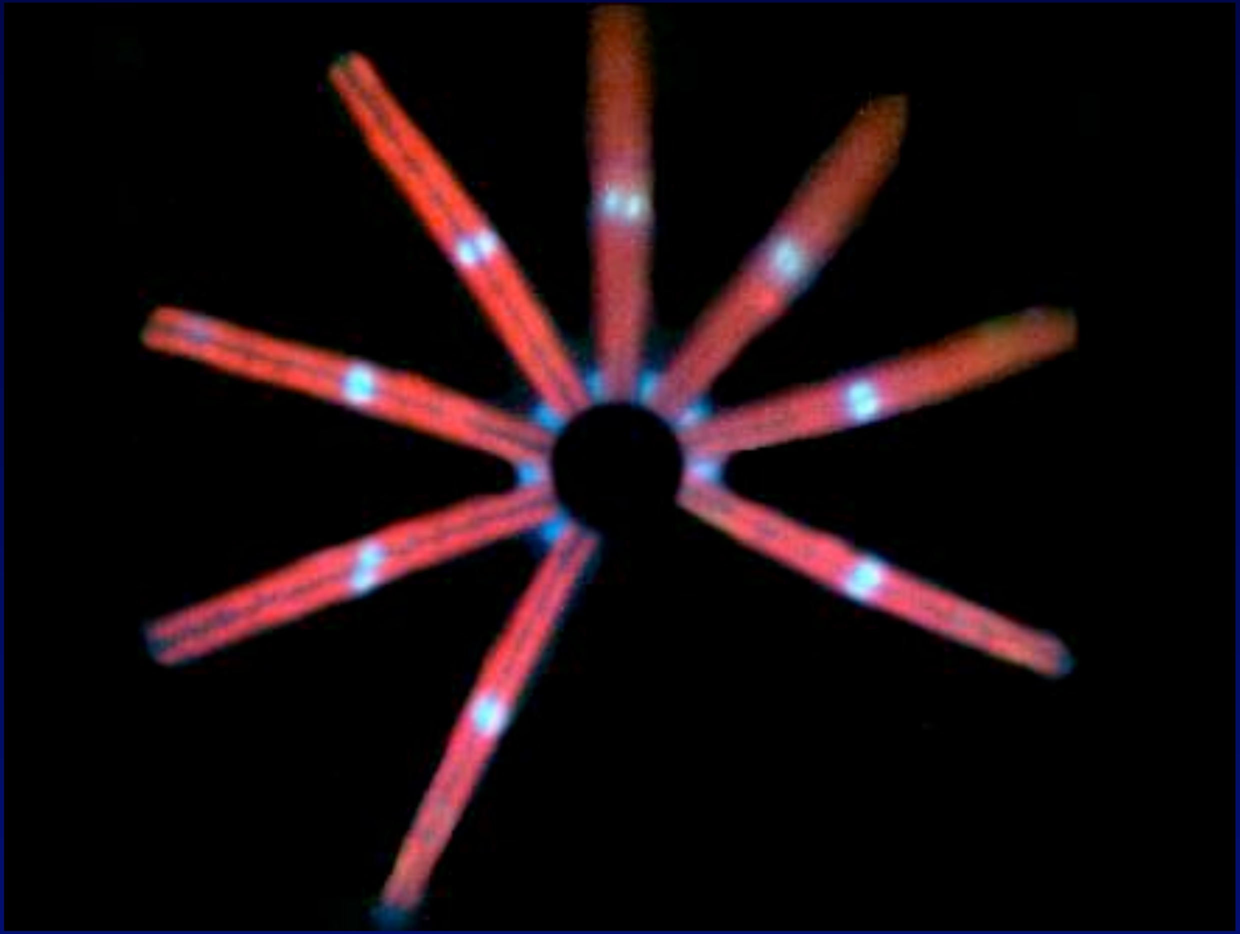
Six vertical profiles of chlorophyll fluorescence (mg m^{-3}) and sigma-t (kg m^{-3}) from a 13 hr time series of 90 profiles.



Tim Cowles, Oregon State University

…but what do fluorometers measure?

chlorophyll fluorescence, not chlorophyll



Sieracki

Physiological effects on fluorescence yield (Fl/Chl) were recognized early

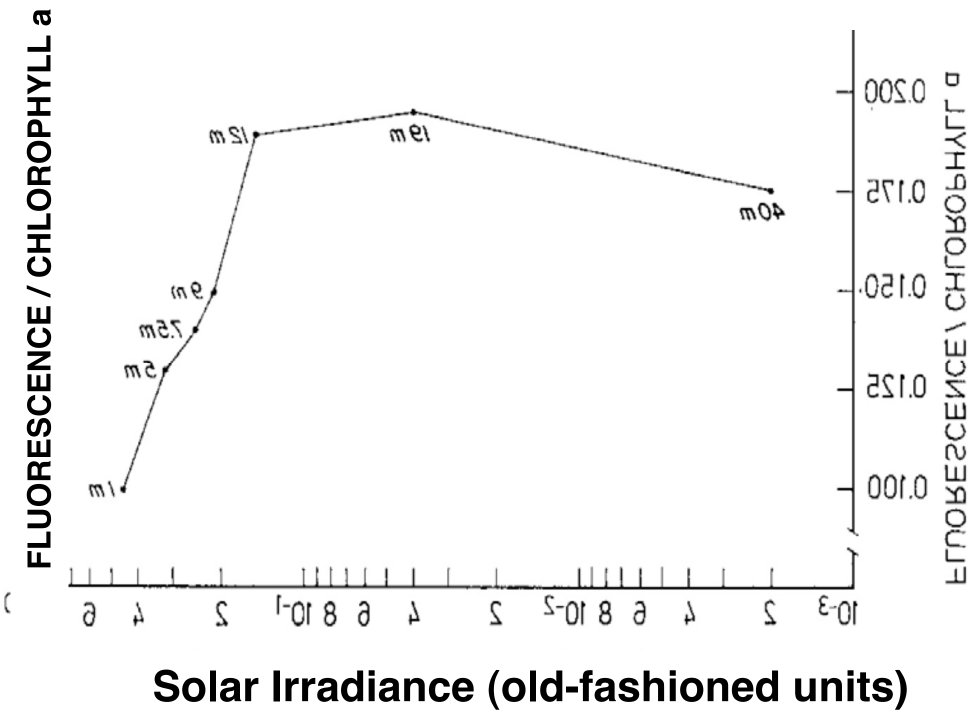


Fig. 4. Fluorescence numbers as function of downwelling solar irradiance (ly/min) for vertical profile off Puerto Vallarta, Mexico. Number next to each point gives depth of sample. Irradiance was measured with the Scripps spectroradiometer

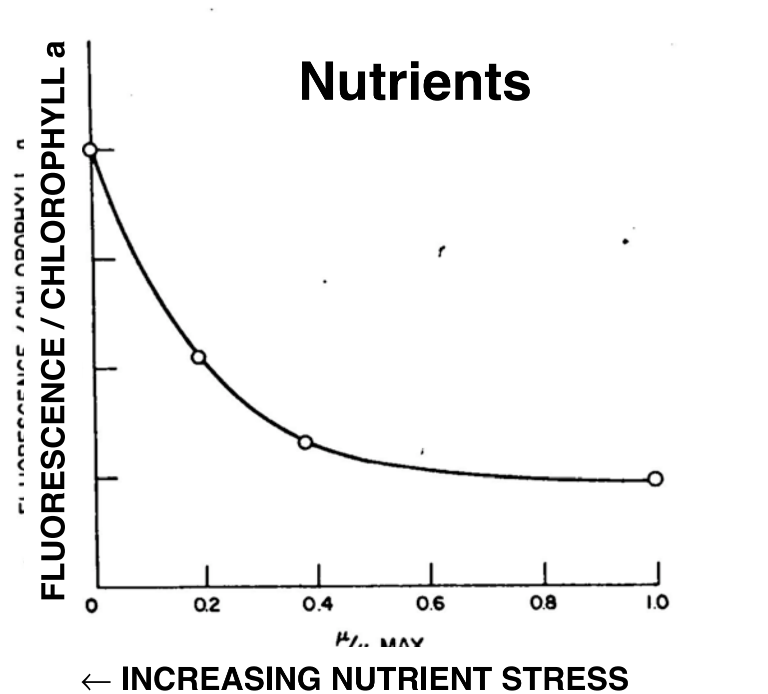


Fig. 8. *Cyclotella nana*. Effect of nitrogen deficiency upon fluorescence number for 4 cultures. Stress was described by the ratio μ/μmax, where μ is specific growth rate of culture (divisions/day), and μmax is maximal specific growth rate (1.6 divisions/day) for culturing conditions

Kiefer DA (1973) Fluorescence properties of natural phytoplankton assemblages. Marine Biology 22:263-269

Loftus ME, Seliger HH (1975) Some limitations of the *in vivo* fluorescence technique. Chesapeake Sci. 16:79-92

Natural variability of fluorescence yield was quantified and tentatively interpreted: effects of nutrition and irradiance

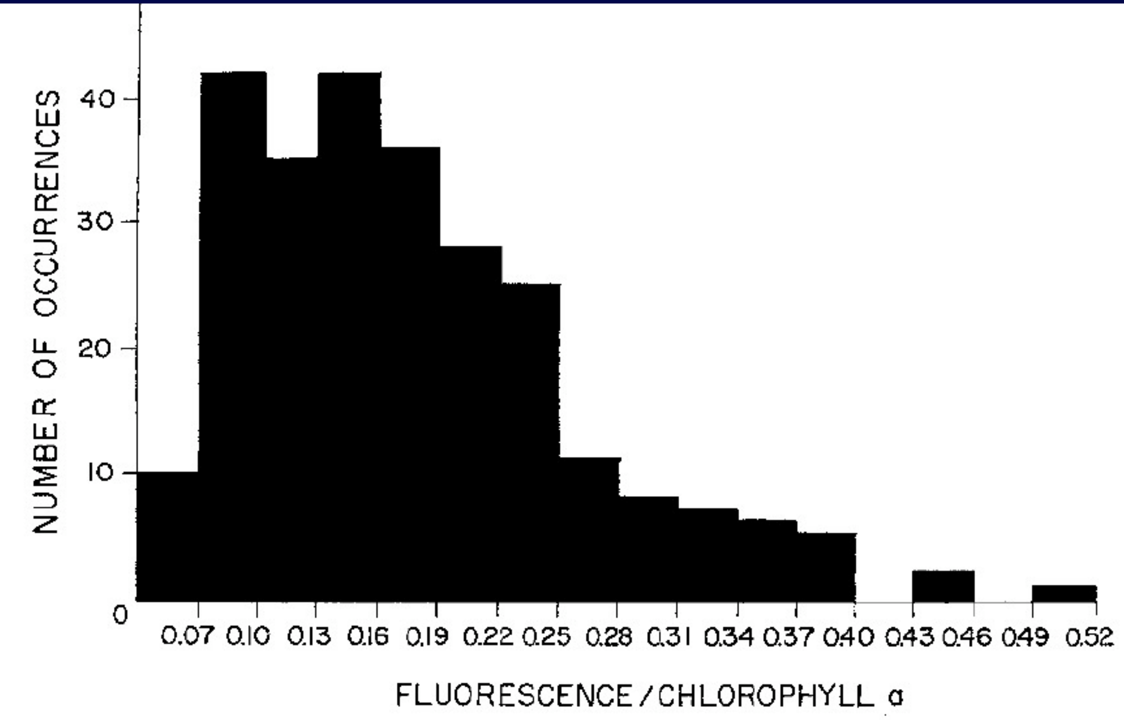


Fig. 1. Frequency polygon for all 250 measurements of fluorescence number made in coastal waters, Lake Tahoe, and Central North Pacific Gyre

Kiefer DA (1973) Fluorescence properties of natural phytoplankton assemblages. Marine Biology 22:263-269

Loftus ME, Seliger HH (1975) Some limitations of the *in vivo* fluorescence technique. Chesapeake Sci. 16:79-92

Variability in the quantum yield of fluorescence:

φ_f (mols photons emitted per mol photons absorbed)

can be expressed in terms of rate constants (k, s^{-1}) for the three possible fates of absorbed photons:

FLUORESCENCE, PHOTOSYNTHESIS, HEAT

$$\varphi_f = \frac{k_f}{k_f + k_p + k_H}$$

From Yannick Huot

Variability in the quantum yield of fluorescence:

φ_f (mols photons emitted per mol photons absorbed)

can be expressed in terms of rate constants (k, s^{-1}) for the three possible fates of absorbed photons:

FLUORESCENCE, PHOTOSYNTHESIS, HEAT

Fluorescence (Constant)

$$\varphi_f = \frac{k_f}{k_f + k_p + k_H}$$

From Yannick Huot

Variability in the quantum yield of fluorescence:

φ_f (mols photons emitted per mol photons absorbed)

can be expressed in terms of rate constants
(*k*, s^{-1}) for the <u>three possible fates</u> of absorbed photons:

FLUORESCENCE, PHOTOSYNTHESIS, HEAT

Fluorescence
(Constant)

$$\varphi_f = \frac{k_f}{k_f + k_p + k_H}$$

Photosynthesis
(Variable)

From Yannick Huot

Variability in the quantum yield of fluorescence:

φ_f (mols photons emitted per mol photons absorbed)

can be expressed in terms of rate constants
(k, s^{-1}) for the three possible fates of absorbed photons:

FLUORESCENCE, PHOTOSYNTHESIS, HEAT

Fluorescence
(Constant)

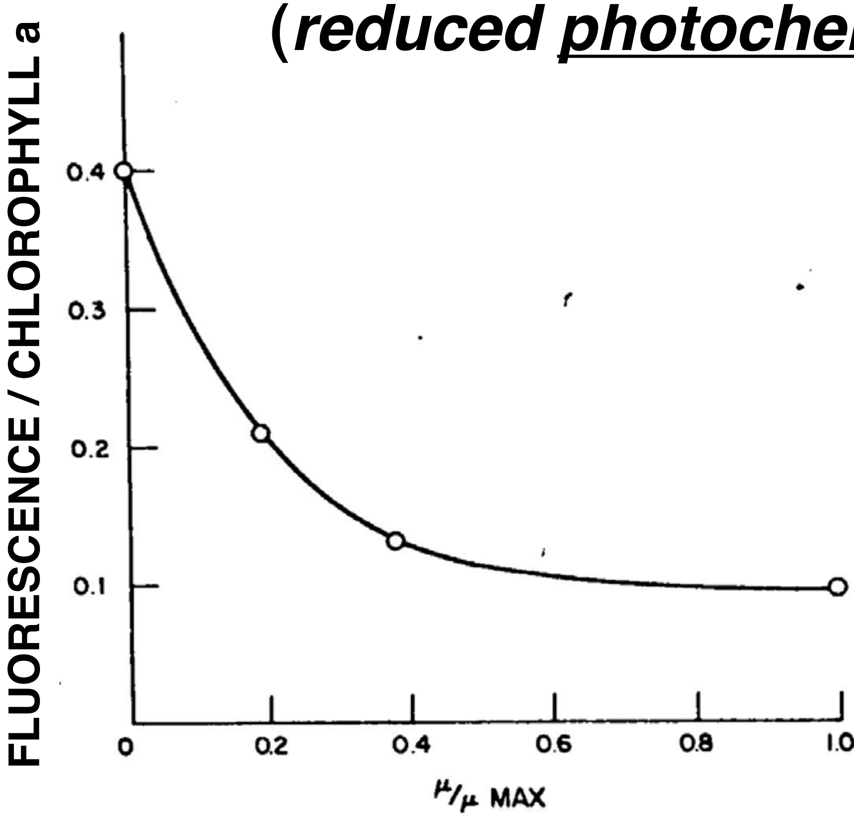
$$\varphi_f = \frac{k_f}{k_f + k_p + k_H}$$

Photosynthesis
(Variable)

Heat
(Variable)

From Yannick Huot

Nutrient Stress
Leading to Higher Fluorescence Yield
(*reduced* ***photochemical quenching***)



← **INCREASING NUTRIENT STRESS**

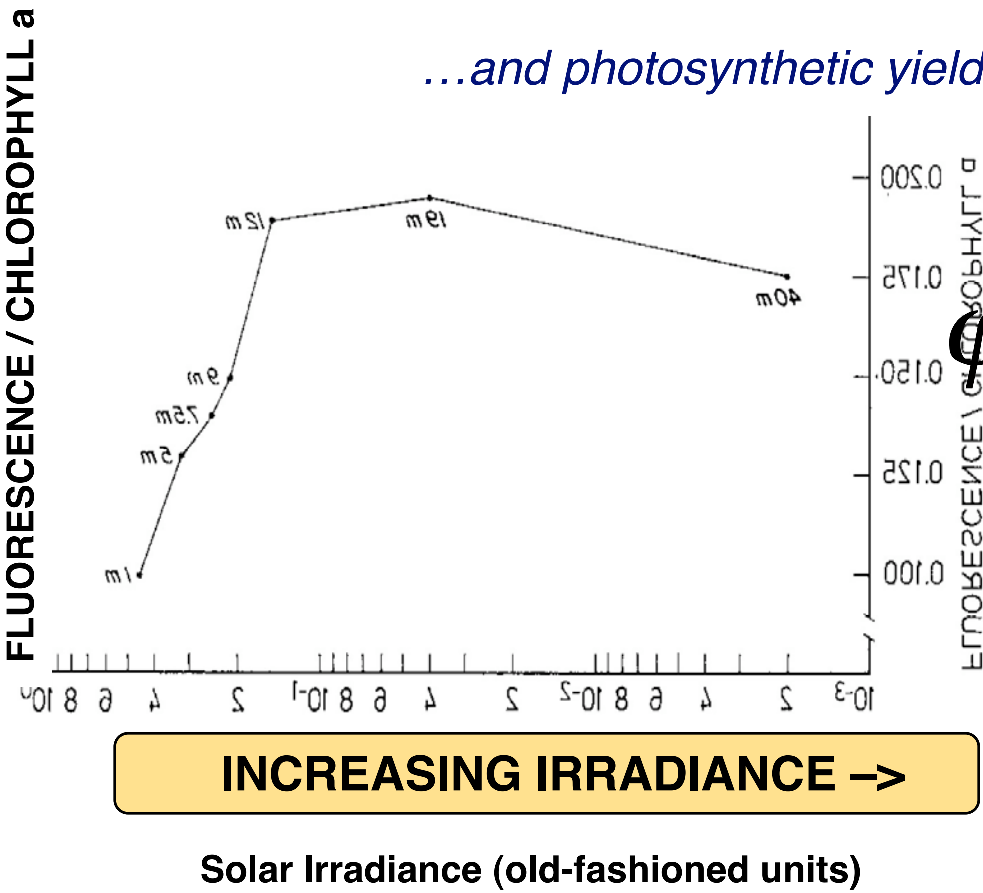
$$\varphi_f = \frac{k_f}{k_f + k_p + k_H}$$

k_p decreases and φ_f increases

Kiefer DA (1973) Marine Biology 22:263-269

Excess Irradiance Leads to Lower Fluorescence Yield (*increased <u>nonphotochemical quenching</u>*)

…and photosynthetic yield is reduced as well

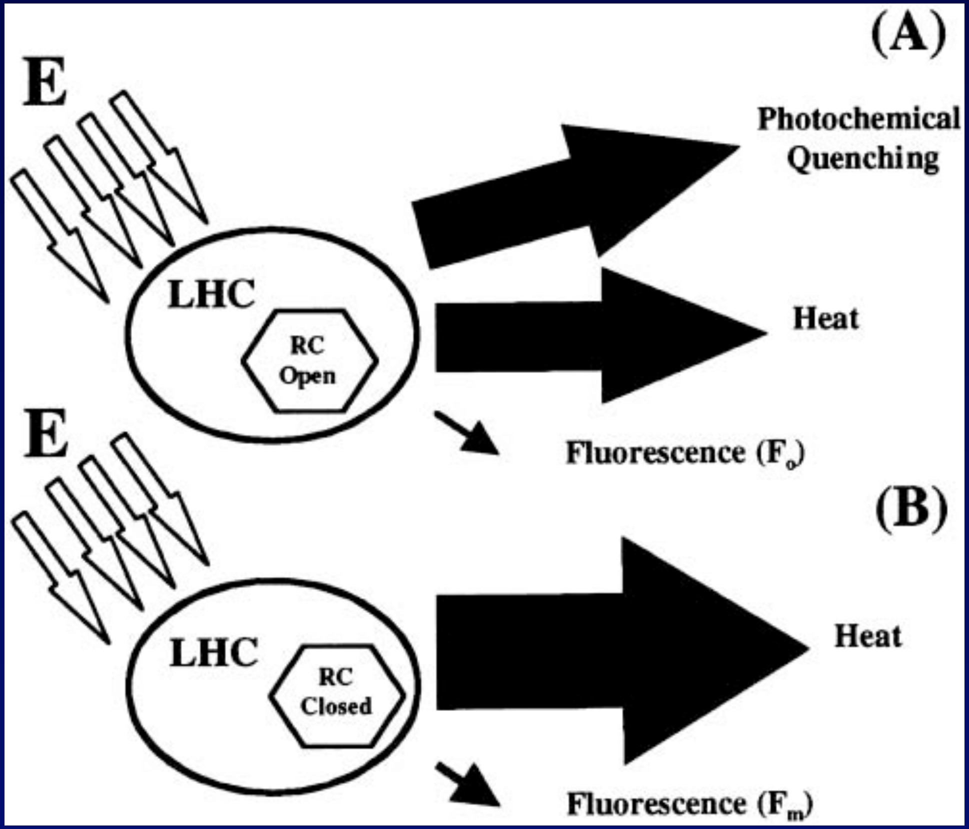


Kiefer DA (1973) Marine Biology 22:263-269

$$\varphi_f = \frac{k_f}{k_f + k_p + k_H}$$

k_H increases and φ_f decreases

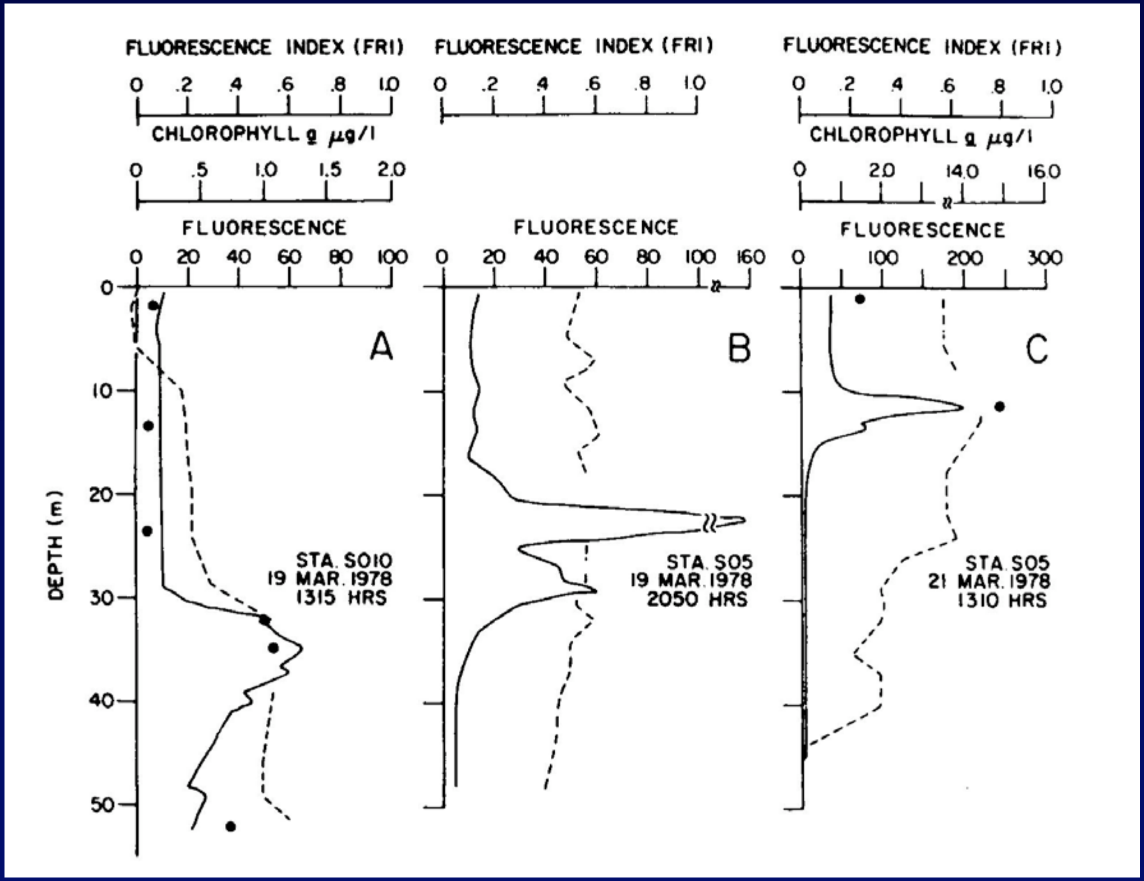
Photosynthetic Efficiency Explored by Measuring Change in Fluorescence upon Closure of Reaction Centers (e.g., Fv/Fm with DCMU)



Samuelsson, G. and G. Öquist (1977). "A method for studying photosynthetic capacities of unicellular algae based on in vivo chlorophyll fluorescence." Plant Physiology 40: 315-319.

