Behavior, physiology and the niche of marine phytoplankton

John J. Cullen

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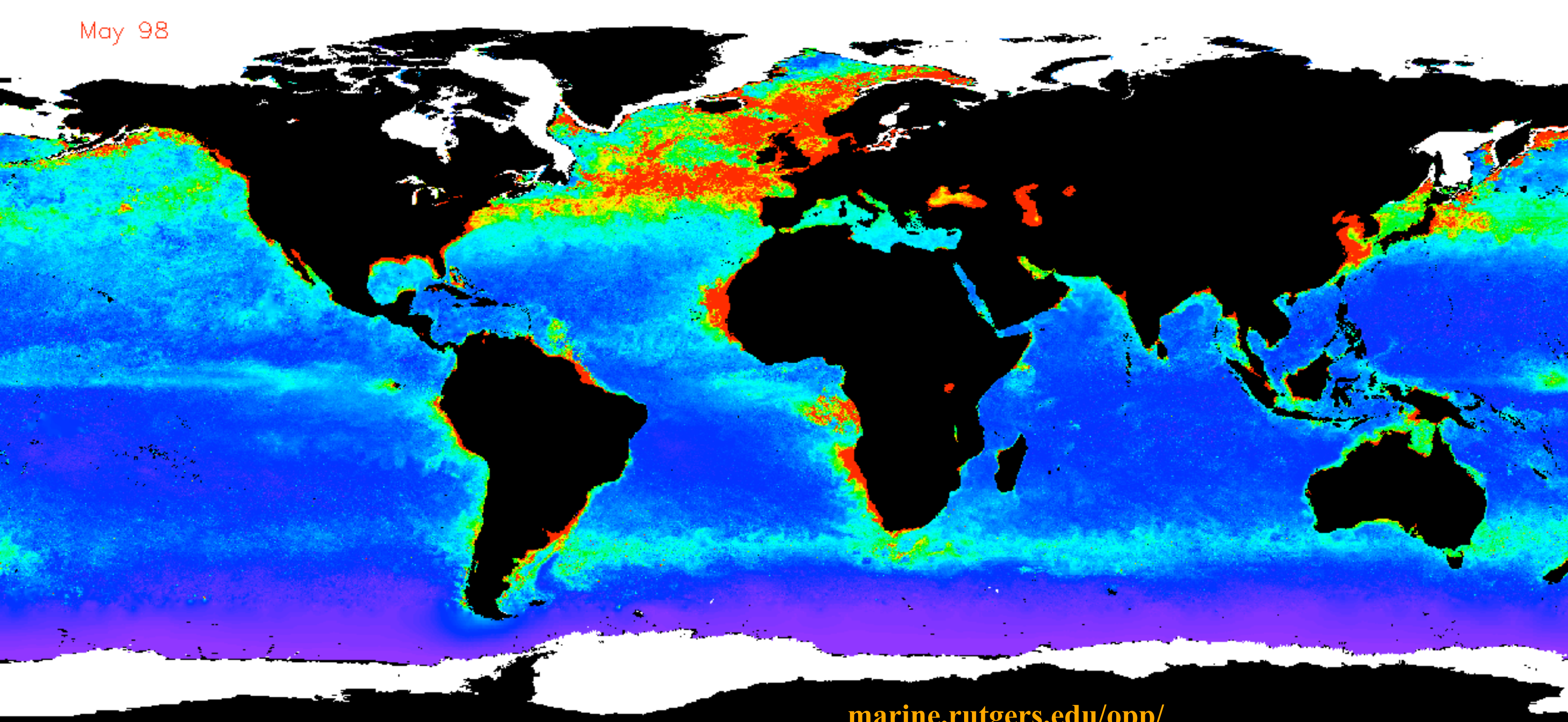
Halifax, Nova Scotia, Canada B3H 4R2

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

Ocean Tracking Network

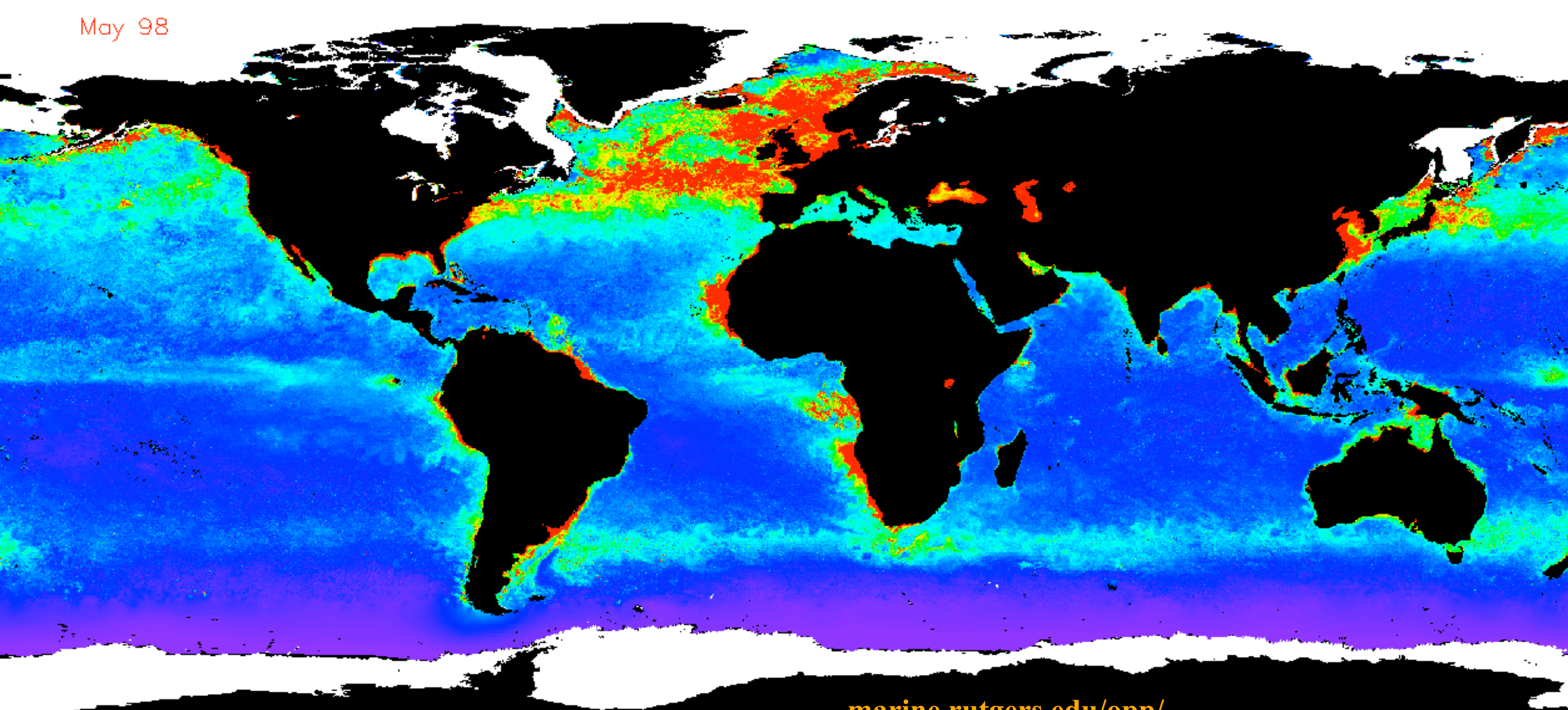
A principal goal of microbial oceanography

Describing and **explaining** the
distributions and ***activities*** of marine microbes



marine.rutgers.edu/opp/

…and using this information to describe the ***causes*** and ***consequences*** of variations in key biogeochemical processes



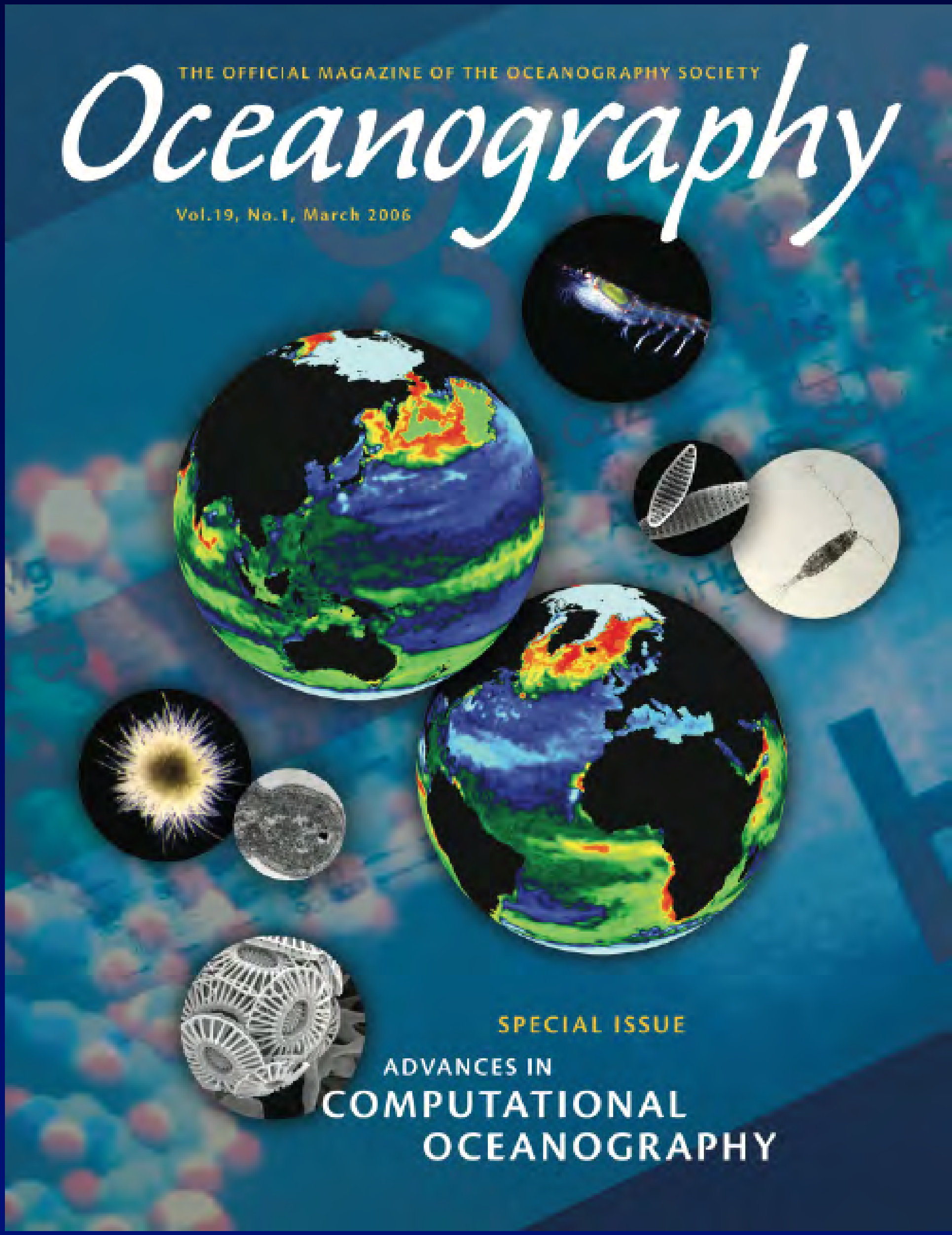
marine.rutgers.edu/opp/

Key biogeochemical processes

- Primary production
- Nitrogen fixation
- Denitrification
- Trace gas production
- …and the many other processes that make those processes possible

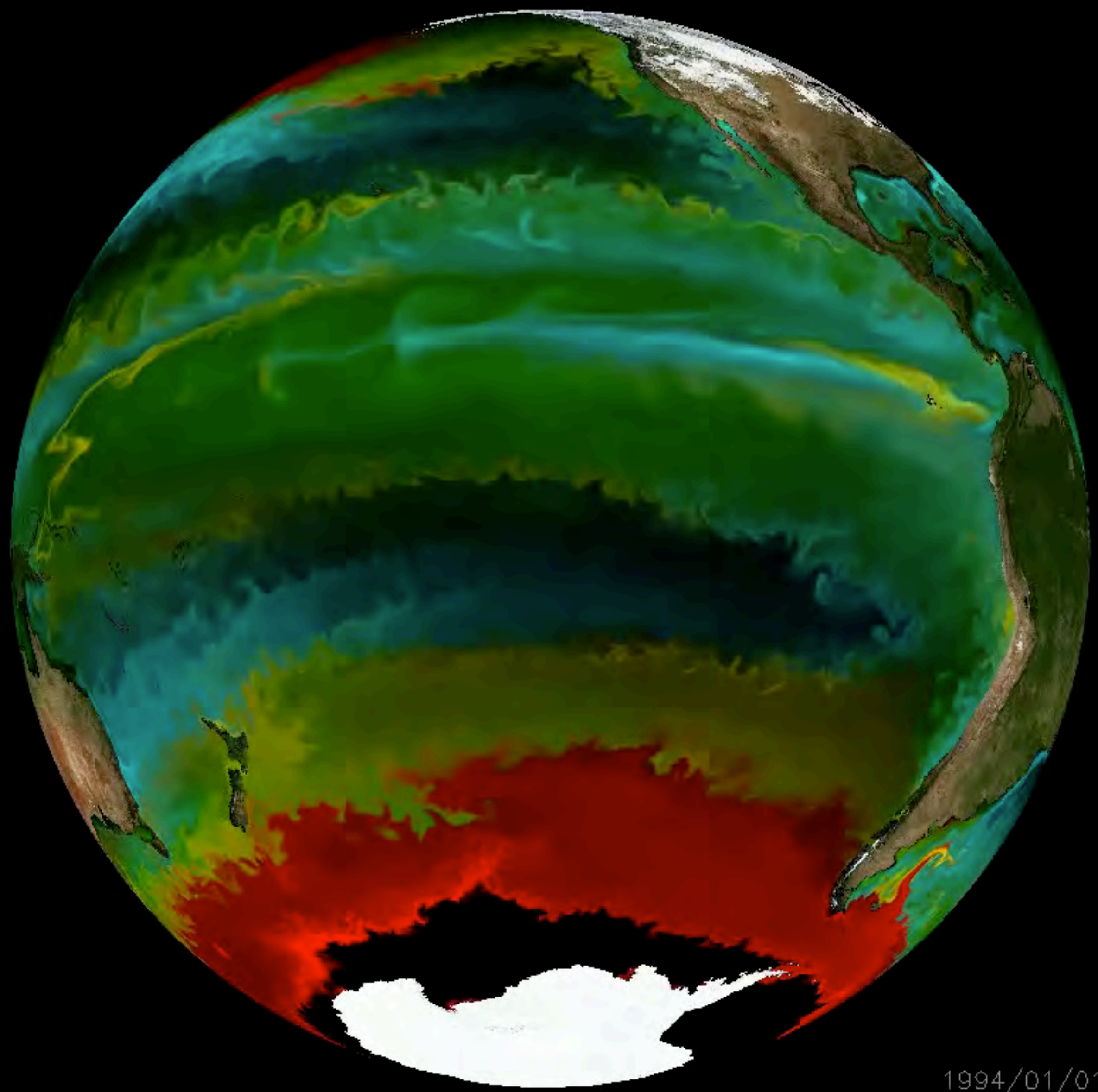
This can be achieved only through an integrated approach

The role of the oceans in Earth systems ecology, and the effects of climate variability on the ocean and its ecosystems, can be understood only by observing, describing, and ultimately predicting the state of the ocean as a physically forced ecological and biogeochemical system.



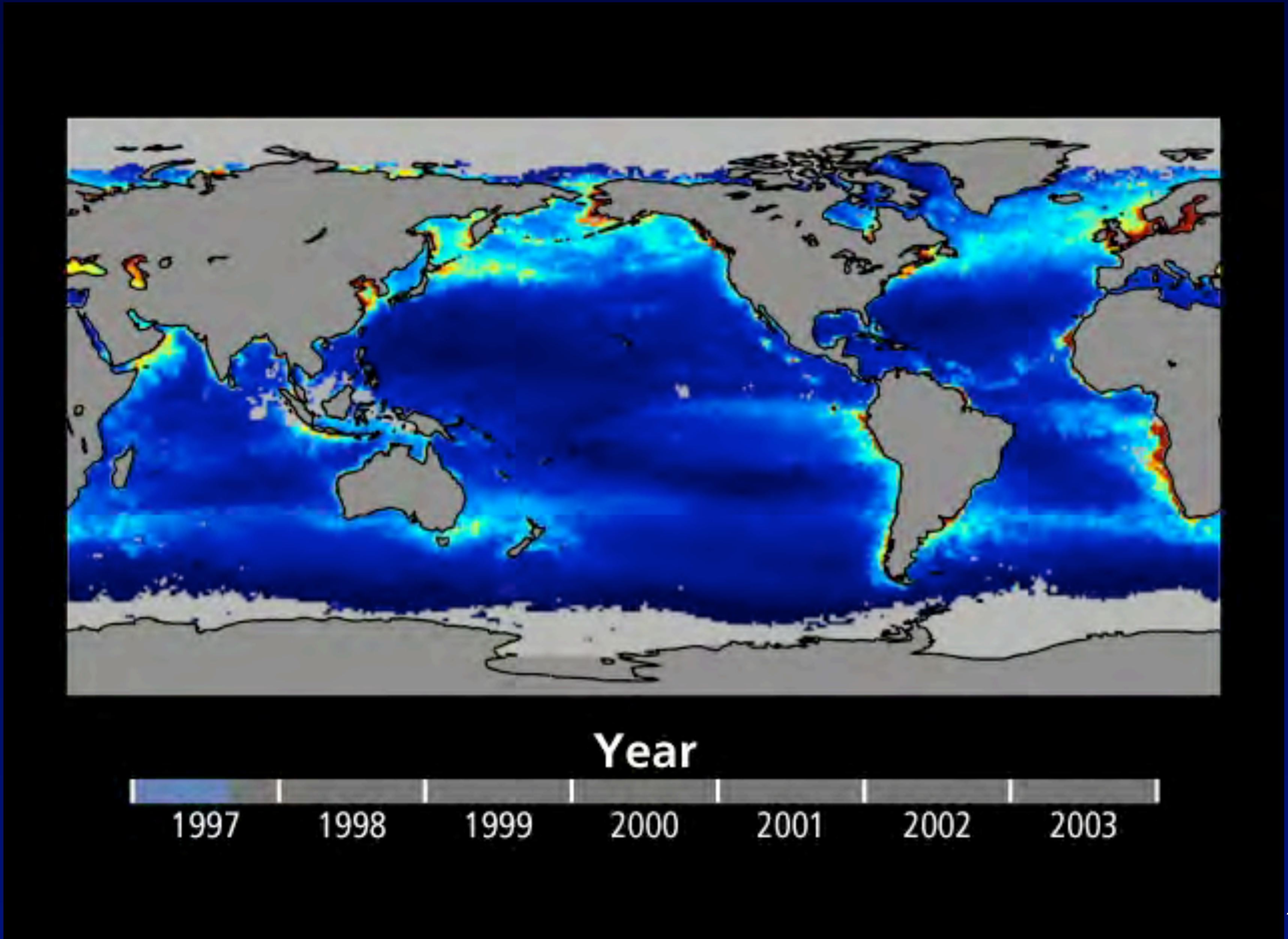
Rothstein et al., Oceanography Mag.

Models integrate information

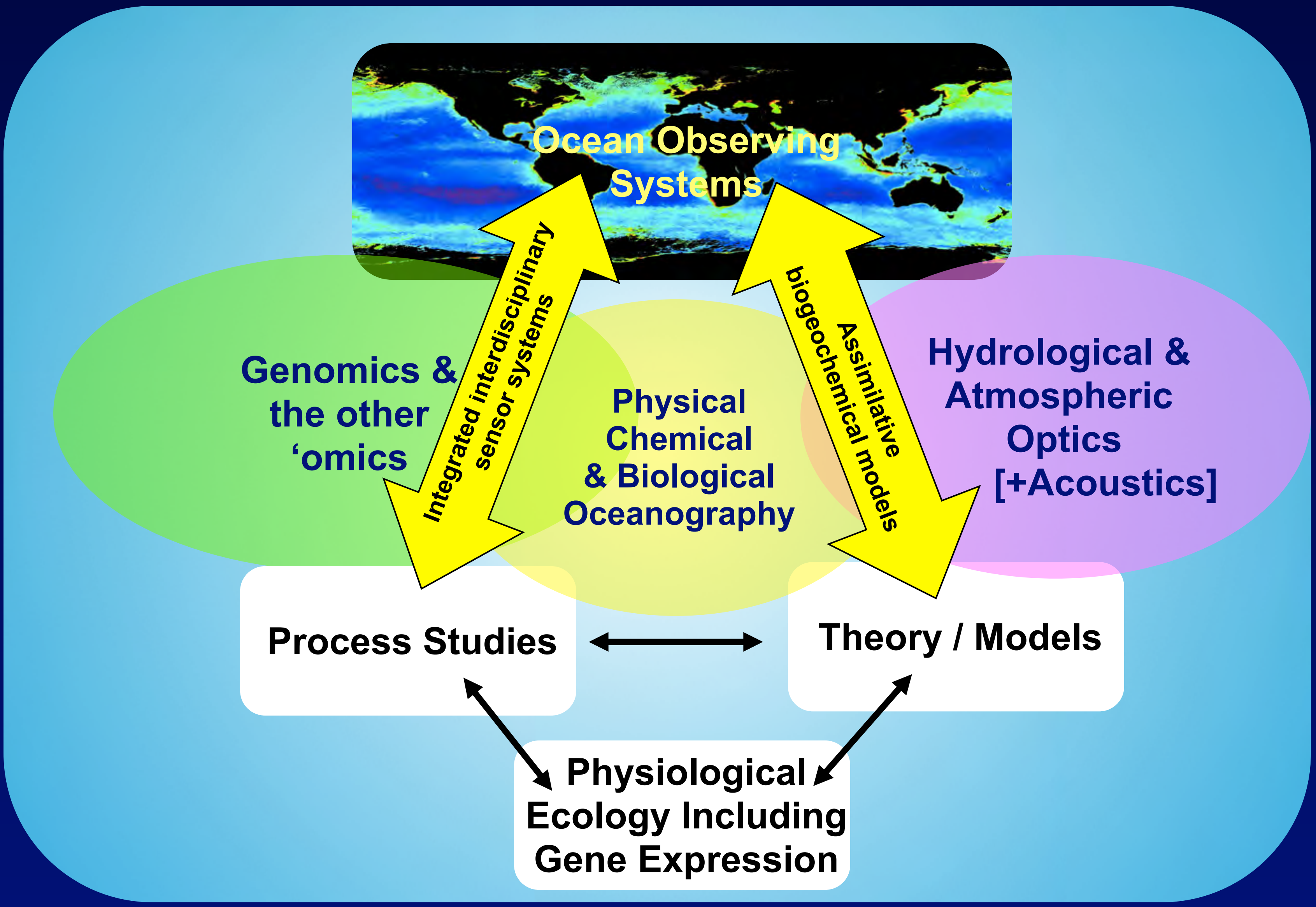


Mick Follows

So do you



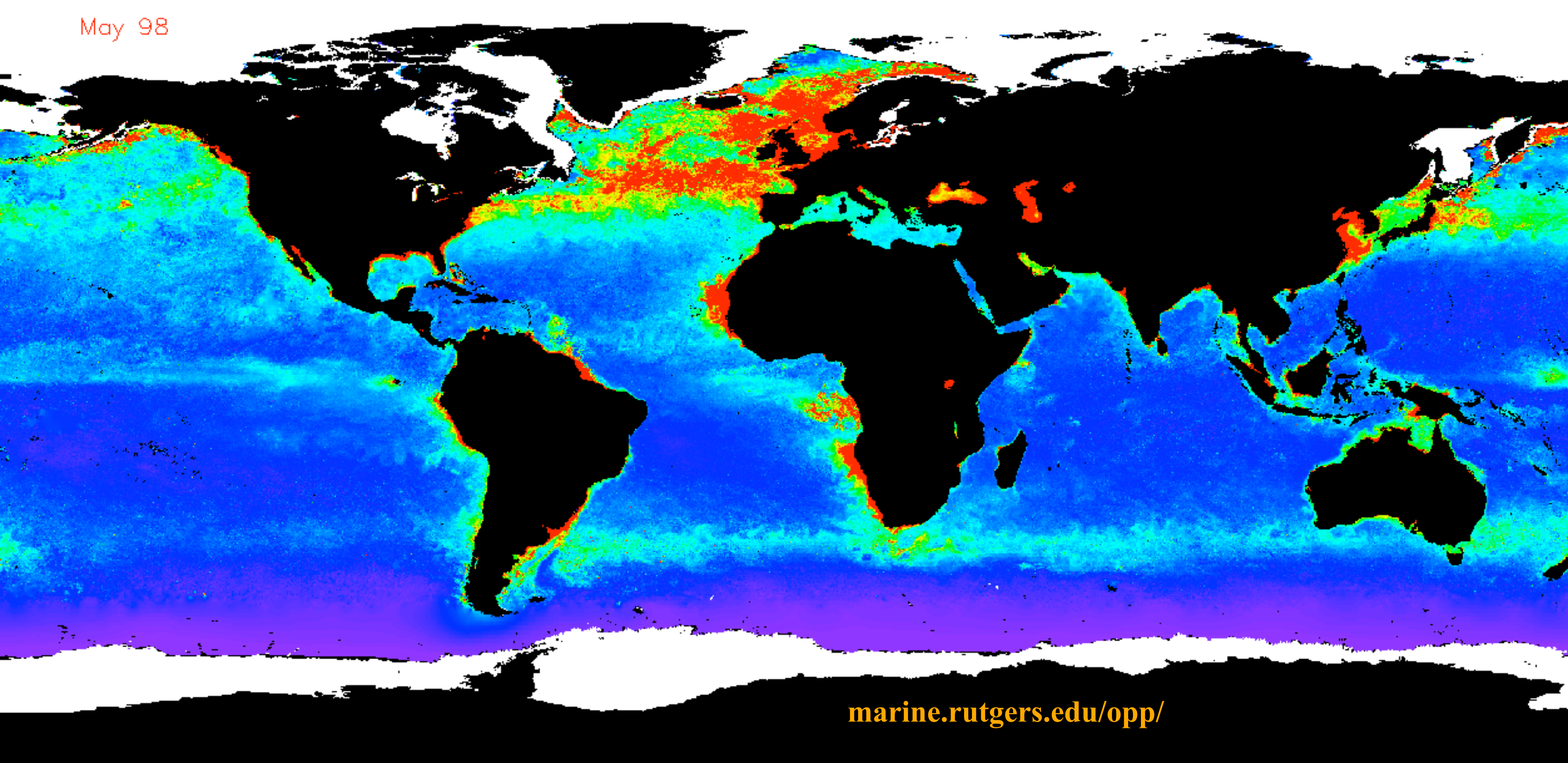
One Ultimate Target



John Cullen: C-MORE 2014

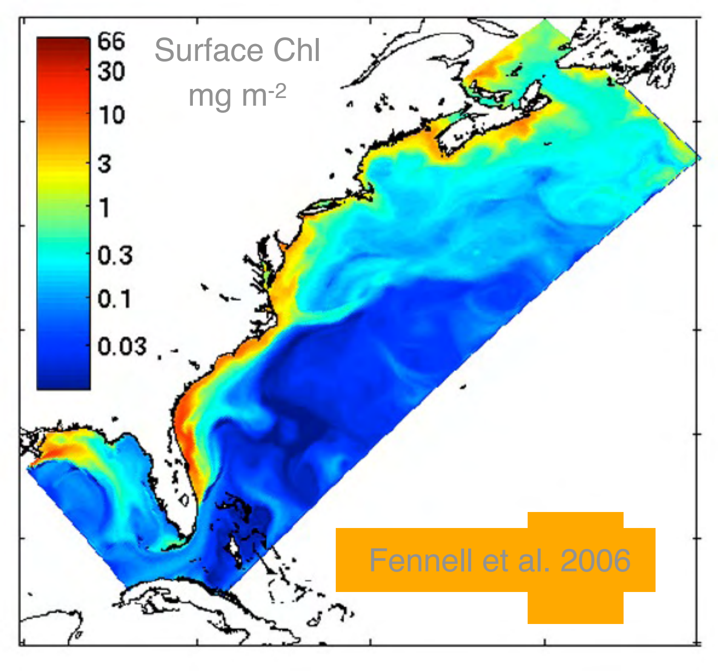
Biological oceanography and phytoplankton ecology

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

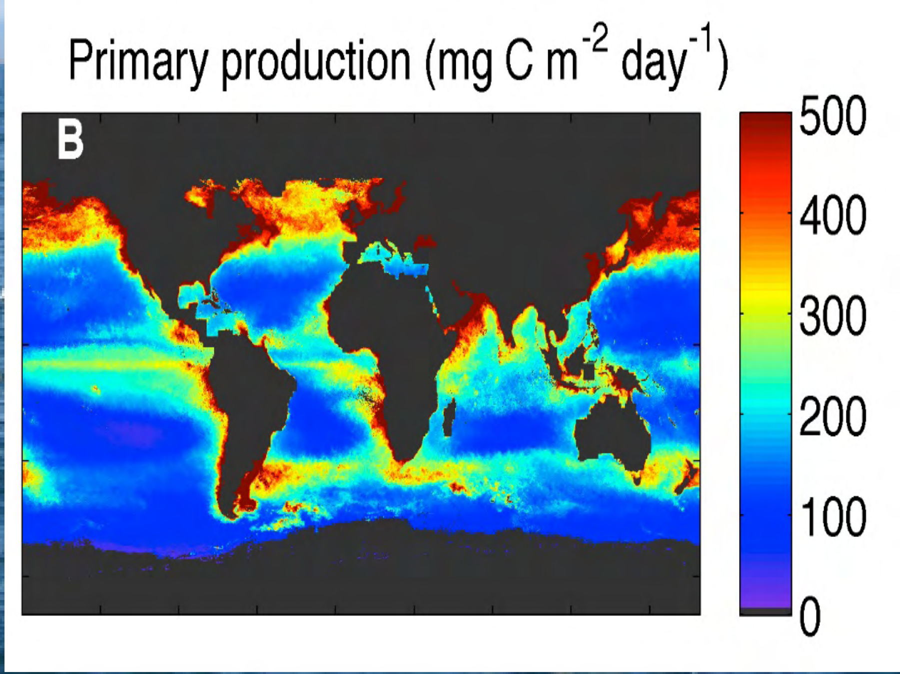


An overview of established approaches to marine modelling

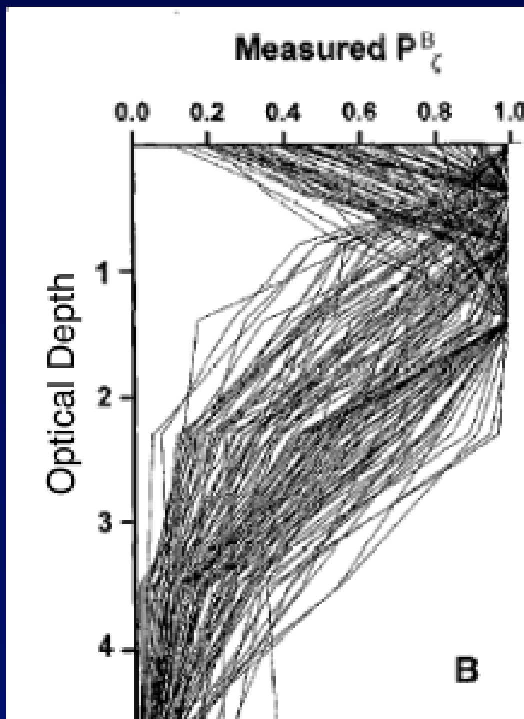
Prognostic Model

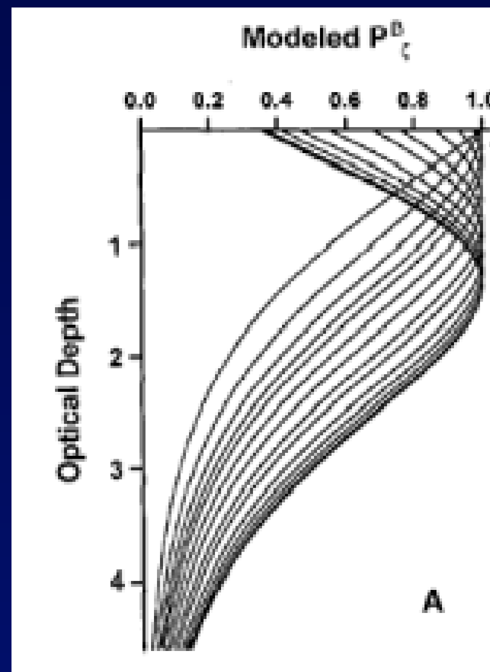


Diagnostic Model



Approach #1: Observation, analysis, inference (empirical, diagnostic models)





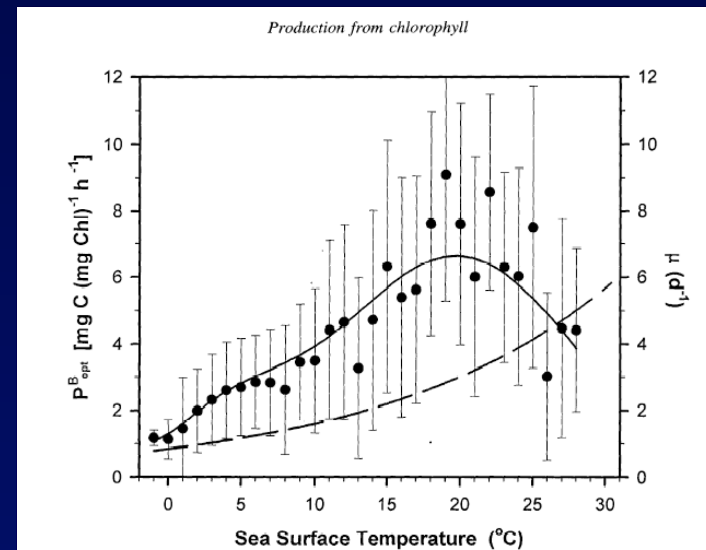


Fig. 7. Measured (●; ±SD) and modeled (——; Eq. 11) median value of the photoadaptive parameter, P^B_{opt}, as a function of sea surface temperature. Dashed curve indicates the theoretical maximum specific growth rate (μ; d^{-1}) of photoautotrophic unicellular algae described by Eppley (1972), which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

Behrenfeld and Falkowski 1997b L&O

Modeling the pattern in the measurements — not necessarily primary productivity!