Parkhill et al. 2001

The first continuous measurements of F_v / F_m employed the Turner Designs



Cullen JJ, Renger EH (1979) Continuous measurement of the DCMU-induced fluorescence response of natural phytoplankton populations. Marine Biology 53:13-20.

See also

Roy S, Legendre L (1979) DCMU-enhanced fluorescence as an index of photosynthetic activity in phytoplankton. Marine Biology 55:93-101

Roy S, Legendre L (1979) Field studies of DCMU-enhanced fluorescence as an index of in situ phytoplankton photosynthetic activity. Canadian Journal of Fisheries and Aquatic Sciences 37:1028-1031

Results were more provocative than conclusive

> We may not know exactly what we are measuring, but the patterns observed are too strong to ignore.

Cullen JJ, Renger EH (1979) Continuous measurement of the DCMU-induced fluorescence response of natural phytoplankton populations. Marine Biology 53:13-20.

Conclusion (early 80's):

PERSPECTIVES

The Deep Chlorophyll Maximum: Comparing Vertical Profiles of Chlorophyll *a*

JOHN J. CULLEN[1]

Department of Fisheries and Oceans, Marine Ecology Laboratory, Bedford Institute of Oceanography, Dartmouth, N.S. B2Y 4A2

CULLEN, J. J. 1982. The deep chlorophyll maximum: comparing vertical profiles of chlorophyll *a*. Can. J. Fish. Aquat. Sci. 39: 791 – 803.

Conclusion (early 80's):

PERSPECTIVES

The Deep Chlorophyll Maximum: Comparing Vertical Profiles of Chlorophyll *a*

JOHN J. CULLEN[1]

Department of Fisheries and Oceans, Marine Ecology Laboratory, Bedford Institute of Oceanography, Dartmouth, N.S. B2Y 4A2

CULLEN, J. J. 1982. The deep chlorophyll maximum: comparing vertical profiles of chlorophyll *a*. Can. J. Fish. Aquat. Sci. 39: 791–803.

Physiological and taxonomic influences on <u>fluorescence yield</u> are sources of both errors and useful information.

Conclusion (early 80's):

PERSPECTIVES

The Deep Chlorophyll Maximum: Comparing Vertical Profiles of Chlorophyll *a*

JOHN J. CULLEN[1]

Department of Fisheries and Oceans, Marine Ecology Laboratory, Bedford Institute of Oceanography, Dartmouth, N.S. B2Y 4A2

CULLEN, J. J. 1982. The deep chlorophyll maximum: comparing vertical profiles of chlorophyll *a*. Can. J. Fish. Aquat. Sci. 39: 791 – 803.

Physiological and taxonomic influences on <u>fluorescence yield</u> are sources of both errors and useful information.

We should <u>measure</u> and <u>interpret</u> the variability of fluorescence yield in nature

1980 - 2006: Systematic comparison of <u>yields</u> fell by the wayside as other powerful approaches were pursued

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]

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

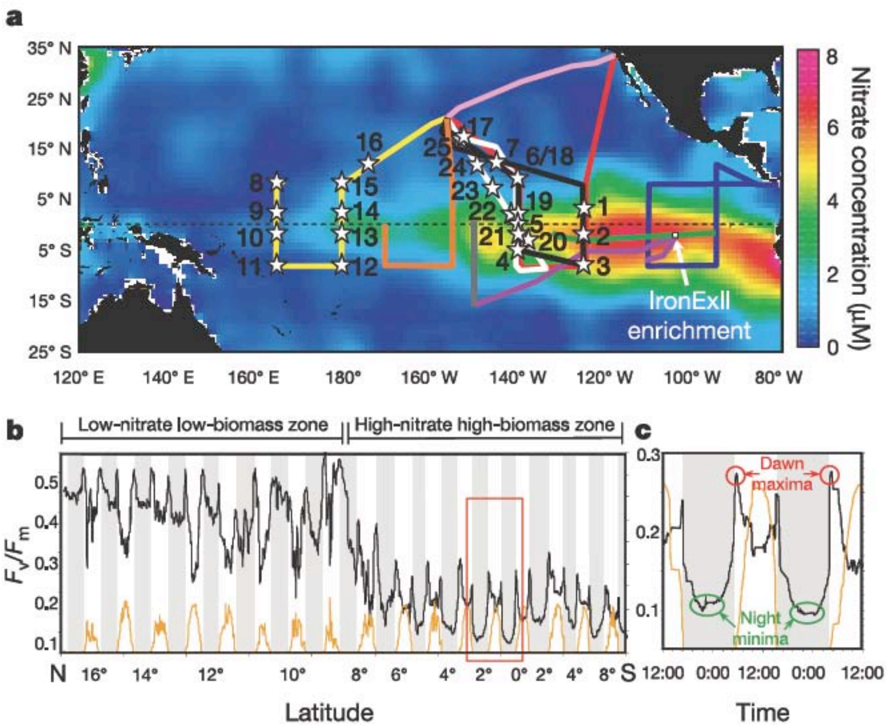


Figure 1 | The tropical Pacific study area. a, Ship transects (lines) and enrichment experiment locations (stars) for the ten field studies. Transect

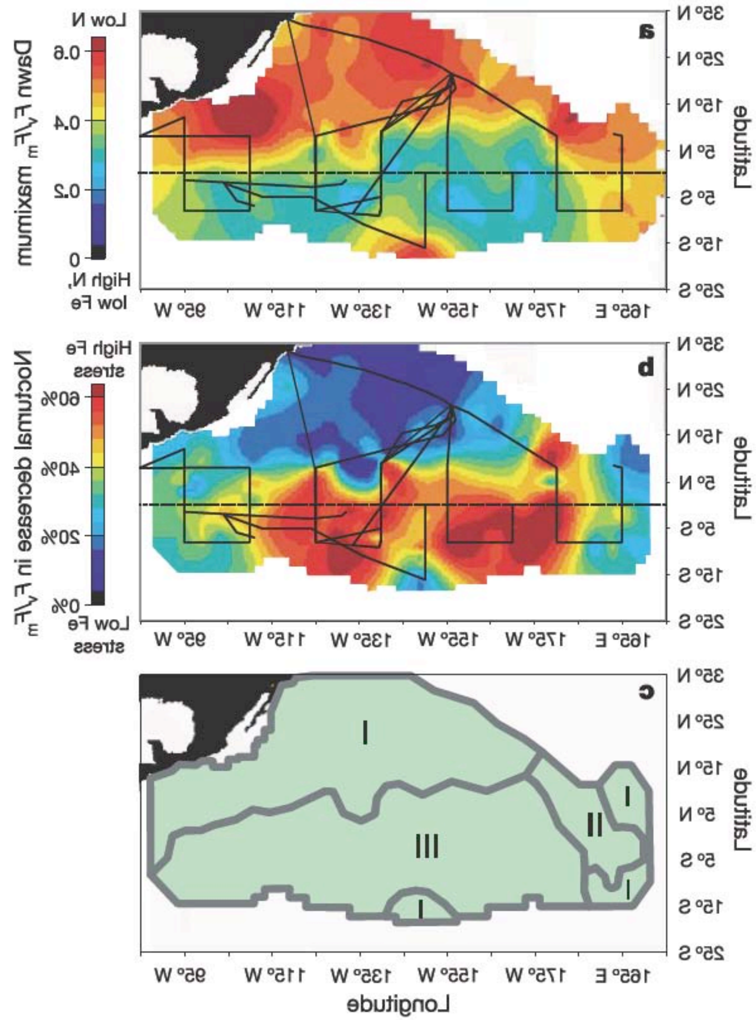


Figure 2 | Fluorescence diagnostics delineate three physiological regime in the tropical Pacific. a, Dawn F_v/F_m maximum. **b,** Nocturnal decrease i

Meantime, sun-induced chlorophyll fluorescence was studied on and off

Morel, A., and L. Prieur (1977), Analysis
Oceanography, 22, 709-722.

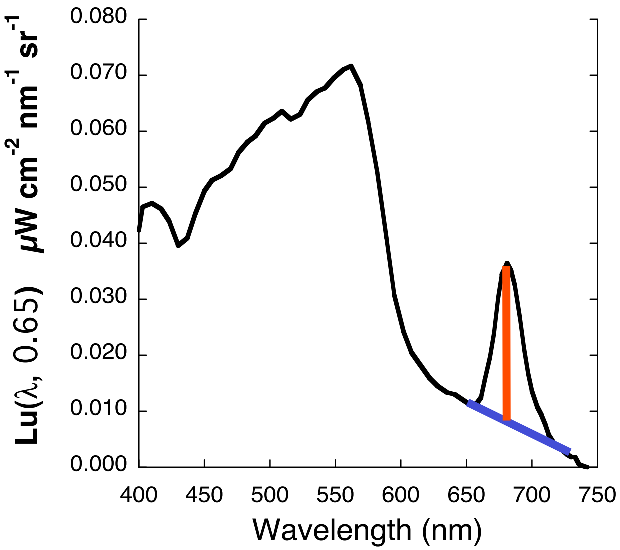
Gordon, H. R. (1979), Estimation of the c
for the remote sensing of chlorophyll a vi
1883-1884.

Topliss, B. J., and T. Platt (1986), Passive
Implications for remote sensing, Deep-Se

Fisher, J., and U. Kronfeld (1990), Sun-st
of oceanic properties, International Journ

Gower, J. F. R., and G. A. Borstad (1990)
fluorescence using an imaging spectrome
11(2), 313-320.

Kiefer, D. A., W. S. Chamberlin, and C. I
chlorophyll a: relationship to photosynthe
South Pacific gyre. Limnol. Oceanogr. 34

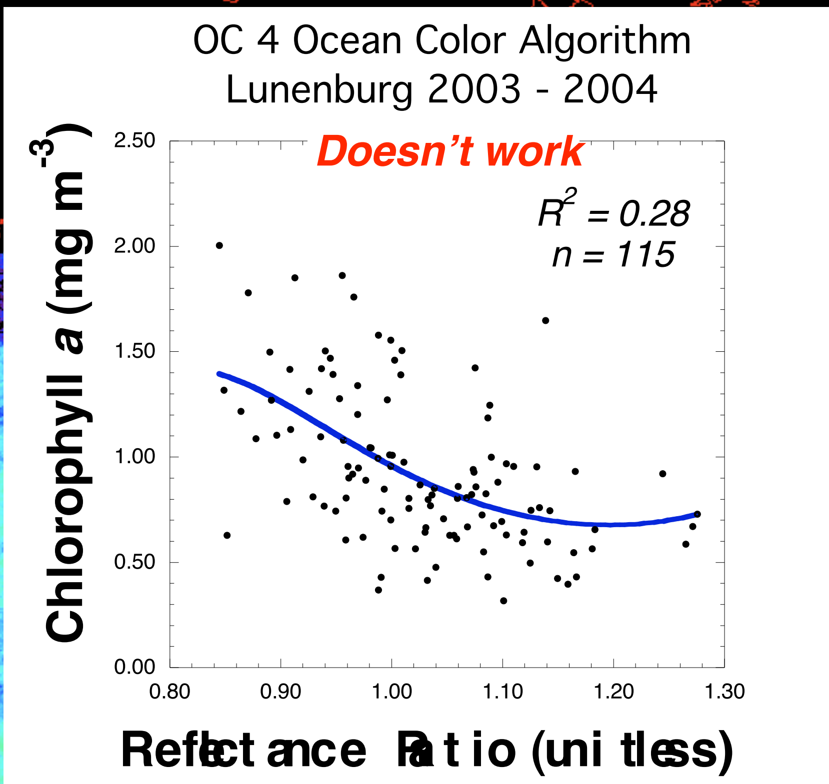


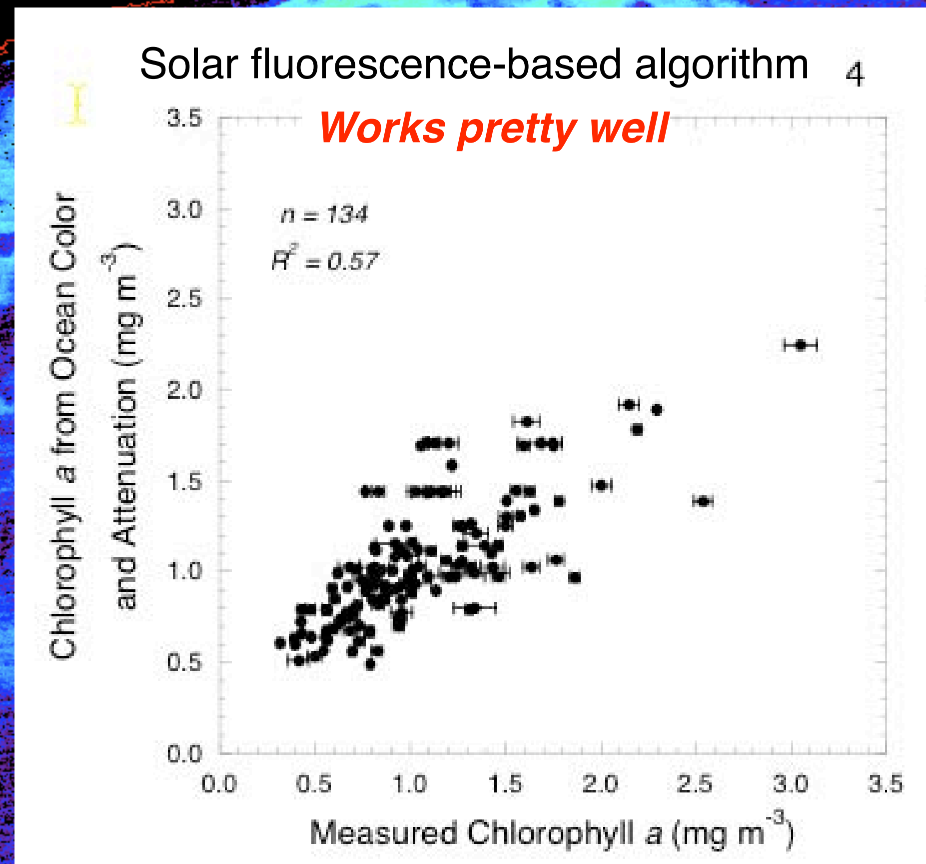
Stegmann, P. M., M. R. Lewis, C. O. Davis, and J. J. Cullen (1992), Primary production estimates from recordings of solar-stimulated fluorescence in the Equatorial Pacific at 150˚W, Journal of Geophysical Research, 97(C1), 627-638.

Babin, M., A. Morel, and B. Gentili (1996), Remote sensing of sea surface sun-induced chlorophyll fluorescence: consequences of natural variations in the optical characteristics of phytoplankton and the quantum yield of chlorophyll a fluorescence, International Journal of Remote Sensing, 17(2), 2417-2448.

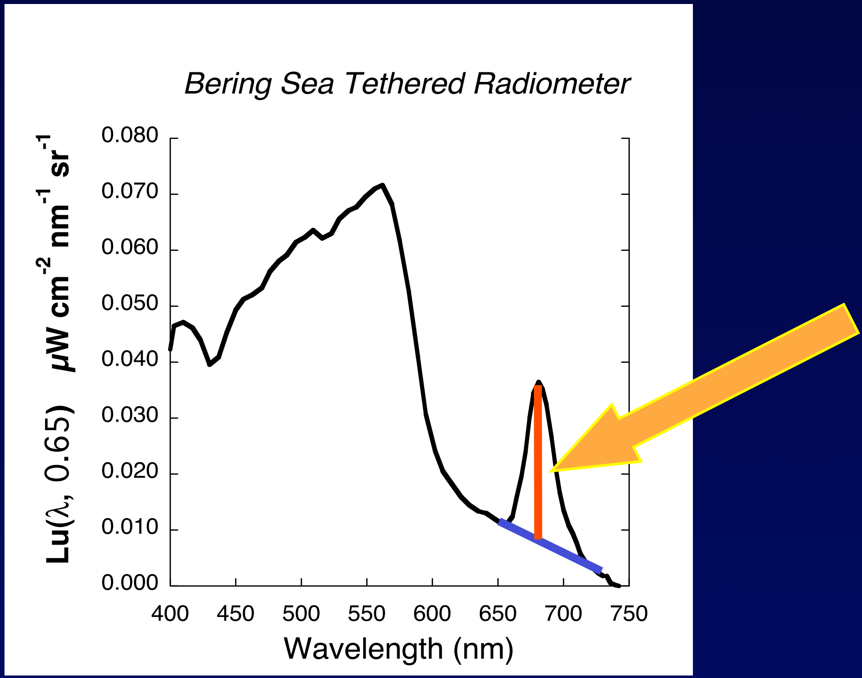
Garcia-Mendoza, E., and H. Maske (1996), The relationship of solar-stimulated natural fluorescence and primary productivity in Mexican Pacific waters, Limnology and Oceanography, 41(8), 1697-1710.

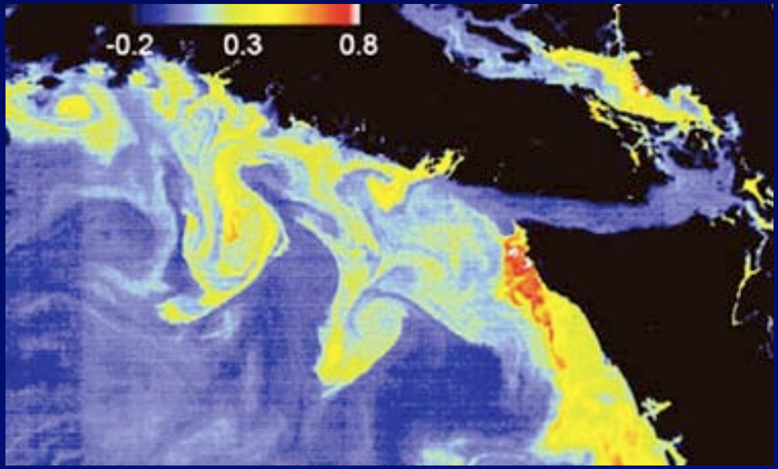
Possibly the only hope for detecting relatively low concentration of phytoplankton in the presence of CDOM and





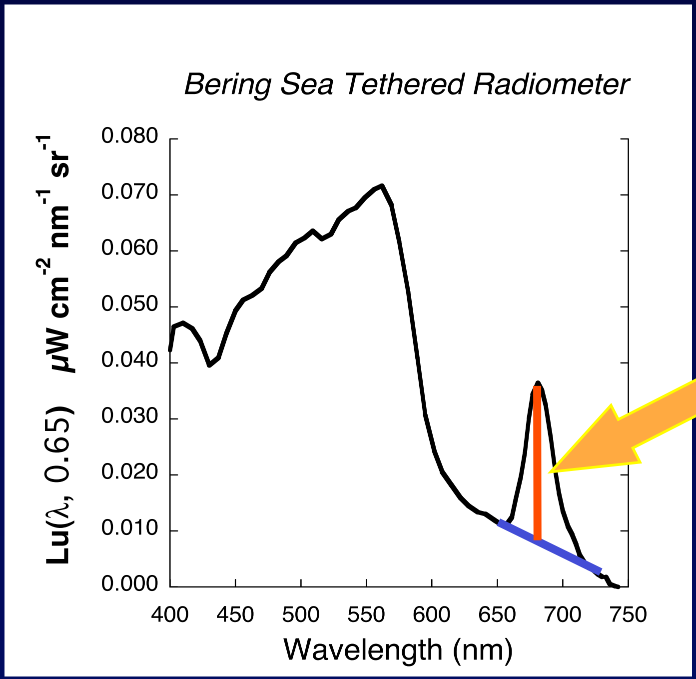
Fluorescence line height (FLH): A proxy for *F*



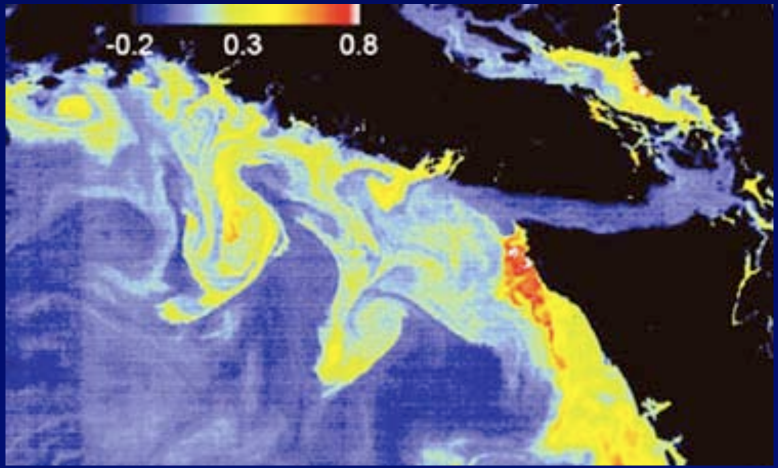


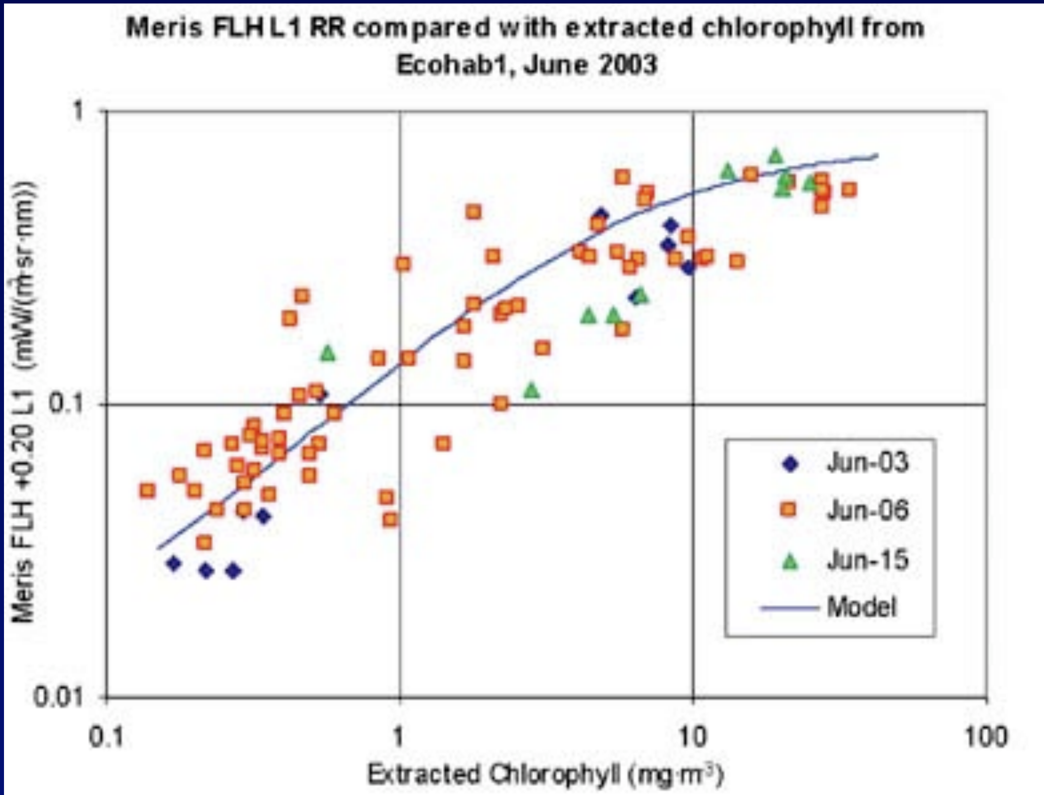
Gayana 68(2) supl. t.I. Proc. : 252-258, 2004 ISSN 0717-652X http://www.scielo.cl/
SATELLITE FLUORESCENCE AS A MEASURE OF OCEAN SURFACE CHLOROPHYLL
Jim Gower & Stephanie King