Biospheric Primary Production During an ENSO Transition

Michael J. Behrenfeld,[1*] James T. Randerson,[2] Charles R. McClain,[1] Gene C. Feldman,[1] Sietse O. Los,[3] Compton J. Tucker,[1] Paul G. Falkowski,[4] Christopher B. Field,[5] Robert Frouin,[6] Wayne E. Esaias,[1] Dorota D. Kolber,[4] Nathan H. Pollack[7]

Result: Quantitative predictions that are as good as the data & assumptions that go into them

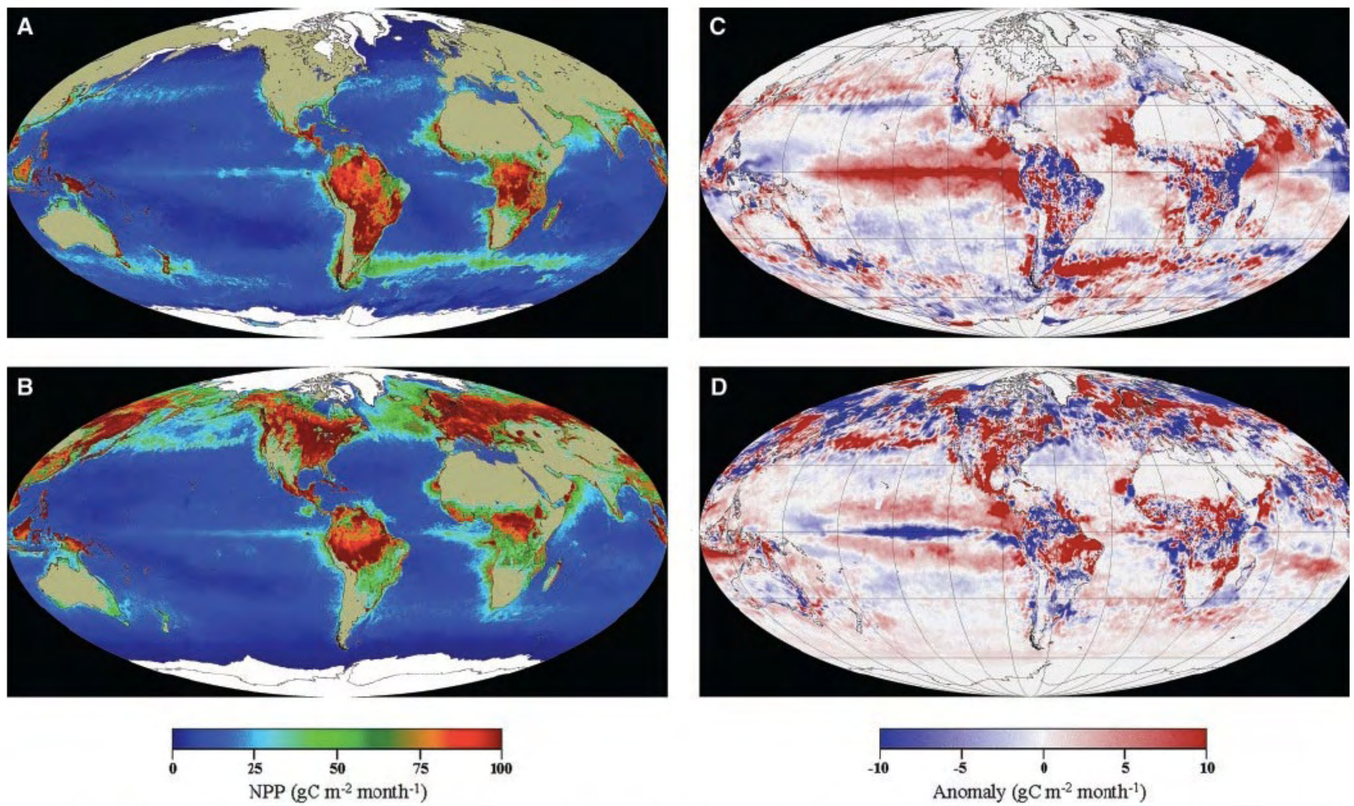
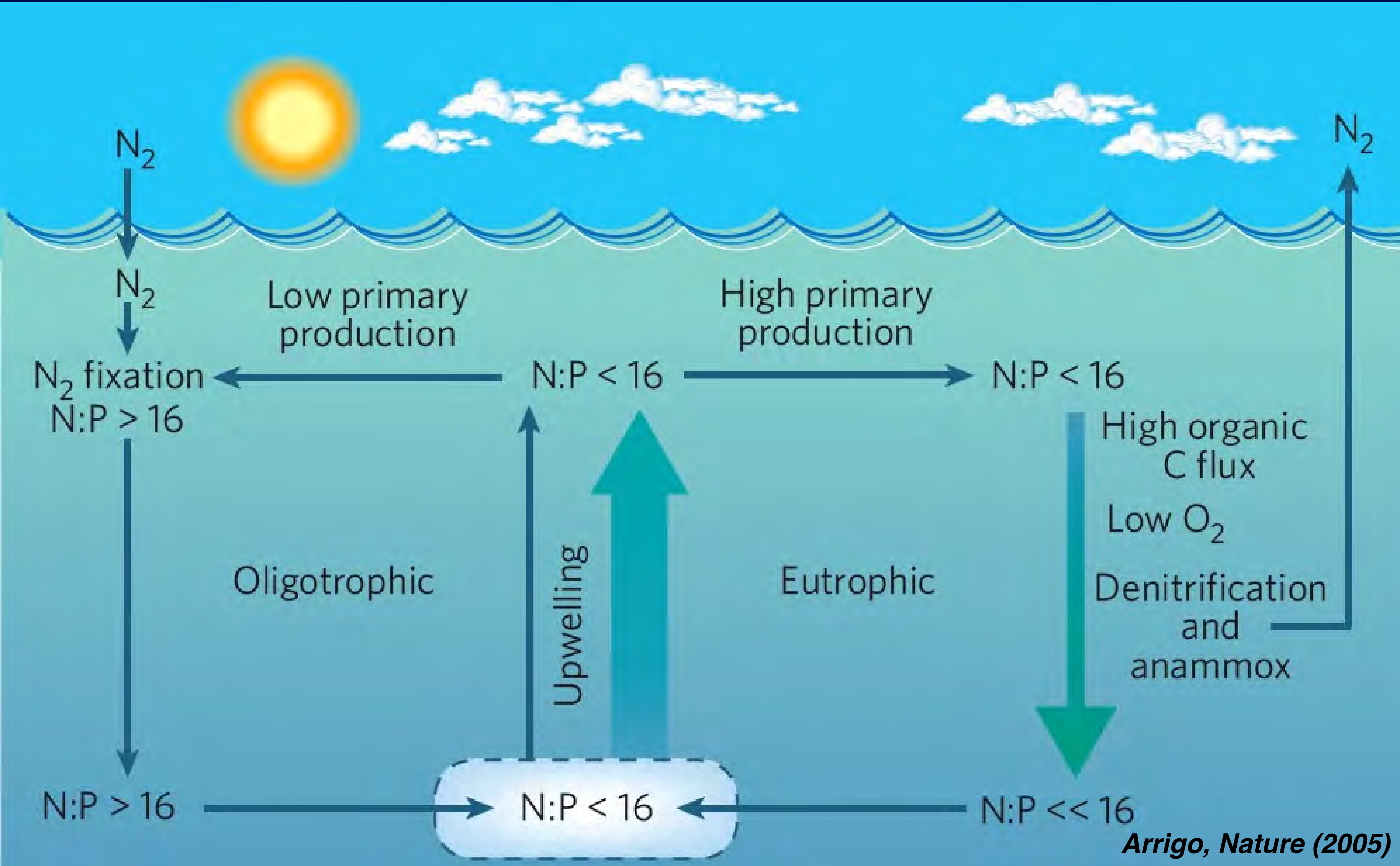


Fig. 2. Seasonal average and interannual differences in biospheric NPP (g C m^{-2} $month^{-1}$) estimated with SeaWiFS data and the integrated ... to La Niña conditions resulted in substantial regional changes in NPP, as illustrated by interannual differences in Austral summer NPP (i.e.,

Approach #2: Observation, analysis, inference (qualitative, mechanistic, predictive models)



Arrigo, Nature (2005)

The testing of qualitative, mechanistic, predictive models may be messy

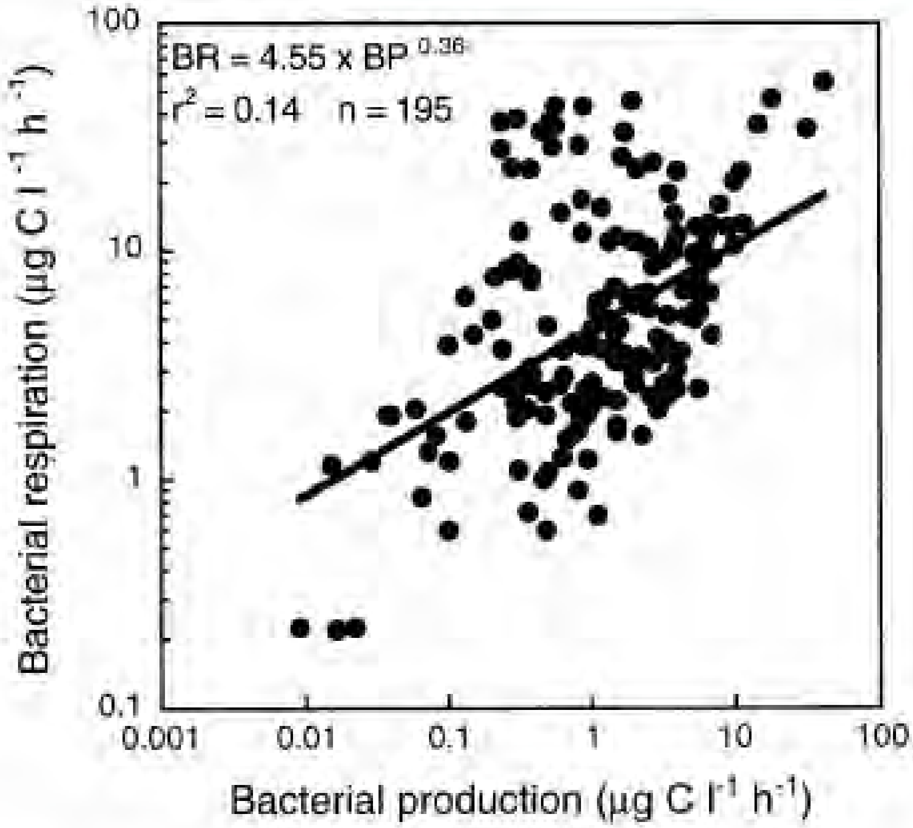


Figure 4. Bacterial respiration as a function of bacterial production in aquatic ecosystems. The data are paired observations of bacterial respiration (*BR*) and production (*BP*); the sources of these data appear in Table 1. The line is the least-squares fit to the log-transformed data.

del Giorgio and Cole (1999)

But predictions can be tested with appropriate observations

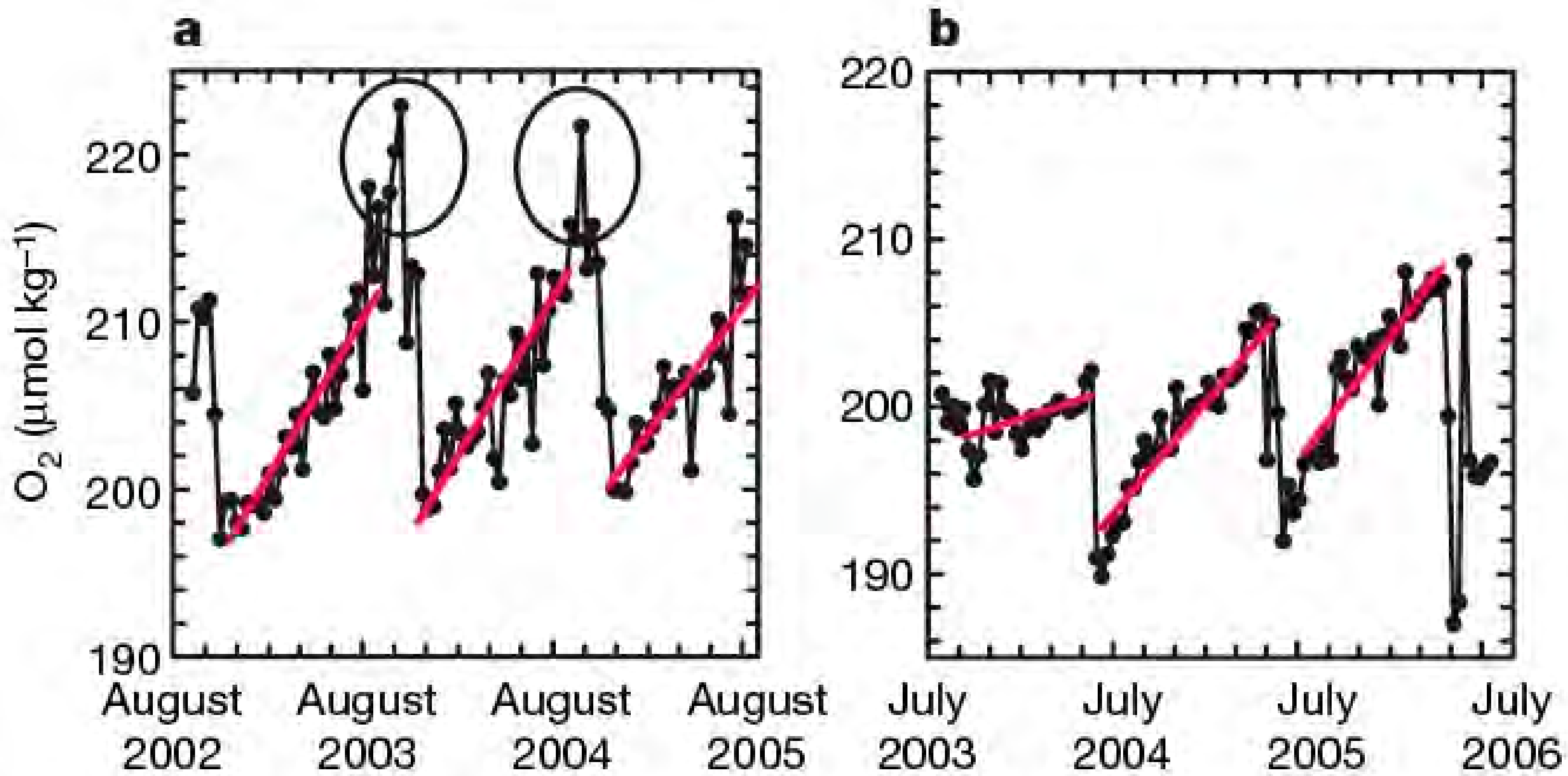


Figure 3 | Oxygen concentrations in the SOM versus time. Oxygen

Riser and Johnson Nature 2008

Diagnostic models can be used to test hypotheses rather than to consolidate and interpret observations

ARTICLE

doi:10.1038/nature09403

Ocean nutrient ratios governed by plankton biogeography

Thomas S. Weber[1] & Curtis Deutsch[1]

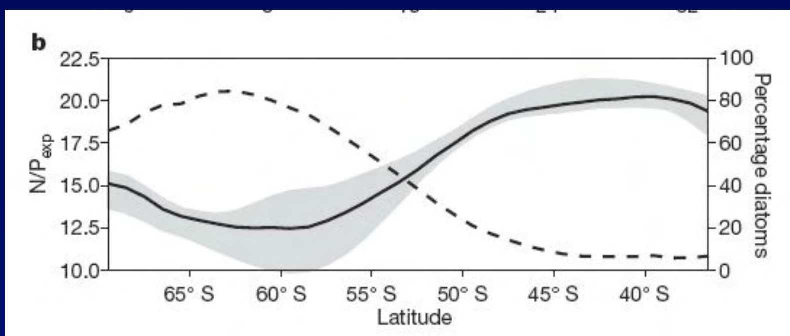


Figure 3 | Diagnosed nutrient export ratios. a, Spatial pattern of N/P_{exp},

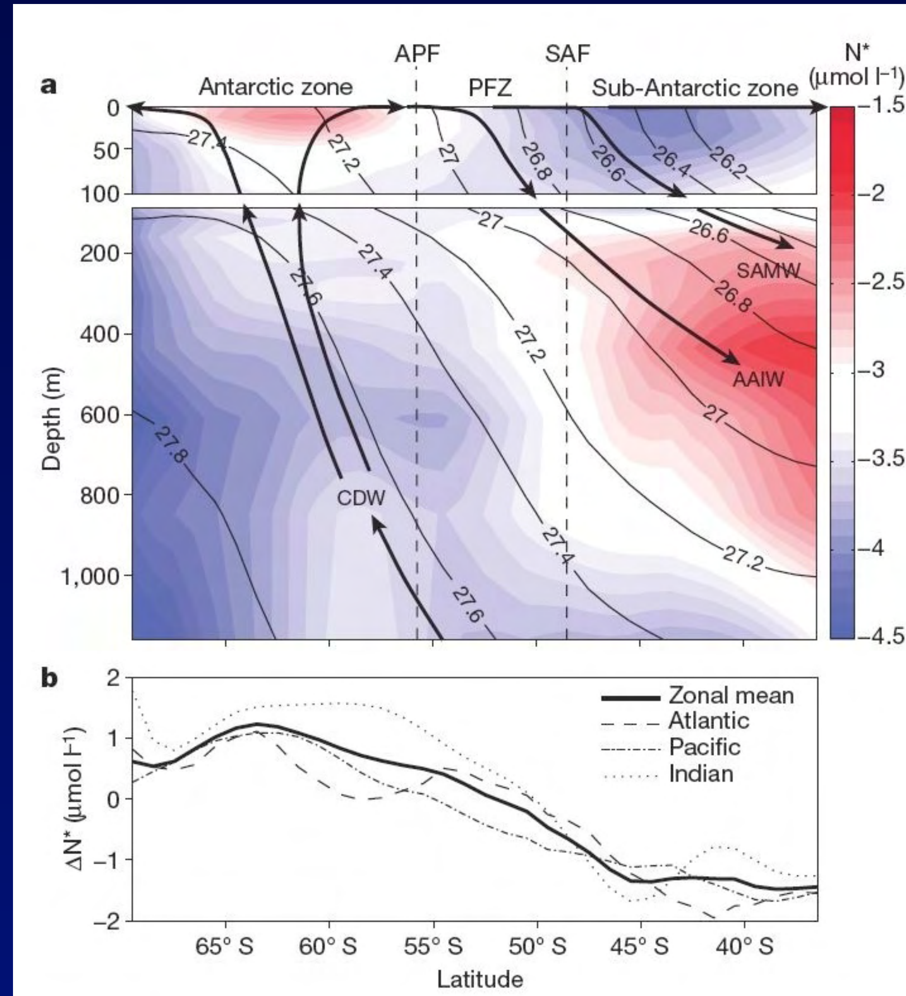
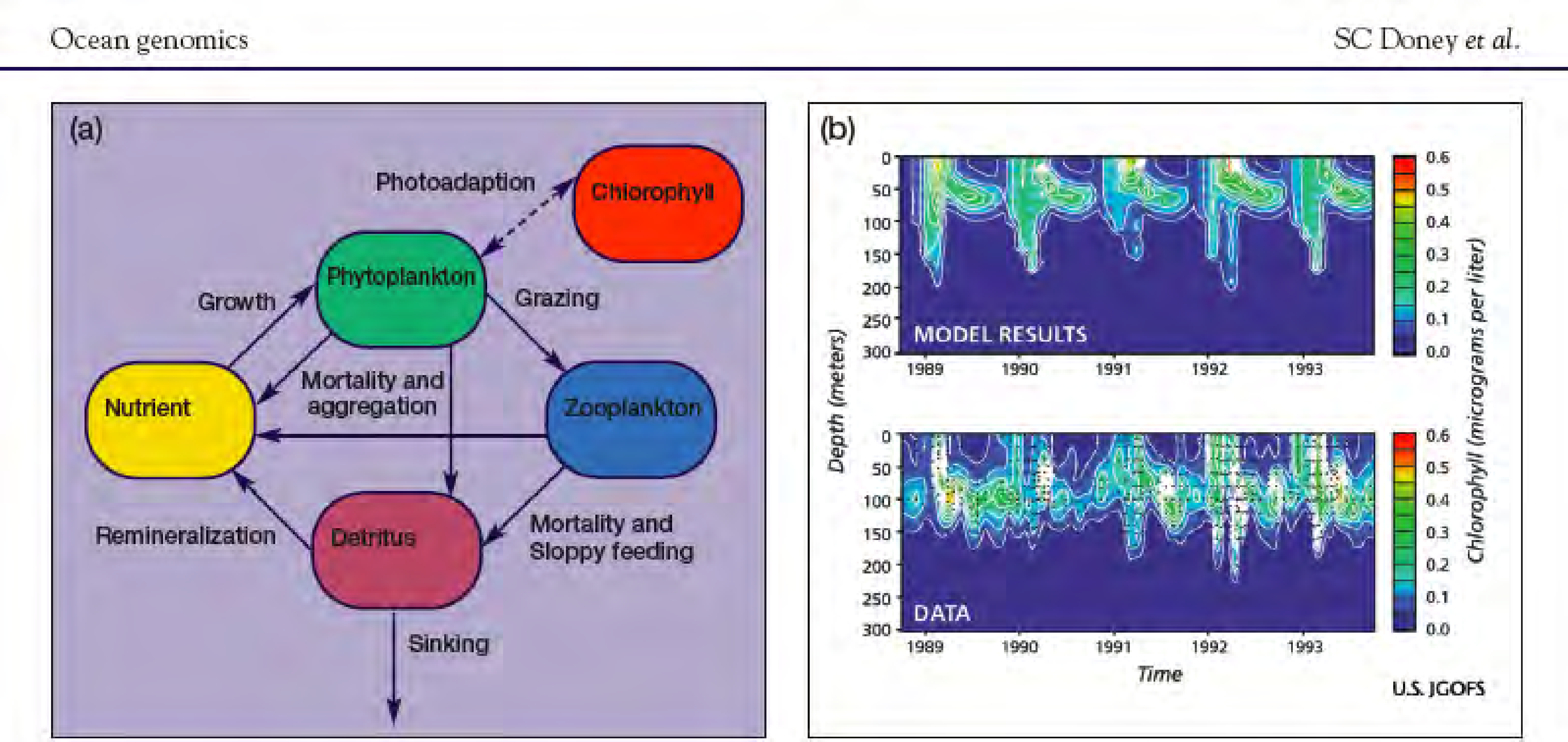


Figure 1 | Observed N* distribution in the Southern Ocean. a, Zonal mean

Approach #3: Prognostic models (quantitative, mechanistic, predictive models) -- e.g., BOCGMs



Doney, S. C., M. R. Abbott, J. J. Cullen, D. M. Karl, and L. Rothstein. 2004. From genes to ecosystems: the ocean's new frontier. Frontiers in Ecology and the Environment 2: 457-466.

Complexity is added to increase realism and to test hypotheses

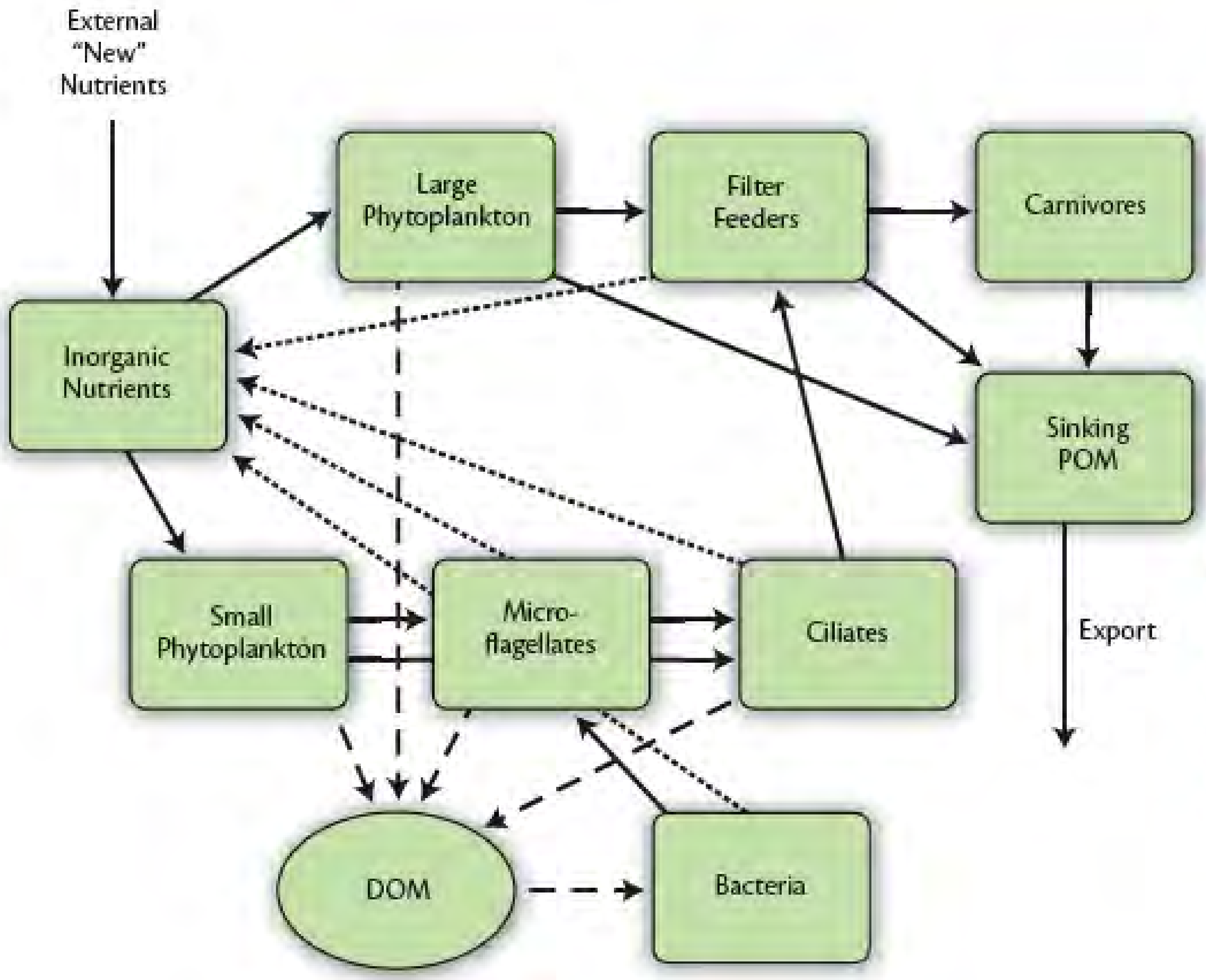
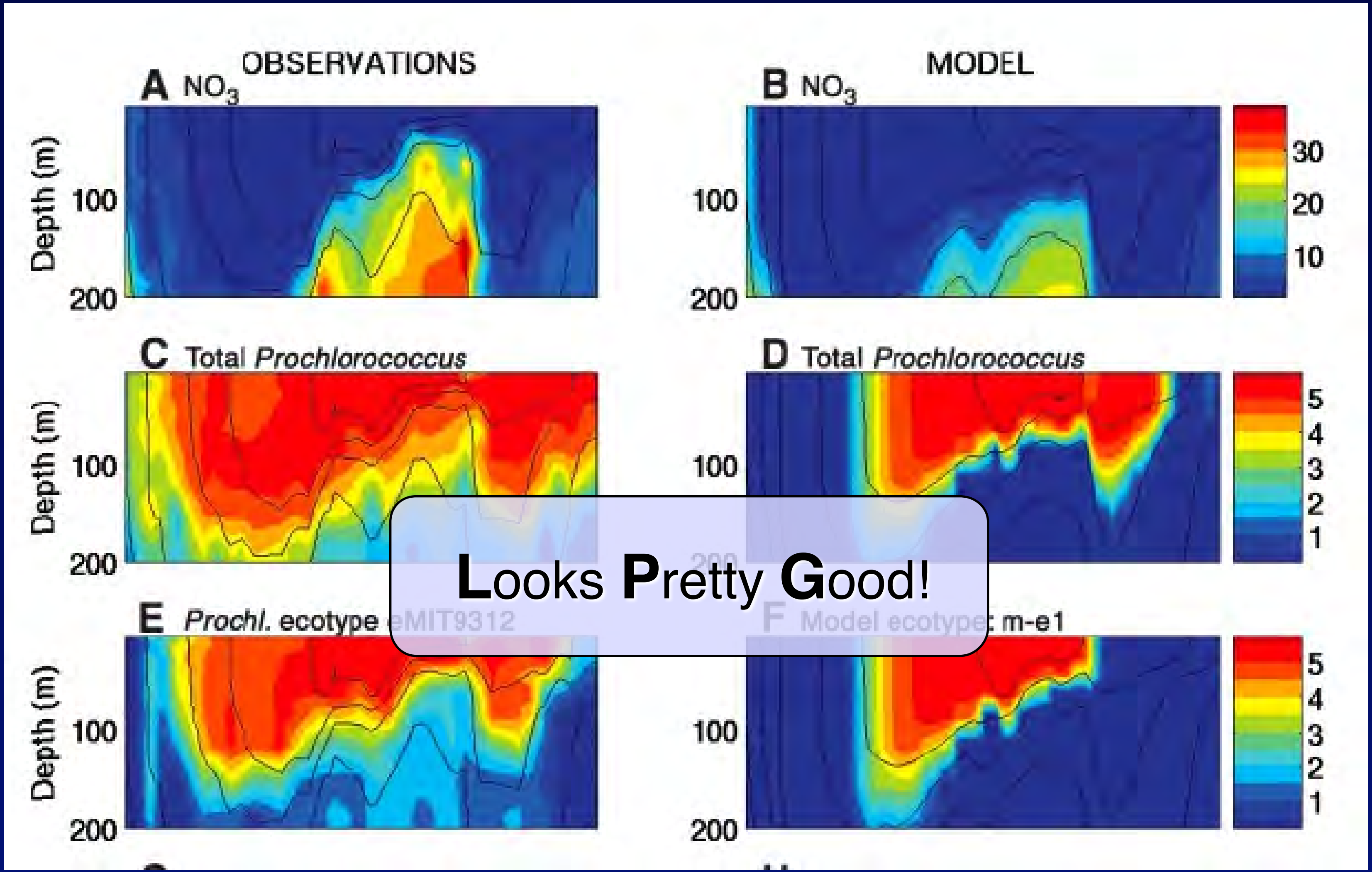


Figure 2. Oceanic plankton food web, after Laws et al. (2000). The upper pathway initiated by large phytoplankton contributes primarily to export from the upper ocean. The lower pathway starting with small phytoplankton results mainly in the recycling of nutrients. Solid arrows: flows of organisms and particulate matter (detritus and fecal pellets). Dashed arrows: flows of dissolved organic matter (DOM). Dotted arrows: flows of regenerated inorganic nutrients. Note that all organisms leak DOM but not all flows are depicted for clarity. All consumers release inorganic nutrients but not all arrows are shown.

Doney, S. C., M. R. Abbott, J. J. Cullen, D. M. Karl, and L. Rothstein. 2004. From genes to ecosystems: the ocean's new frontier. Frontiers in Ecology and the Environment 2: 457-466.

Conventionally tested by the "LPG" criterion — but that is changing



Follows, M. J., S. Dutkiewicz, S. Grant, and S. W. Chisholm. 2007. Emergent biogeography of microbial communities in a model ocean. Science 315: 1843-1846.

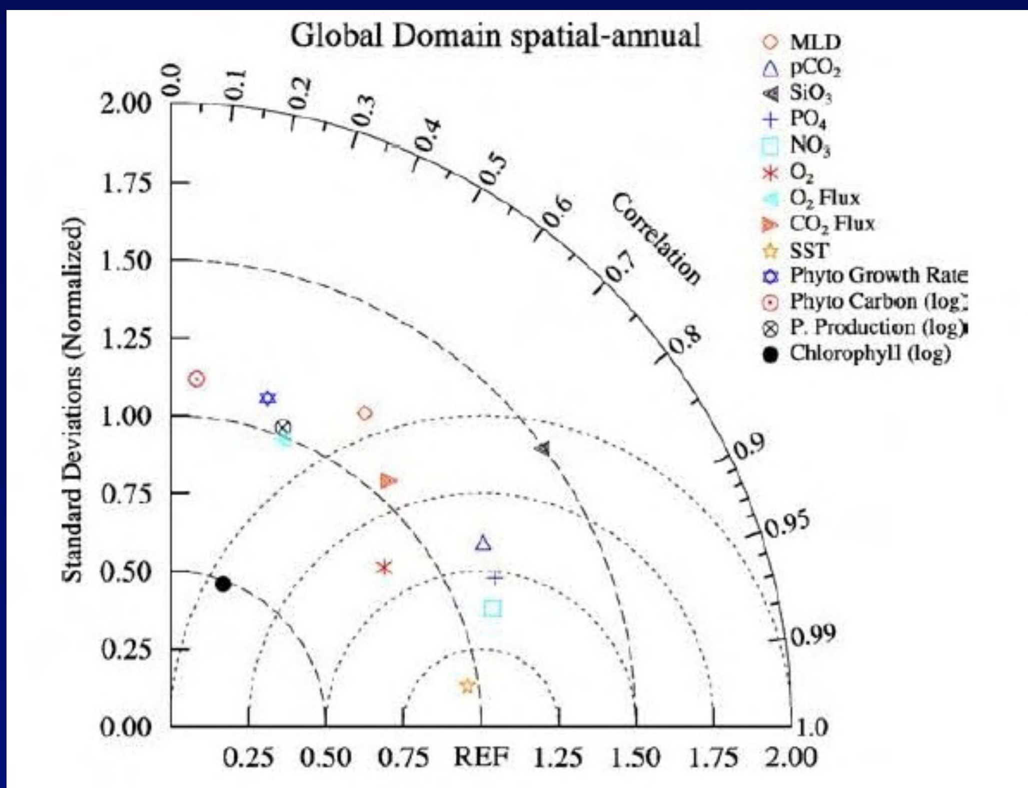
Contents lists available at ScienceDirect

Journal of Marine Systems

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

Skill metrics for confronting global upper ocean ecosystem-biogeochemistry models against field and remote sensing data

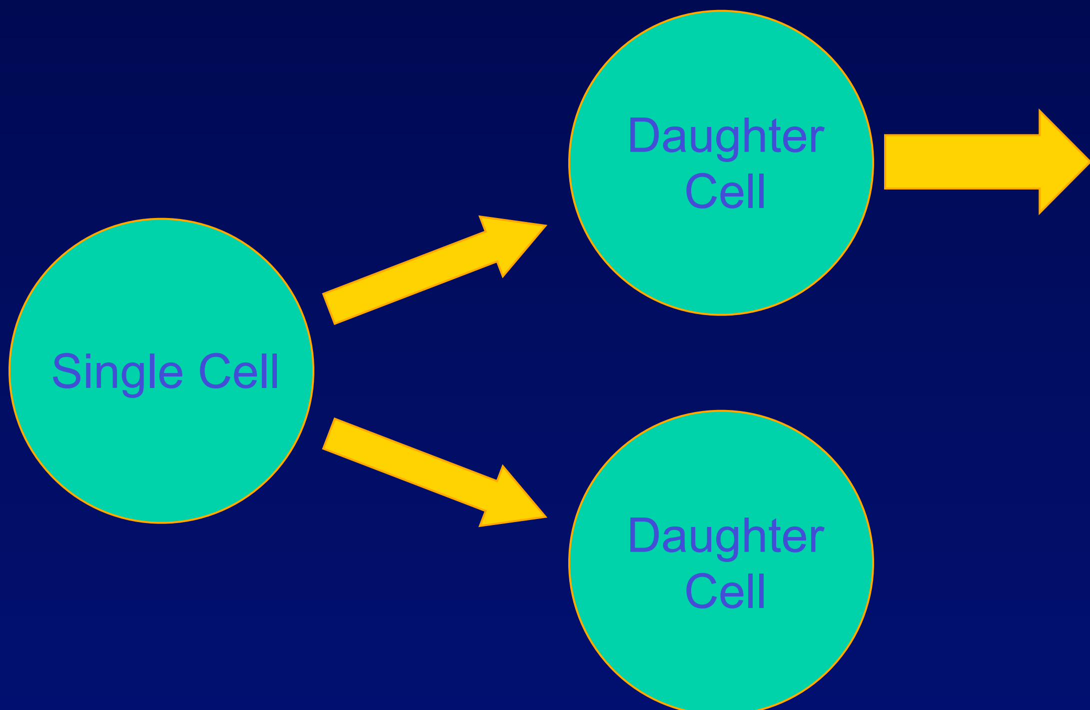
Scott C. Doney[a,*], Ivan Lima[a], J. Keith Moore[b], Keith Lindsay[c], Michael J. Behrenfeld[d], Toby K. Westberry[d], Natalie Mahowald[e], David M. Glover[a], Taro Takahashi[f]



e.g., Taylor diagrams

Fundamentally, ecosystem models should predict population dynamics

Growth



Loss

Accumulate (Bloom)

Be eaten

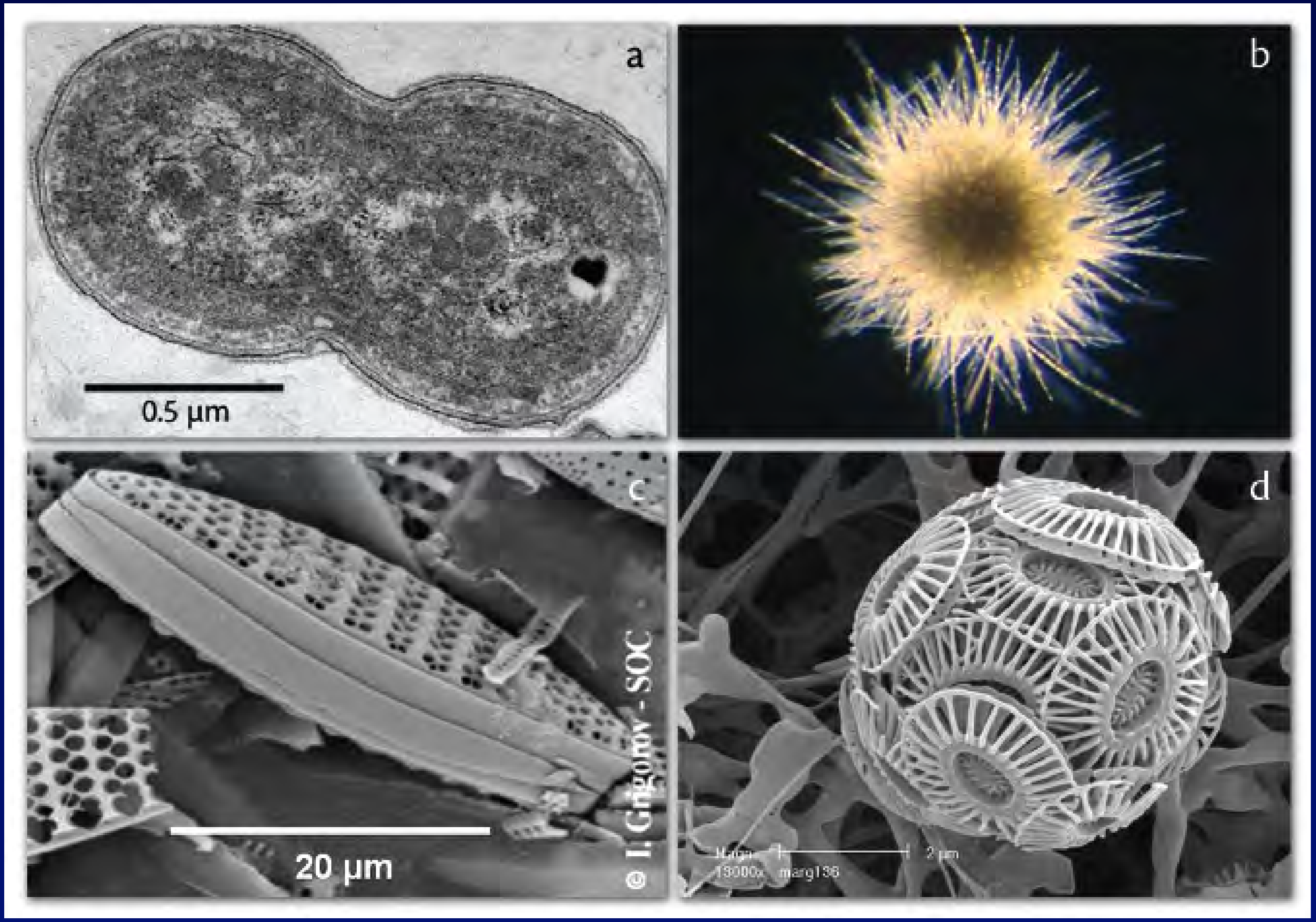
Blow up (viral lysis)

Sink

Die (e.g., apoptosis)

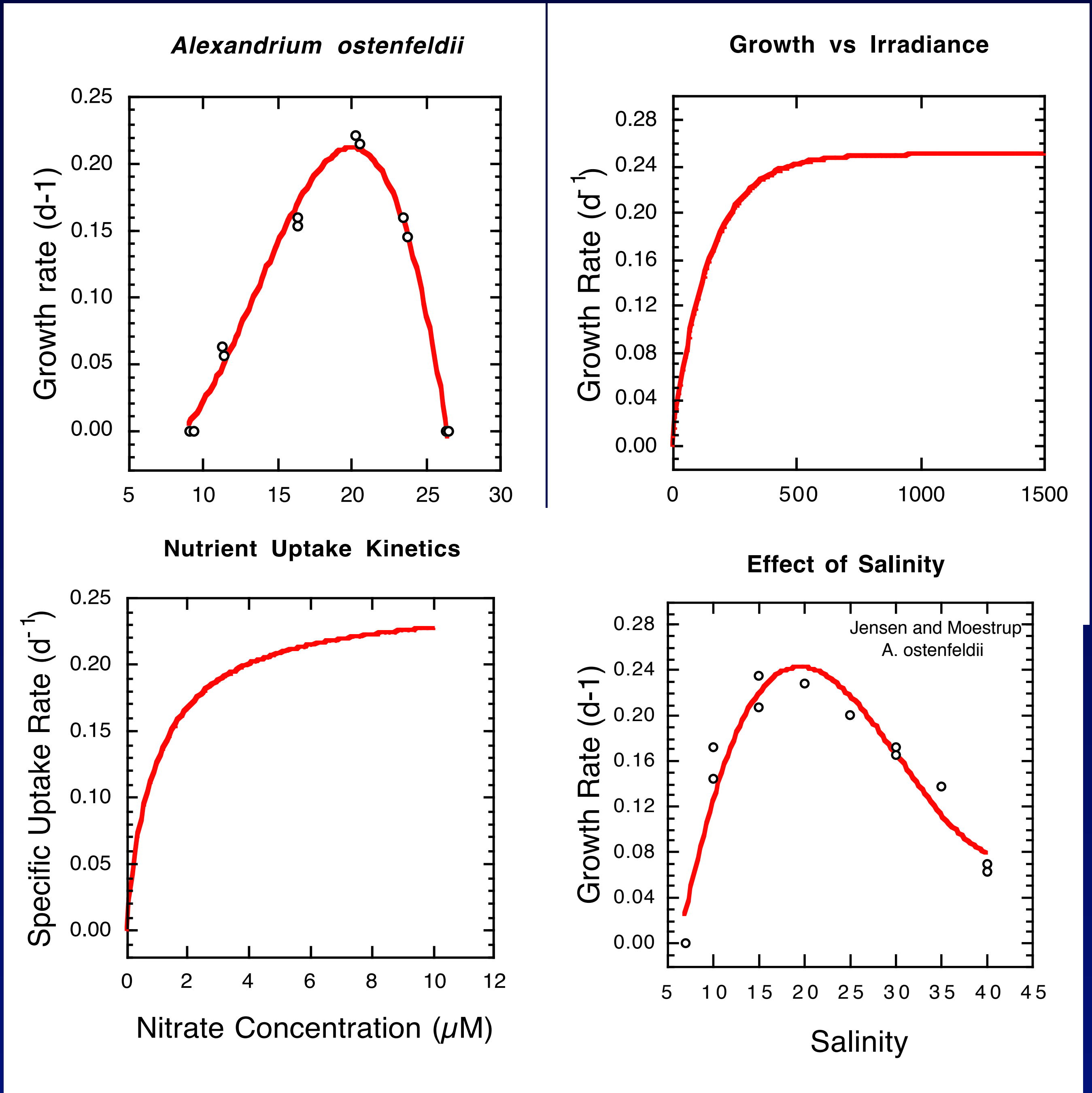
A bit weird, because "population" refers to species, and many species are often lumped

Biogeochemical models must include functional groups

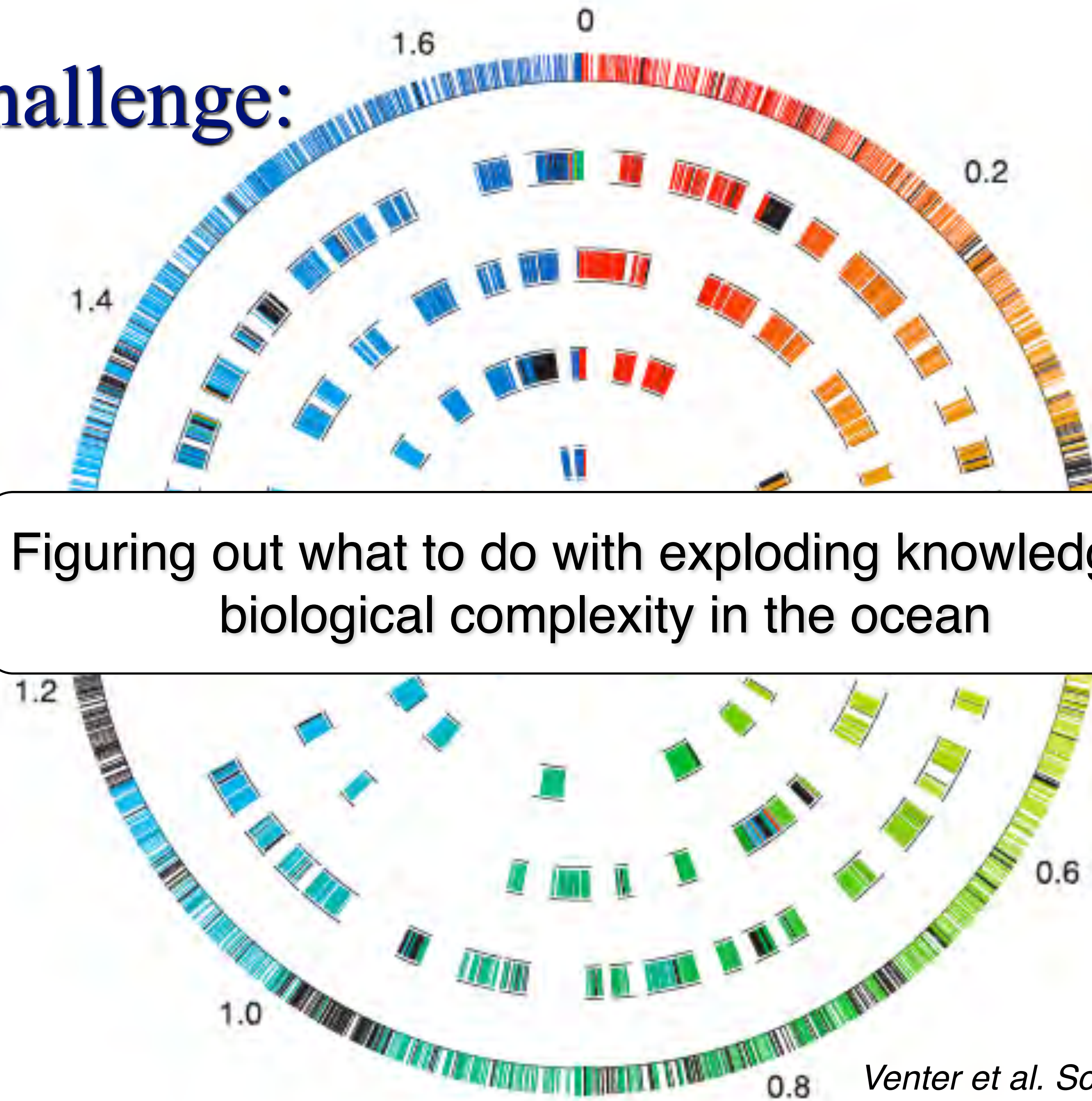


Critical to know the Environmental Influences on the Growth of Phytoplankton:

Temperature
Light
Daylength
Nutrients



Challenge:



Figuring out what to do with exploding knowledge of biological complexity in the ocean

Venter et al. Science 2004

A big part of the answer is here

Modeling Diverse Communities of Marine Microbes

Michael J. Follows and Stephanie Dutkiewicz

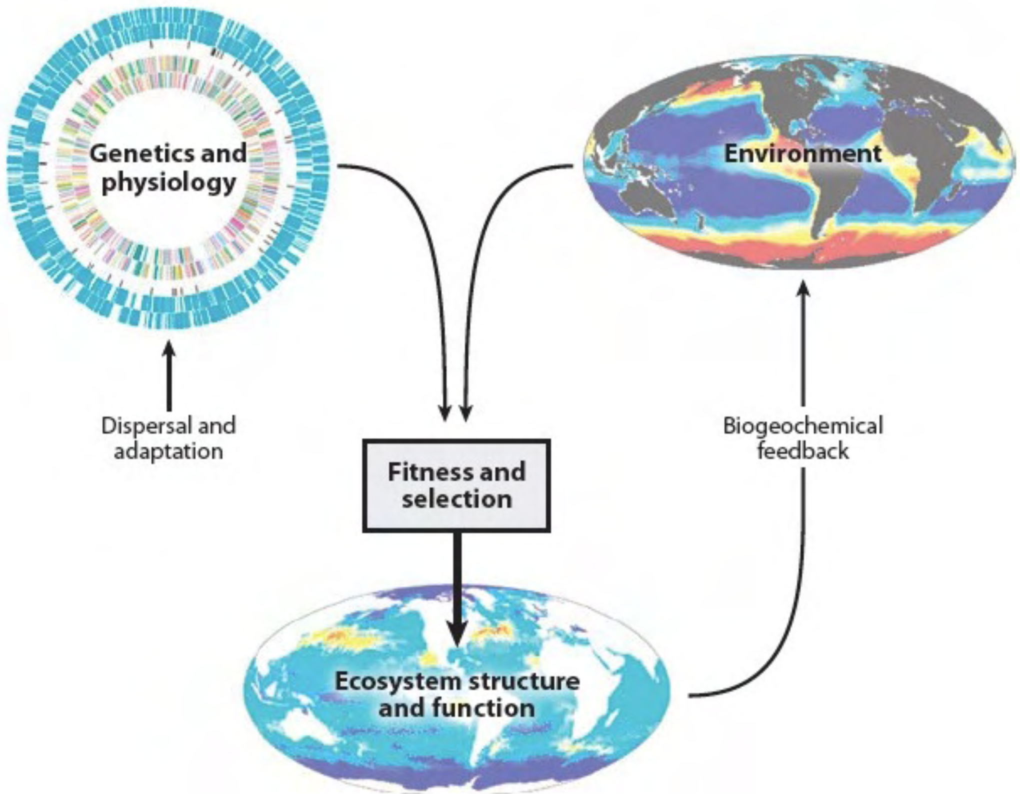
Earth, Atmospheric, and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, Massachusetts 02139; email: mick@ocean.mit.edu, stephd@mit.edu

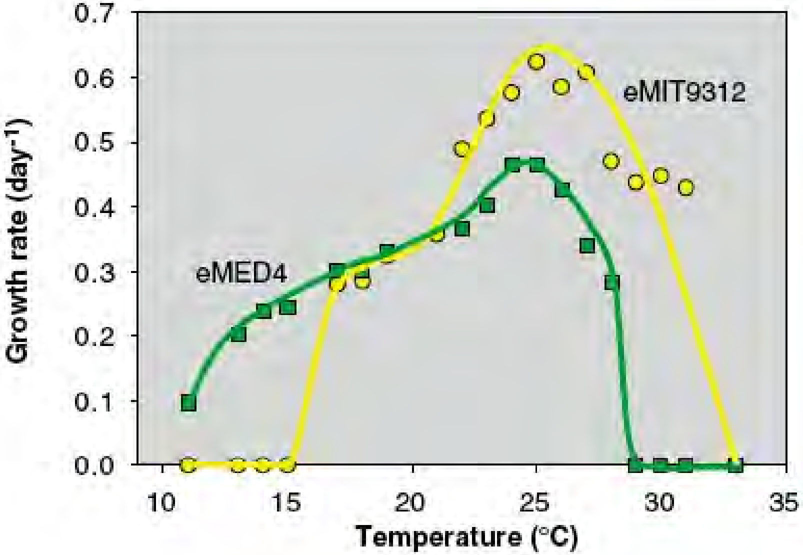
Annu. Rev. Mar. Sci. 2011. 3:427–51

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

This article's doi: 10.1146/annurev-marine-120709-142848

1941-1405/11/0115-0427$20.00



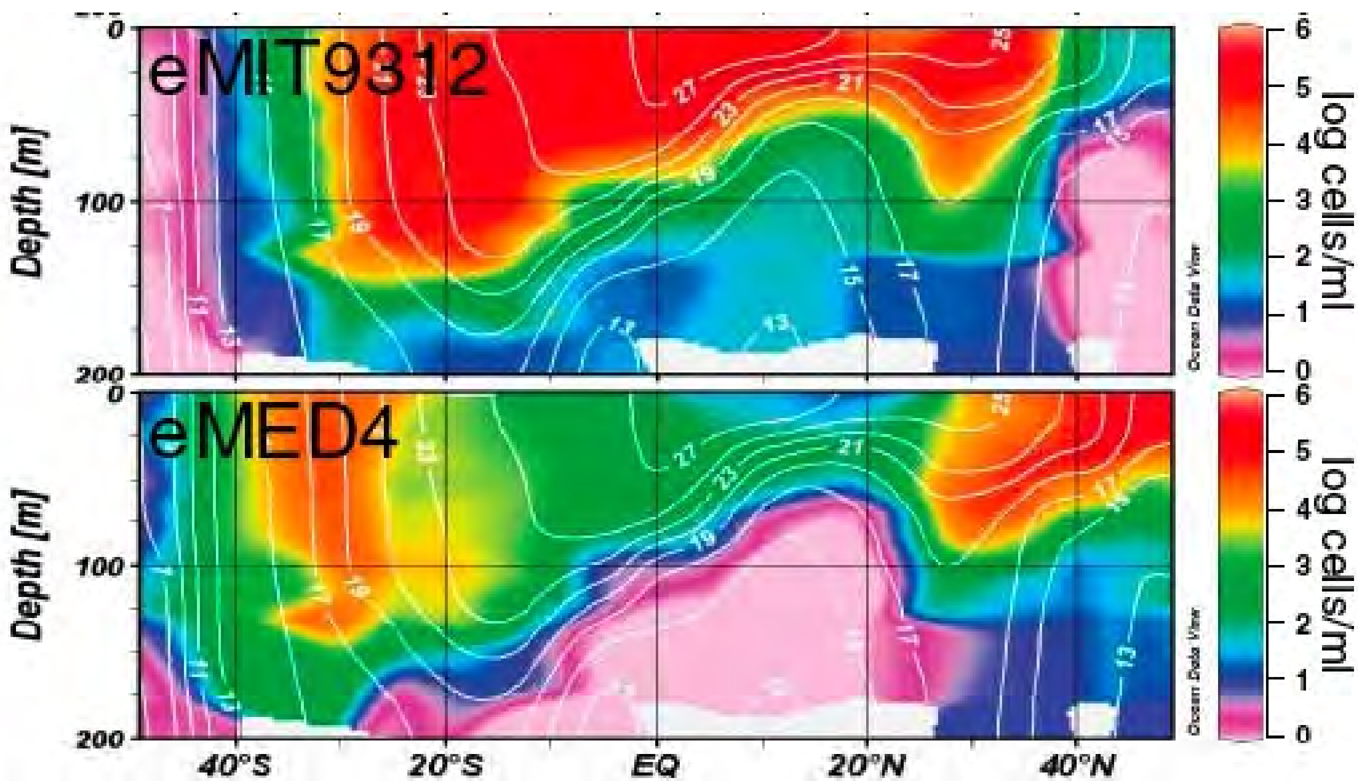


Growth *vs* Temperature

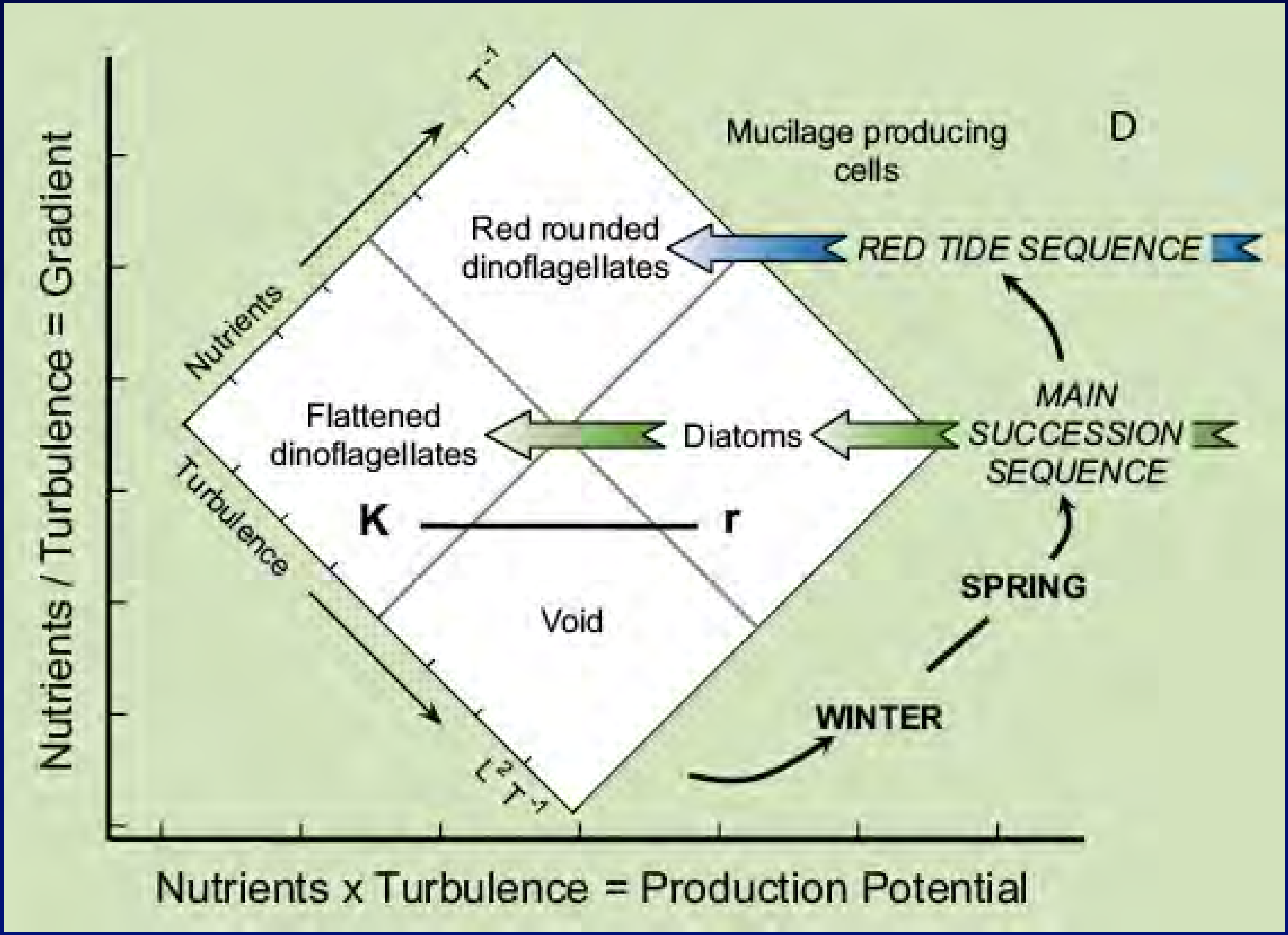
SCIENCE VOL 311 24 MARCH 2006 1737

Niche Partitioning Among *Prochlorococcus* Ecotypes Along Ocean-Scale Environmental Gradients