Fluorescence line height (FLH): A proxy for *F*



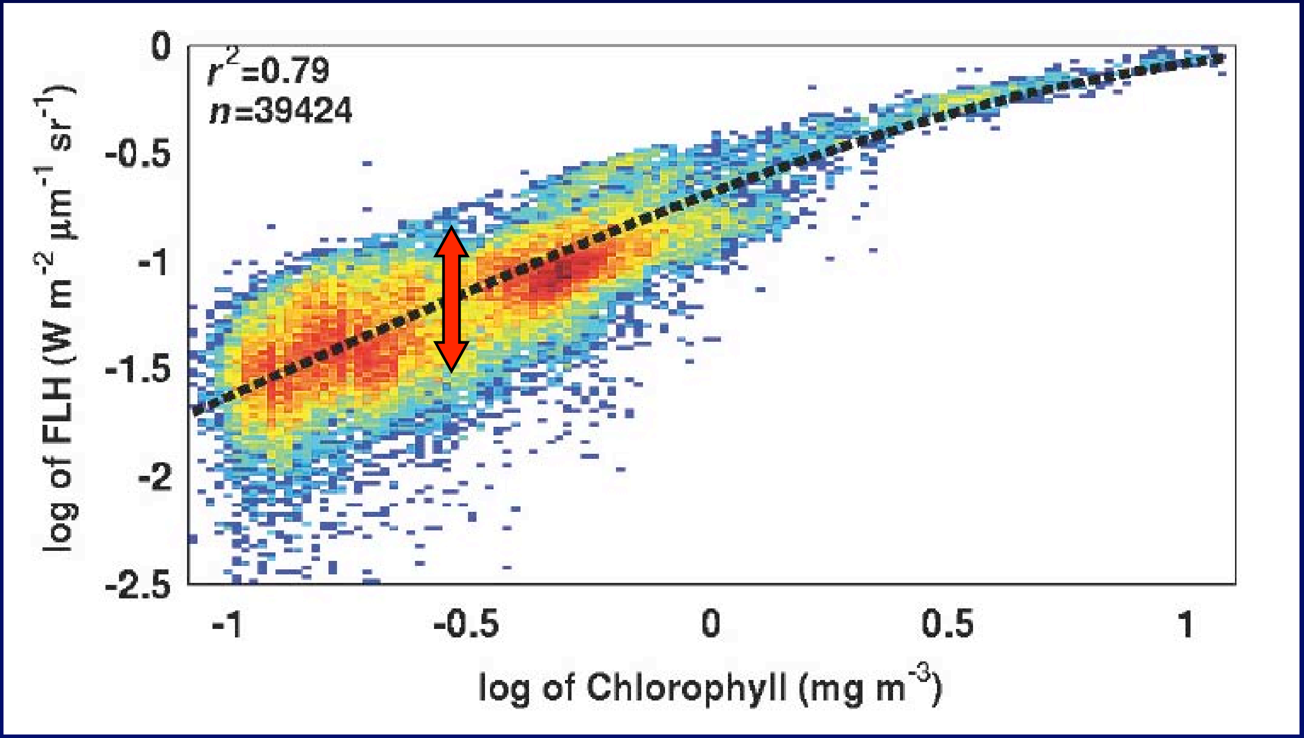
it can sometimes provide reasonable estimates of Chlorophyll (especially when the range of Chl is very large)





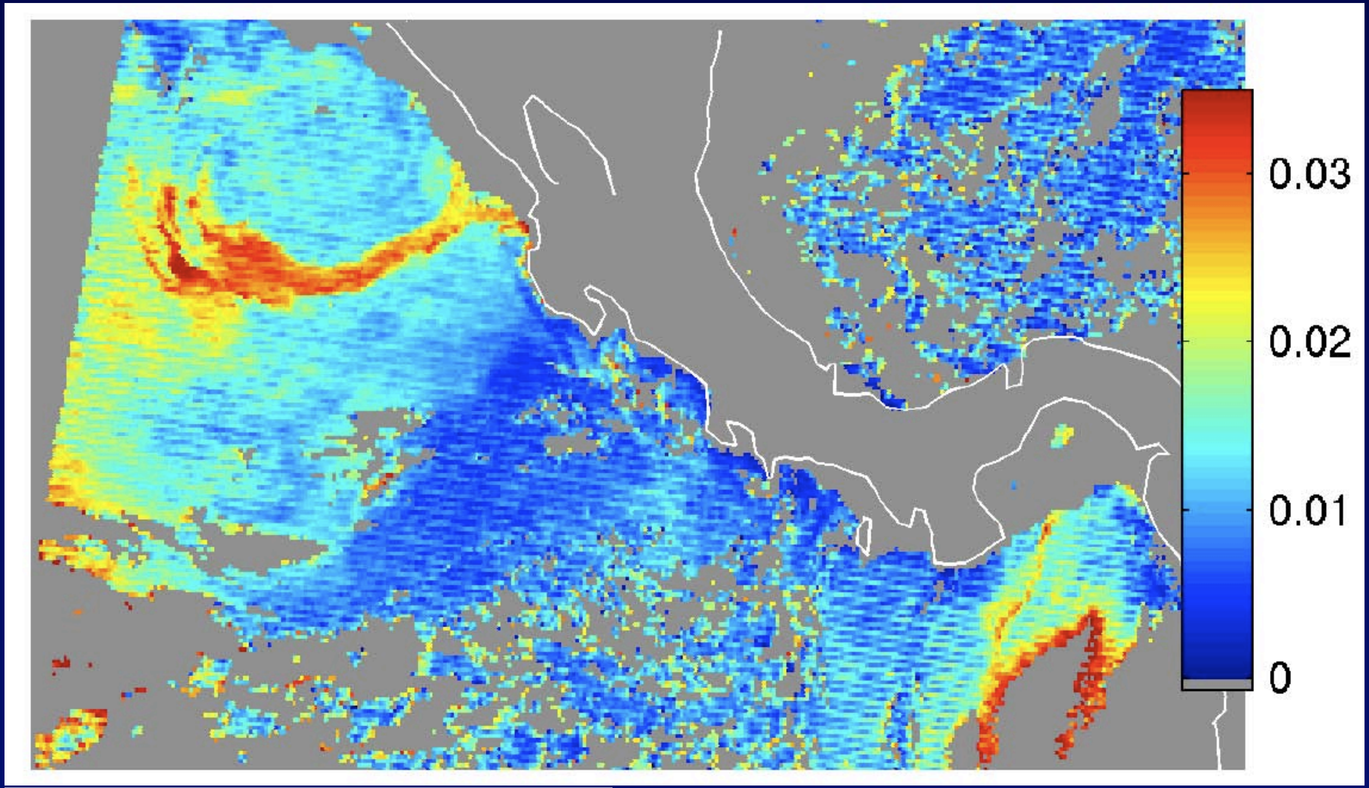
Gayana 68(2) supl. t.I. Proc. : 252-258, 2004 ISSN 0717-652X http://www.scielo.cl/
SATELLITE FLUORESCENCE AS A MEASURE OF OCEAN SURFACE CHLOROPHYLL
Jim Gower & Stephanie King

But fluorescence yield is highly variable in nature



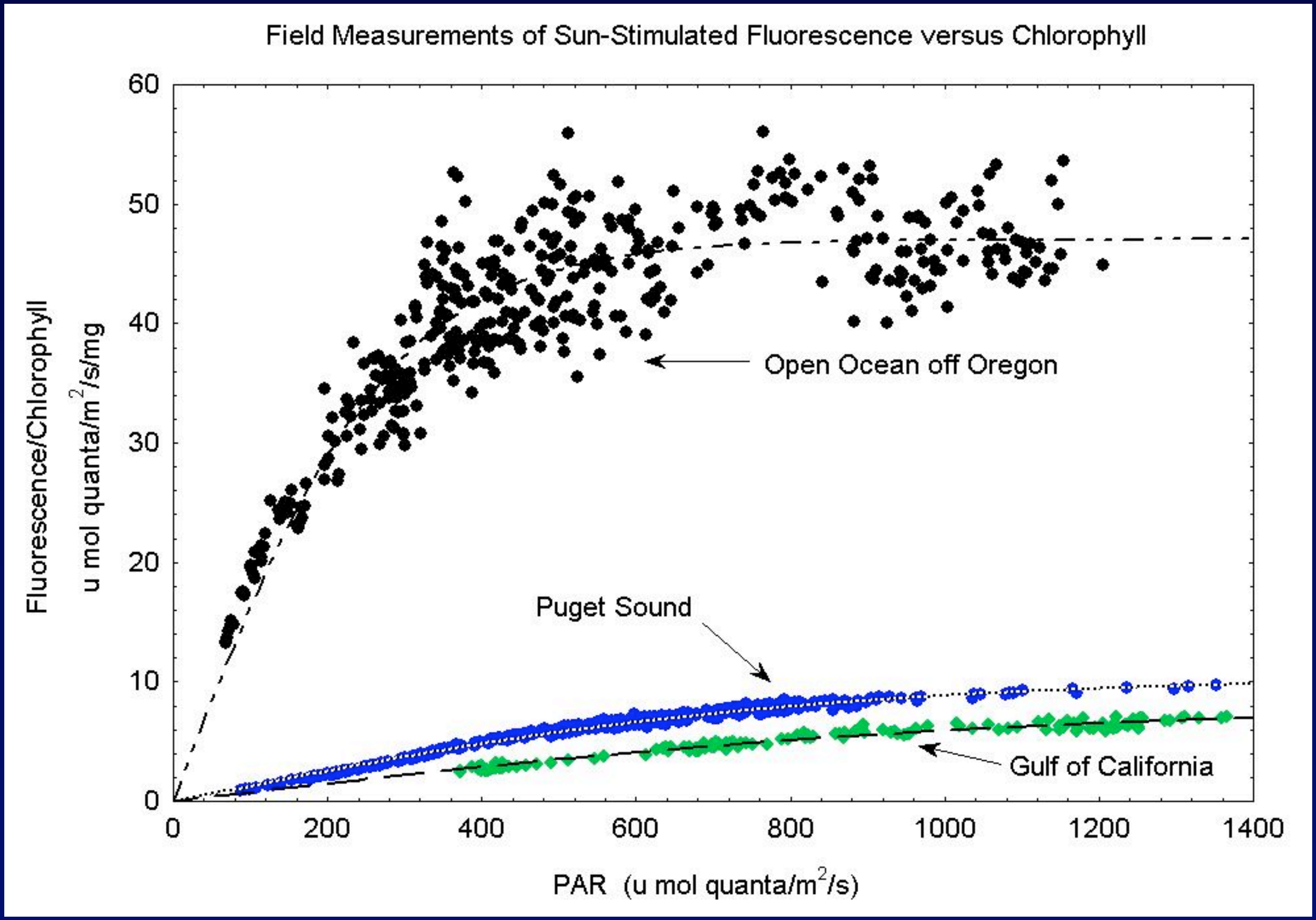
Huot et al. 2005
L&O Methods

Apparently huge variability of fluorescence yield in nature (ca. 10x) is clearly tied to environmental forcing



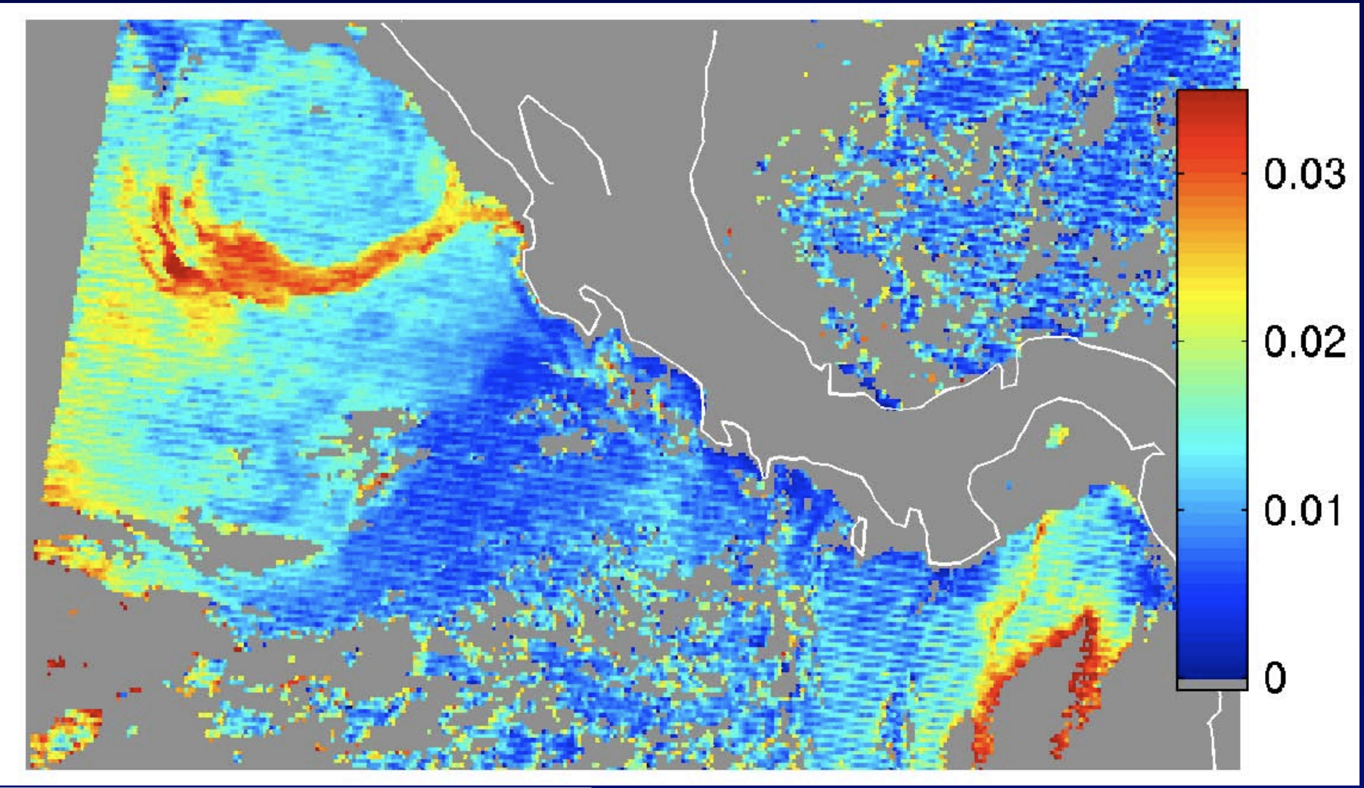
Estimated fluorescence quantum yield: Huot et al. 2005 L&O Methods

Satellites detect fluorescence in full sunlight. *In situ* radiometers can measure <u>*F* vs *E*</u>. It also varies greatly!



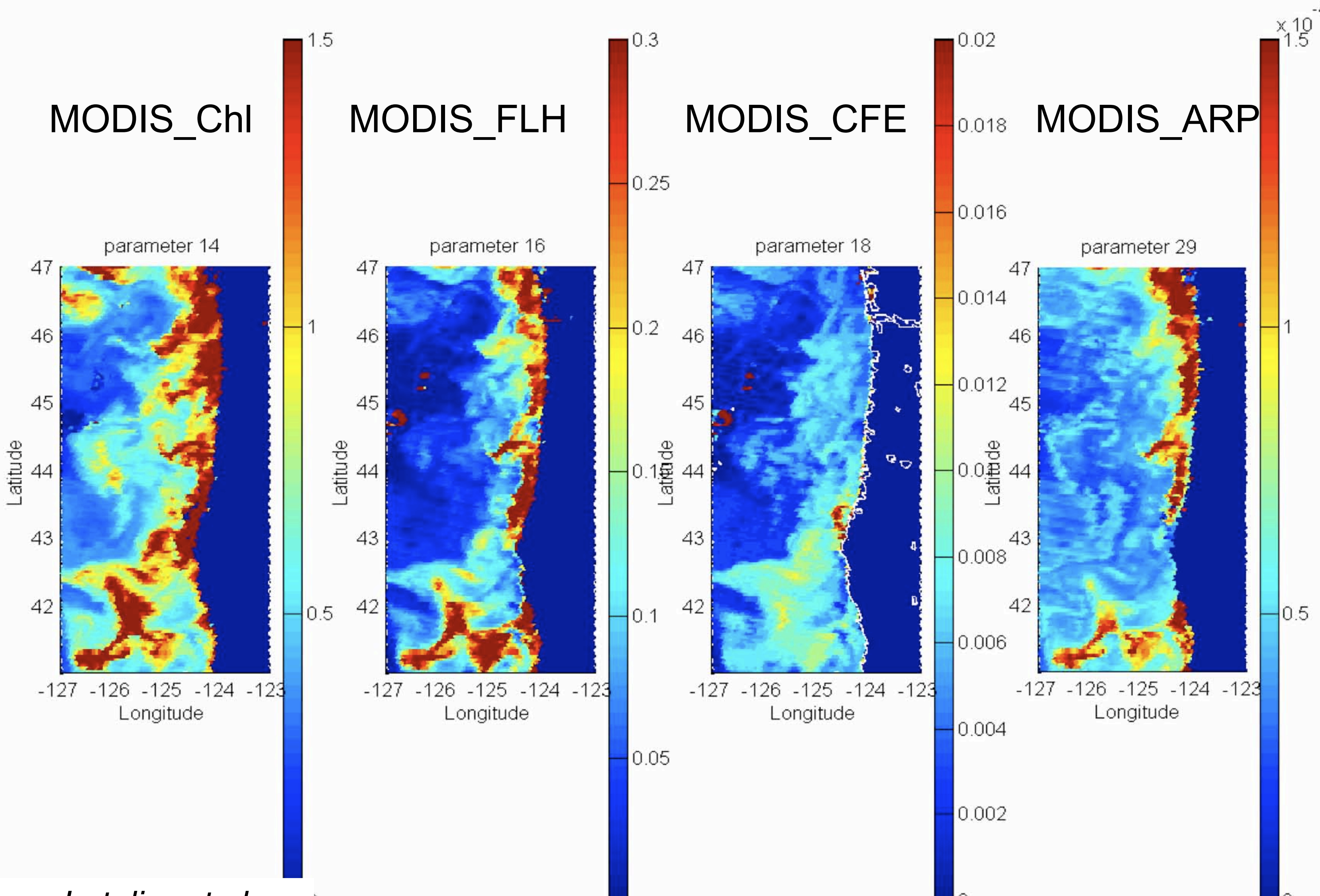
Ricardo Letelier, Mark Abbott, Jasmine Nahorniak
College of Oceanic and Atmospheric Sciences
Oregon State University

This signal should not be ignored!



Estimated fluorescence quantum yield: Huot et al. 2005 L&O Methods

A big goal: Interpreting natural variability of φ_f as detected from space



Letelier et al.

A number of processes must be considered to relate FLH quantitatively and mechanistically to the biomass and physiology of phytoplankton

Recent examples:
Babin et al. (1996)
Ostrawska et al. (1997)
Maritorena and Morel (2000)
Morrison (2003)
Huot et al. (2005)
Laney et al. (2005)

$$FLH = L_{uf}\left(683,0^{-}\right) =$$

$$\frac{1}{4\pi}\cdot\frac{1}{C_f}\cdot\varphi_f\cdot\mathring{E}(\mathrm{PAR},0^{-})\cdot chl\cdot\overline{a_{\varphi}^{*}}\cdot Q_a^{*}\left(683\right)\cdot[\overline{K_{abs}}+a_f\left(683\right)]^{-1}$$

A number of processes must be considered to relate FLH quantitatively and mechanistically to the biomass and physiology of phytoplankton

Recent examples:
Babin et al. (1996)
Ostrawska et al. (1997)
Maritorena and Morel (2000)
Morrison (2003)
Huot et al. (2005)
Laney et al. (2005)

Correction for backscatter and Raman scatter

$$FLH = L_{uf}\left(683, 0^{-}\right) =$$

$$\frac{1}{4\pi}\cdot\frac{1}{C_f}\cdot\varphi_f\cdot\overset{o}{E}(\mathrm{PAR},0^{-})\cdot chl\cdot\overline{a_{\varphi}^{*}}\cdot Q_a^{*}\left(683\right)\cdot[\overline{K_{abs}}+a_f\left(683\right)]^{-1}$$

A number of processes must be considered to relate FLH <u>*quantitatively*</u> *and* <u>*mechanistically*</u> *to the biomass and physiology of phytoplankton*

Recent examples:
Babin et al. (1996)
Ostrawska et al. (1997)
Maritorena and Morel (2000)
Morrison (2003)
Huot et al. (2005)
Laney et al. (2005)

$$FLH = L_{uf}\left(683,0^{-}\right) =$$

$$\frac{1}{4\pi}\cdot\frac{1}{C_f}\cdot\varphi_f\cdot\overset{o}{E}(\mathrm{PAR},0^{-})\cdot chl\cdot\overline{a_{\varphi}^{*}}\cdot Q_a^{*}\left(683\right)\cdot[\overline{K_{abs}}+a_f\left(683\right)]^{-1}$$

A number of processes must be considered to relate FLH quantitatively and mechanistically to the biomass and physiology of phytoplankton

Recent examples:
Babin et al. (1996)
Ostrawska et al. (1997)
Maritorena and Morel (2000)
Morrison (2003)
Huot et al. (2005)
Laney et al. (2005)

$$FLH = L_{uf}\left(683, 0^{-}\right) =$$

$$\frac{1}{4\pi} \cdot \frac{1}{C_f} \cdot \varphi_f \cdot \overset{\circ}{E}(\mathrm{PAR}, 0^{-}) \cdot chl \cdot \overline{a_{\varphi}^{*}} \cdot Q_a^{*}\left(683\right) \cdot [\overline{K_{abs}} + a_f\left(683\right)]^{-1}$$

Volume emission to upwelling radiance

A number of processes must be considered to relate FLH quantitatively and mechanistically to the biomass and physiology of phytoplankton

Recent examples:
Babin et al. (1996)
Ostrawska et al. (1997)
Maritorena and Morel (2000)
Morrison (2003)
Huot et al. (2005)
Laney et al. (2005)

$$FLH = L_{uf}\left(683,0^{-}\right) =$$

$$\frac{1}{4\pi}\cdot\frac{1}{C_f}\cdot\varphi_f\cdot\overset{o}{E}(\mathrm{PAR},0^{-})\cdot chl\cdot\overline{a_{\varphi}^{*}}\cdot Q_a^{*}\left(683\right)\cdot[\overline{K_{abs}}+a_f\left(683\right)]^{-1}$$

A number of processes must be considered to relate FLH quantitatively and mechanistically to the biomass and physiology of phytoplankton

Recent examples:
Babin et al. (1996)
Ostrawska et al. (1997)
Maritorena and Morel (2000)
Morrison (2003)
Huot et al. (2005)
Laney et al. (2005)

$$FLH = L_{uf}\left(683,0^{-}\right) =$$

$$\frac{1}{4\pi}\cdot\frac{1}{C_f}\cdot\varphi_f\cdot\mathring{E}(\mathrm{PAR},0^{-})\cdot chl\cdot\overline{a_{\varphi}^{*}}\cdot Q_a^{*}\left(683\right)\cdot[\overline{K_{abs}}+a_f\left(683\right)]^{-1}$$

Full spectral emission to 683 nm

A number of processes must be considered to relate FLH quantitatively and mechanistically to the biomass and physiology of phytoplankton

Recent examples:
Babin et al. (1996)
Ostrawska et al. (1997)
Maritorena and Morel (2000)
Morrison (2003)
Huot et al. (2005)
Laney et al. (2005)

$$FLH = L_{uf}\left(683,0^{-}\right) =$$

$$\frac{1}{4\pi}\cdot\frac{1}{C_f}\cdot\varphi_f\cdot\overset{o}{E}(\mathrm{PAR},0^{-})\cdot chl\cdot\overline{a_{\varphi}^{*}}\cdot Q_a^{*}\left(683\right)\cdot[\overline{K_{abs}}+a_f\left(683\right)]^{-1}$$

A number of processes must be considered to relate FLH quantitatively and mechanistically to the biomass and physiology of phytoplankton

Recent examples:
Babin et al. (1996)
Ostrawska et al. (1997)
Maritorena and Morel (2000)
Morrison (2003)
Huot et al. (2005)
Laney et al. (2005)

Quantum yield of fluorescence — function of *E* & physiology

$$FLH = L_{uf}\left(683,0^{-}\right) =$$

$$\frac{1}{4\pi}\cdot\frac{1}{C_f}\cdot\varphi_f\cdot\mathring{E}(\mathrm{PAR},0^{-})\cdot chl\cdot\overline{a_{\varphi}^{*}}\cdot Q_a^{*}\left(683\right)\cdot[\overline{K_{abs}}+a_f\left(683\right)]^{-1}$$