Zackary I. Johnson,[1,2]* Erik R. Zinser,[1,3]* Allison Coe,[1] Nathan P. McNulty,[1] E. Malcolm S. Woodward,[4] Sallie W. Chisholm[1]†

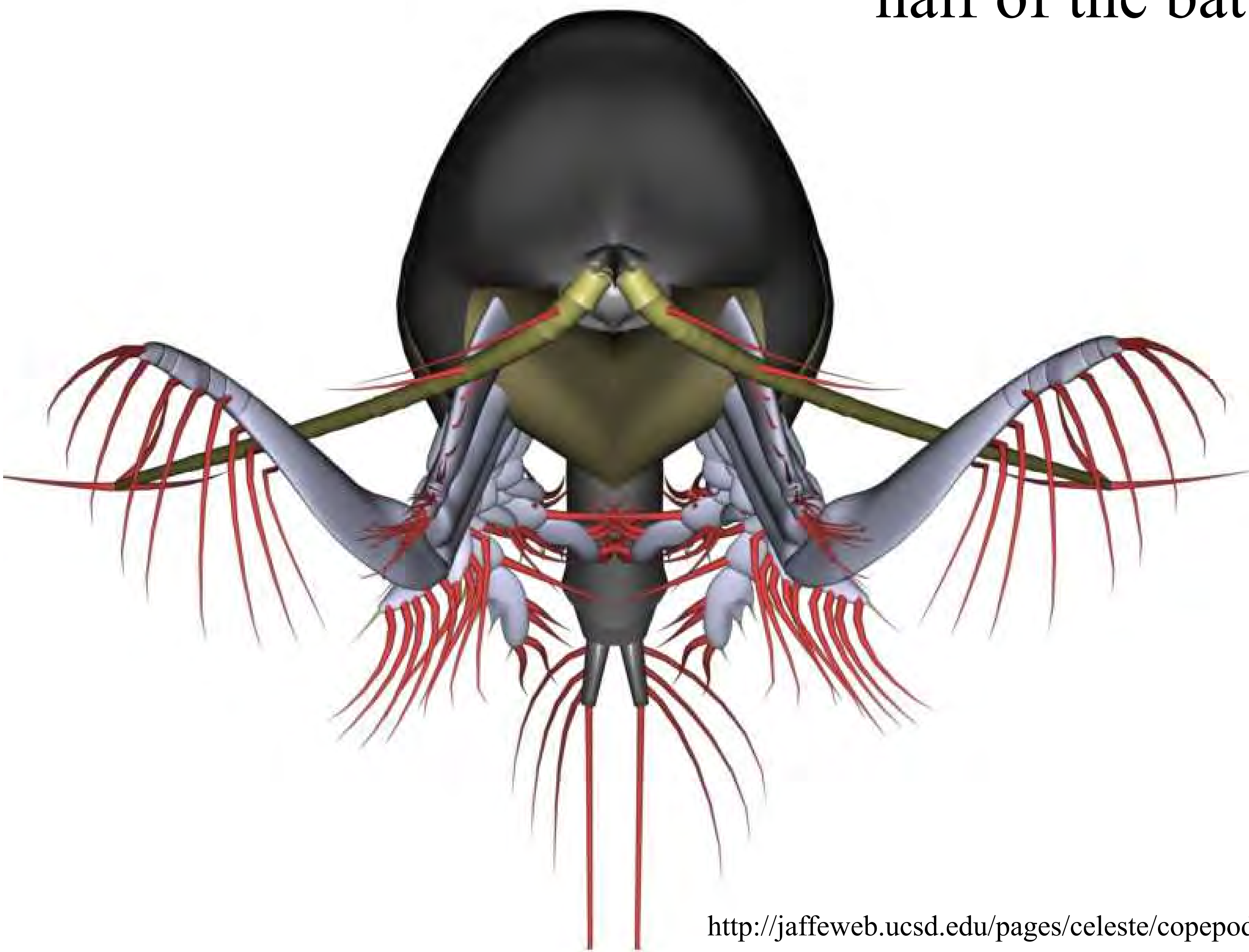


Many other things define the growth-niche of marine phytoplankton



From Margalef et al. 1979 in Cullen et al. Oceanography Mag. 2007

And cell division is only half of the battle!



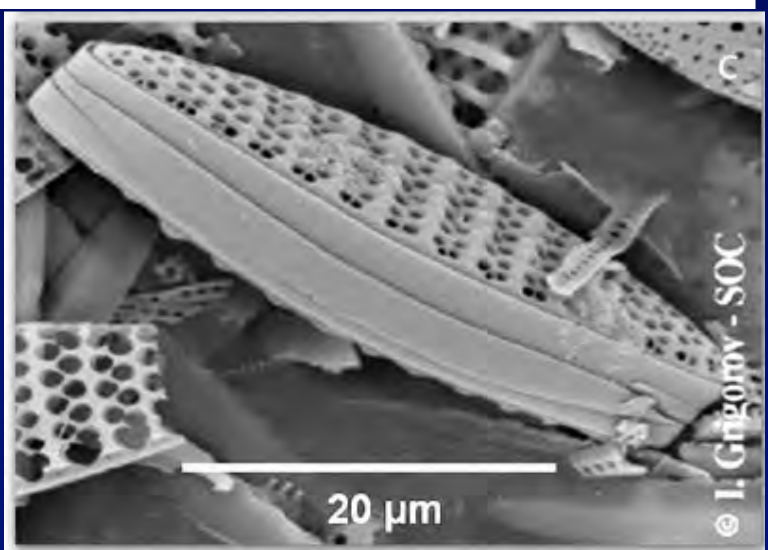
http://jaffeweb.ucsd.edu/pages/celeste/copepods.html

Reduction of loss can be as good as an increase of growth rate

Architecture and material properties of diatom shells provide effective mechanical protection

Christian E. Hamm*, Rudolf Merkel†‡, Olaf Springer§, Piotr Jurkojc§, Christian Maier†, Kathrin Prechtel† & Victor Smetacek*

NATURE | VOL 421 | 20 FEBRUARY 2003 | www.nature.com/nature



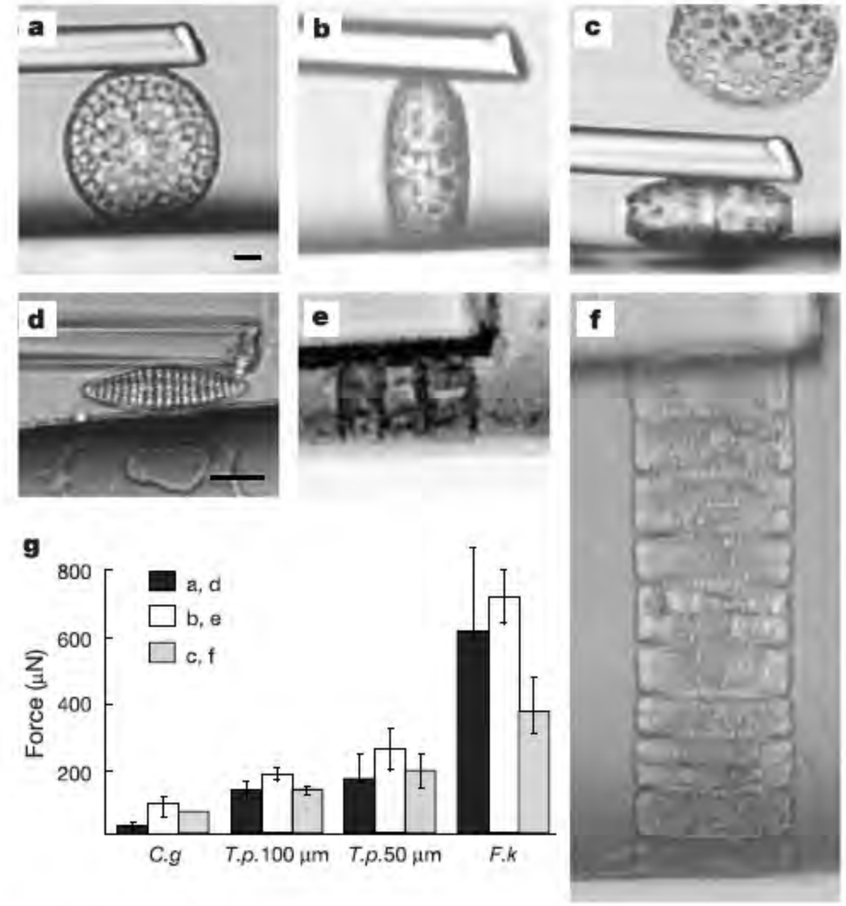
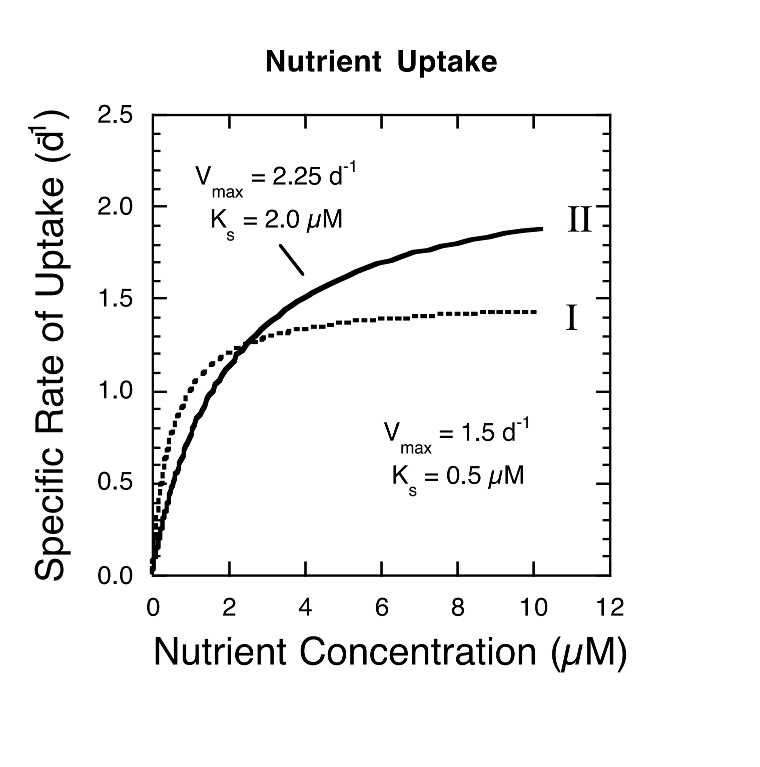


Figure 1 Glass needle tests: Live single cells of *T. punctigera* (**a**–**c**) and *F. kerguelensis* (**d**–**f**), in chains (**e**, **f**). Pressures applied along the girdle bands, (**a**, **d**), across the girdle bands (**b**, **e**), and across the centre of the valves (**c**, **f**). **g**, Forces necessary to break *Coscinodiscus granii* (*C.g.*), *Thalassiosira punctigera* (*T.p.*) with diameters of 100 and 50 µm, and *Fragilariopsis kerguelensis* (*F.k.*). *C. granii* has a geometry similar to that of *T. punctigera*. Scale bars, 10 µm.

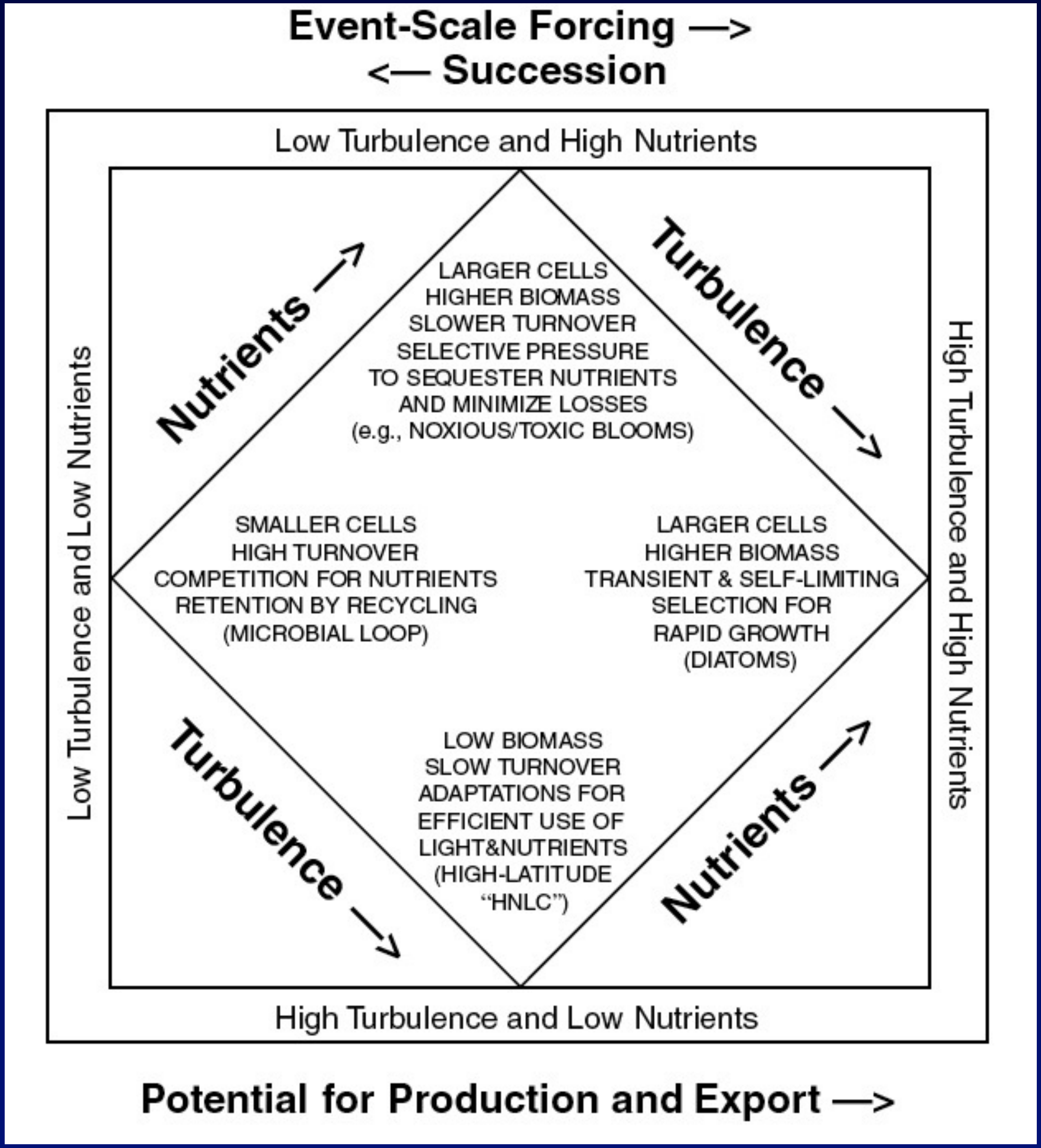
So rapid growth is not the only strategy for survival / selection

It's the gene, stupid!



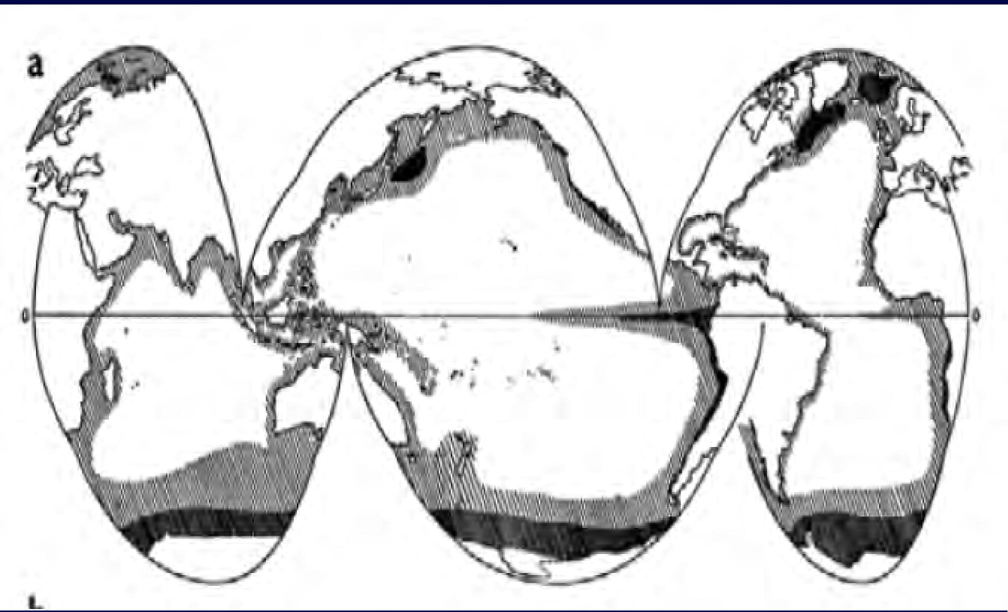
www.andyslocum.com/images/tortoise&hare.jpg

Same framework

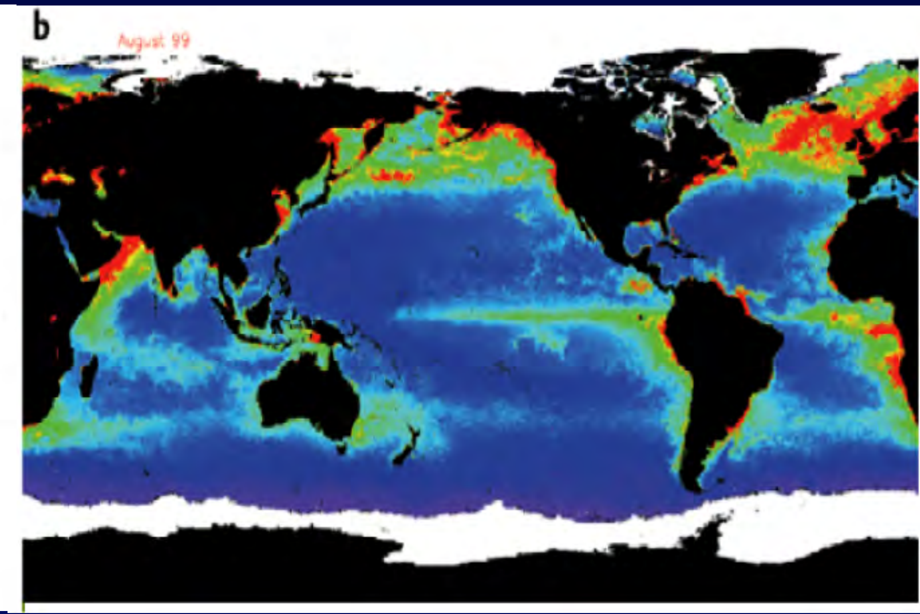


From Margalef et al. 1979 in Cullen et al. The Sea 2002

Top-down or bottom-up control?



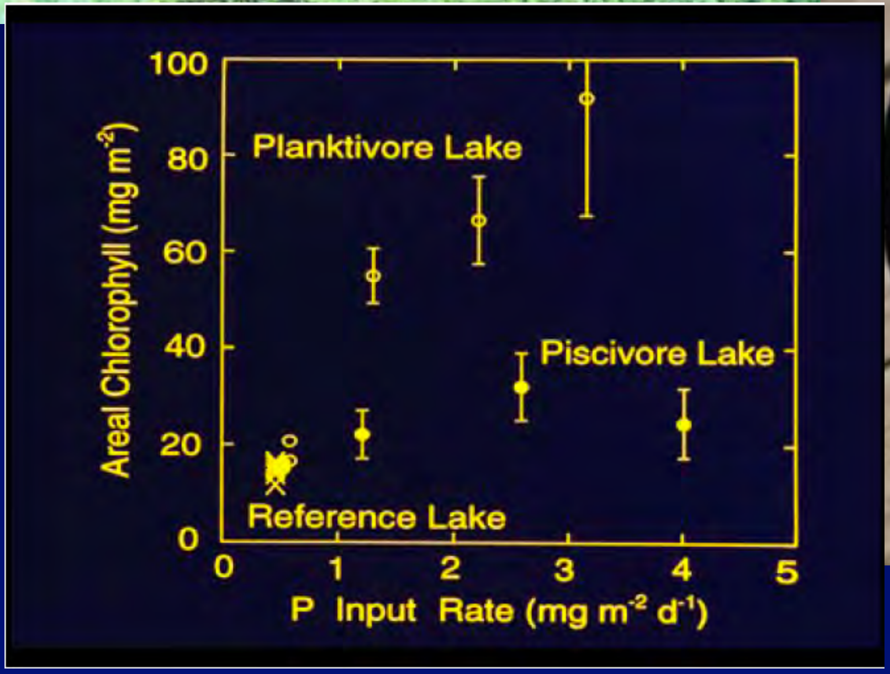
Sverdrup's (1955) map of productivity based on vertical convection, upwelling and turbulent diffusion



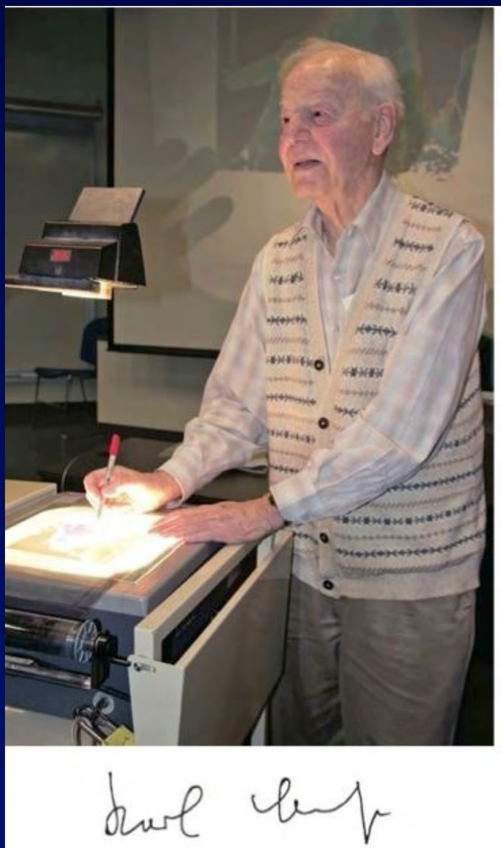
Global productivity estimated from remote sensing (Falkowski et al. 1998)

As presented by John McGowan (Oceanography Mag., 2004)

Top-down control



Top-down control

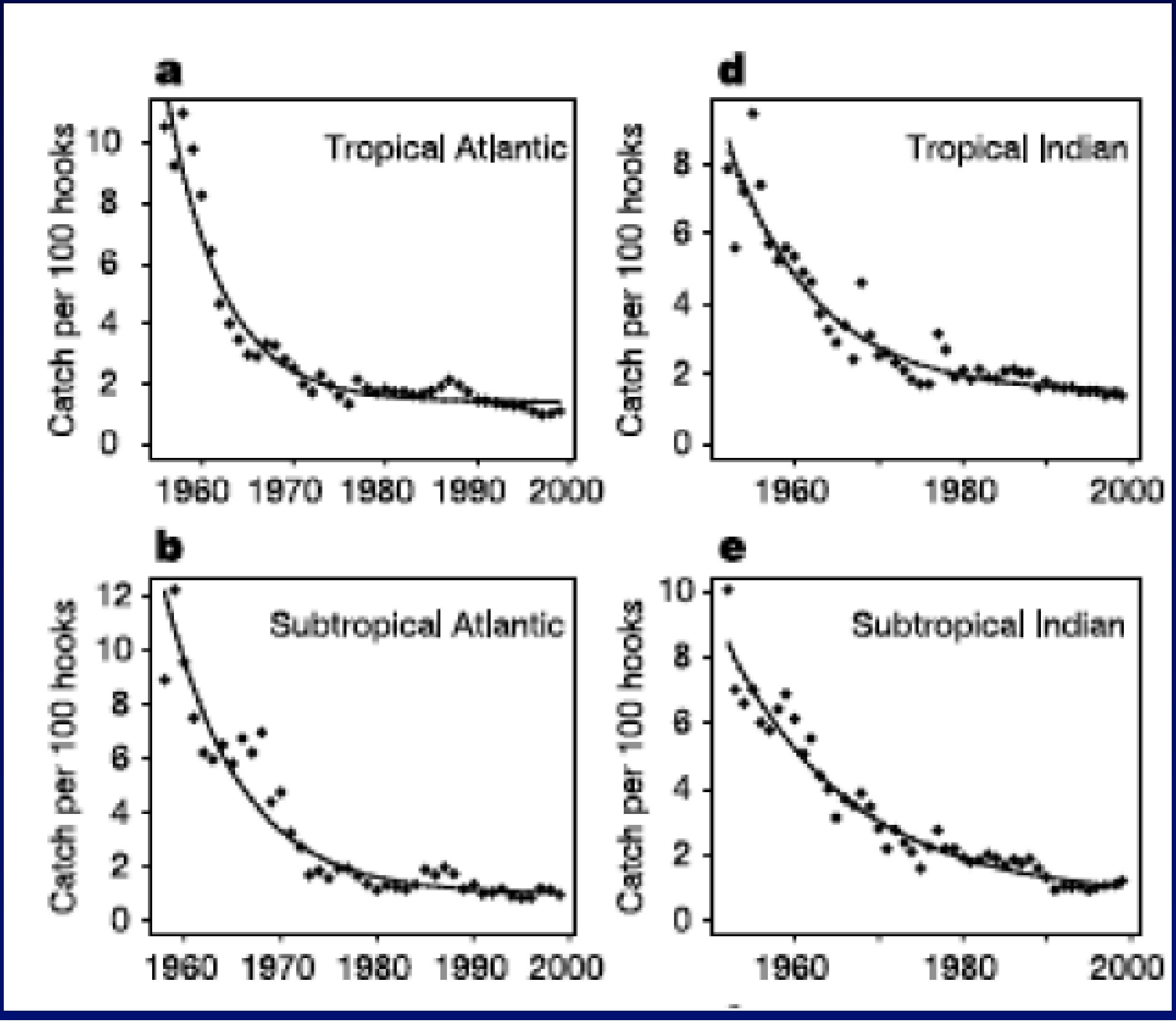


Reflections About Chance in *My* Career, and on the Top-Down Regulated World

Karl Banse

School of Oceanography, University of Washington, Seattle, Washington 98195-7940;
email: banse@uw.edu

Global test of the top-down hypothesis?



Decline of fish stocks since 1960

Myers and Worm Nature 2003

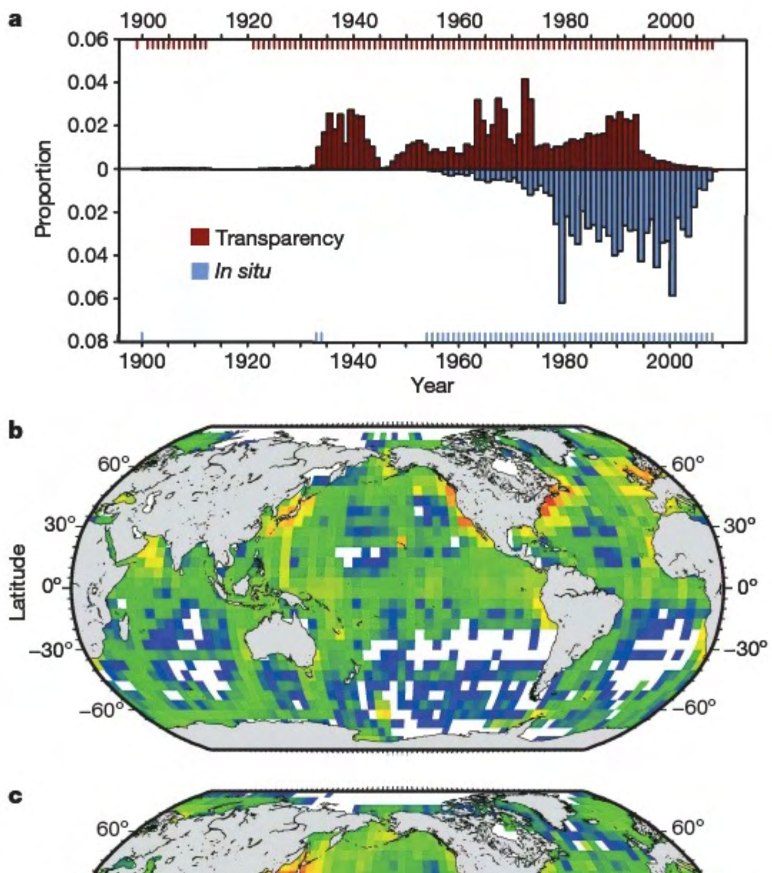
Top-down effects?

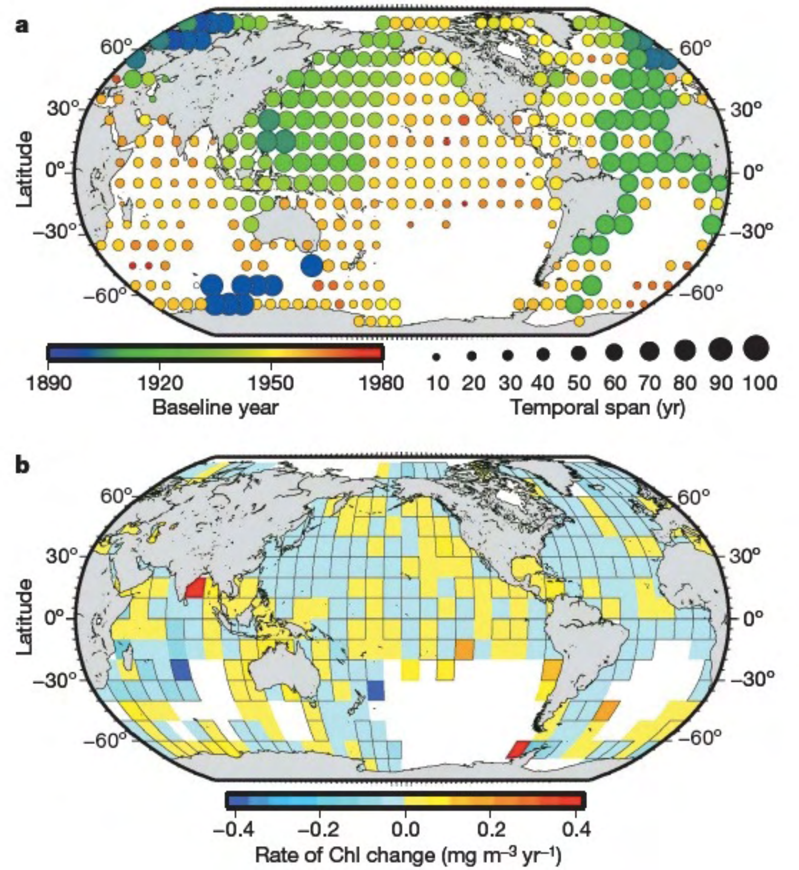
Vol 466 | 29 July 2010 | doi:10.1038/nature09268 nature

Global phytoplankton decline over the past century

Daniel G. Boyce[1], Marlon R. Lewis[2] & Boris Worm[1]

In the oceans, ubiquitous microscopic phototrophs (phytoplankton) account for approximately half the production of organic matter on Earth. Analyses of satellite-derived phytoplankton concentration (available since 1979) have suggested decadal-scale fluctuations linked to climate forcing, but the length of this record is insufficient to resolve longer-term trends. Here we combine available ocean transparency measurements and *in situ* chlorophyll observations to estimate the time





BRIEF COMMUNICATIONS ARISING

Does blending of chlorophyll data bias temporal trend?

ARISING FROM D. G. Boyce, M. R. Lewis & B. Worm *Nature* **466**, 591–596 (2010)

David L. Mackas[1]
[1]Institute of Ocean Sciences, Fisheries and Oceans Canada, PO Box 6000, Sidney, British Columbia, V8L 4B2, Canada.
e-mail: Dave.Mackas@dfo-mpo.gc.ca

A measured look at ocean chlorophyll trends

Ryan R. Rykaczewski[1,2] **& John P. Dunne**[2]
[1]University Corporation for Atmospheric Research, Boulder, Colorado 80307-3000 USA.

Is there a decline in marine phytoplankton?

Links to useful references

Abigail McQuatters-Gollop[1], **Philip C. Reid**[1], **Martin Edwards**[1], **Peter H. Burkill**[1], **Claudia Castellani**[1], **Sonia Batten**[1], **Winfried Gieskes**[2], **Doug Beare**[3], **Robert R. Bidigare**[4], **Erica Head**[5], **Rod Johnson**[6], **Mati Kahru**[7], **J. Anthony Koslow**[7] **& Angelica Pena**[8]
[1]Sir Alister Hardy Foundation for Ocean Science, The Laboratory, Citadel Hill, Plymouth, PL1 2PB, UK.
e-mail: abiqua@sahfos.ac.uk
[2]University of Groningen, ESRIG, Dept. Ocean Ecosystems, Nijenborgh 4,

Many scientific controversies get sorted out in time

Progress in Oceanography 122 (2014) 163–173

Contents lists available at ScienceDirect

Progress in Oceanography

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

ELSEVIER

PROGRESS IN OCEANOGRAPHY

Estimating global chlorophyll changes over the past century

CrossMark

Daniel G. Boyce [a,b,c,*], Michael Dowd [d], Marlon R. Lewis [e], Boris Worm [a]

Bottom-up processes

It can be argued that a similarly parsimonious set of factors determines the distribution of pelagic biomes, each with its characteristic flora and fauna... ***Copepods and whales do not determine which groups of plants will flourish; like the phytoplankton, they are themselves expressions of the regional physical oceanographic regime.***

(Alan Longhurst's section of Cullen et al., 2002, *The Sea*)

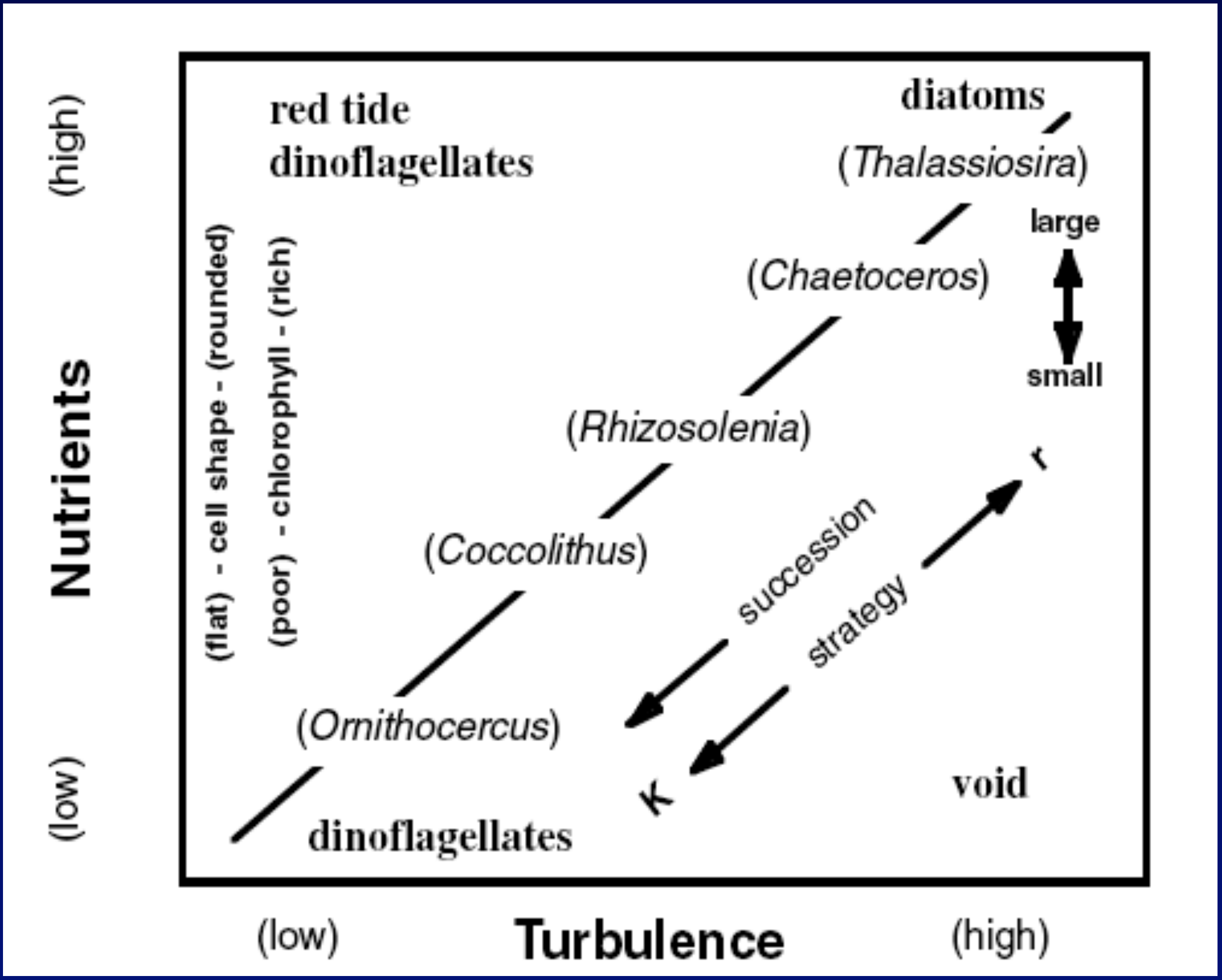
Vol. 83: 291–303, 1992 | MARINE ECOLOGY PROGRESS SERIES
Mar. Ecol. Prog. Ser. | Published July 16

Grazing and iron limitation in the control of phytoplankton stock and nutrient concentration: a chemostat analogue of the Pacific equatorial upwelling zone

B. W. Frost, N. C. Franzen

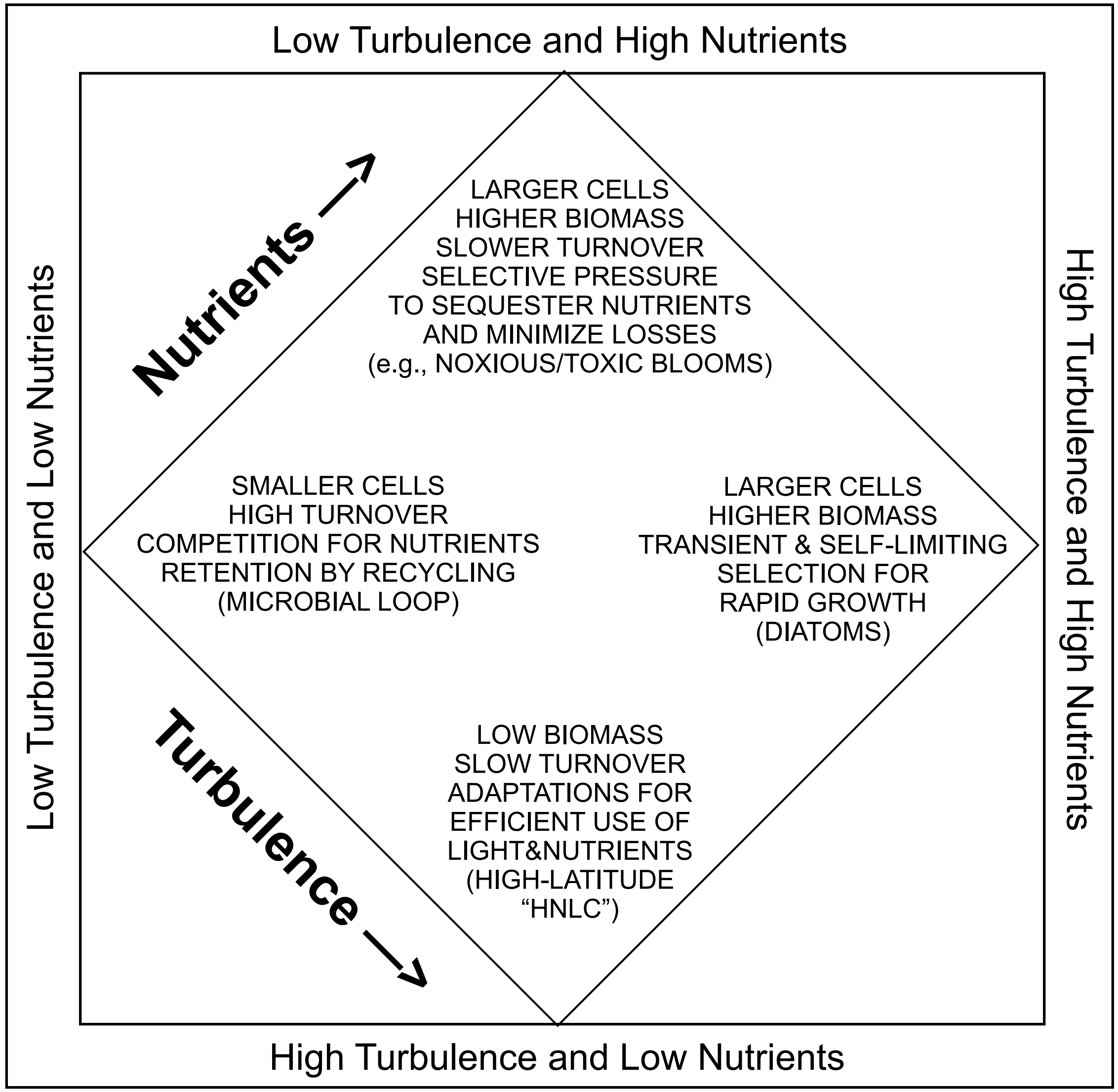
A Tool for Making Sense of Physically Forced Ecosystem Dynamics:

Margalef's Mandala



Event-Scale Forcing —>

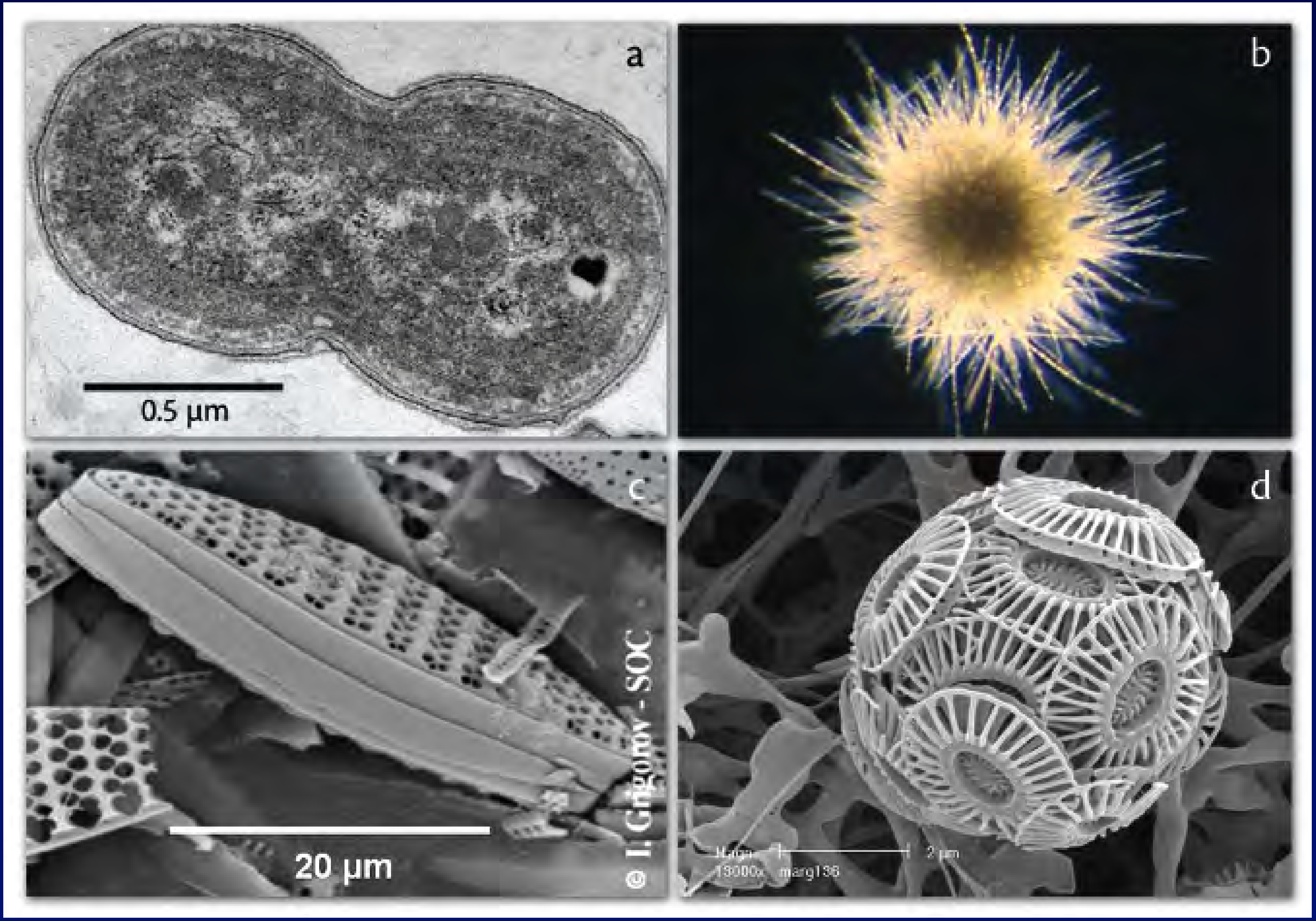
<— Succession



Potential for Production and Export —>

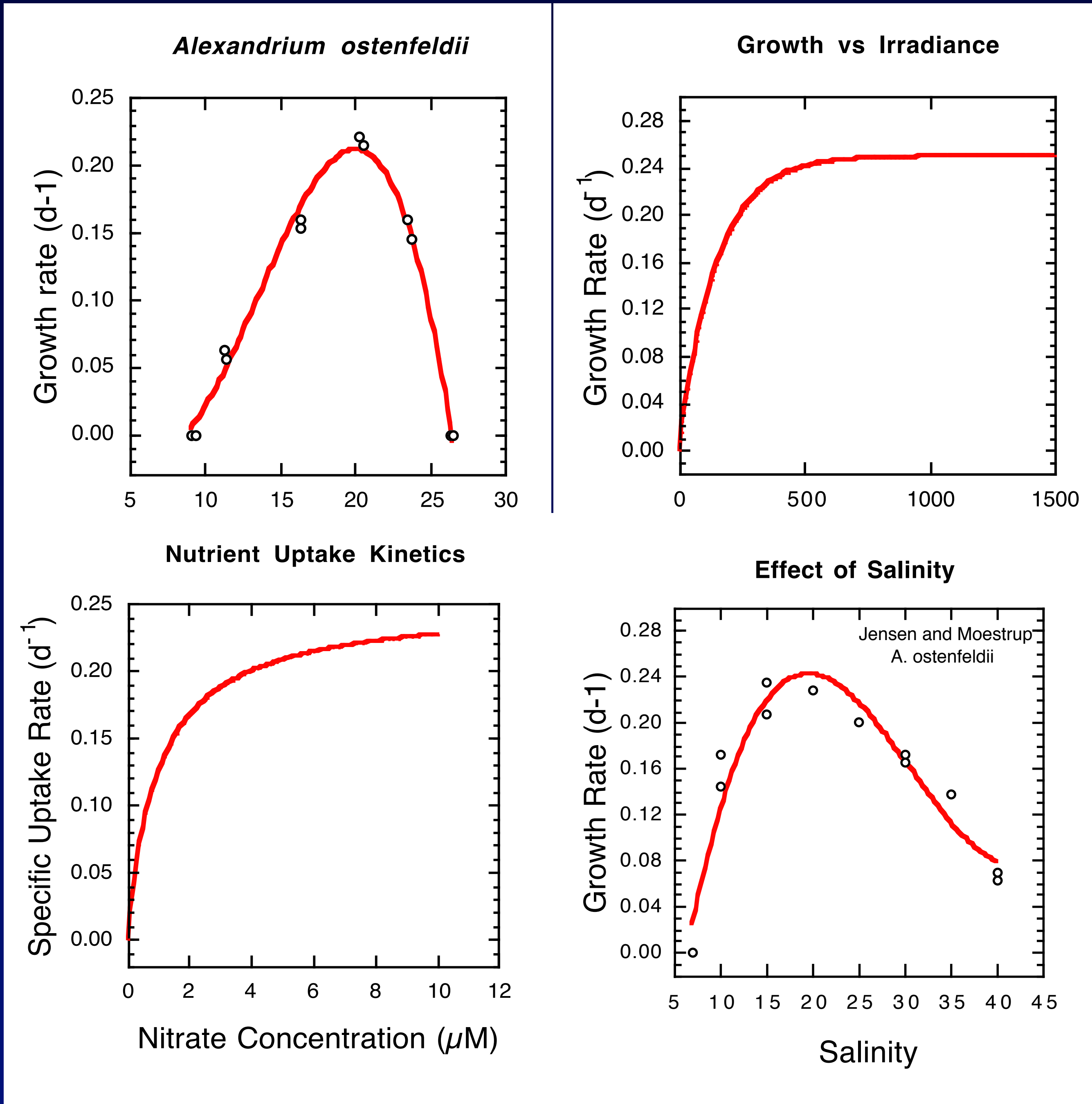
Cullen et al. 2002, The Sea

The challenge: quantitative description of the niches of functional groups



Critical to know the Environmental Influences on the Growth of Phytoplankton:

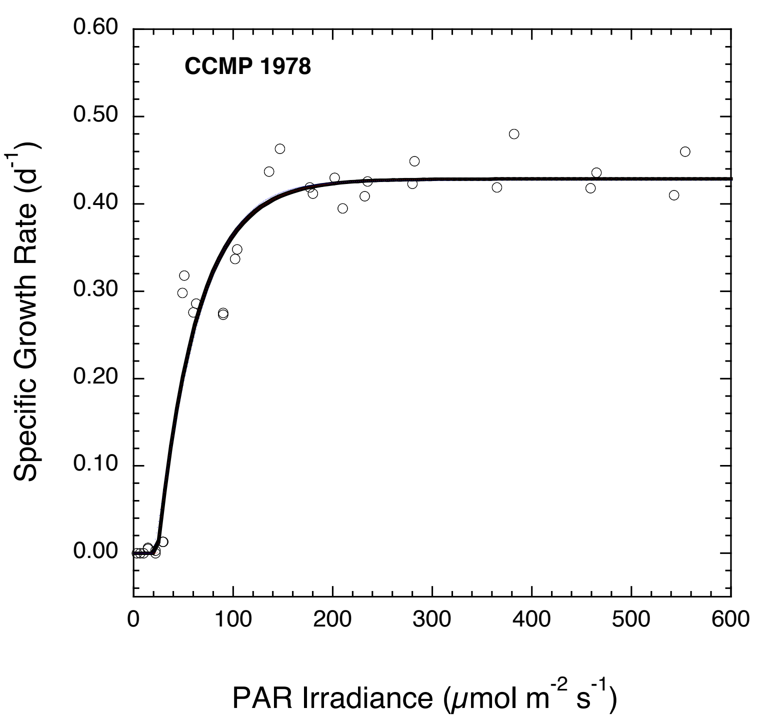
Temperature
Light
Daylength
Nutrients



Ecosystem modeling ground zero:

Acclimated growth rate: genotypic

Cullen et al. in prep



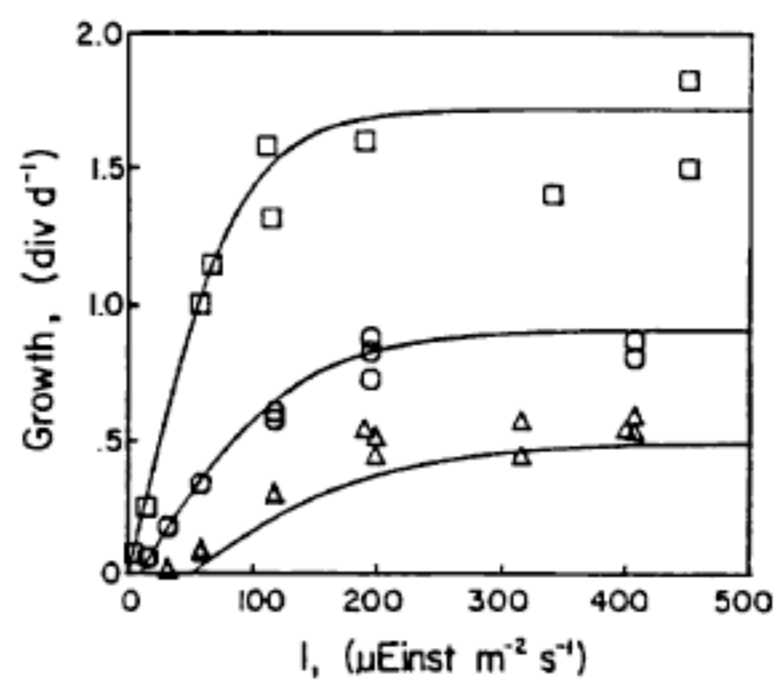
$$\mu(E) = (\mu_{\max})(1 - e^{-(E-K_C)/(K_E - K_C)}) \quad \text{if } E > K_C$$

$$\mu(E) = 0 \quad \text{if } E \leq K_C$$

Journal of Plankton Research Vol.9 no.3 pp.459–482, 1987

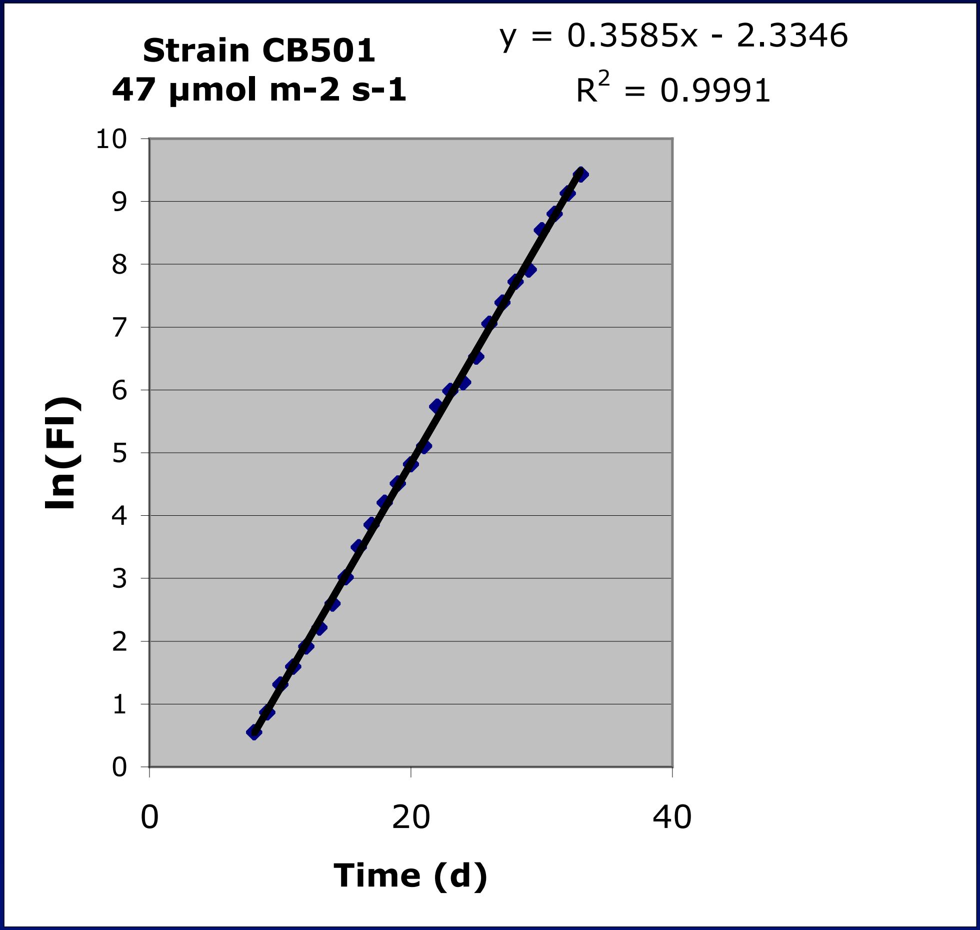
On the causes of interspecific differences in the growth–irradiance relationship for phytoplankton. Part I. A comparative study of the growth–irradiance relationship of three marine phytoplankton species: *Skeletonema costatum*, *Olisthodiscus luteus* and *Gonyaulax tamarensis*

Christopher Langdon[1]



Species evolve different functions through ***adaptation*** and selection

μ as a function of *T* and *E* may not be relevant for describing growth rate in dynamic environments



Alexandrium fundyense

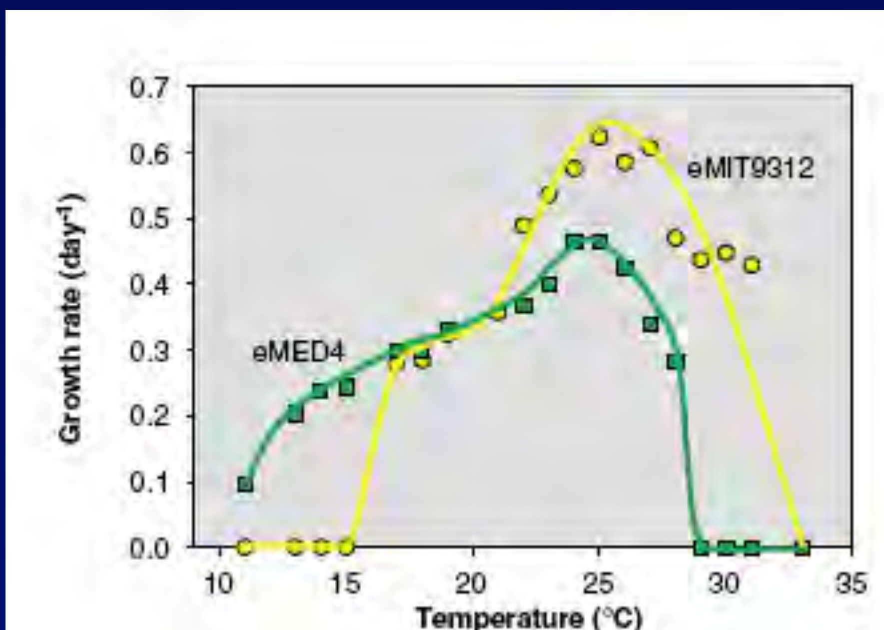
Growth determined using the method of Brand and Guillard

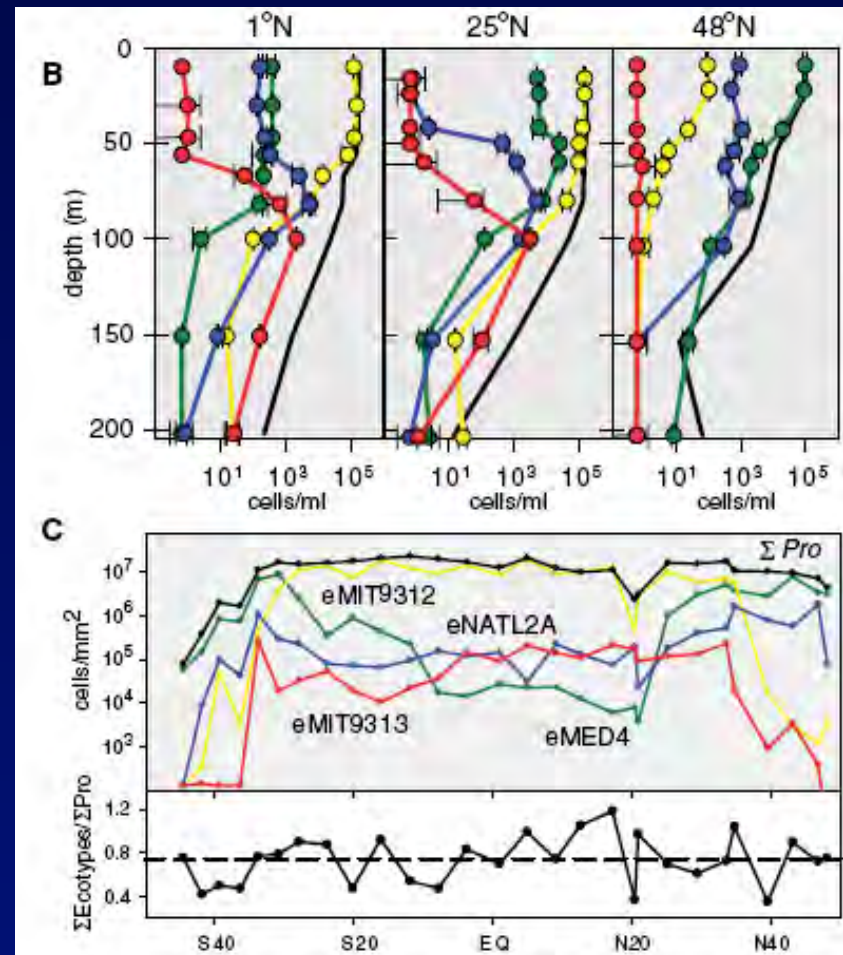
Brand, L. E. and Guillard, R. R. L. (1981). A method for the rapid and precise determination of acclimated phytoplankton reproduction rates. *J. Plankton Res.* 3: 191-201.