A number of processes must be considered to relate FLH quantitatively and mechanistically to the biomass and physiology of phytoplankton

Recent examples:
Babin et al. (1996)
Ostrawska et al. (1997)
Maritorena and Morel (2000)
Morrison (2003)
Huot et al. (2005)
Laney et al. (2005)

$$FLH = L_{uf}\left(683, 0^{-}\right) =$$

$$\frac{1}{4\pi} \cdot \frac{1}{C_f} \cdot \varphi_f \cdot \overset{o}{E}(\mathrm{PAR}, 0^{-}) \cdot chl \cdot \overline{a_{\varphi}^{*}} \cdot Q_a^{*}\left(683\right) \cdot [\overline{K_{abs}} + a_f\left(683\right)]^{-1}$$

A number of processes must be considered to relate FLH quantitatively and mechanistically to the biomass and physiology of phytoplankton

Recent examples:
Babin et al. (1996)
Ostrawska et al. (1997)
Maritorena and Morel (2000)
Morrison (2003)
Huot et al. (2005)
Laney et al. (2005)

$$FLH = L_{uf}\left(683, 0^-\right) =$$

$$\frac{1}{4\pi} \cdot \frac{1}{C_f} \cdot \varphi_f \cdot \overset{o}{E}(\mathrm{PAR}, 0^-) \cdot chl \cdot \overline{a_{\varphi}^{*}} \cdot Q_a^{*}(683) \cdot [\overline{K_{abs}} + a_f(683)]^{-1}$$

Incident scalar PAR

A number of processes must be considered to relate FLH quantitatively and mechanistically to the biomass and physiology of phytoplankton

Recent examples:
Babin et al. (1996)
Ostrawska et al. (1997)
Maritorena and Morel (2000)
Morrison (2003)
Huot et al. (2005)
Laney et al. (2005)

$$FLH = L_{uf}\left(683,0^{-}\right) =$$

$$\frac{1}{4\pi}\cdot\frac{1}{C_f}\cdot\varphi_f\cdot\overset{\circ}{E}(\mathrm{PAR},0^{-})\cdot chl\cdot\overline{a_{\varphi}^{*}}\cdot Q_a^{*}\left(683\right)\cdot[\overline{K_{abs}}+a_f\left(683\right)]^{-1}$$

A number of processes must be considered to relate FLH quantitatively and mechanistically to the biomass and physiology of phytoplankton

Recent examples:
Babin et al. (1996)
Ostrawska et al. (1997)
Maritorena and Morel (2000)
Morrison (2003)
Huot et al. (2005)
Laney et al. (2005)

$$FLH = L_{uf}\left(683,0^{-}\right) =$$

$$\frac{1}{4\pi} \cdot \frac{1}{C_f} \cdot \varphi_f \cdot \mathring{E}(\mathrm{PAR},0^{-}) \cdot \underbrace{chl \cdot \overline{a_{\varphi}^{*}}}\cdot Q_a^{*}\left(683\right) \cdot [\overline{K_{abs}} + a_f\left(683\right)]^{-1}$$

Chl * irradiance-weighted
specific absorption
coefficient

A number of processes must be considered to relate FLH quantitatively and mechanistically to the biomass and physiology of phytoplankton

Recent examples:
Babin et al. (1996)
Ostrawska et al. (1997)
Maritorena and Morel (2000)
Morrison (2003)
Huot et al. (2005)
Laney et al. (2005)

$$FLH = L_{uf}\left(683,0^{-}\right) =$$

$$\frac{1}{4\pi}\cdot\frac{1}{C_f}\cdot\varphi_f\cdot\overset{\circ}{E}(\mathrm{PAR},0^{-})\cdot chl\cdot\overline{a_{\varphi}^{*}}\cdot Q_a^{*}\left(683\right)\cdot[\overline{K_{abs}}+a_f\left(683\right)]^{-1}$$

A number of processes must be considered to relate FLH quantitatively and mechanistically to the biomass and physiology of phytoplankton

Recent examples:
Babin et al. (1996)
Ostrawska et al. (1997)
Maritorena and Morel (2000)
Morrison (2003)
Huot et al. (2005)
Laney et al. (2005)

$$FLH = L_{uf}\left(683,0^{-}\right) =$$

$$\frac{1}{4\pi}\cdot\frac{1}{C_f}\cdot\varphi_f\cdot\mathring{E}(\mathrm{PAR},0^{-})\cdot chl\cdot\overline{a_{\varphi}^{*}}\cdot Q_a^{*}\left(683\right)\cdot[\overline{K_{abs}}+a_f\left(683\right)]^{-1}$$

Internal reabsorption of fluoresced photons

A number of processes must be considered to relate FLH quantitatively and mechanistically to the biomass and physiology of phytoplankton

Recent examples:
Babin et al. (1996)
Ostrawska et al. (1997)
Maritorena and Morel (2000)
Morrison (2003)
Huot et al. (2005)
Laney et al. (2005)

$$FLH = L_{uf}\left(683, 0^-\right) =$$

$$\frac{1}{4\pi} \cdot \frac{1}{C_f} \cdot \varphi_f \cdot \overset{\circ}{E}(\mathrm{PAR}, 0^-) \cdot chl \cdot \overline{a_\varphi^*} \cdot Q_a^*\left(683\right) \cdot [\overline{K_{abs}} + a_f\left(683\right)]^{-1}$$

A number of processes must be considered to relate FLH quantitatively and mechanistically to the biomass and physiology of phytoplankton

Recent examples:
Babin et al. (1996)
Ostrawska et al. (1997)
Maritorena and Morel (2000)
Morrison (2003)
Huot et al. (2005)
Laney et al. (2005)

Attenuation of downwelling absorbed radiation

$$FLH = L_{uf}\left(683, 0^{-}\right) =$$

$$\frac{1}{4\pi} \cdot \frac{1}{C_f} \cdot \varphi_f \cdot \overset{o}{E}(\mathrm{PAR}, 0^{-}) \cdot chl \cdot \overline{a_{\varphi}^{*}} \cdot Q_a^{*}\left(683\right) \cdot [\overline{K_{abs}} + a_f\left(683\right)]^{-1}$$

A number of processes must be considered to relate FLH ***quantitatively*** *and* ***mechanistically*** *to the biomass and physiology of phytoplankton*

Recent examples:
Babin et al. (1996)
Ostrawska et al. (1997)
Maritorena and Morel (2000)
Morrison (2003)
Huot et al. (2005)
Laney et al. (2005)

$$FLH = L_{uf}\left(683,0^{-}\right) =$$

$$\frac{1}{4\pi}\cdot\frac{1}{C_f}\cdot\varphi_f\cdot\mathring{E}(\mathrm{PAR},0^{-})\cdot chl\cdot\overline{a_{\varphi}^{*}}\cdot Q_a^{*}\left(683\right)\cdot[\overline{K_{abs}}+a_f\left(683\right)]^{-1}$$

A number of processes must be considered to relate FLH quantitatively and mechanistically to the biomass and physiology of phytoplankton

Recent examples:
Babin et al. (1996)
Ostrawska et al. (1997)
Maritorena and Morel (2000)
Morrison (2003)
Huot et al. (2005)
Laney et al. (2005)

$$FLH = L_{uf}\left(683,0^{-}\right) =$$

Attenuation of upwelling fluoresced radiation

$$\frac{1}{4\pi}\cdot\frac{1}{C_f}\cdot\varphi_f\cdot\mathring{E}(\mathrm{PAR},0^{-})\cdot chl\cdot\overline{a_{\varphi}^{*}}\cdot Q_a^{*}\left(683\right)\cdot[\overline{K_{abs}}+a_f\left(683\right)]^{-1}$$

A number of processes must be considered to relate FLH ***quantitatively*** *and* ***mechanistically*** *to the biomass and physiology of phytoplankton*

Recent examples:
Babin et al. (1996)
Ostrawska et al. (1997)
Maritorena and Morel (2000)
Morrison (2003)
Huot et al. (2005)
Laney et al. (2005)

$$FLH = L_{uf}\left(683, 0^{-}\right) =$$

$$\frac{1}{4\pi} \cdot \frac{1}{C_f} \cdot \varphi_f \cdot \mathring{E}(\mathrm{PAR}, 0^{-}) \cdot chl \cdot \overline{a_{\varphi}^{*}} \cdot Q_a^{*}\left(683\right) \cdot [\overline{K_{abs}} + a_f\left(683\right)]^{-1}$$

It’s not really all that bad, and it’s needed to retrieve physiological variables

Recent examples:
Babin et al. (1996)
Ostrawska et al. (1997)
Maritorena and Morel (2000)
Morrison (2003)
Huot et al. (2005)
Laney et al. (2005)

$$FLH = L_{uf}\left(683,0^{-}\right) = \frac{1}{4\pi}\cdot\frac{1}{C_f}\cdot\varphi_f\cdot\mathring{E}(\mathrm{PAR},0^{-})\cdot chl\cdot\underbrace{\overline{a_{\varphi}^{*}}}\cdot Q_a^{*}\left(683\right)\cdot[\overline{K_{abs}}+a_f\left(683\right)]^{-1}$$

Correction for backscatter and Raman scatter

Quantum yield of fluorescence — function of *E* & physiology

Attenuation of downwelling absorbed radiation

Attenuation of upwelling fluoresced radiation

Volume emission to upwelling radiance

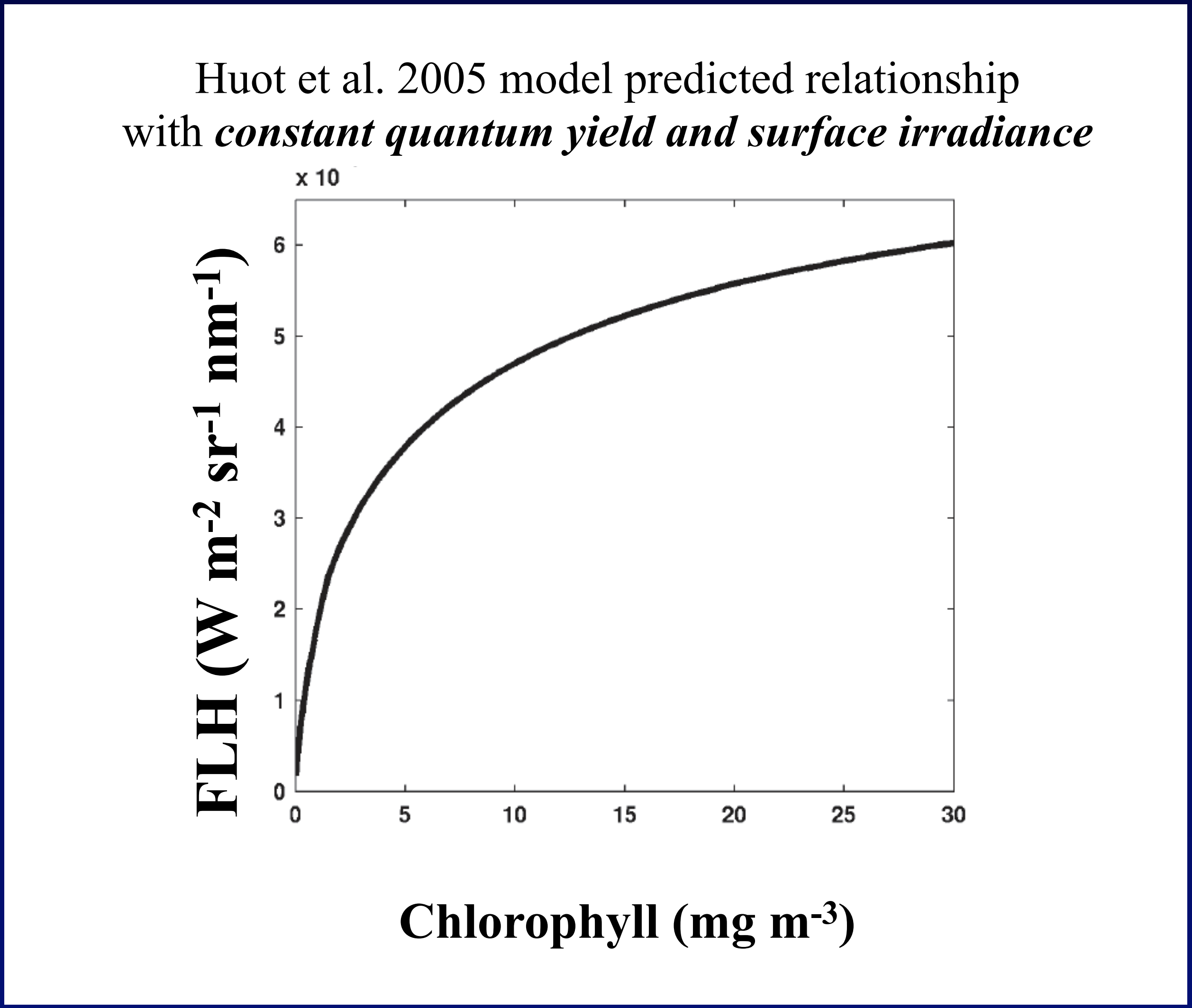
Full spectral emission to 683 nm

Incident scalar PAR

Chl * irradiance-weighted specific absorption coefficient

Internal reabsorption of fluoresced photons

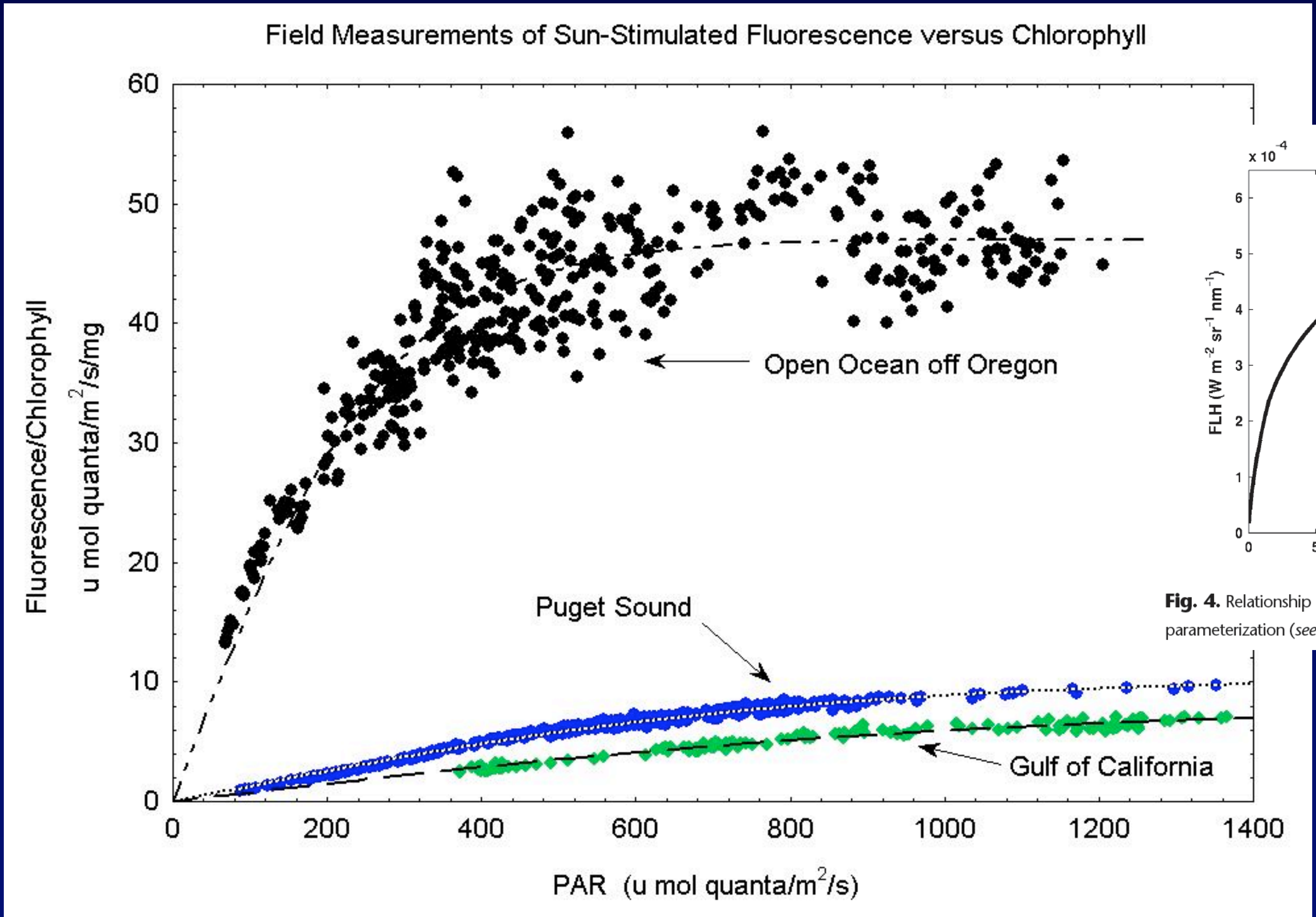
These all contribute to the observed nonlinear relationships between FLH and Chlorophyll



See Babin et al. 1996; Gower et al. 2004

Roots in papers by Morel and Prieur 1977, Neville and Gower (1977), Gordon (1979)

But φ_f *varies — a lot*



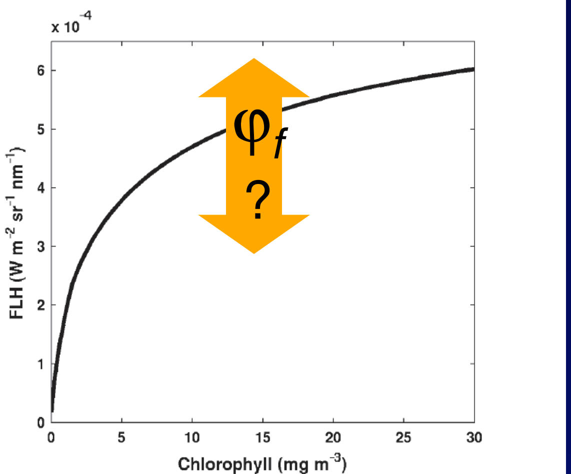
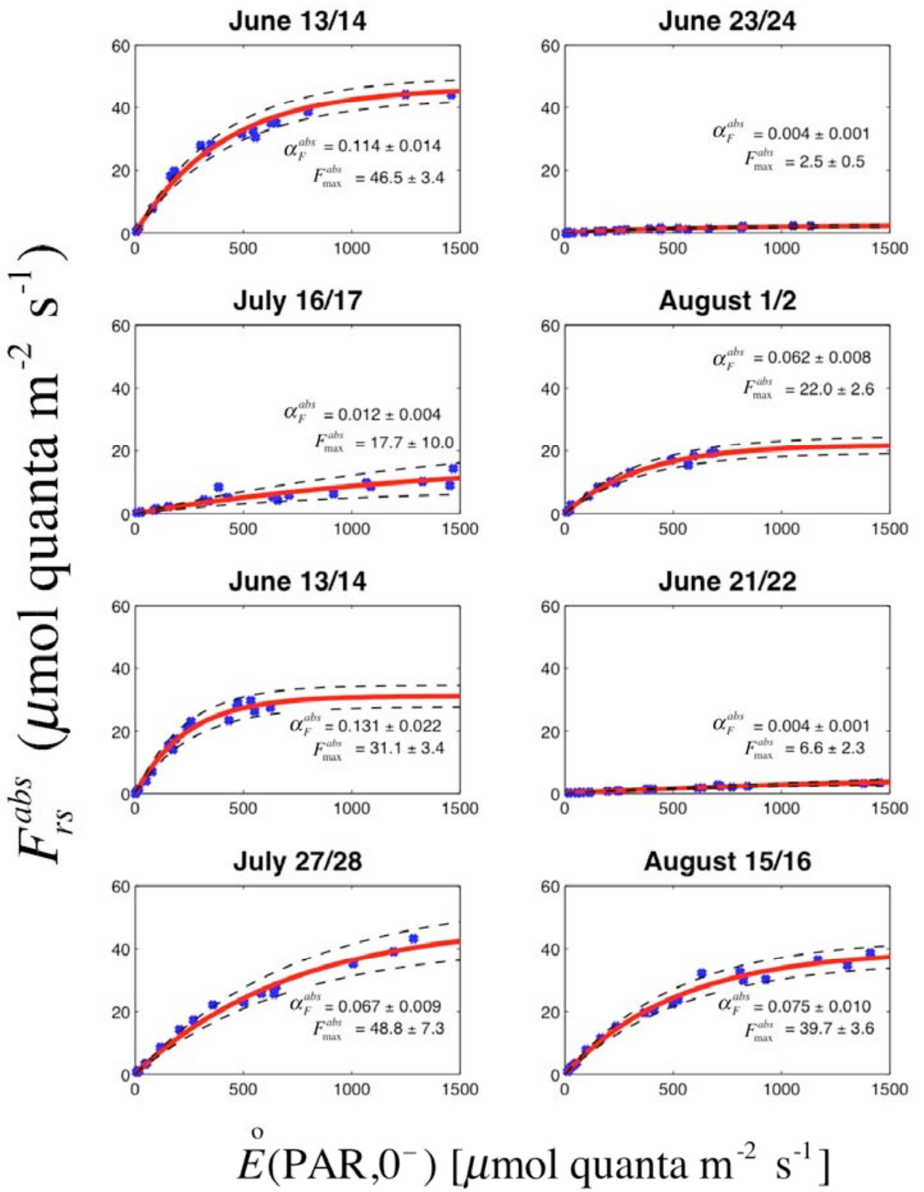


Fig. 4. Relationship between the *FLH* and chlorophyll concentration with our parameterization (*see* Eq. 20) using $\varphi_{chl} = 0.012$ and $\mathring{E}_{PAR} = 1750$ µmol m^{-2} s^{-1}.