But it is an excellent start for identifying niches

Niche Partitioning Among *Prochlorococcus* Ecotypes Along Ocean-Scale Environmental Gradients

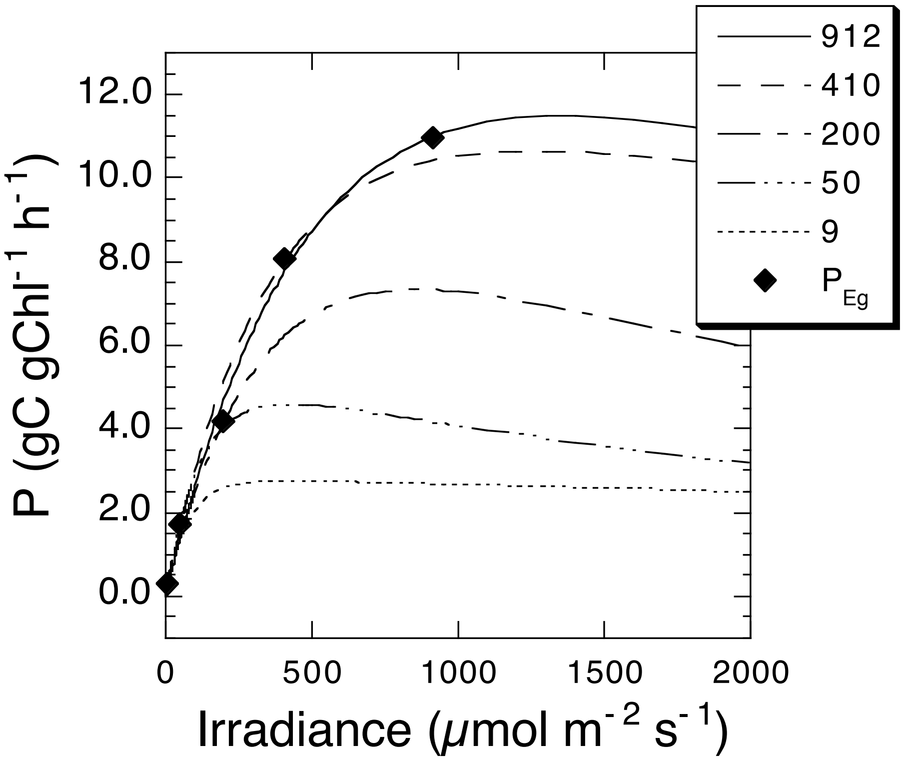
Zackary I. Johnson,[1,2]* Erik R. Zinser,[1,3]* Allison Coe,[1] Nathan P. McNulty,[1] E. Malcolm S. Woodward,[4] Sallie W. Chisholm[1]†

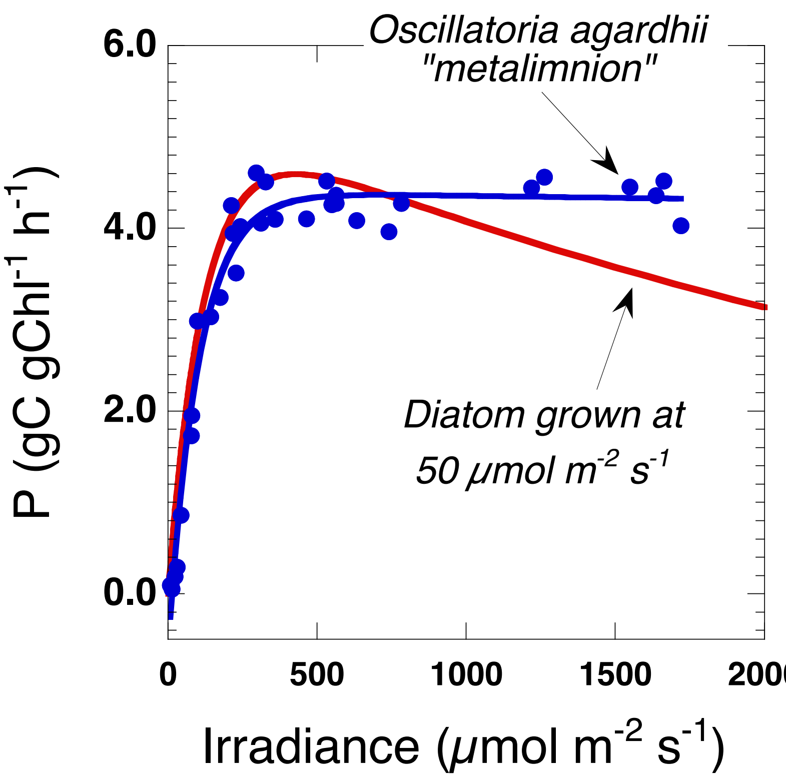




SCIENCE VOL 311 24 MARCH 2006

Photosynthesis vs Irradiance: phenotypic

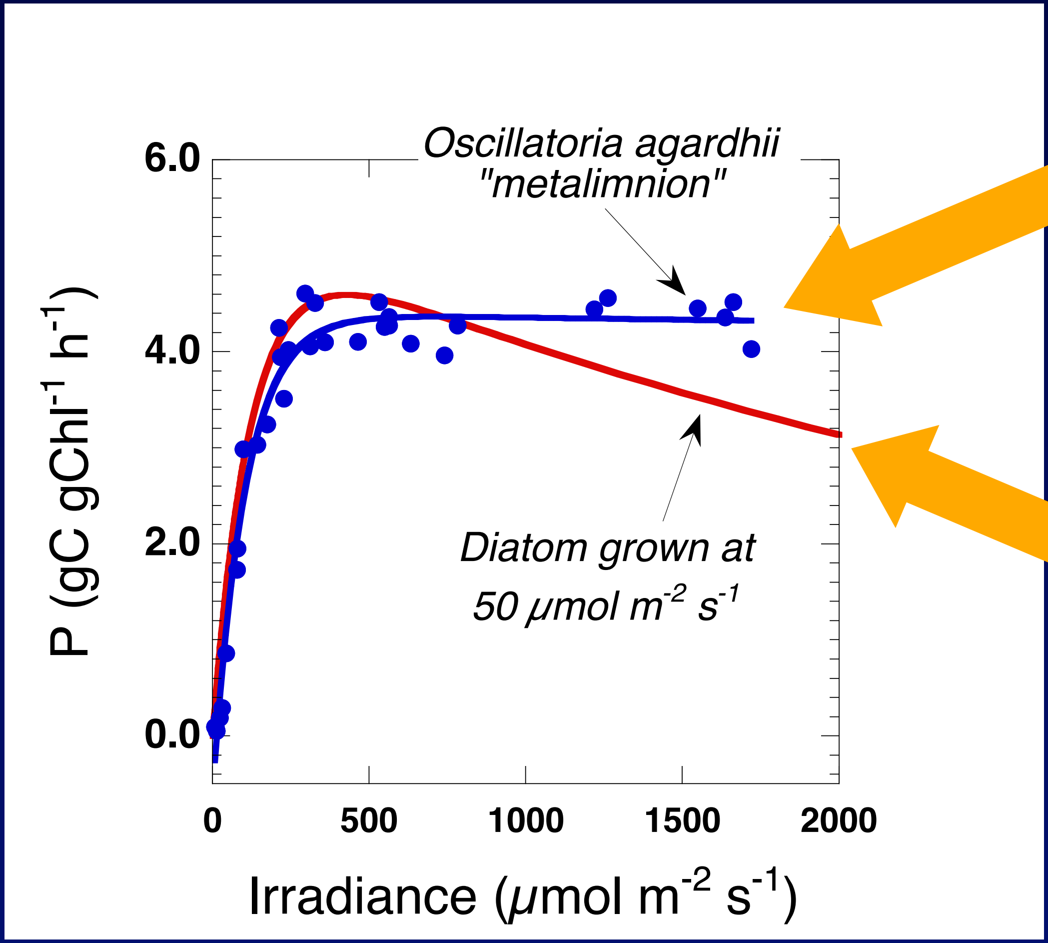




Species develop different functions through ***acclimation***

John Cullen: C-MORE 2014

Photosynthesis vs Irradiance: phenotypic



Layer former

Mixer

Strategies to respond to environmental variability are adaptations

Adaptations to oceanic vs coastal conditions

Vol. 41: 275–282, 1987 | MARINE ECOLOGY – PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published December 14

Thalassiosira oceanica and _T. pseudonana_: two different photoadaptational responses

E. Sakshaug[1], S. Demers[2], C. M. Yentsch[3]

Photosynthetic architecture differs in coastal and oceanic diatoms

Robert F. Strzepek[1+] & Paul J. Harrison[2+]

NATURE | VOL 431 | 7 OCTOBER 2004 | www.nature.com/nature

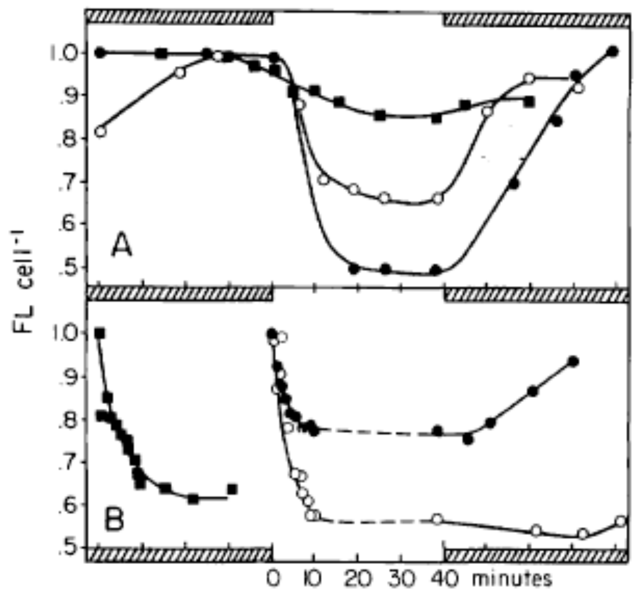


Fig. 5. *Thalassiosira pseudonana and T. oceanica*. Short-term changes of *in vivo* fluorescence per cell normalized to the highest observed value in each experiment. (A) *T. pseudonana* at 600 (○) or 800 µmol m^{-2} s^{-1} (●) exposed to 2800, and then to 600 or 800 µmol m^{-2} s^{-1} and *T. oceanica* (■) at 800 µmol m^{-2} s^{-1} exposed to 2800 and then to 800 µmol m^{-2} s^{-1}. (B) Changes in *in vivo* fluorescence per cell of *T. pseudonana* after addition of gramicidin; (■) cultures at 800 µmol m^{-2} s^{-1}; (○) cultures at 2800 µmol m^{-2} s^{-1} followed by darkness; (●) control (no gramicidin), cultures at 800 µmol m^{-2} s^{-1} followed by darkness. Horizontal bars: period of low light or darkness according to descriptions above

Oceanic species has much reduced capability for regulation

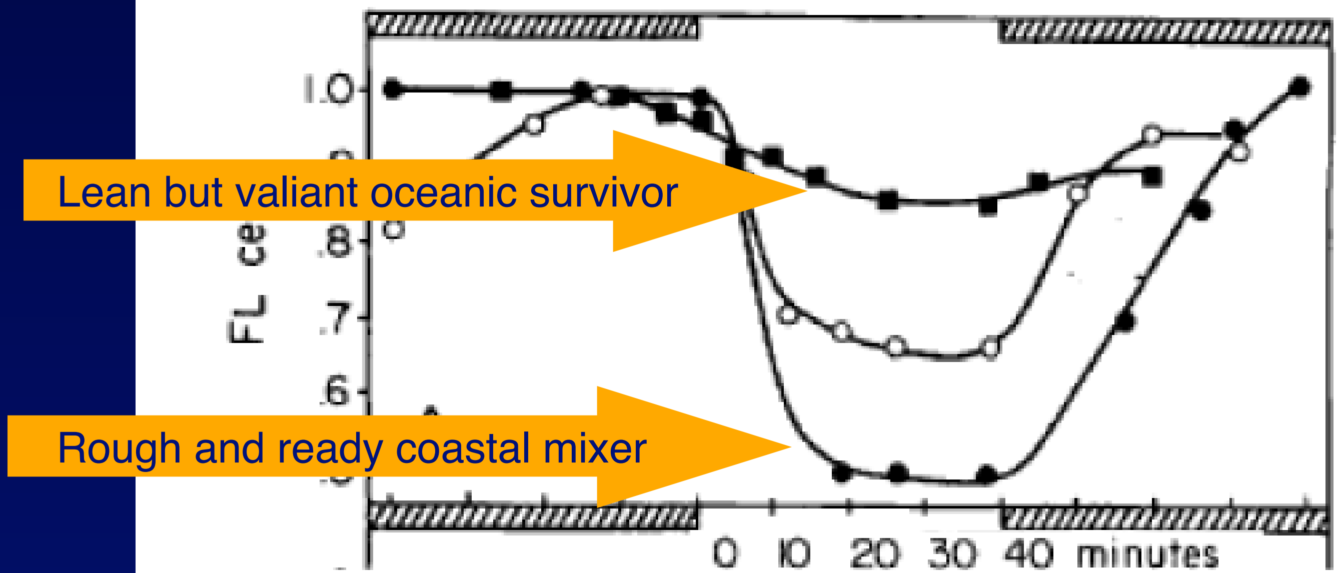
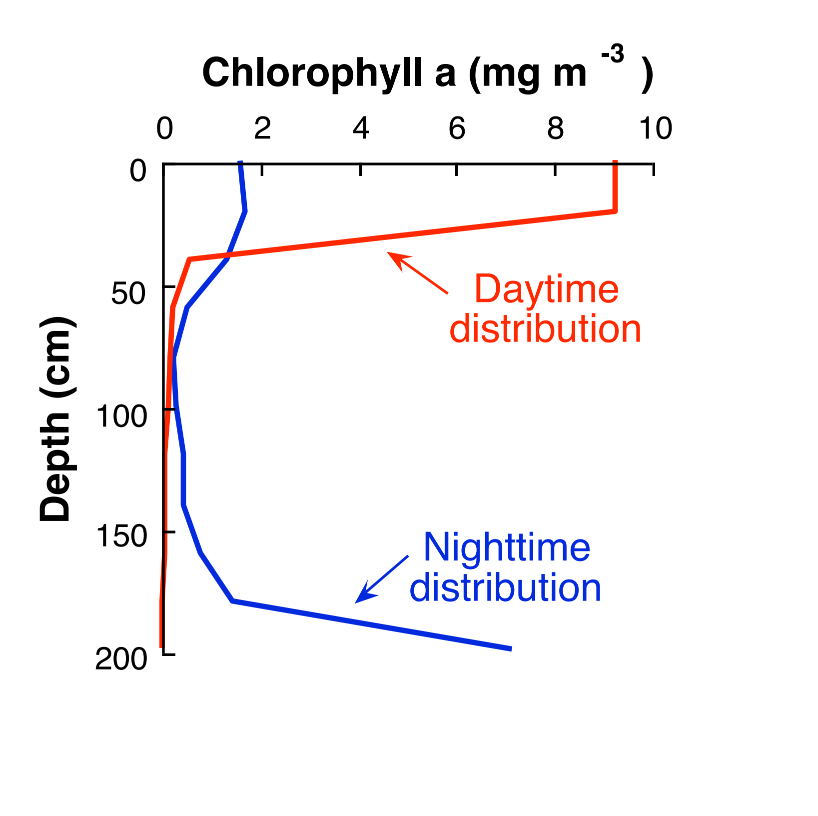


Fig. 5. *Thalassiosira pseudonana and T. oceanica*. Short-term changes of *in vivo* fluorescence per cell normalized to the highest observed value in each experiment. (A) *T. pseudonana* at 600 (○) or 800 μmol m^{-2} s^{-1} (●) exposed to 2800, and then to 600 or 800 μmol m^{-2} s^{-1} and *T. oceanica* (■) at 800 μmol m^{-2} s^{-1} exposed to 2800 and then to 800 μmol m^{-2} s^{-1}.

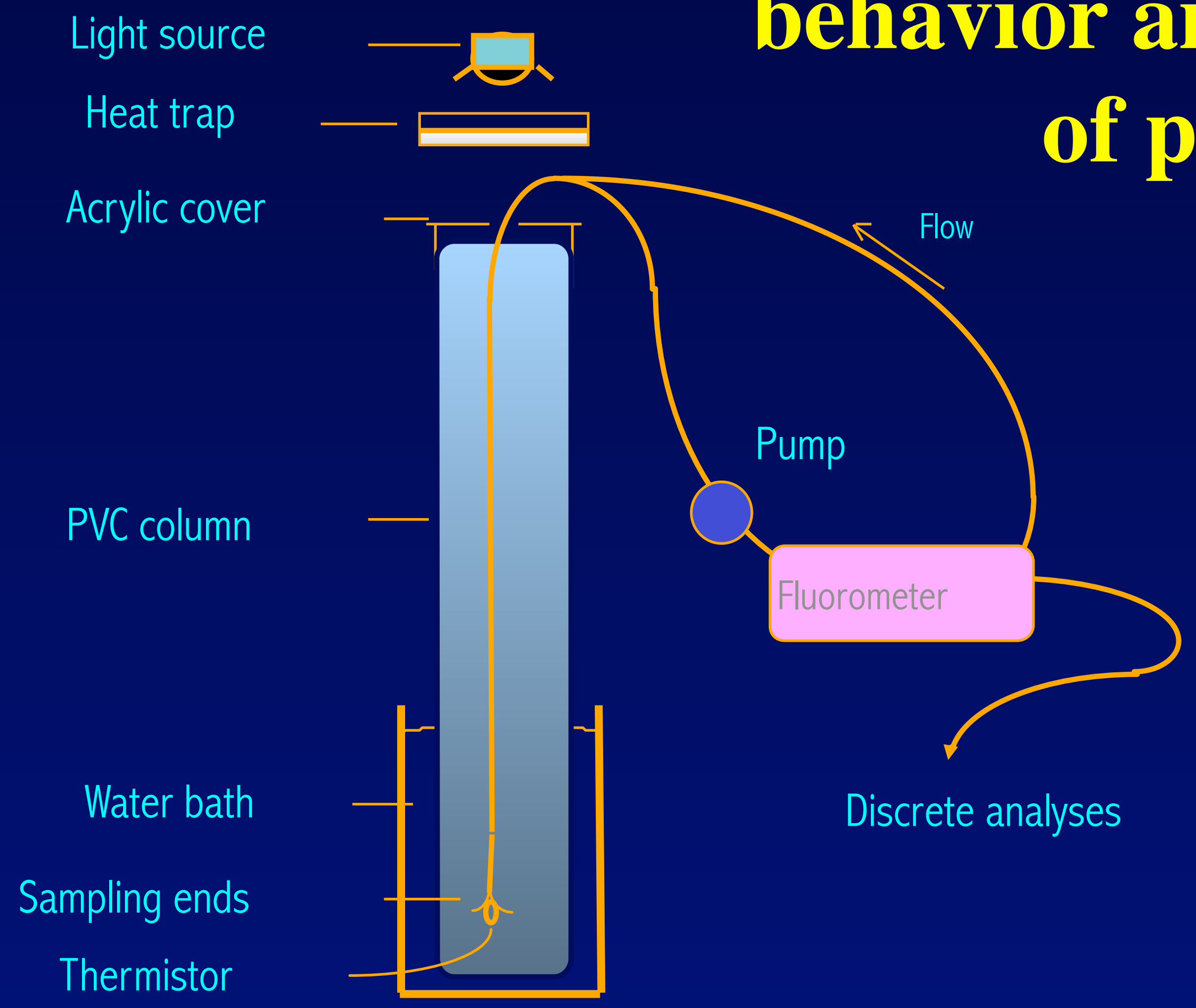
And what about vertical migrators?



Nutrient concentration?

Temperature?

“Cheap Tank” — A useful tool for studying the behavior and physiology of phytoplankton



Other mesocosms have been used in a few labs (e.g., M. Estrada)

Migration studies

Excellent tool for describing behavior in natural gradients of environmental factors

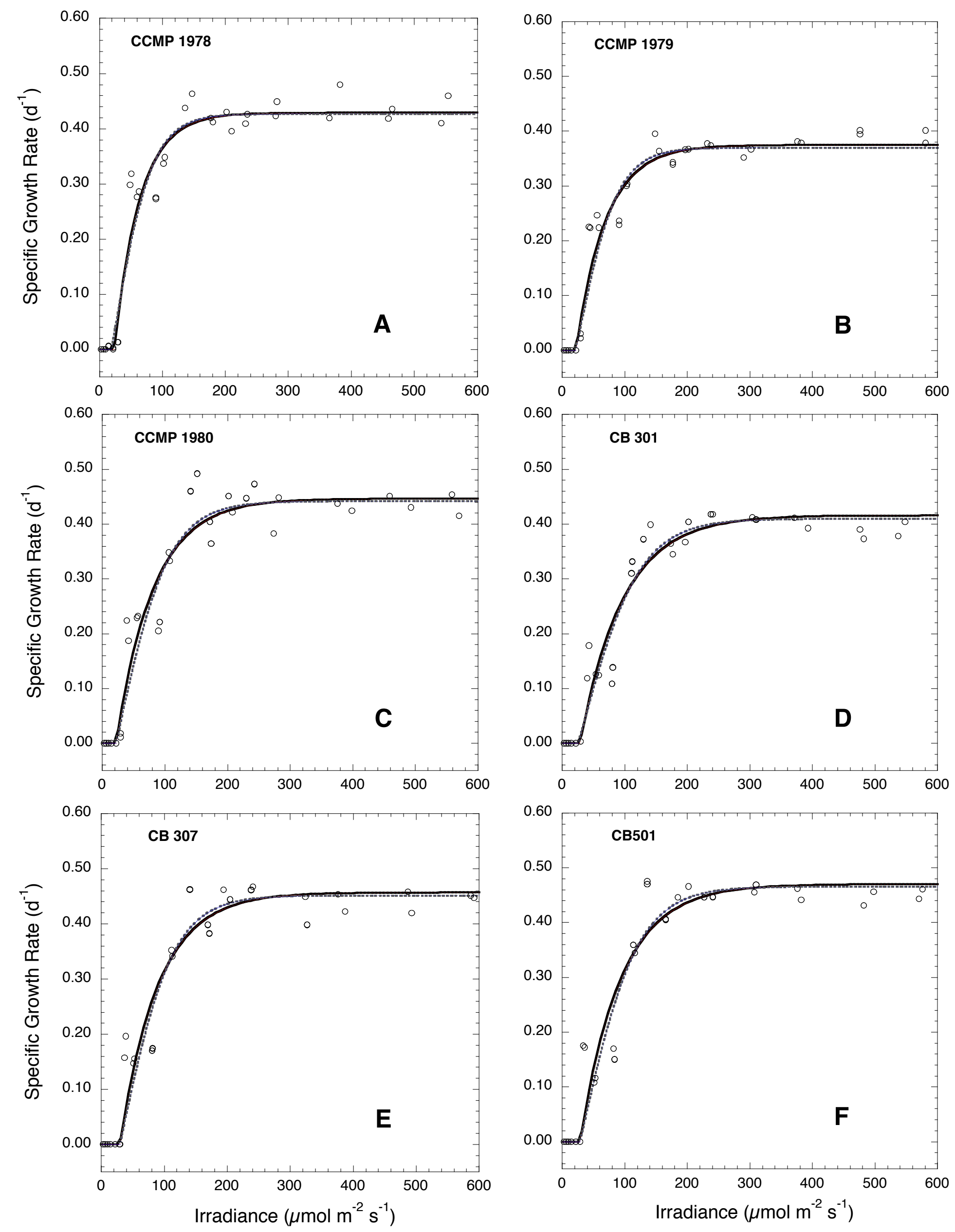
Difficult to specify growth rate in nature

Good for examining interspecific and intraspecific variability in ecologically important traits

Alexandrium fundyense

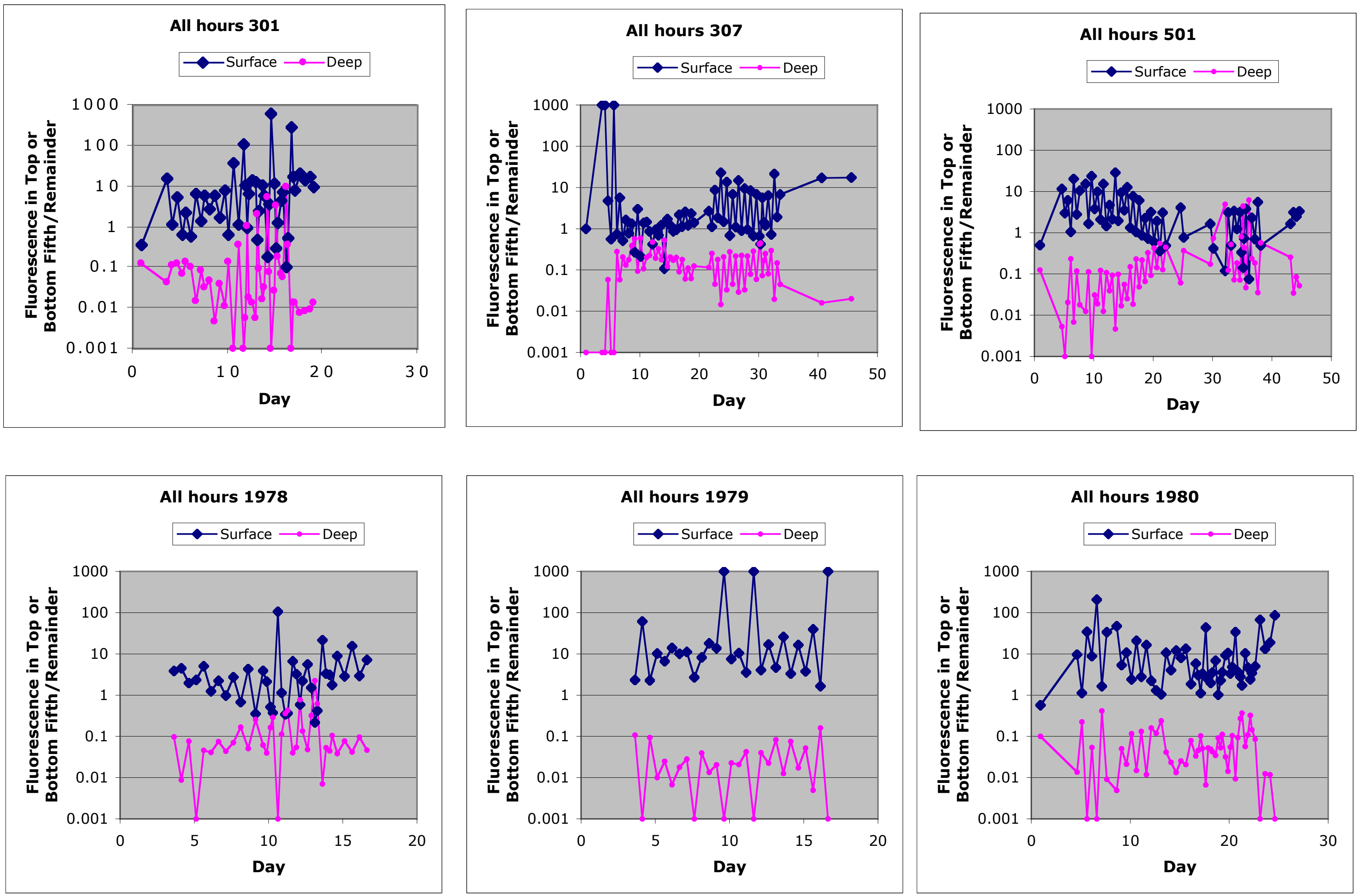
Results for 6 strains:

Growth Rate vs Irradiance



Behavior showed significant variability:

Aggregation at top vs bottom all hours



Top Layer < 5 μM

Bottom Layer < 5 μM

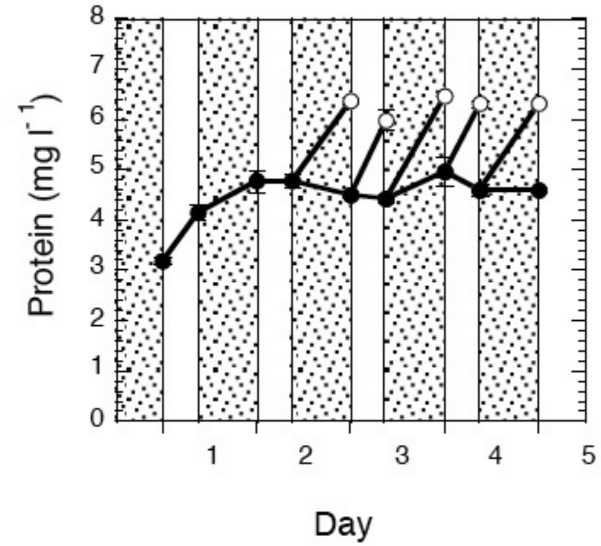
Nitrate Restored

Bouncing around Redfield

NATO ASI Series, Vol. G 41
Physiological Ecology of Harmful Algal Blooms
Edited by D.M. Anderson, A.D. Cembella, and G. M. Hallegraeff

Behavior, physiology and the niche of depth-regulating phytoplankton

John J. Cullen and J. Geoffrey MacIntyre



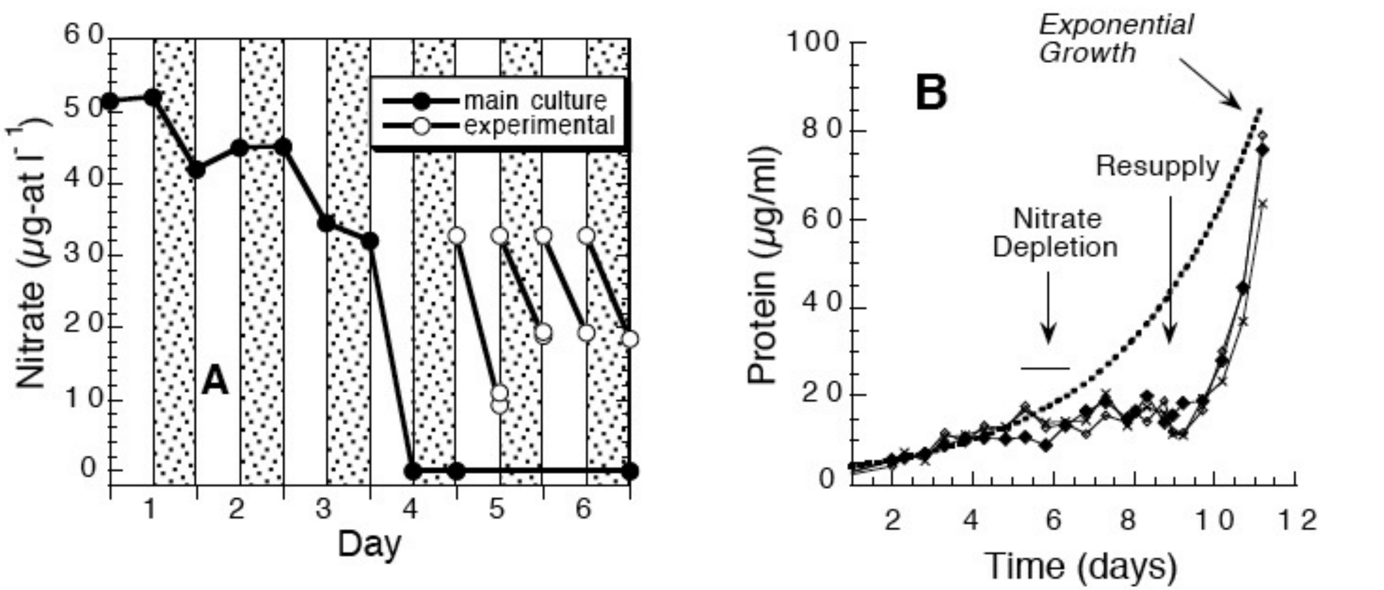


Fig. 4. Uptake and assimilation of nitrate after N-starvation. A. The diatom *Skeletonema*

Bouncing around Redfield

Vol. 87: 123–134, 1992 | MARINE ECOLOGY PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published October 8

Stoichiometric variations of N, P, C and O_2 during a *Gymnodinium catenatum* red tide and their interpretation

F. Fraga, F. F. Pérez, F. G. Figueiras, A. F. Ríos

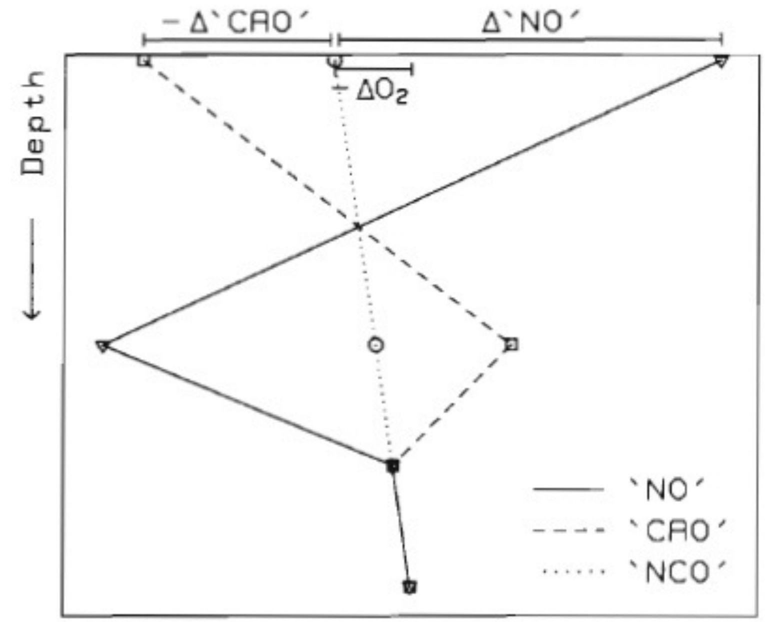


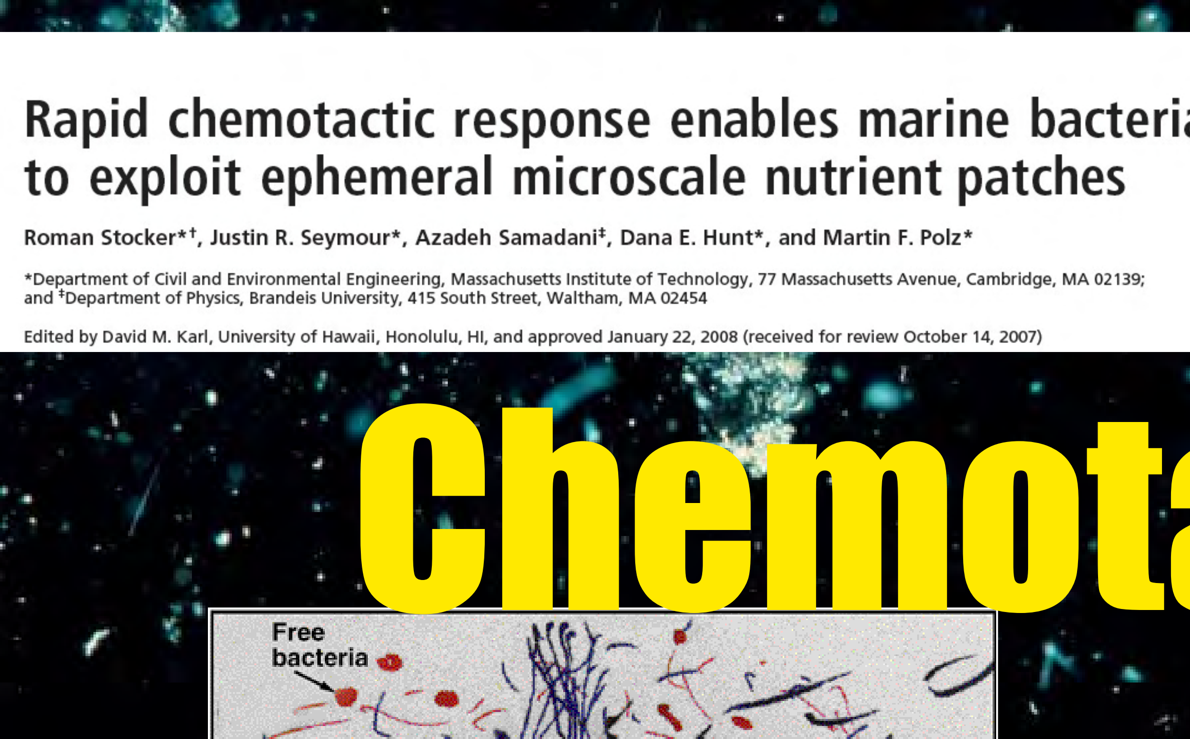
Fig. 5. Theoretical scheme of vertical variation of the chemical parameters 'NO' or 'PO', 'CAO' and 'NCO' or 'PCO' according to the data given in Table 3. The loss of oxygen ($-\Delta O_2$) to the atmosphere is also shown and decreases linearly with depth

Rapid chemotactic response enables marine bacteria to exploit ephemeral microscale nutrient patches

Roman Stocker*†, Justin R. Seymour*, Azadeh Samadani‡, Dana E. Hunt*, and Martin F. Polz*

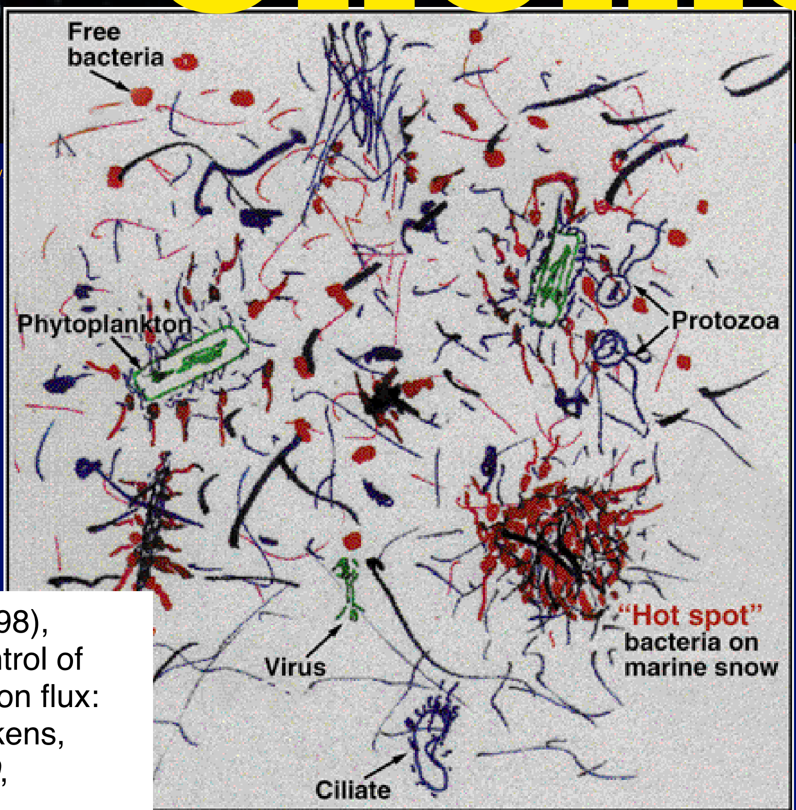
*Department of Civil and Environmental Engineering, Massachusetts Institute of Technology, 77 Massachusetts Avenue, Cambridge, MA 02139; and ‡Department of Physics, Brandeis University, 415 South Street, Waltham, MA 02454

Edited by David M. Karl, University of Hawaii, Honolulu, HI, and approved January 22, 2008 (received for review October 14, 2007)

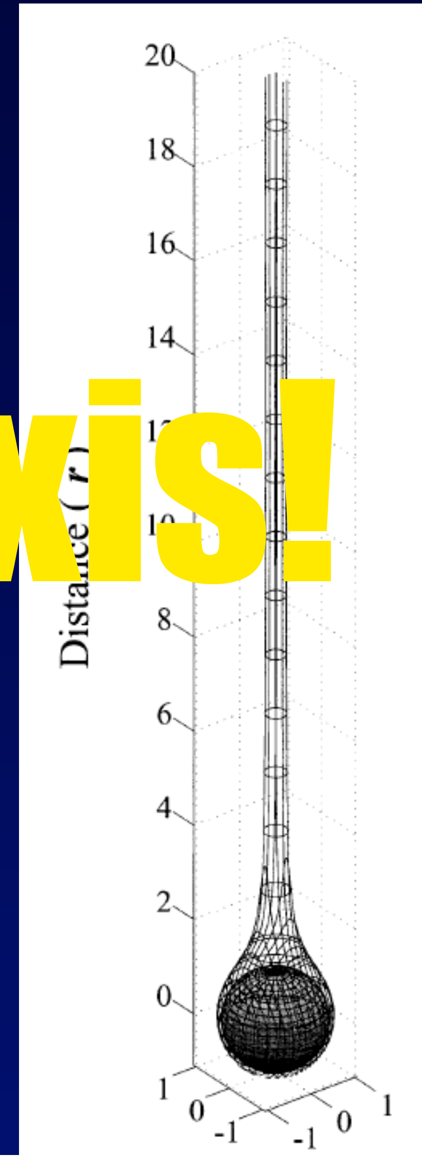


Chemotaxis!

http://



Azam, F. (1998), Microbial control of oceanic carbon flux: The plot thickens, *Science*, *280*, 694-696.



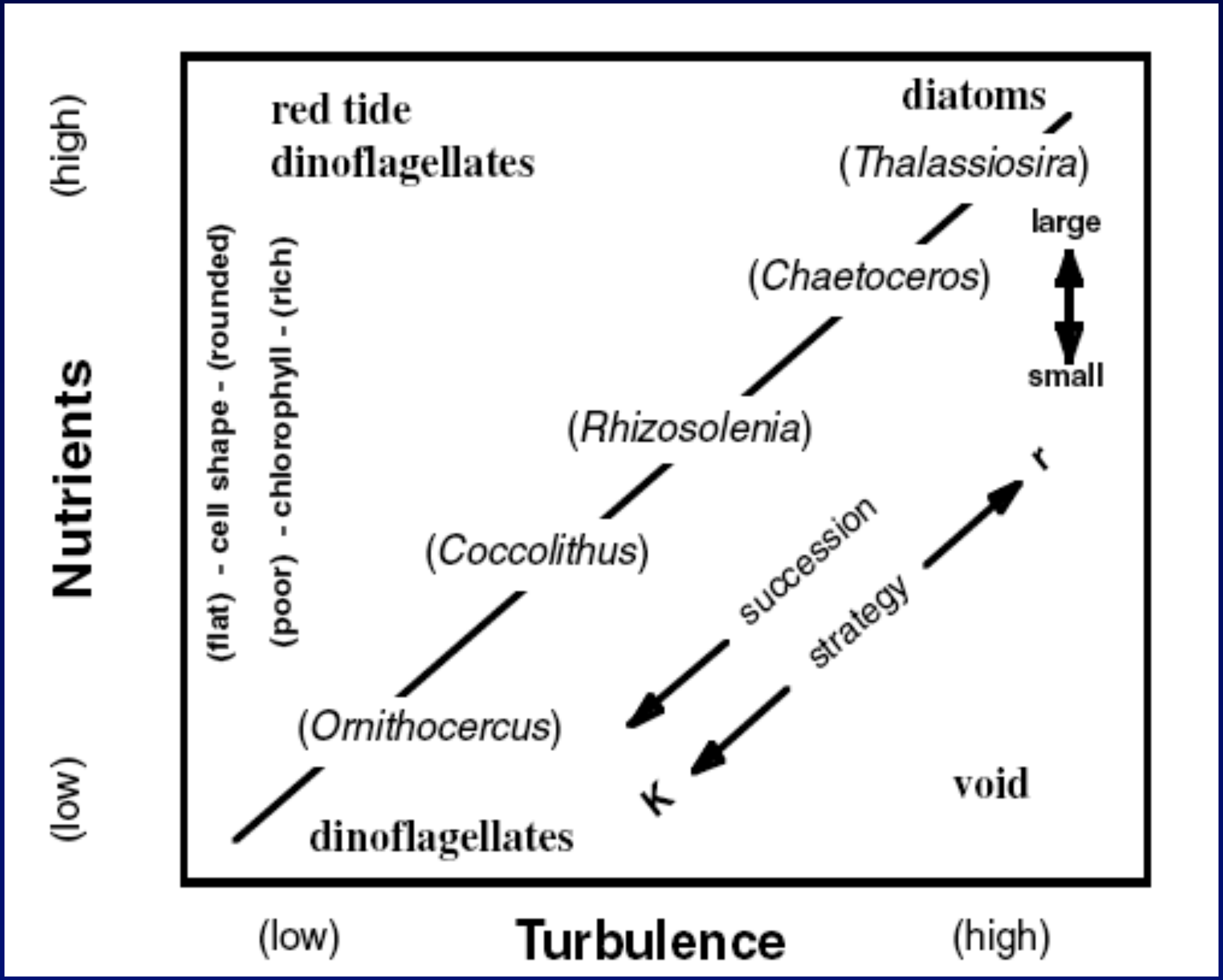
Limnol. Oceanogr., 46(6), 2001, 1309–1318
© 2001, by the American Society of Limnology and Oceanography, Inc.

Marine snow, organic solute plumes, and optimal chemosensory behavior of bacteria

Thomas Kiørboe
Danish Institute for Fisheries Research, Kavalergaarden 6, DK-2920 Charlottenlund, Denmark

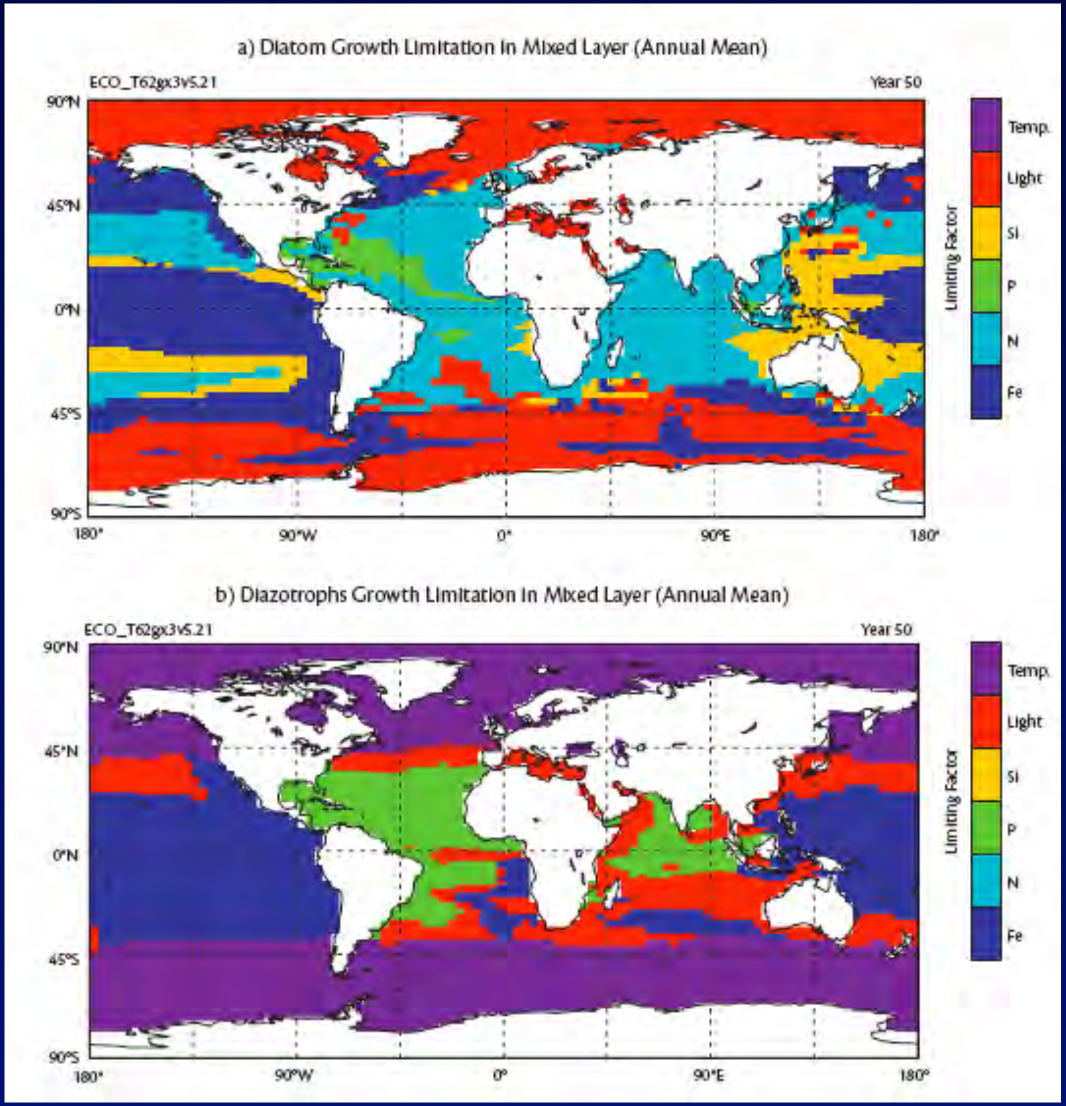
George A. Jackson
Department of Oceanography, Texas A&M University, College Station, Texas 77843

Niches abound!



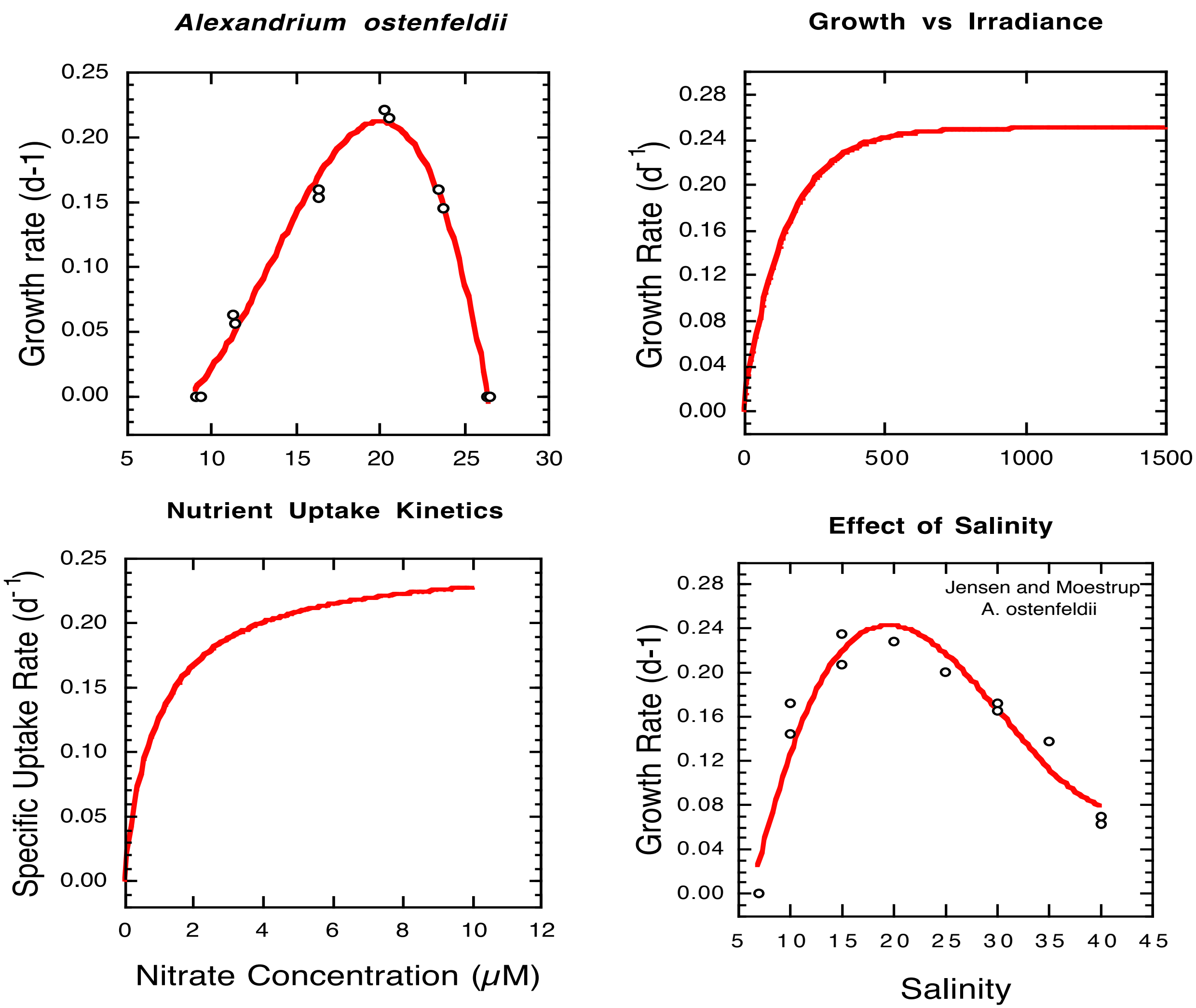
John Cullen: C-MORE 2014

But what about quantitative prediction?

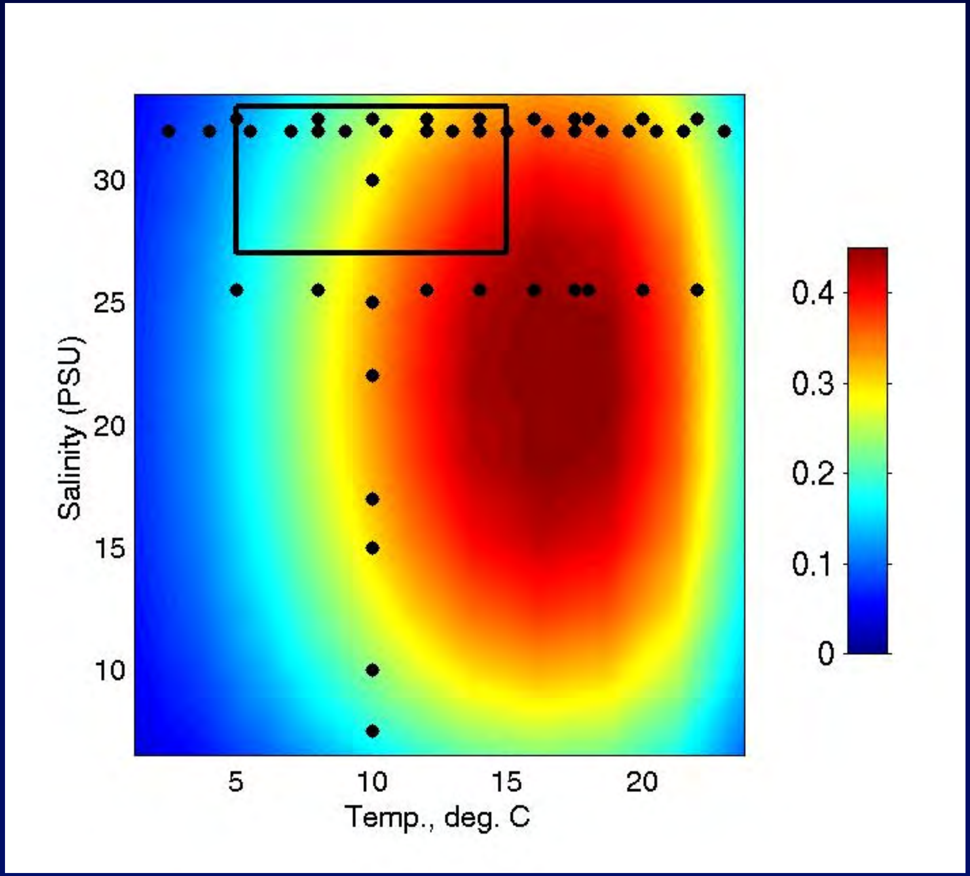


Rothstein et al. Oceanography Mag. 2006

Growth must be described as a function of environmental conditions



Functions can be Developed



McGillicuddy, Stock, Anderson, and Signell WHOI

$$\mu = f(D, E, N, T)$$

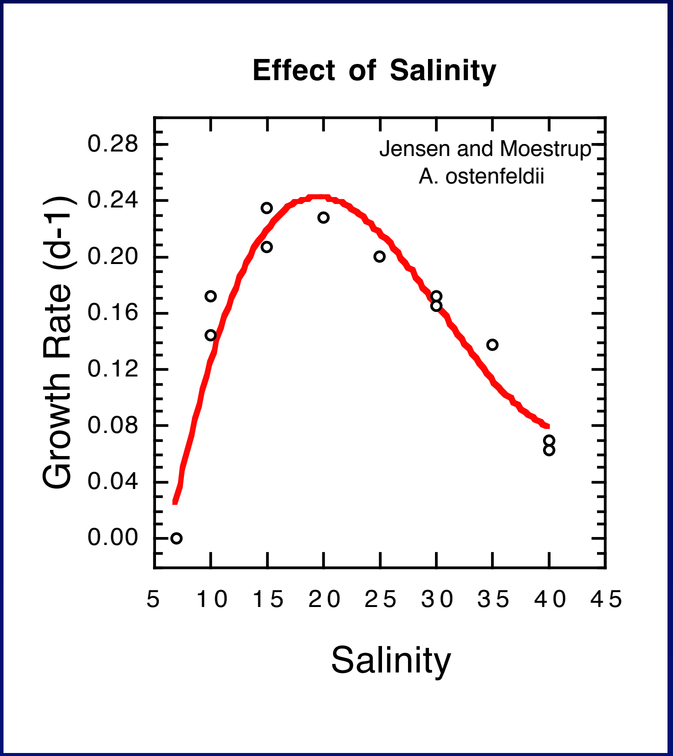
(Daylength, Irradiance, Temperature, Nutrients)

…but

- Requires a huge amount of work with cultures
- Algae should be acclimated to each set of conditions
  - This can require several weeks
- Conditions in nature are almost never so stable
  - Phytoplankton are subject to vertical mixing
  - Vertical migration
- All combinations of *Daylength, Irradiance, Nutrients* and *Temperature* are essentially impossible to test

Summary: μ as a function of environmental conditions

Good for identifying environmental ranges and optima



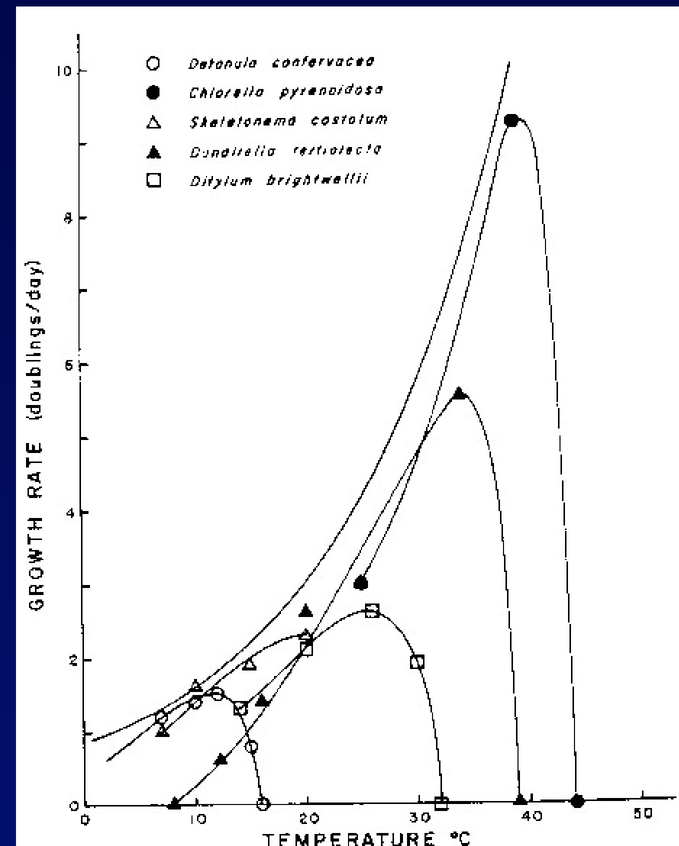
Summary: μ as a function of environmental conditions

Excellent for describing differences between species

(and variations among strains of the same species)

Ancient example:

Gallagher, J. C. (1982). Physiological variation and electrophoretic banding patterns of genetically different seasonal populations of *Skeletonema costatum* (Bacillariophyceae). *J. Phycol.* 18: 148-162.