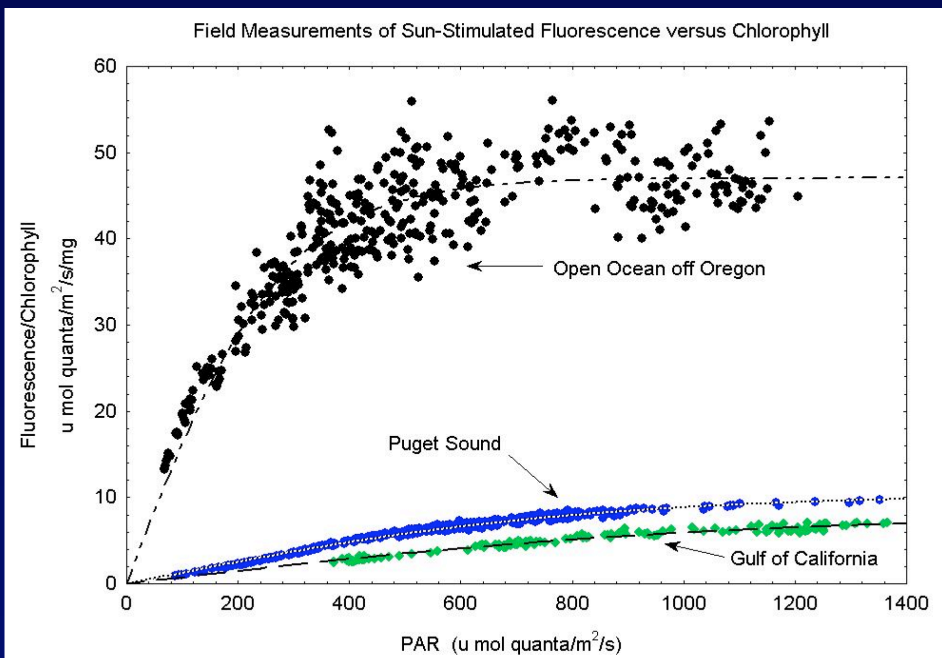
Ricardo Letelier, Mark Abbott, Jasmine Nahorniak
COAS, Oregon State University

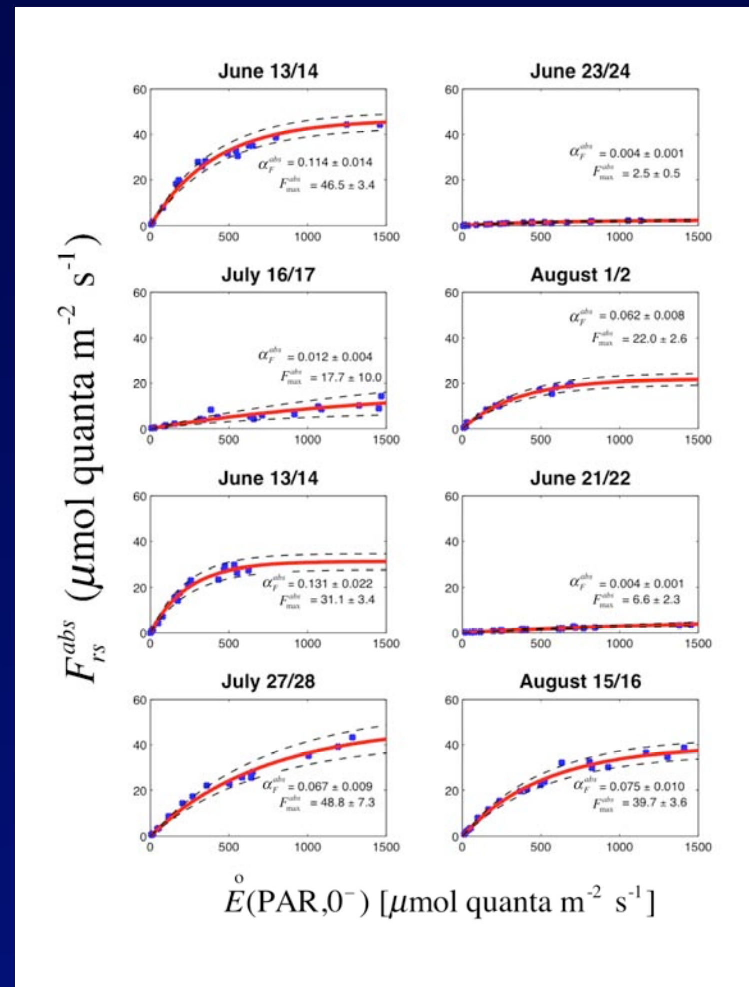
…we observed the same kind of variability in the Bering Sea



Data from optical drifters
Schallenberg et al., submitted (JGR Oceans)

Goal: Explain this kind of variability in fluorescence yield in terms of φ_f and the optical properties of phytoplankton and the water





Approach

Approach

- Retrieve fluorescence normalized to absorbed radiation (F^{abs}) and surface irradiance, E

Approach

- Retrieve fluorescence normalized to absorbed radiation (F^{abs}) and surface irradiance, *E*

Approach

- Retrieve fluorescence normalized to absorbed radiation (F^{abs}) and surface irradiance, E
- Ascribe variation of F^{abs} vs E to natural variability of φ_f vs E

Approach

- Retrieve fluorescence normalized to absorbed radiation (F^{abs}) and surface irradiance, E
- Ascribe variation of F^{abs} vs E to natural variability of φ_f vs E

Approach

- Retrieve fluorescence normalized to absorbed radiation (F^{abs}) and surface irradiance, E
- Ascribe variation of F^{abs} vs E to natural variability of φ_f vs E
- Relate inferred variability of φ_f vs E to phytoplankton physiology

Approach

- Retrieve fluorescence normalized to absorbed radiation (F^{abs}) and surface irradiance, E
- Ascribe variation of F^{abs} vs E to natural variability of φ_f vs E
- Relate inferred variability of φ_f vs E to phytoplankton physiology

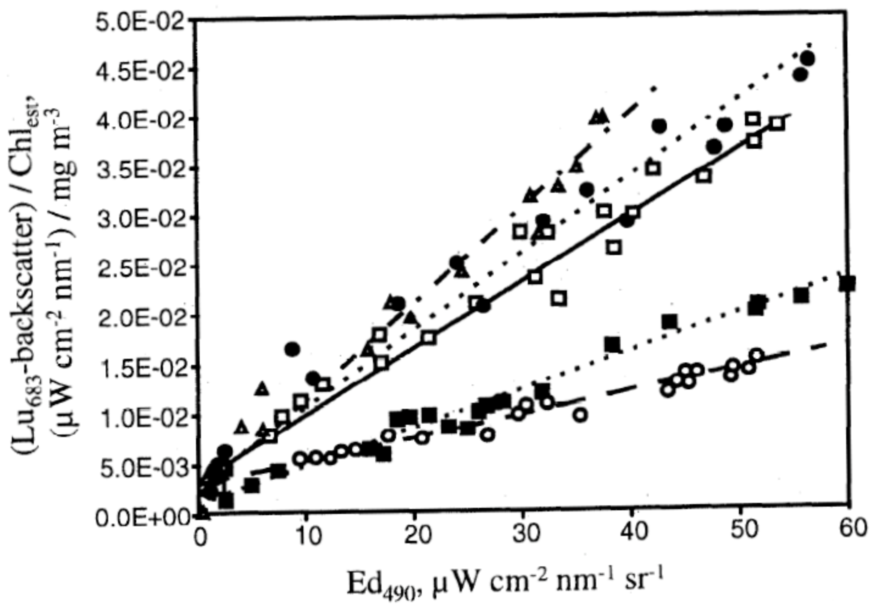
Approach

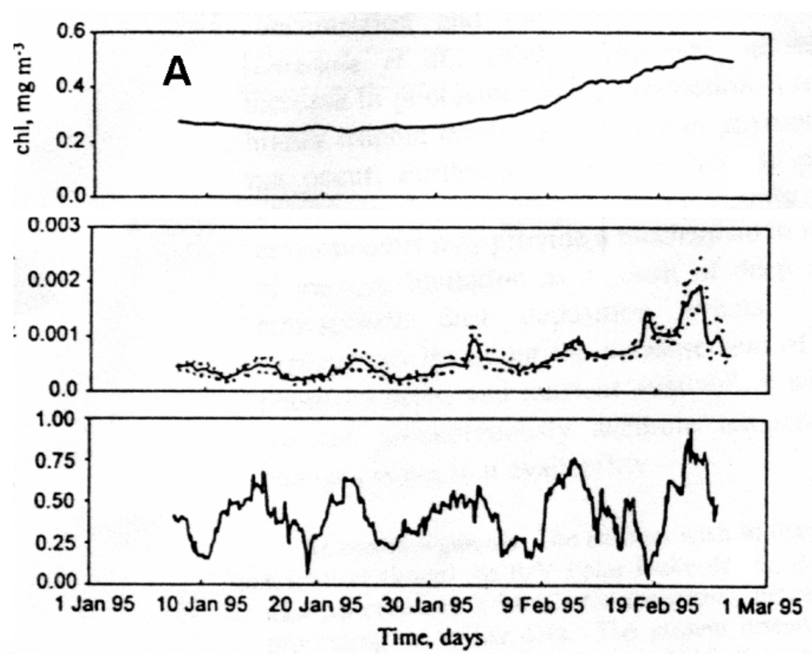
- Retrieve fluorescence normalized to absorbed radiation (F^{abs}) and surface irradiance, E
- Ascribe variation of F^{abs} vs E to natural variability of φ_f vs E
- Relate inferred variability of φ_f vs E to phytoplankton physiology
- Relate physiological status to environmental factors

The working hypothesis from the drifter studies was that high fluorescence yield corresponds to nutrient stressed assemblages

Chlorophyll natural fluorescence response to upwelling events in the Southern Ocean

Letelier et al. 1997, GRL

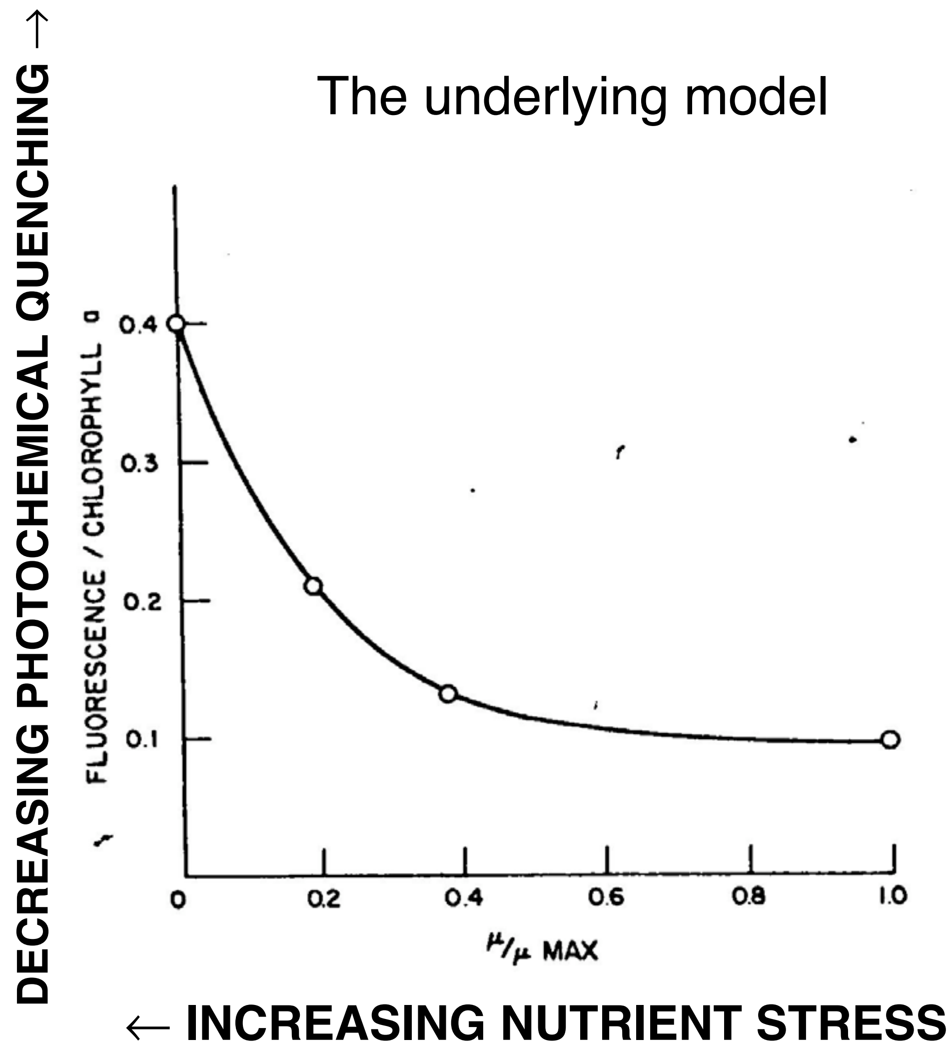




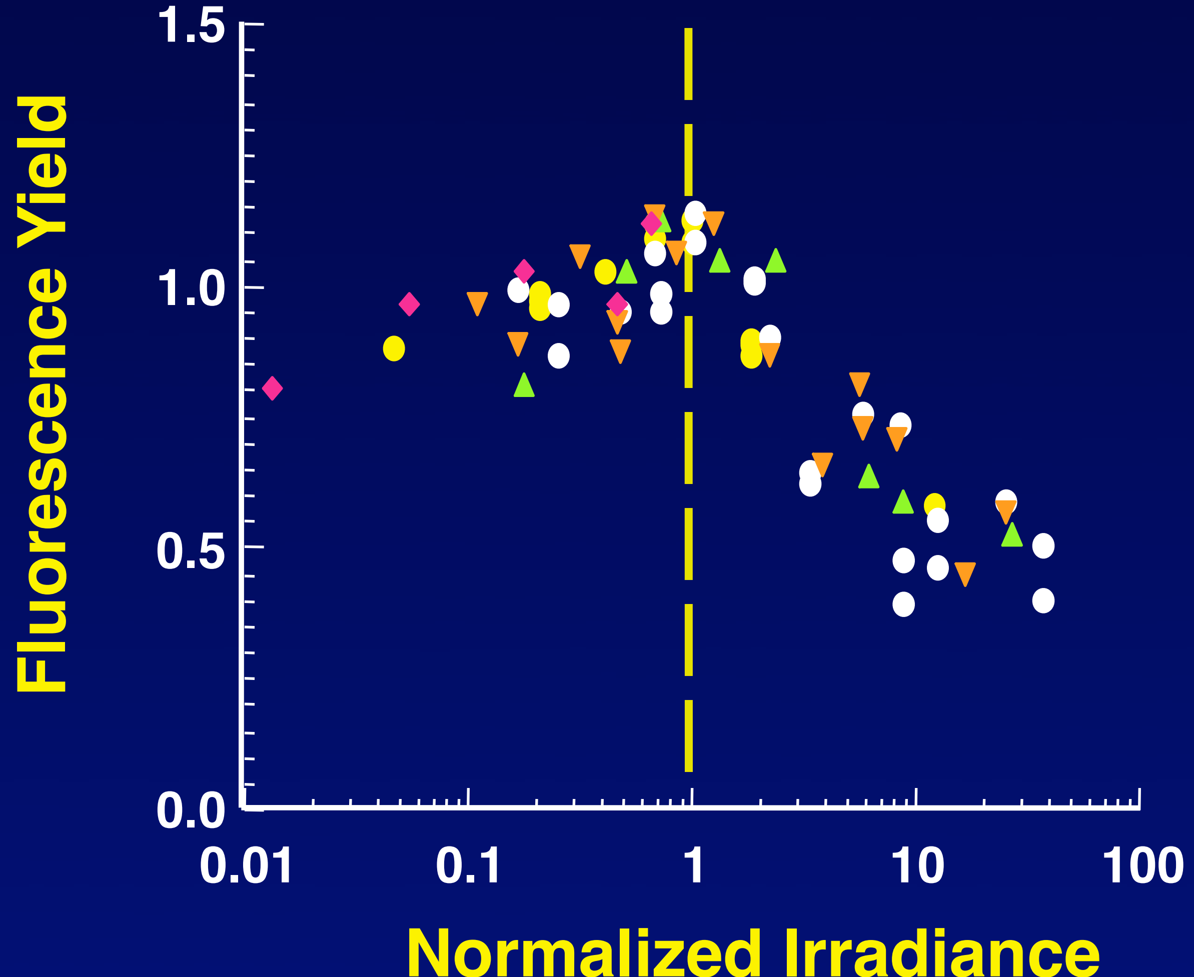
FLH/Chl vs *E* slope varied, reflecting variation in φ_f

φ_f covaried with inferred upwelling: high nutrient input - low fluorescence yield

The underlying model



But nonphotochemical quenching was recognized as a factor:

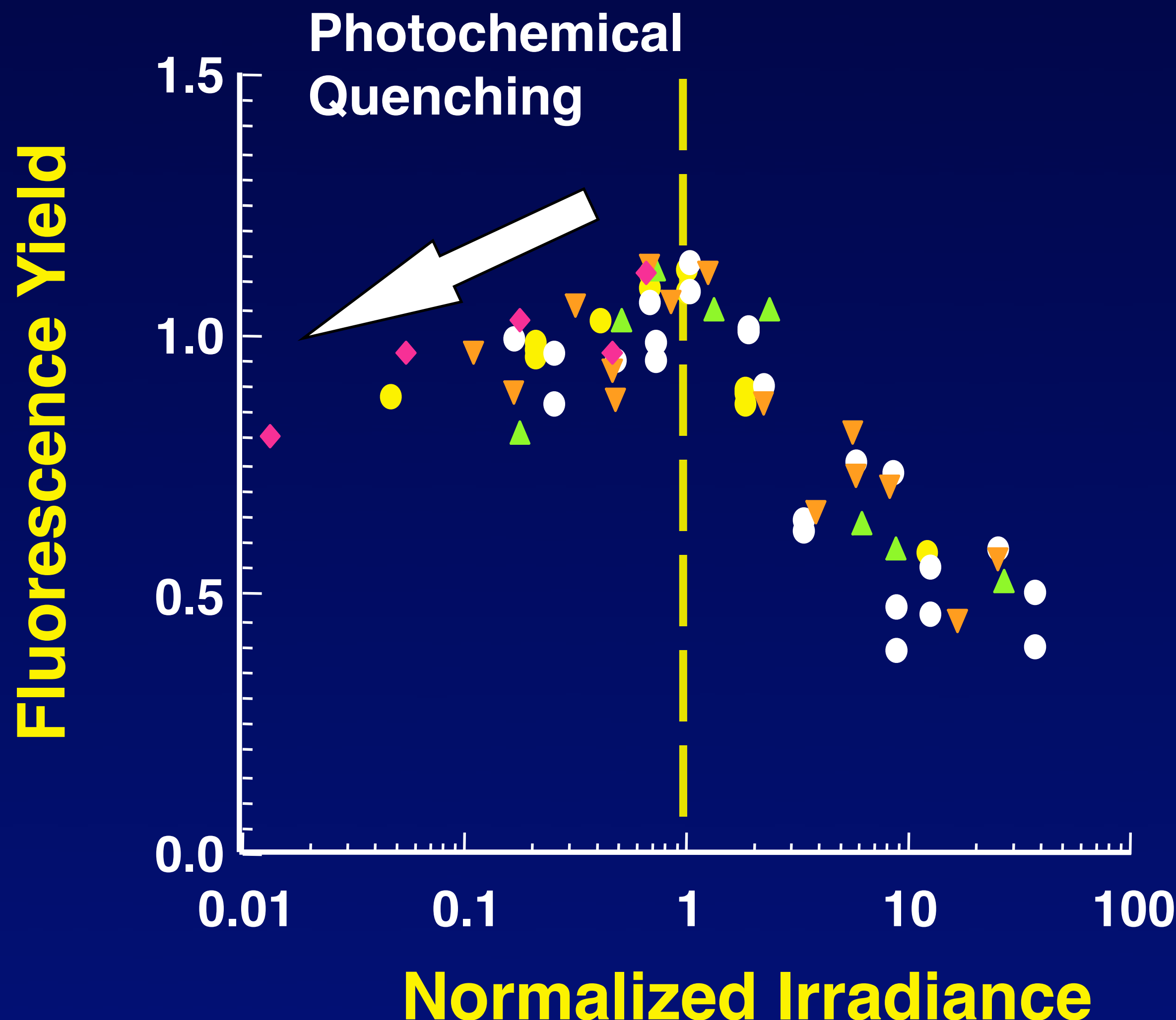


Each data set is normalized to a different irradiance of maximal fluorescence yield

Cullen, J.J., Á.M. Ciotti, R.F. Davis and P.J. Neale. 1997. The relationship between near-surface chlorophyll and solar-stimulated fluorescence: biological effects. In: Ocean Optics XIII, S.G. Ackleson and R. Frouin, eds. Proc. SPIE 2963: 272-277.

But nonphotochemical quenching was recognized as a factor:

Photosynthesis decreases φ_f (subsaturating irradiance)



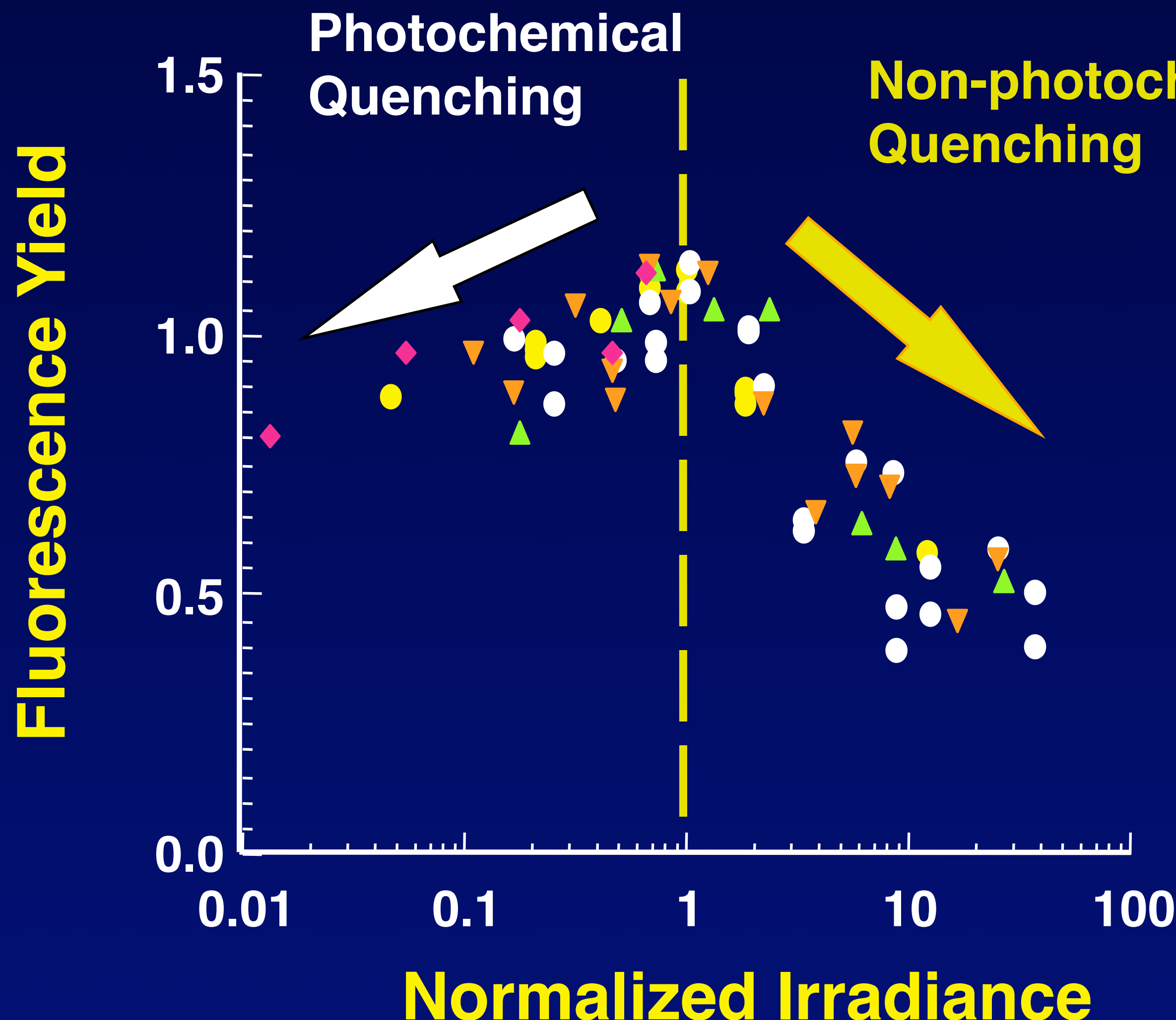
Each data set is normalized to a different irradiance of maximal fluorescence yield

Cullen, J.J., Á.M. Ciotti, R.F. Davis and P.J. Neale. 1997. The relationship between near-surface chlorophyll and solar-stimulated fluorescence: biological effects. In: Ocean Optics XIII, S.G. Ackleson and R. Frouin, eds. Proc. SPIE 2963: 272-277.

But nonphotochemical quenching was recognized as a factor:

Photosynthesis decreases φ_f (subsaturating irradiance)

Heat dissipation decreases φ_f (supersaturating irradiance)



Each data set is normalized to a different irradiance of maximal fluorescence yield

Cullen, J.J., Á.M. Ciotti, R.F. Davis and P.J. Neale. 1997. The relationship between near-surface chlorophyll and solar-stimulated fluorescence: biological effects. In: Ocean Optics XIII, S.G. Ackleson and R. Frouin, eds. Proc. SPIE 2963: 272-277.

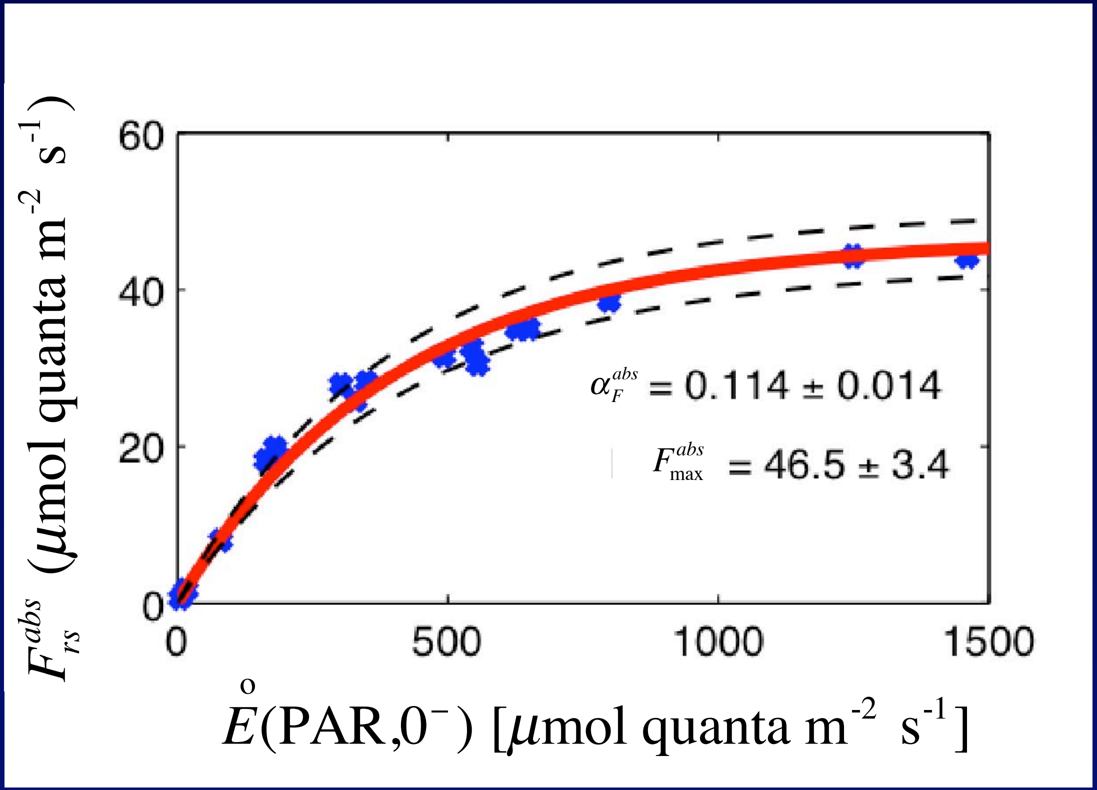
Moving beyond FLH:

Direct estimation of quantum yield vs irradiance relationship

$$F_{rs}^{abs} = \frac{\left(L_u(683) - L_{ub}(683)\right) \cdot 4\pi \cdot C_f}{chl_{rs} \cdot \bar{a}_{\varphi}^{*}(chl_{rs}) \cdot Q_a^{*}(chl_{rs})} \cdot \left[\bar{K}_{abs}(chl_{rs}) + \kappa_f(chl_{rs})\right]$$

Optical drifter in the Bering Sea: quantum yield is

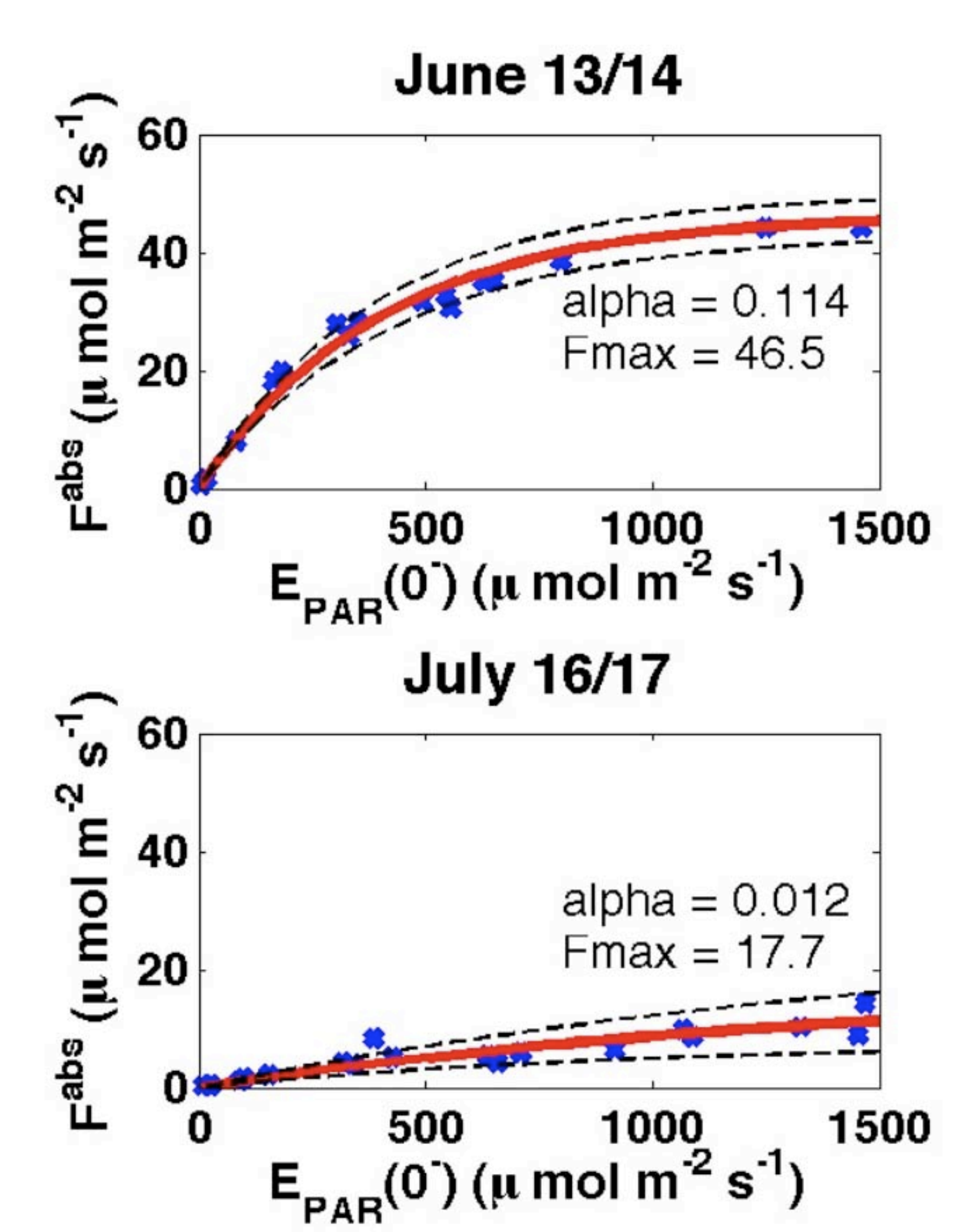
$$F_{rs}^{abs} \,/\, \overset{o}{E}(\mathrm{PAR}, 0^-)$$



Schallenberg et al. 2008, JGR Oceans

Results from the Bering Sea

Conclusion is the same: large variation, with high fluorescence yield associated with nutrient stress.

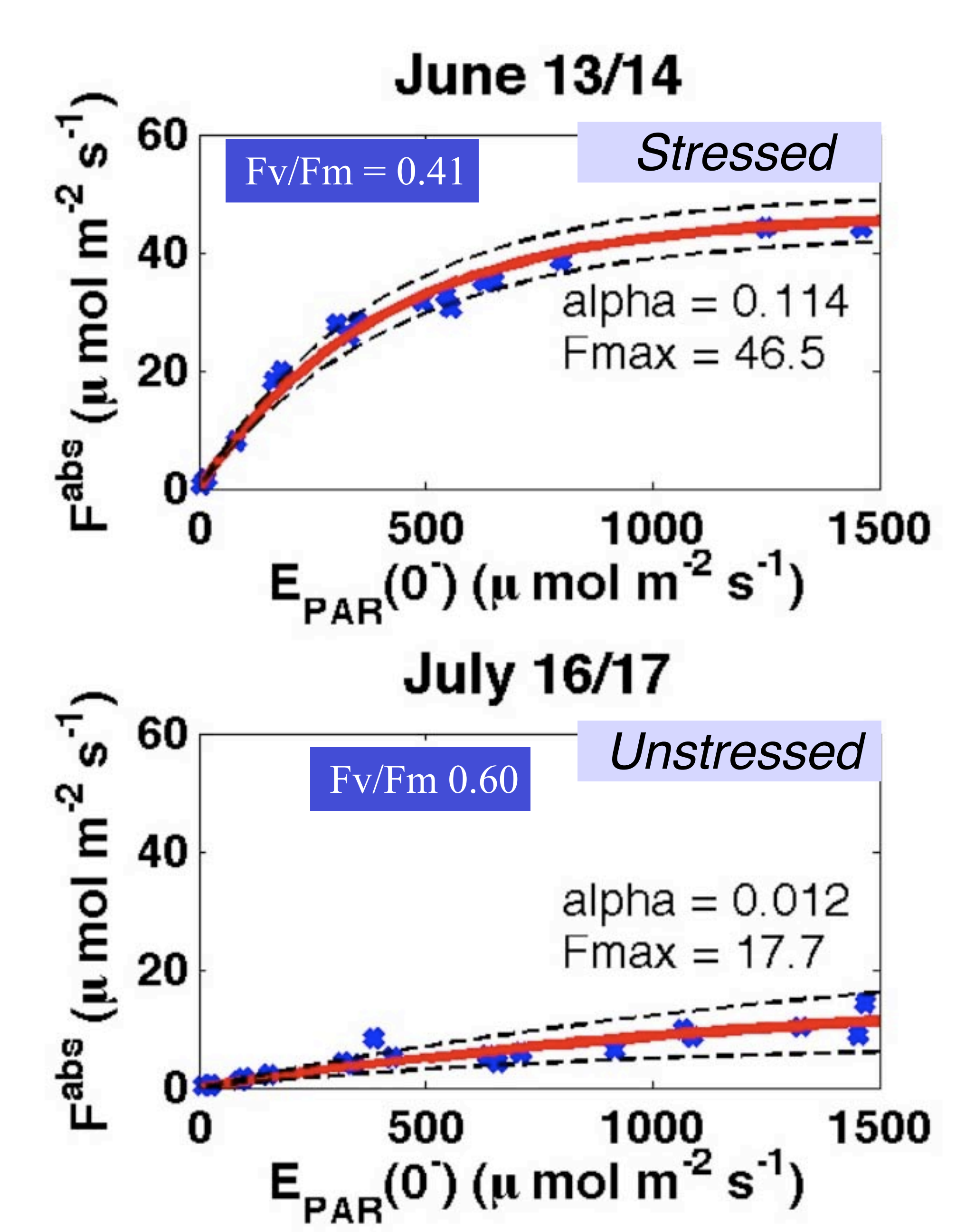


Schallenberg et al. 2008, JGR Oceans

Results from the Bering Sea

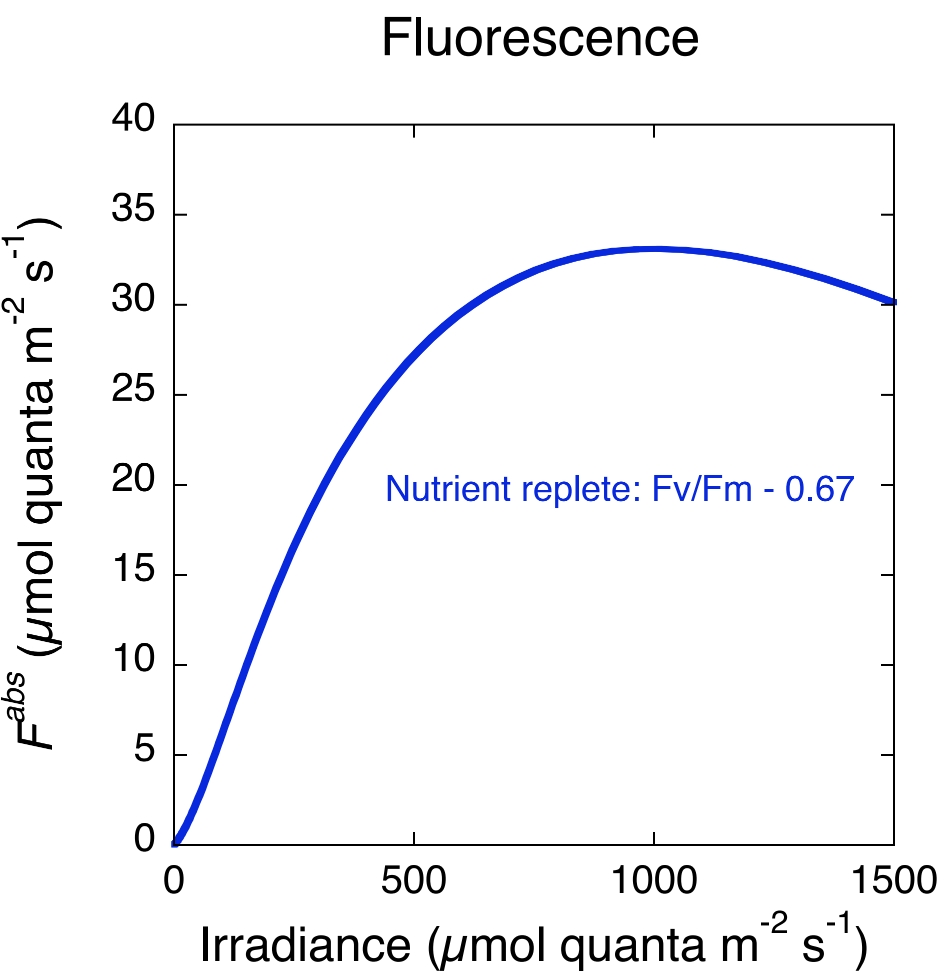
Conclusion is the same: large variation, with high fluorescence yield associated with nutrient stress.

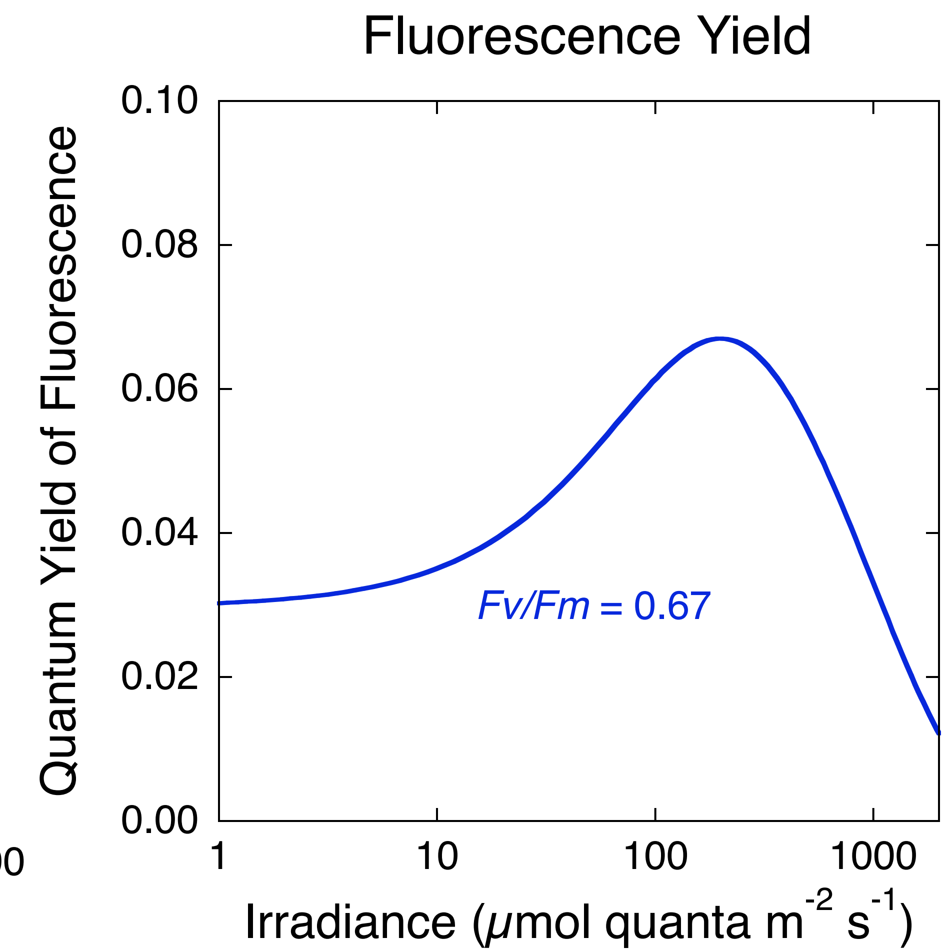
Backed up with direct measures of photosynthetic efficiency, *Fv*/*F*m



Schallenberg et al. 2008, JGR Oceans

What is the effect of nutrient stress on F vs E in this system?



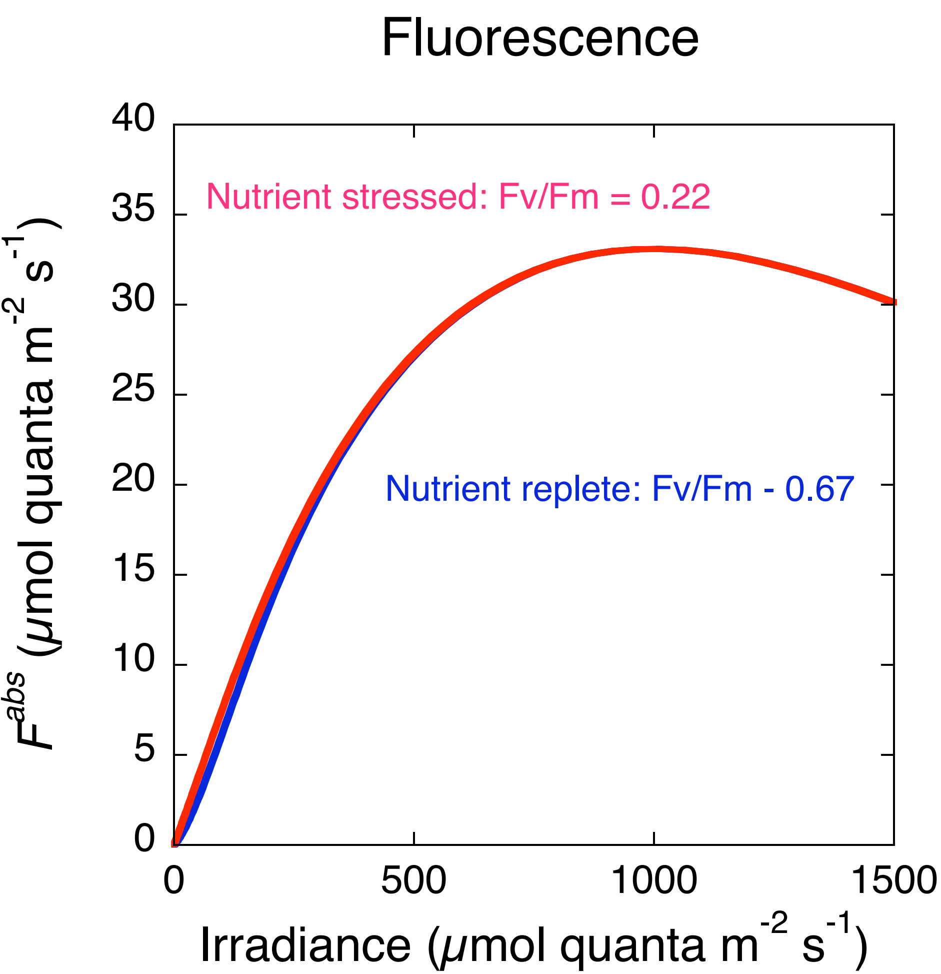


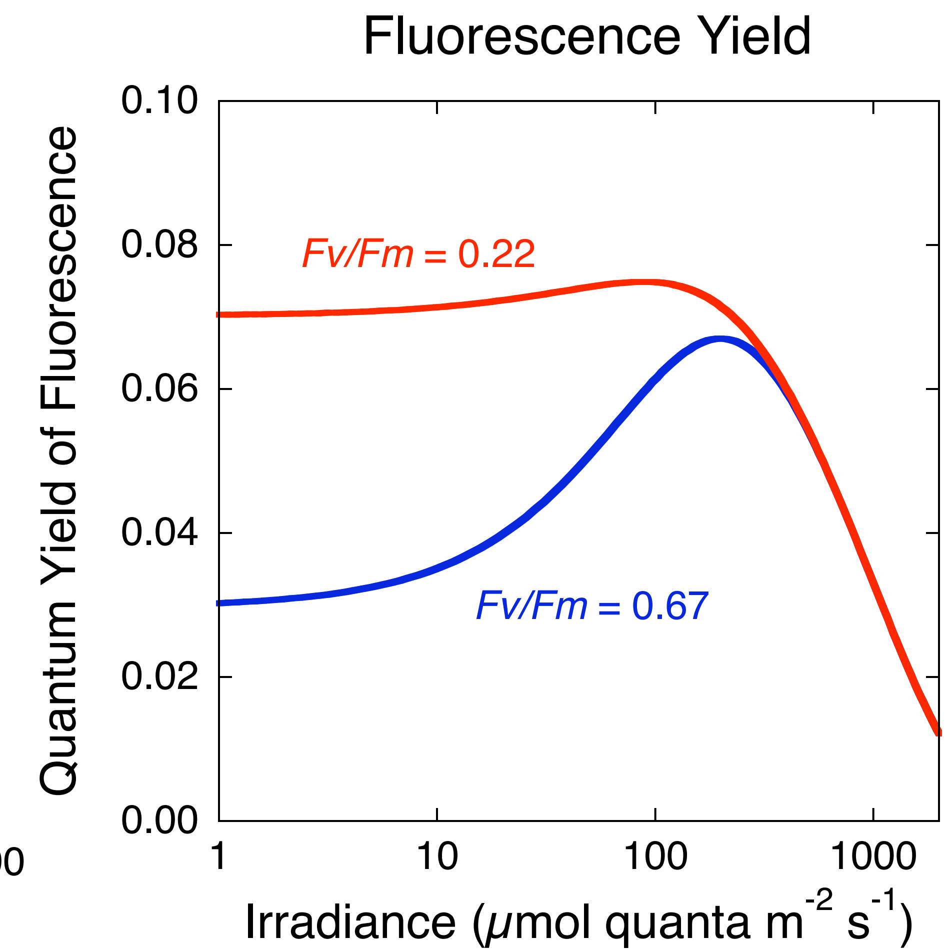
Schallenberg et al. 2008, JGR Oceans

Analysis after Morrison (2003) L&O

Not much!