Even more ancient:

Eppley, R. W. 1972. Temperature and phytoplankton growth in the sea. Fish. Bull. **70:** 1063-1085.

John Cullen: C-MORE 2014

Can we assume that adaptation provides all the raw genetic material for aggregate super-bugs?

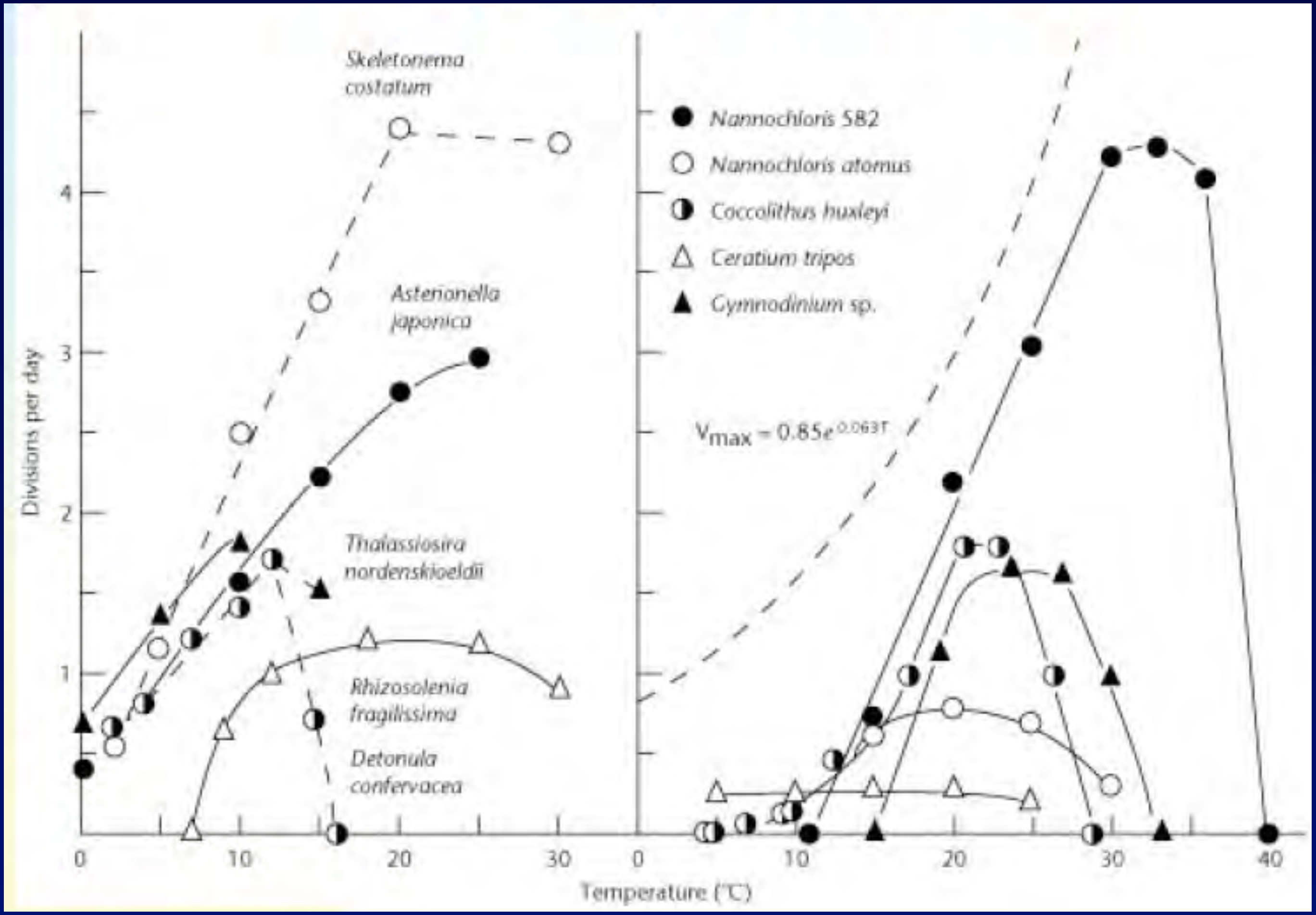


Figure from C.B. Miller, "Biological Oceanography" after Smayda, 1976

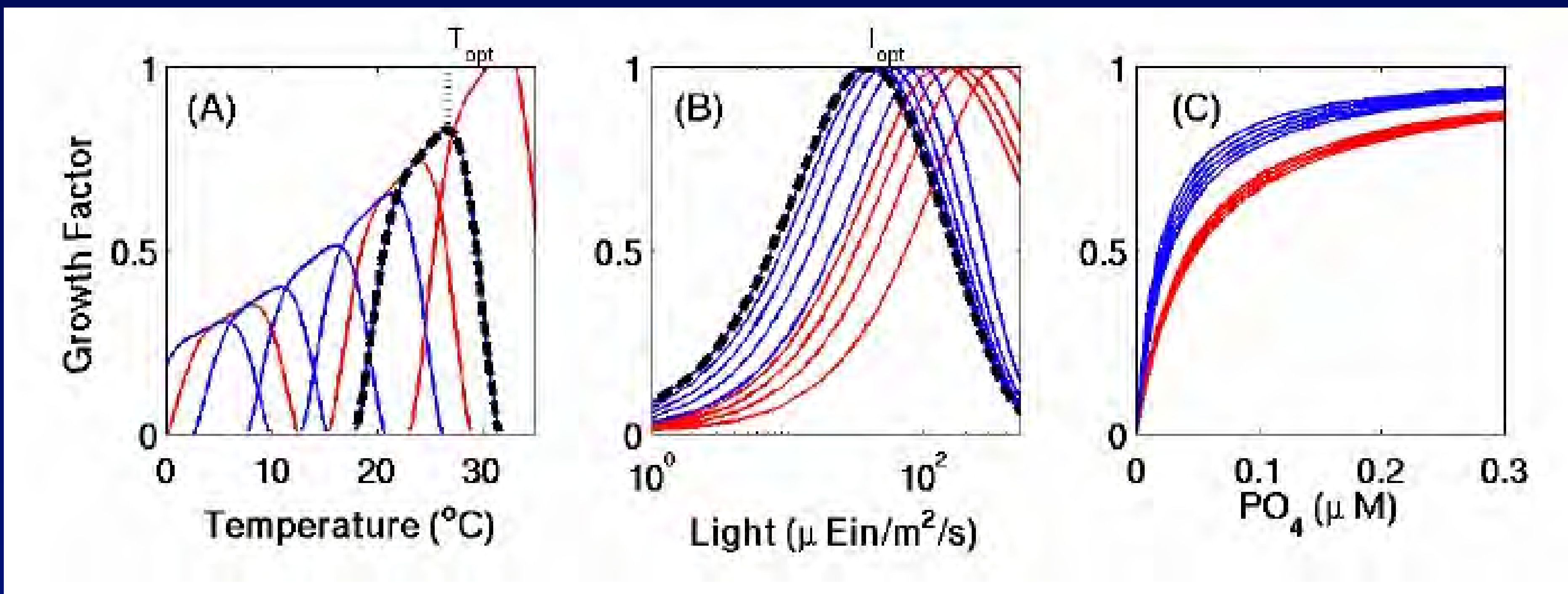
see Eppley, R. W. 1972. Temperature and phytoplankton growth in the sea. Fish. Bull. 70: 1063-1085.

A novel approach

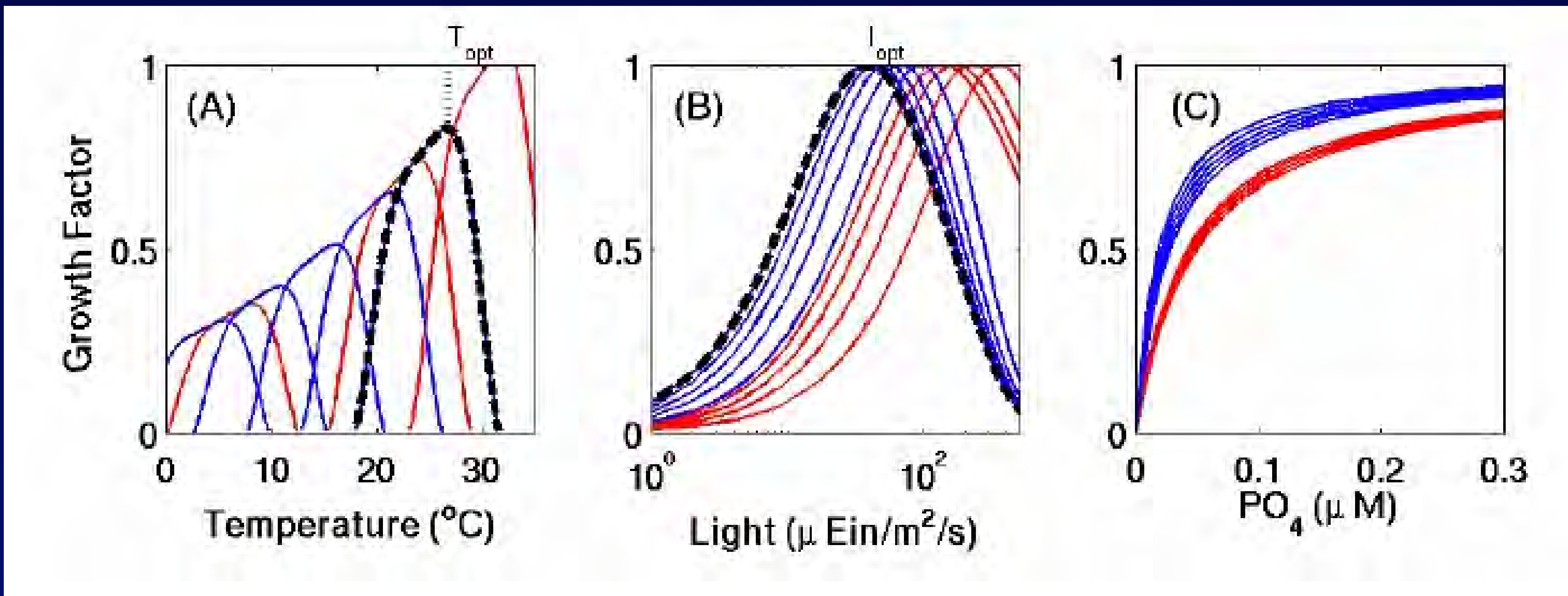
Emergent Biogeography of Microbial Communities in a Model Ocean

Michael J. Follows,[1*] Stephanie Dutkiewicz,[1] Scott Grant,[1,2] Sallie W. Chisholm[3]

SCIENCE VOL 315 30 MARCH 2007 1843



Everything (well, a lot of things) is everywhere and the environment selects



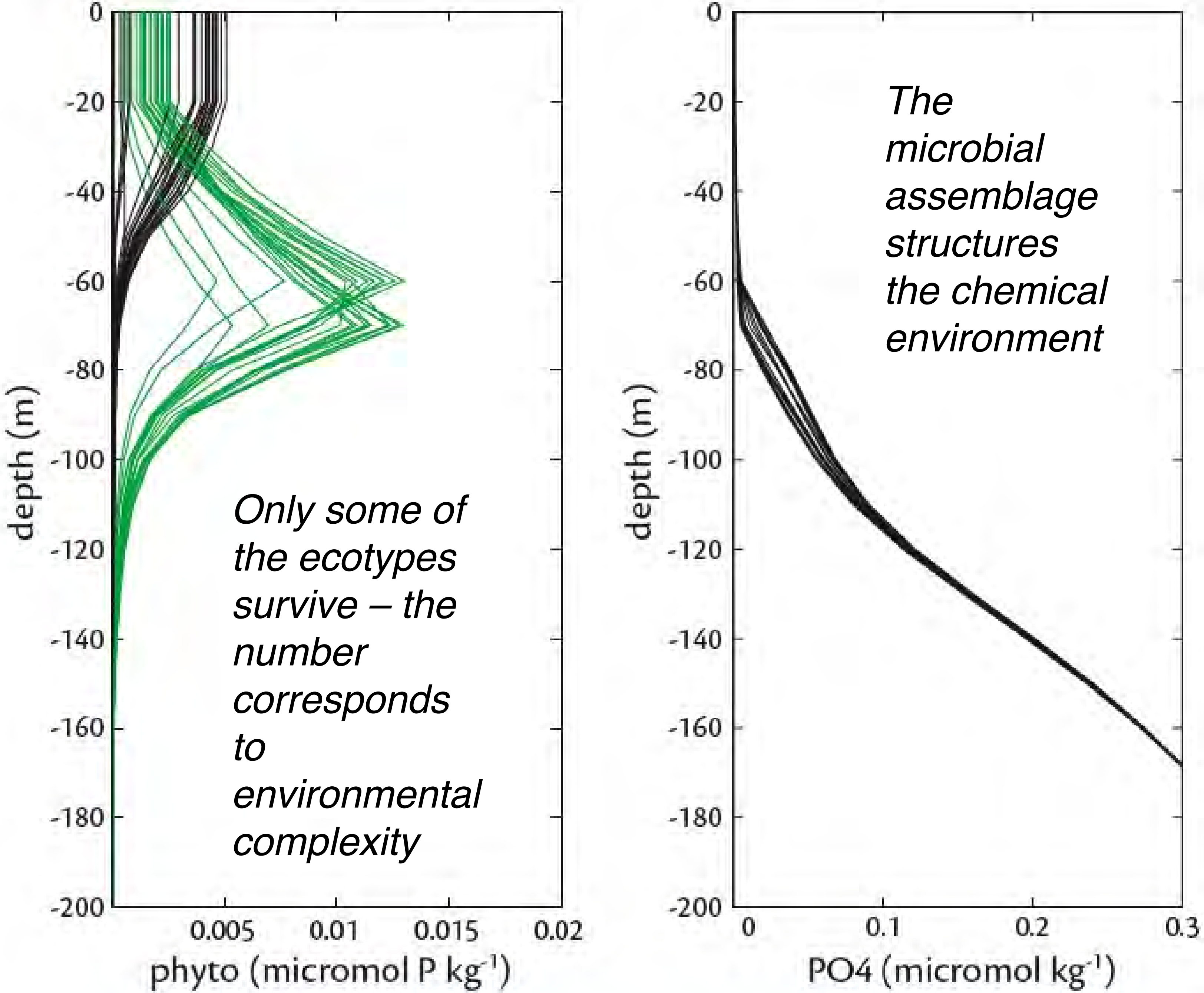
Emergent Biogeography of Microbial Communities in a Model Ocean

Michael J. Follows,[1*] Stephanie Dutkiewicz,[1] Scott Grant,[1,2] Sallie W. Chisholm[3]

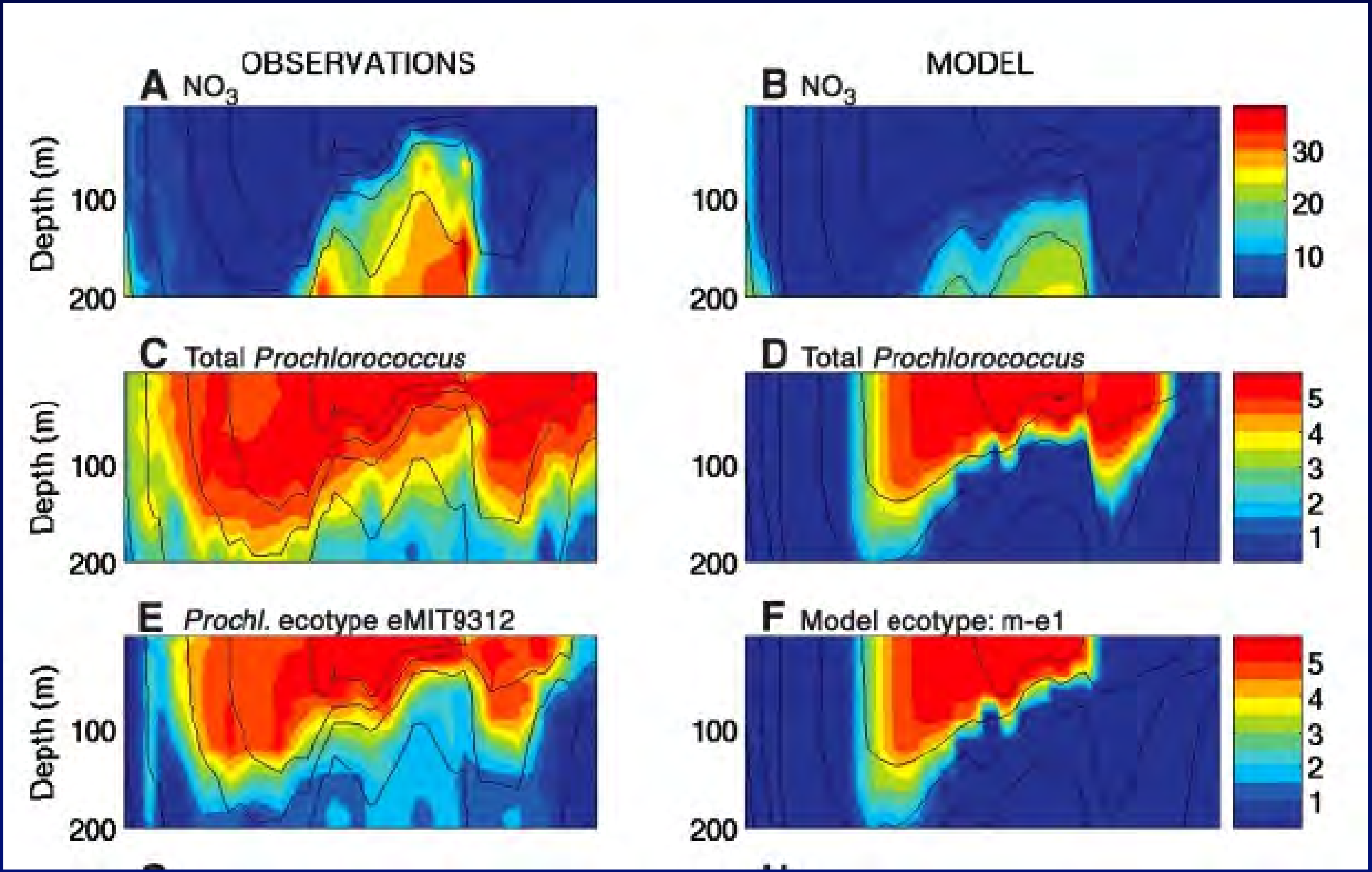
SCIENCE VOL 315 30 MARCH 2007 1843

Natural selection *in silico*

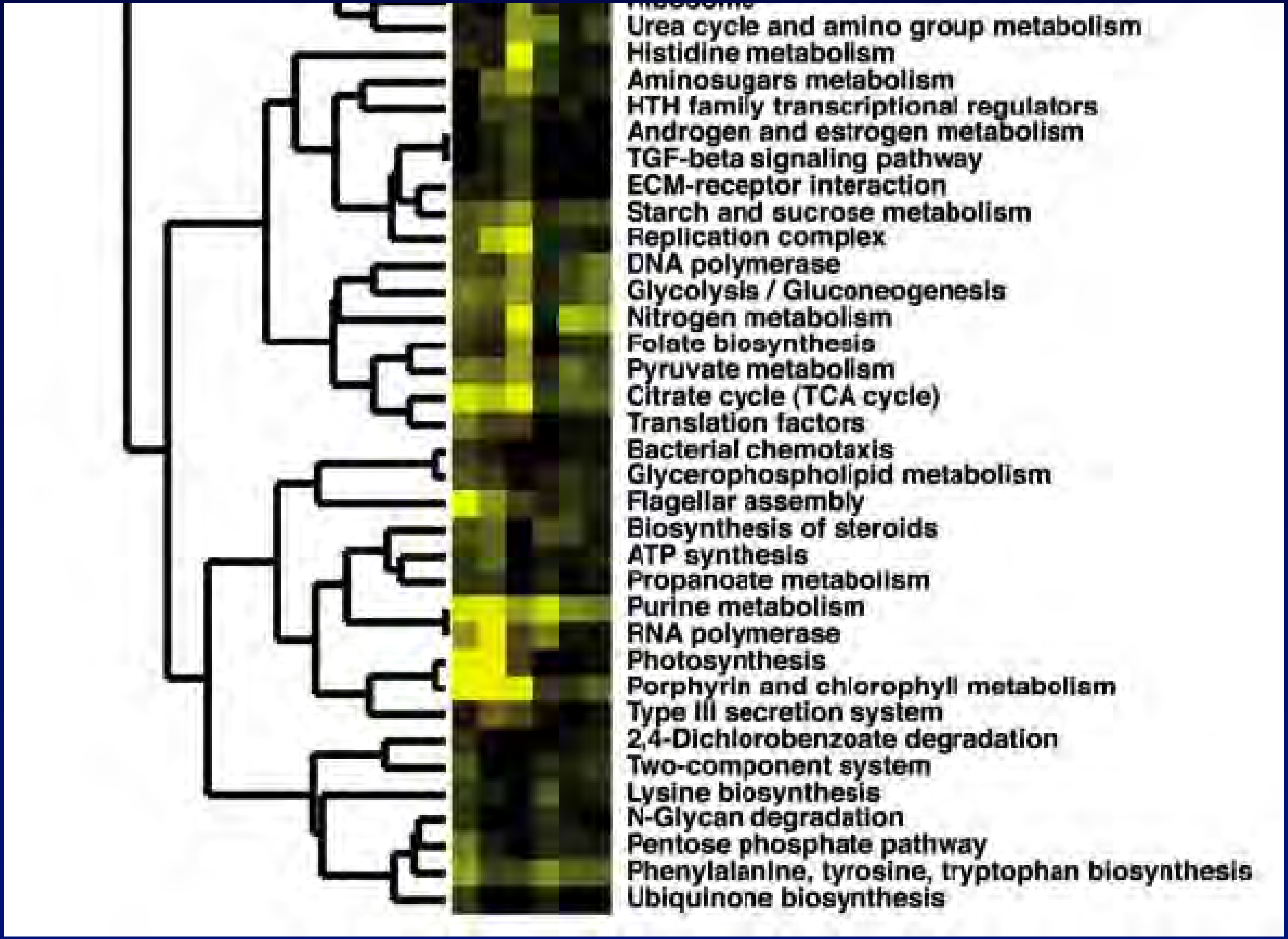
Rothstein et al. 2006



A test of our understanding of what structures marine ecosystems (LPG)



Future steps:
Assembly and natural selection of microbial communities guided by metagenomics



John Cullen: C-MORE 2014

A big part of the answer is here

Modeling Diverse Communities of Marine Microbes

Michael J. Follows and Stephanie Dutkiewicz

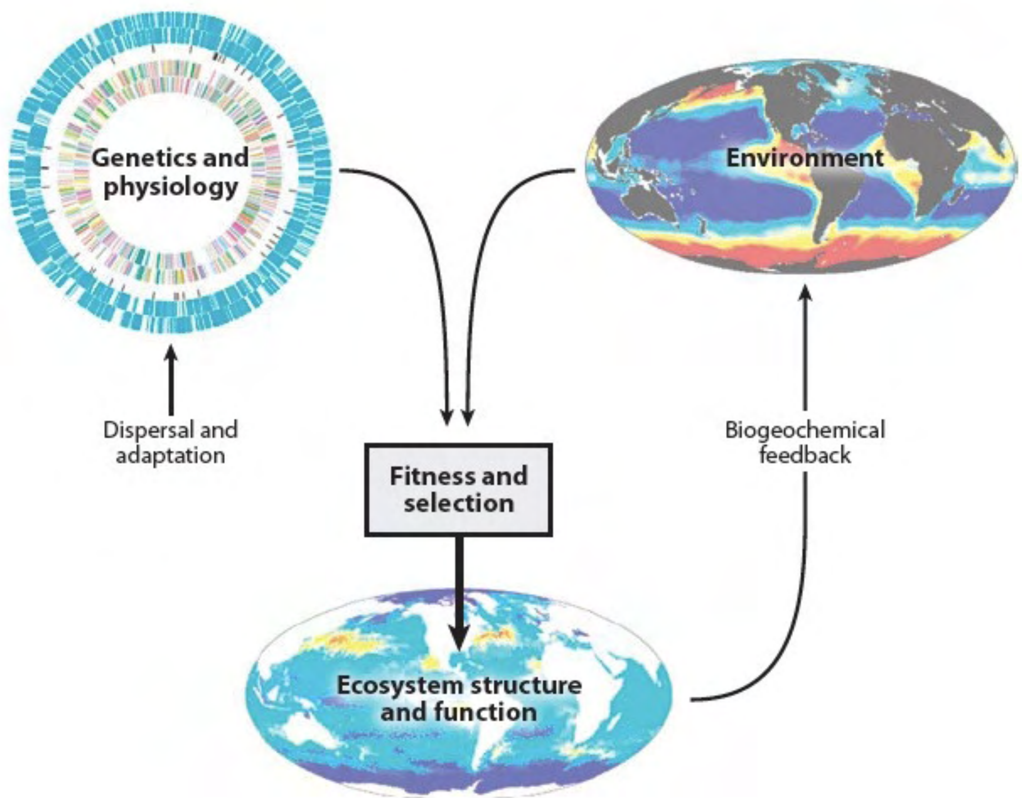
Earth, Atmospheric, and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, Massachusetts 02139; email: mick@ocean.mit.edu, stephd@mit.edu

Annu. Rev. Mar. Sci. 2011. 3:427–51

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

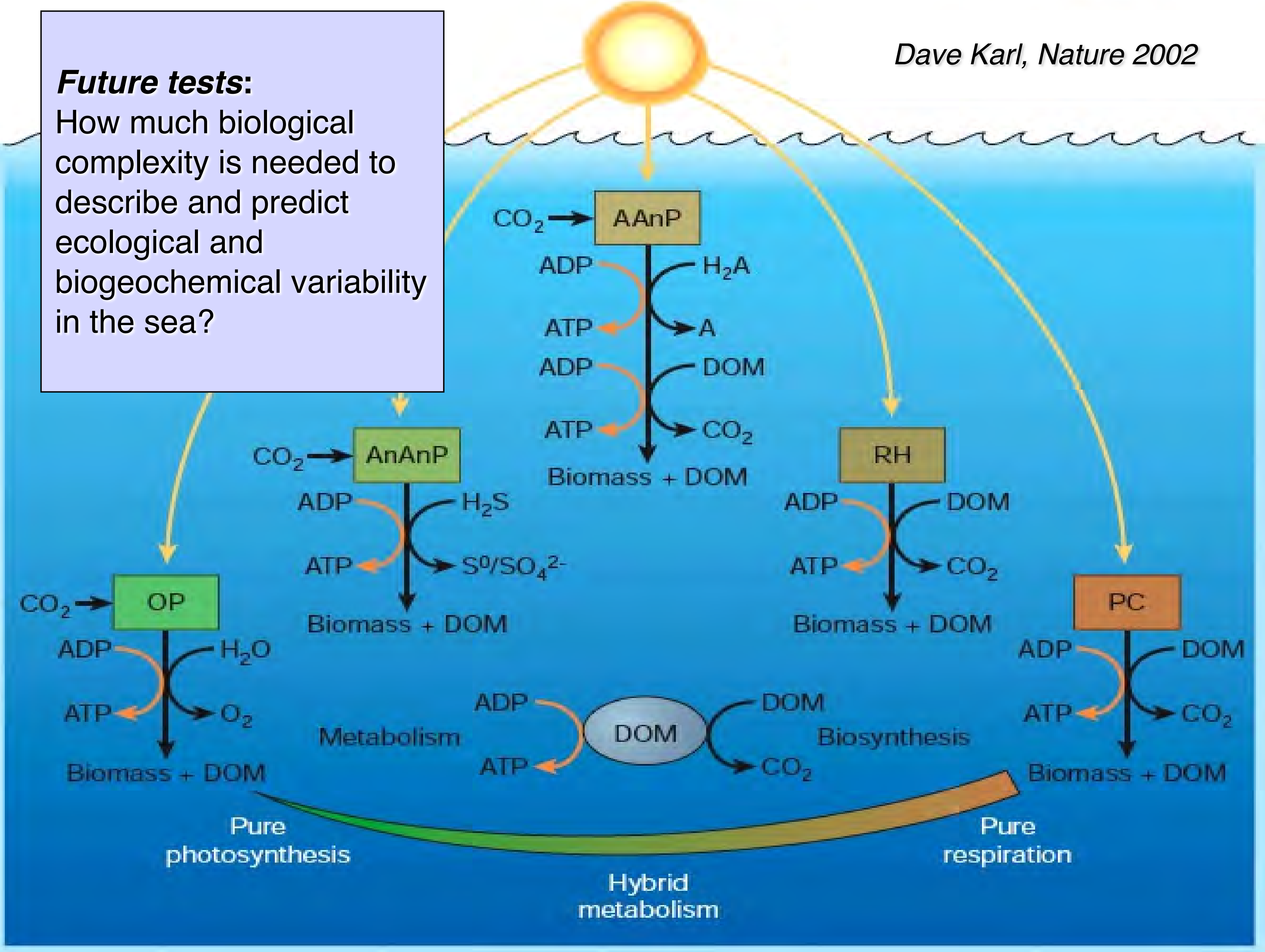
This article's doi:
10.1146/annurev-marine-120709-142848

1941-1405/11/0115-0427$20.00



***Future tests*:**
How much biological complexity is needed to describe and predict ecological and biogeochemical variability in the sea?

Dave Karl, Nature 2002



Conclusions

Relationships between environmental variability and microbial diversity must be described and ultimately predicted to understand the ecology and biogeochemistry of the sea

Niches abound:

wide range of environmental tolerances

specialized life-styles (nutrient requirements, alternate modes of photosynthesis

physiological plasticity vs specialization for stable environments

Complexity will never be fully described with numerical models

The degree of model complexity can and should be related to the ecological/biogeochemical question and its scale.

This can be done — but models must be verified by measurements!

Mahalo!