(*considering only photochemical quenching*)

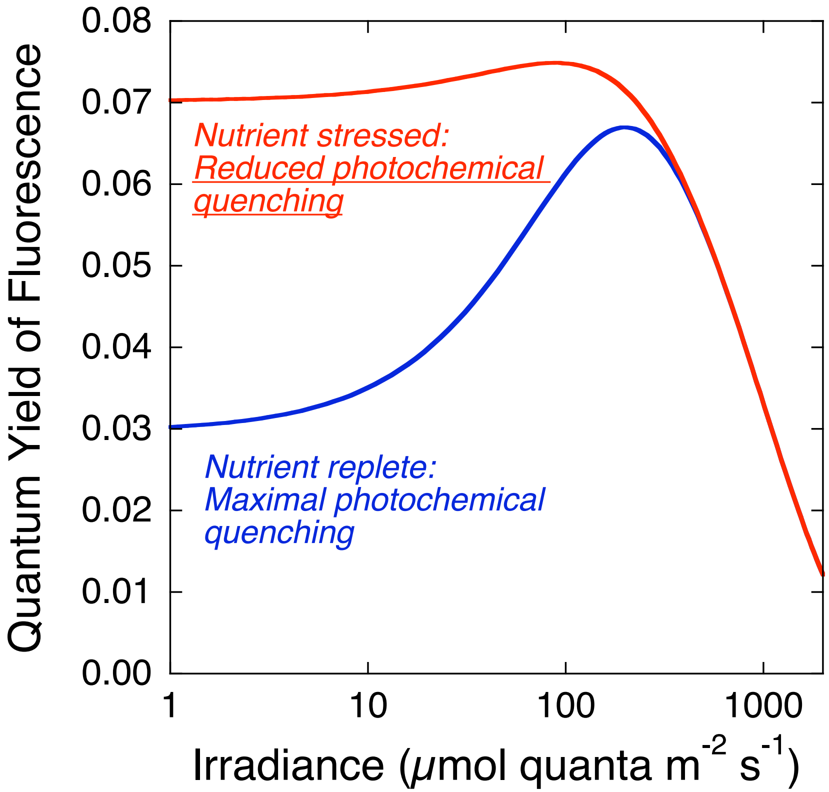


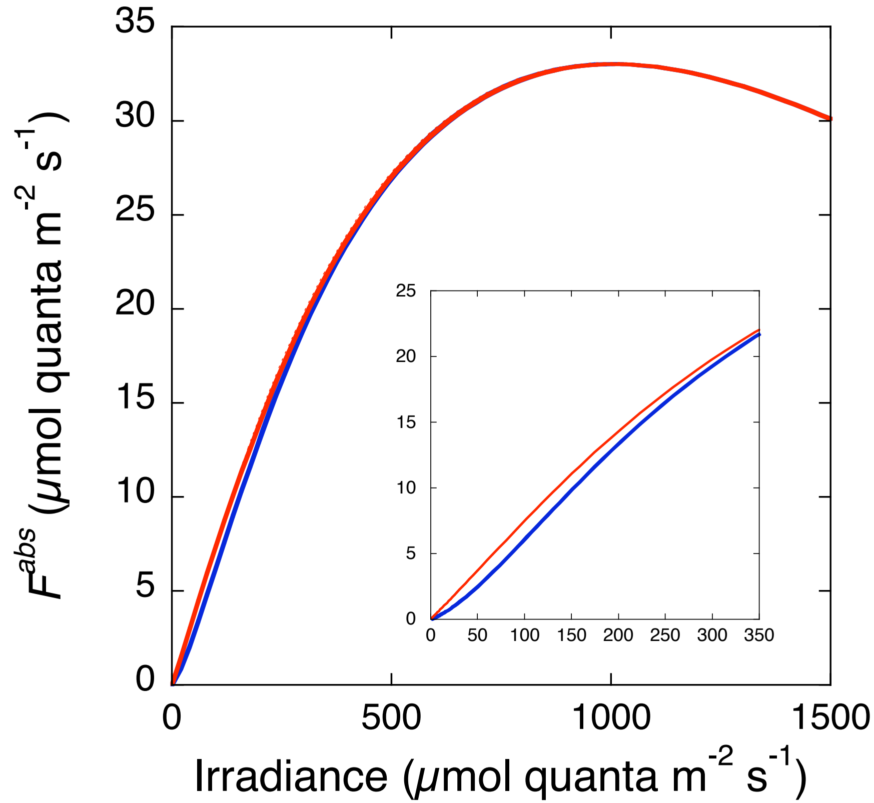


Schallenberg et al. 2008, JGR Oceans

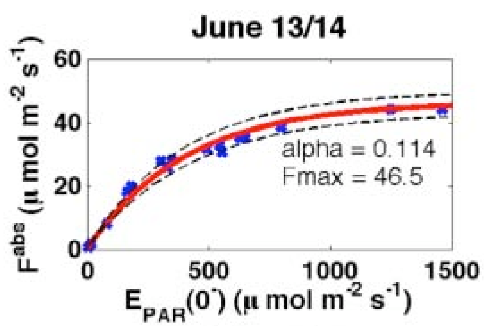
Analysis after Morrison (2003) L&O

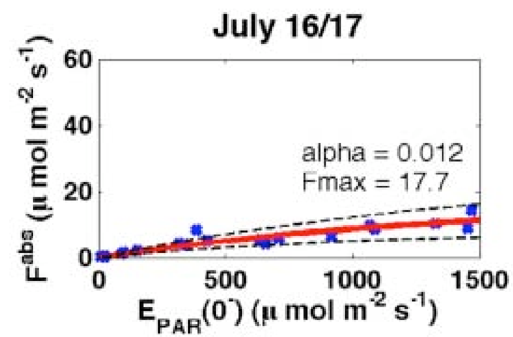
Big differences in near-surface sun-induced fluorescence yield are not due to effects of nutrition on photochemical quenching





Stressed

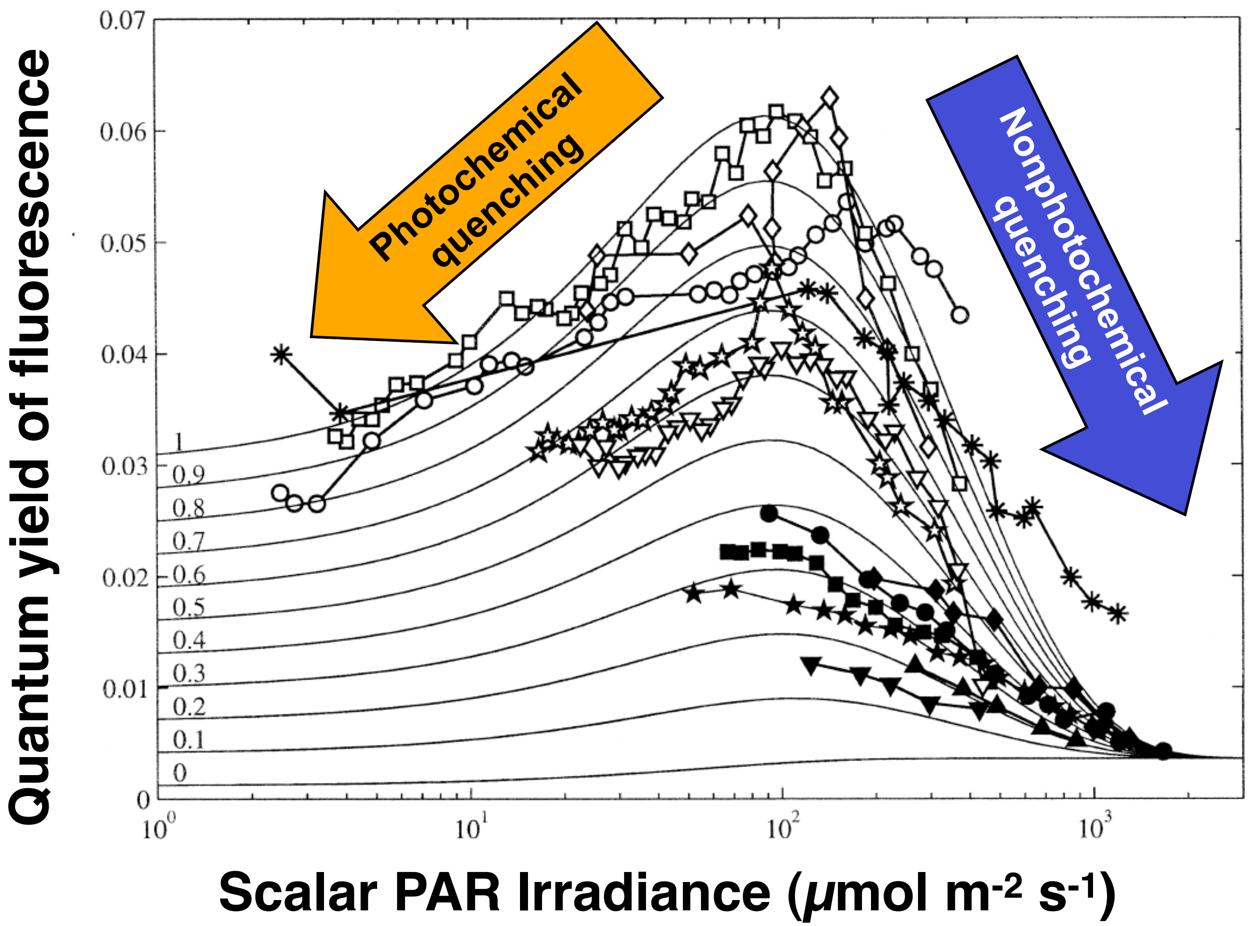




Unstressed

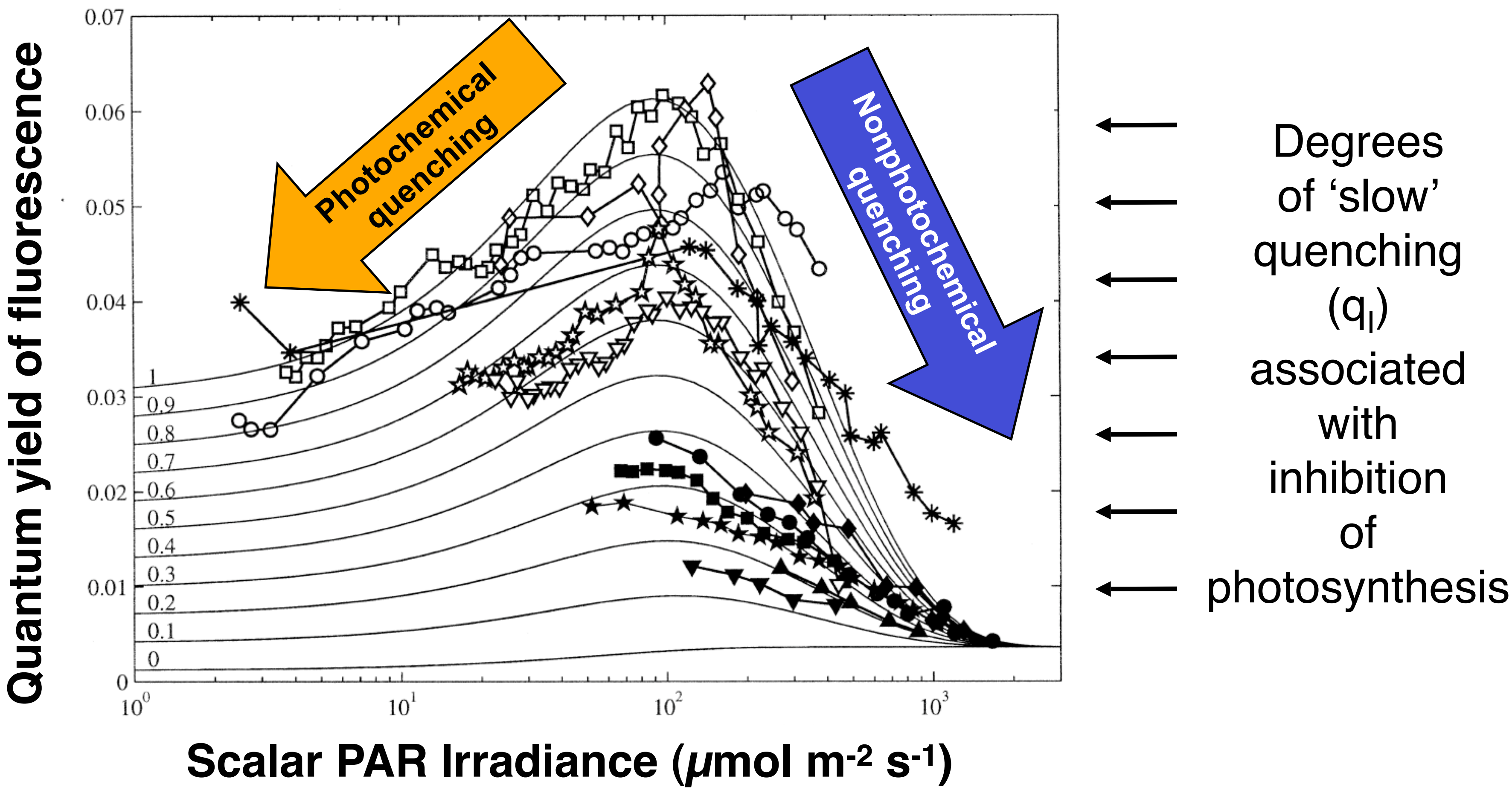
Morrison (2003, L&O):

A third process must be considered: q_i



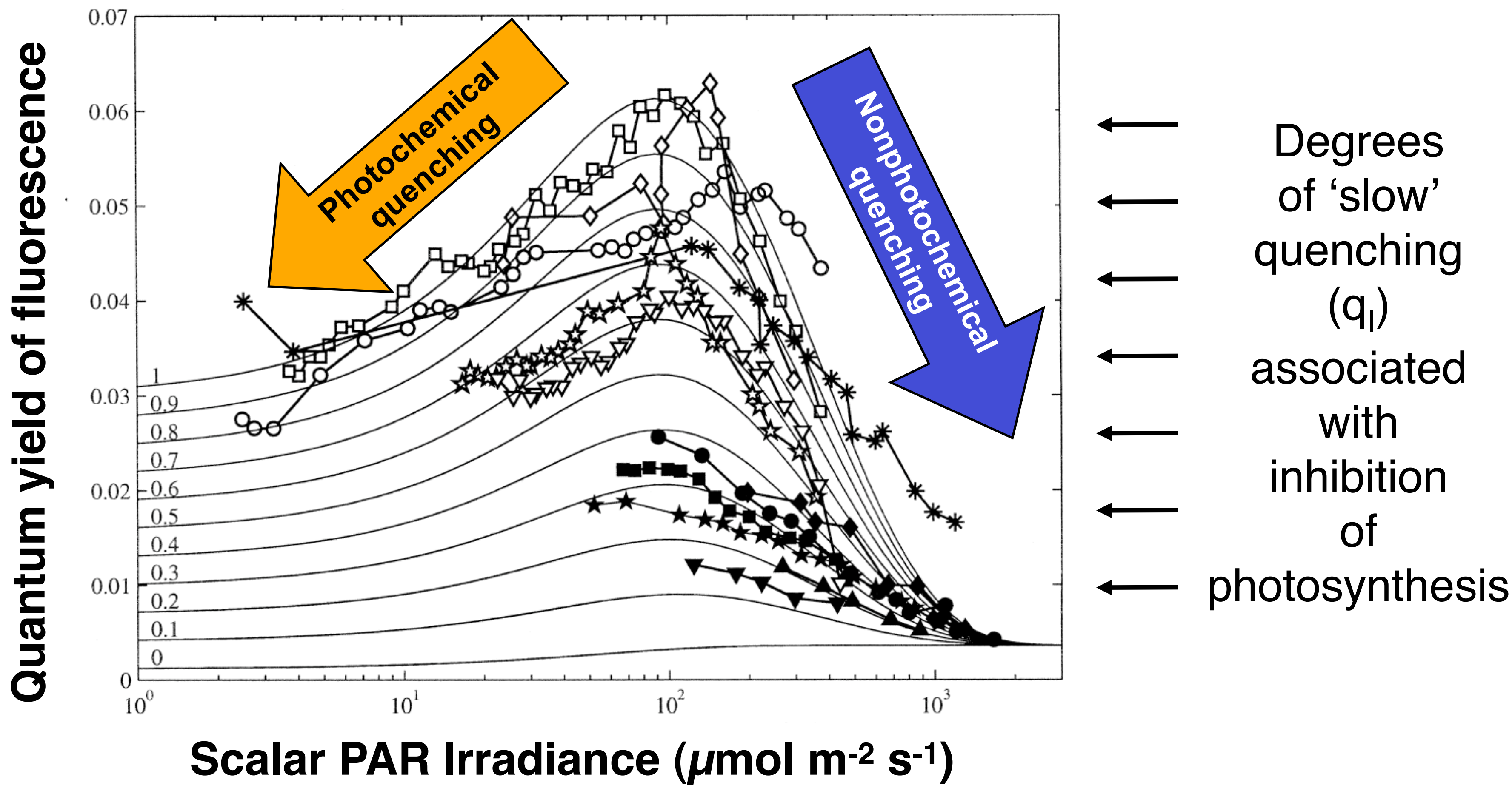
Morrison (2003, L&O):

A third process must be considered: q_i



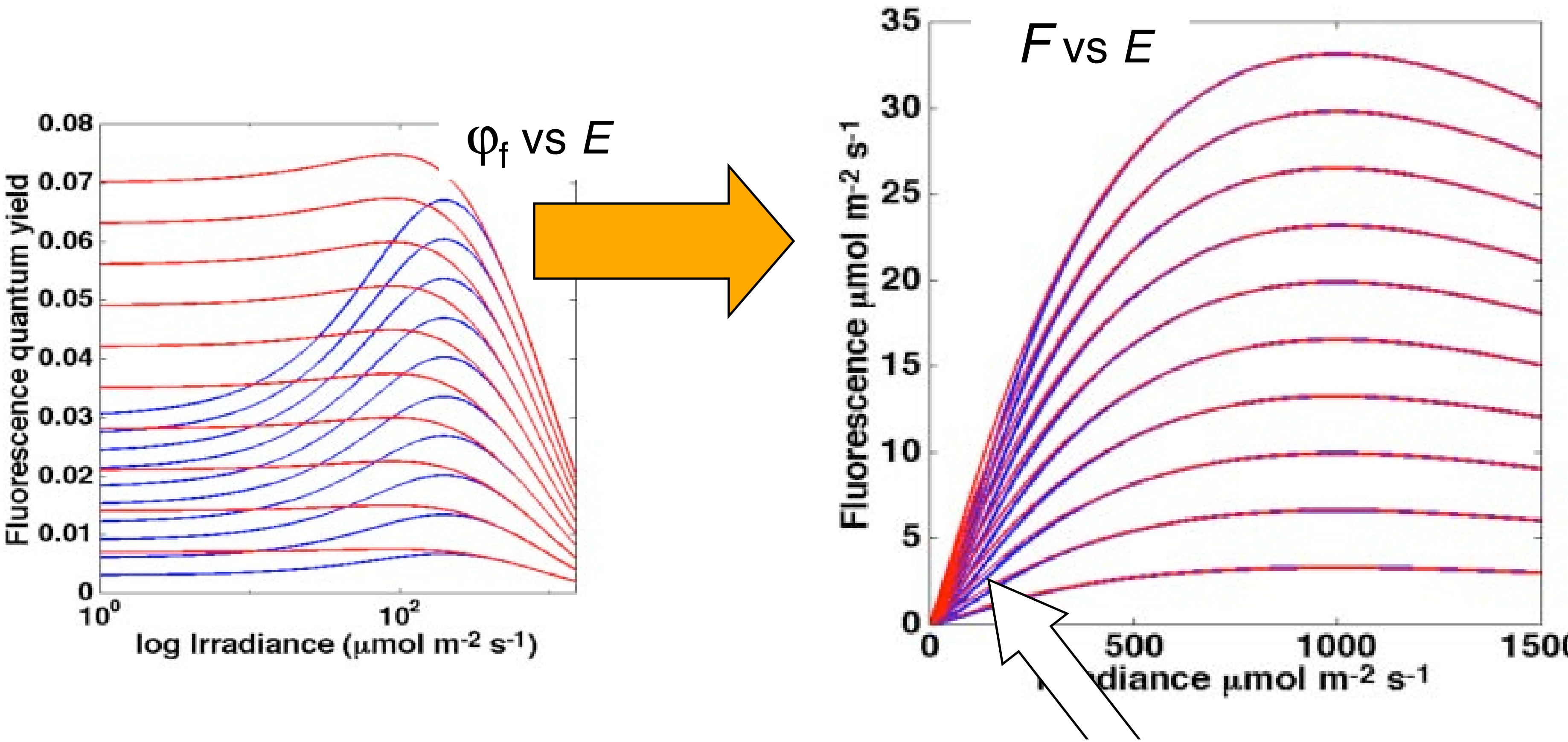
Morrison (2003, L&O):

A third process must be considered: q_i



This quenching leads to reduced photosynthetic efficiency in low light

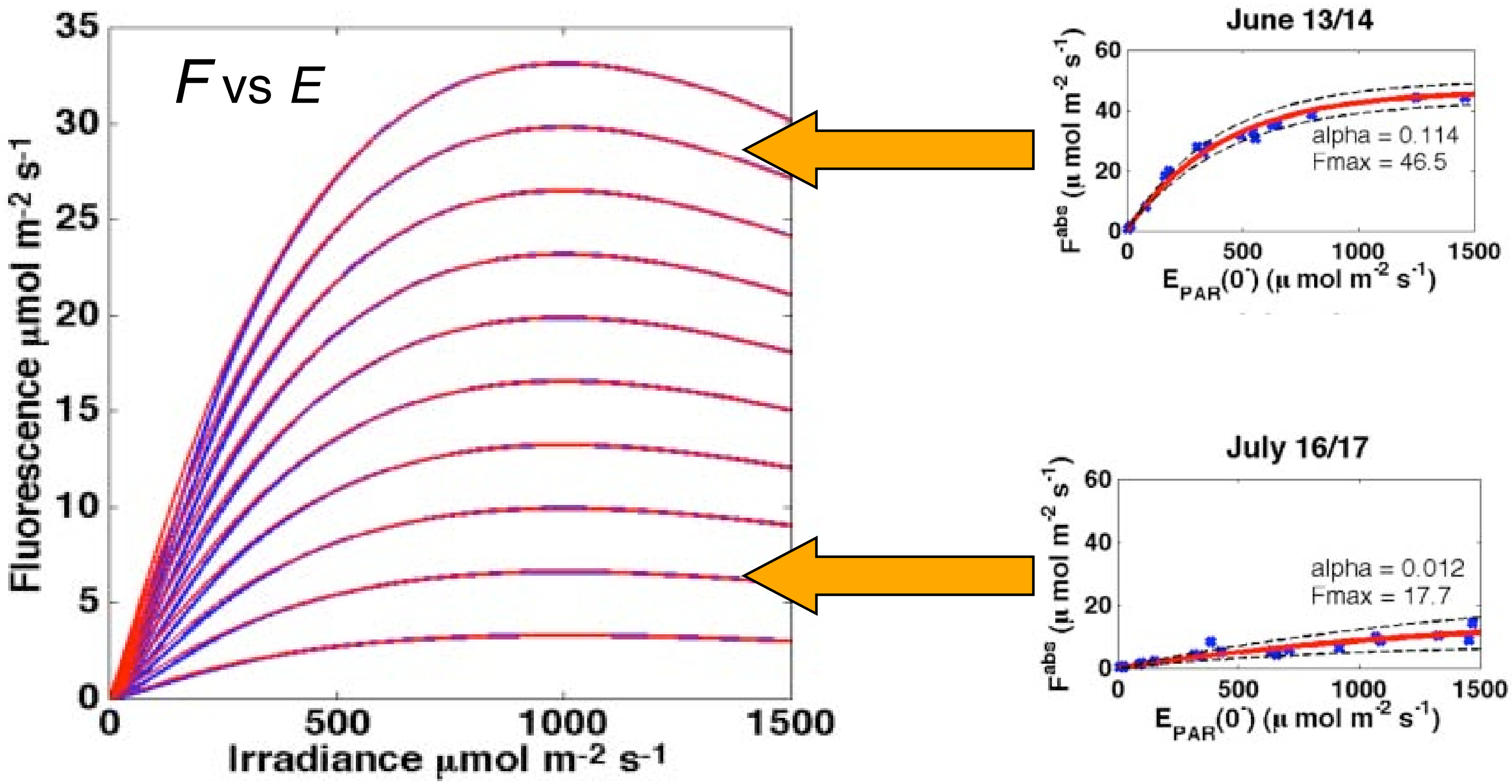
Inference: Variability in surface *F* vs *E* is dominated by nonphotochemical quenching (NPQ), not effects of nutrition on photochemical quenching



Competition between photosynthesis and fluorescence affects only this curvature

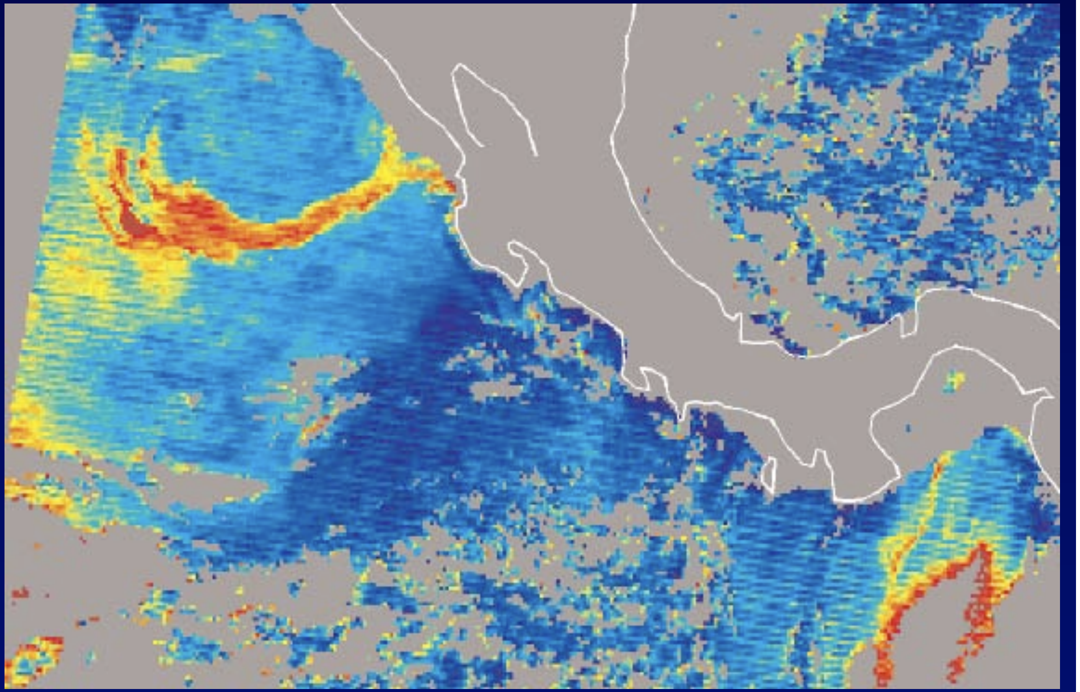
Schallenberg et al. 2008, JGR Oceans

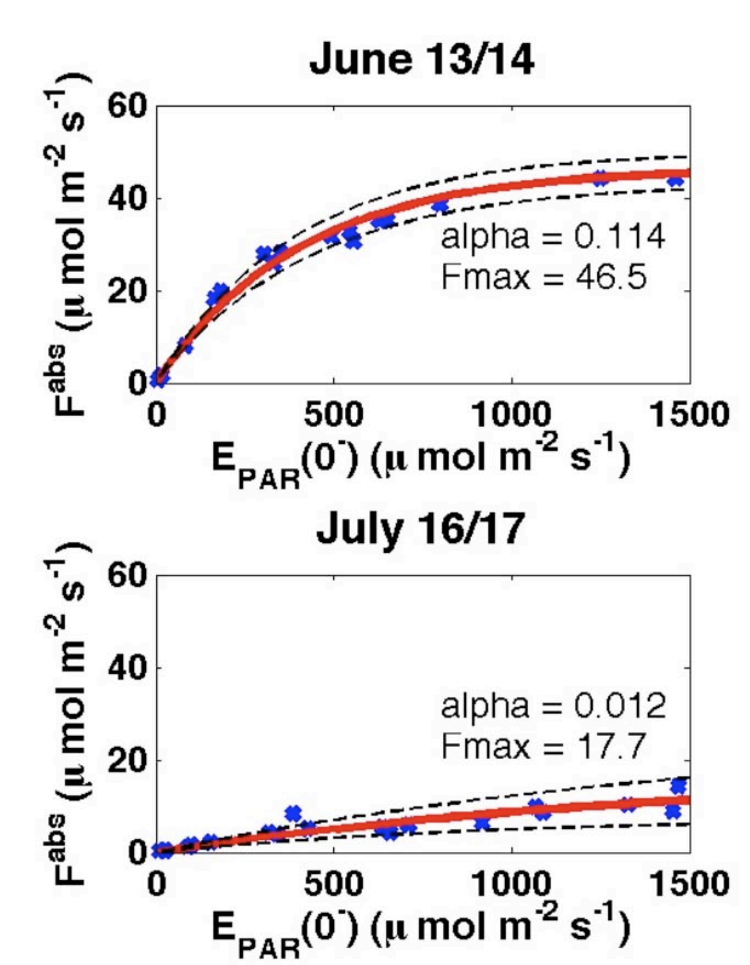
An influence of nutrition on NPQ?



Schallenberg et al. 2008, JGR Oceans

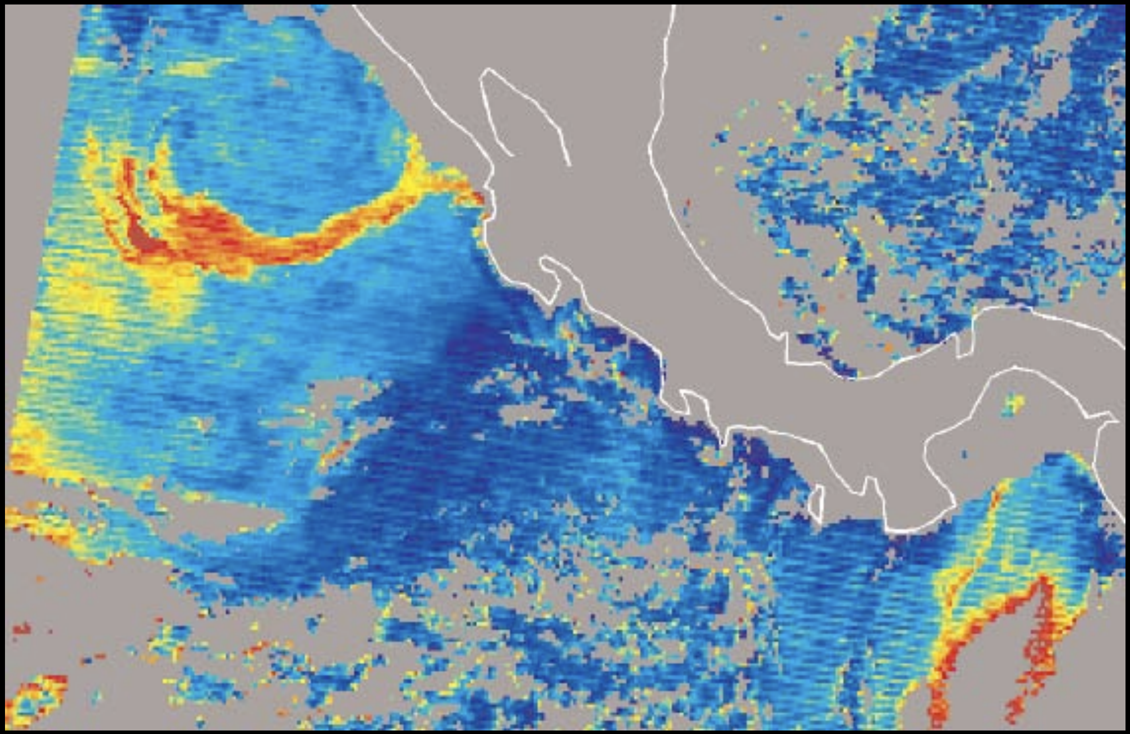
Working hypothesis: variability in the quantum yield of near-surface SICF in the ocean is driven by the slow component of nonphotochemical quenching, q_I.





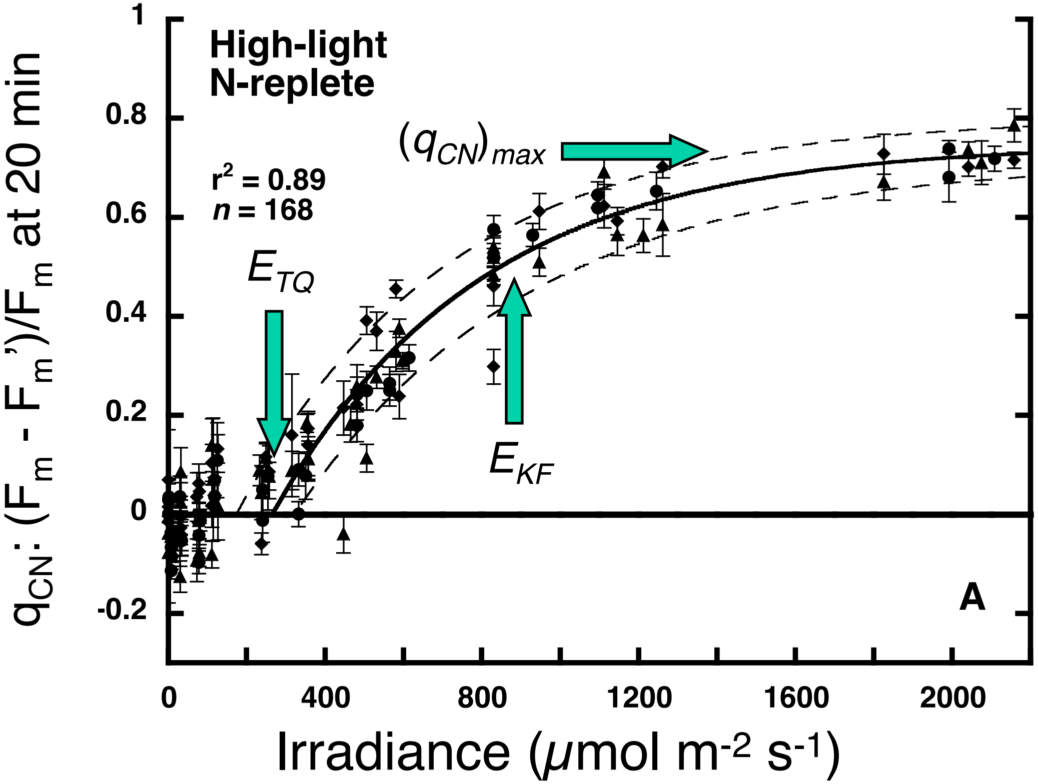
…the phenomenology of which is nearly unknown

Interpreting this…



…thus requires an understanding of NPQ vs $E = f$ (physiological state, species)

Careful, quantitative analysis of variable fluorescence vs *E* vs time



Parallel incubations: rapid light curves cause artifacts

A. Barnett (M.Sc. thesis)
see also Laney et al 2005

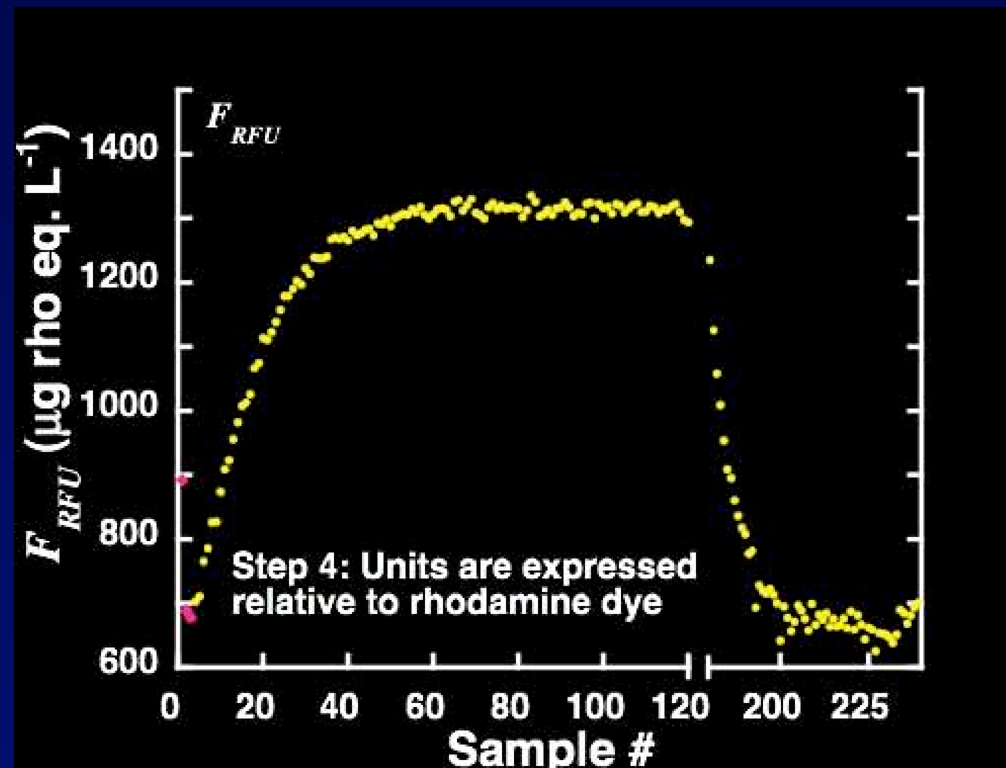
The FIRe Brigade is pursuing robust, quantitative procedures

Comprehensive characterization of a variable fluorescence assessment system: the Fluorescence Induction Relaxation fluorometer

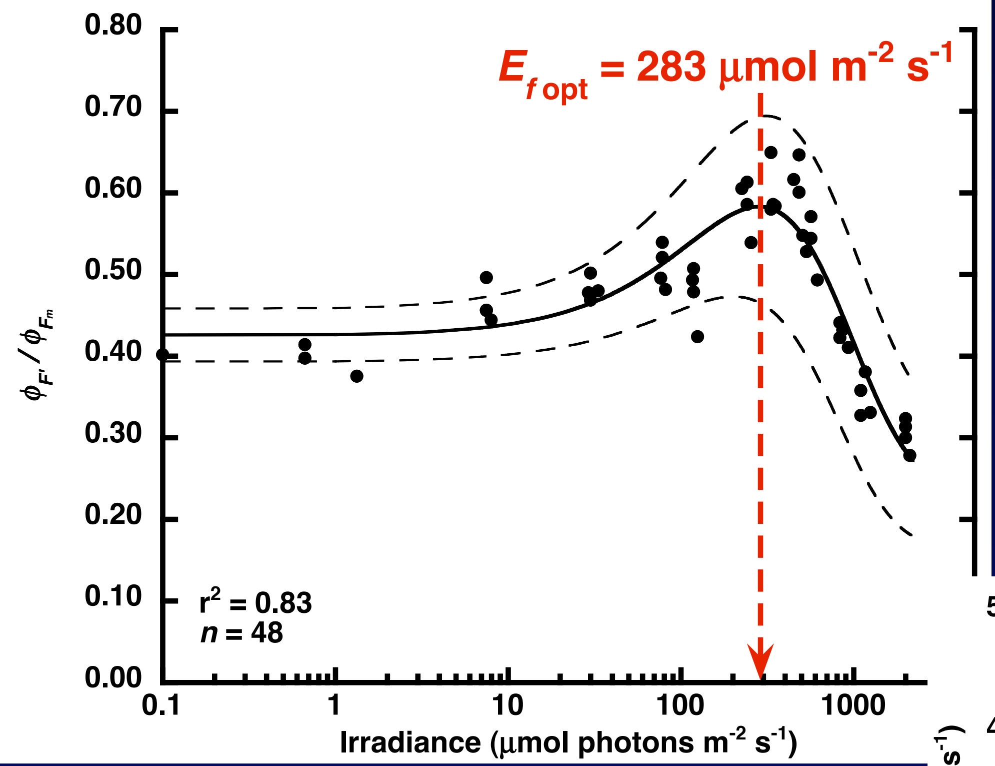
Audrey B. Barnett, Flavienne Bruyant, Caitlin B. Newport, Richard F. Davis, John J. Cullen

Analysis of raw data!
Reference standards!
Blanks!
Statistical estimates of errors!
F vs E vs time

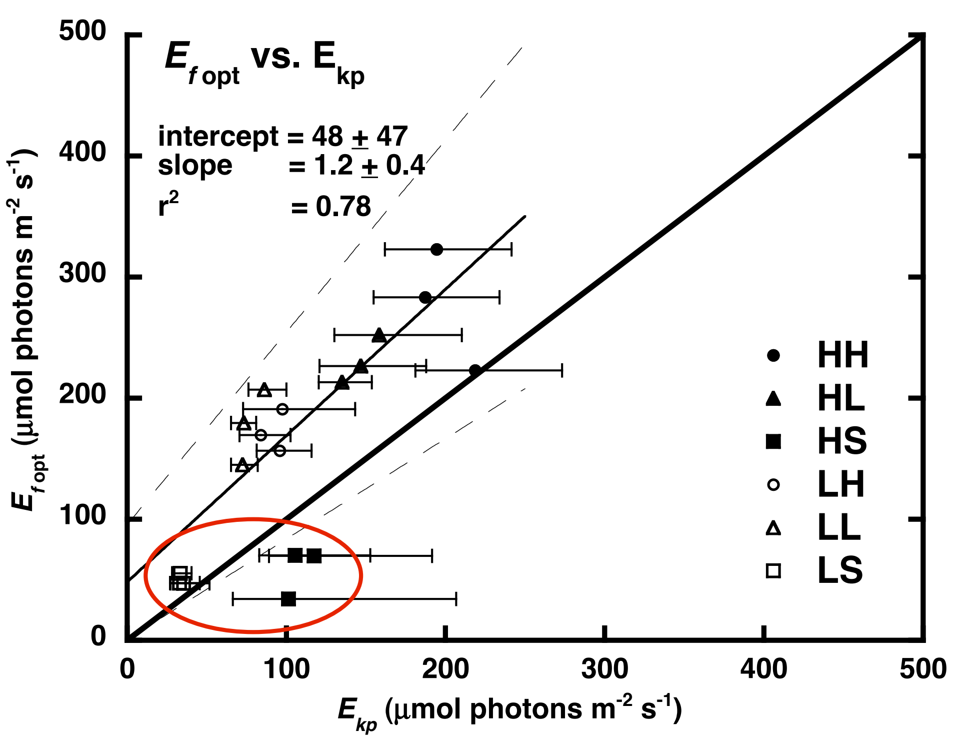
FIRe Fluorometer System



SATLANTIC



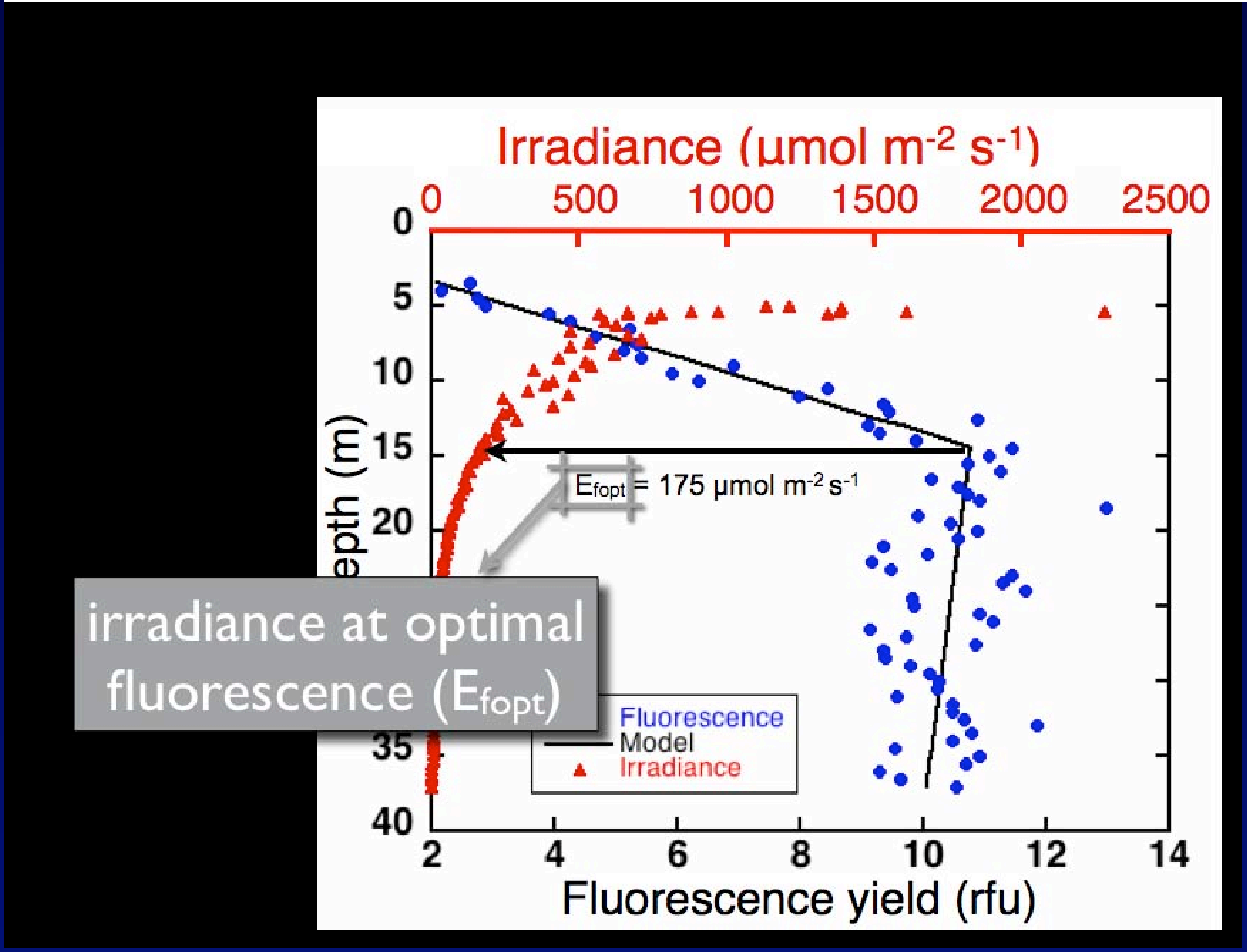
Relating *F* vs *E* to *P* vs *E* during parallel incubations



Not rapid light curves

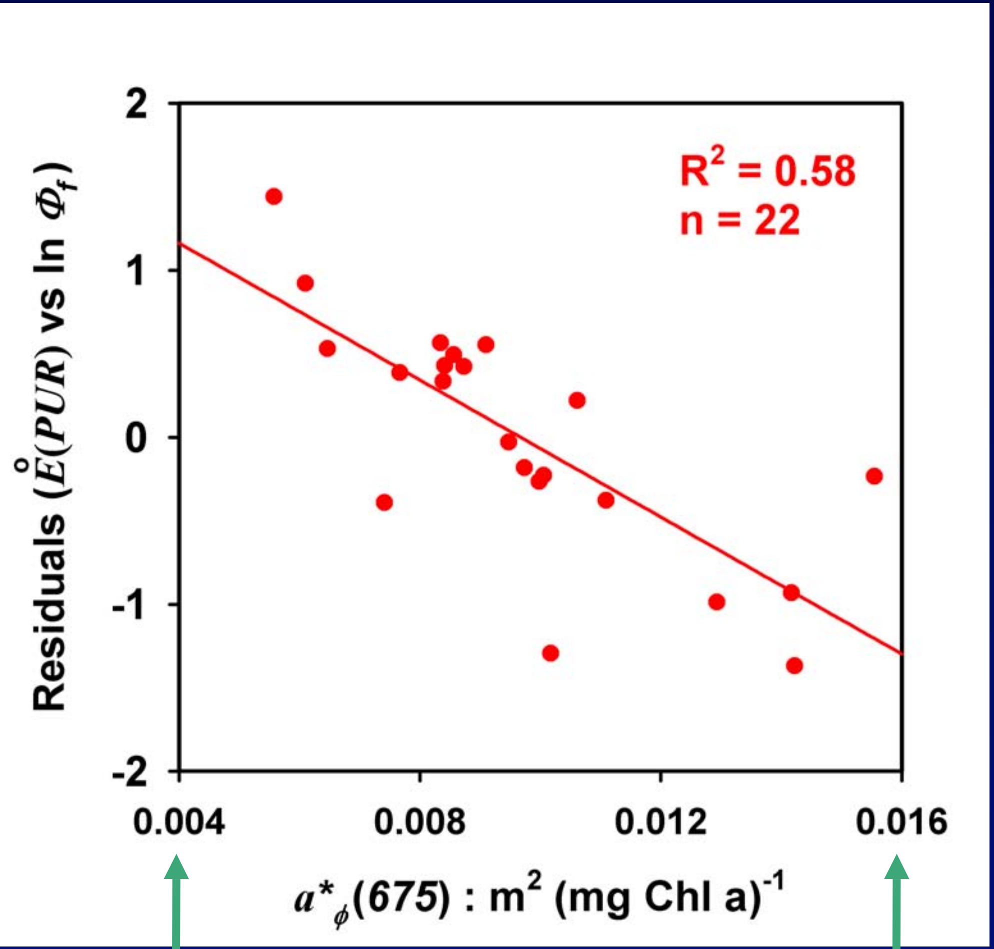
A. Barnett (M.Sc. thesis)

And retrieving similar information from vertical profiles using "any old fluorometer"



Adam Comeau

Systematic analysis of natural variability of ϕ_f



high packaging

low packaging

Susanne Craig

Large, densely pigmented cells	⇨	High ϕ_f
Small, weakly pigmented cells	⇨	Low ϕ_f

Summary

Thank you!

Summary

Fluorescence yield is variable for many reasons

Thank you!

Summary

Fluorescence yield is variable for many reasons

The foundations of studying variations in fluorescence yield go back 50 years. They should not be ignored.

Thank you!

Summary

Fluorescence yield is variable for many reasons

The foundations of studying variations in fluorescence yield go back 50 years. They should not be ignored.

Sun-induced fluorescence yield varies greatly in nature (about 10x), directly driven by physiological processes.

Thank you!

Summary

Fluorescence yield is variable for many reasons

The foundations of studying variations in fluorescence yield go back 50 years. They should not be ignored.

Sun-induced fluorescence yield varies greatly in nature (about 10x), directly driven by physiological processes.

This is not a simple effect of nutrient stress on fluorescence yield.

Thank you!

Summary

Fluorescence yield is variable for many reasons

The foundations of studying variations in fluorescence yield go back 50 years. They should not be ignored.

Sun-induced fluorescence yield varies greatly in nature (about 10x), directly driven by physiological processes.

This is not a simple effect of nutrient stress on fluorescence yield.

We don't know enough about the physiological influences on sun-induced chlorophyll fluorescence to interpret the variability effectively. We can propose explanations, but these would be hypotheses only.

Thank you!

Summary

Fluorescence yield is variable for many reasons

The foundations of studying variations in fluorescence yield go back 50 years. They should not be ignored.

Sun-induced fluorescence yield varies greatly in nature (about 10x), directly driven by physiological processes.

This is not a simple effect of nutrient stress on fluorescence yield.

We don’t know enough about the physiological influences on sun-induced chlorophyll fluorescence to interpret the variability effectively. We can propose explanations, but these would be hypotheses only.

Careful, quantitative analysis — both in the lab and in the field — will provide new and powerful interpretations of SICF.

Thank you!