Behavior, physiology and the niche of marine phytoplankton

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Microbial Oceanography Summer Course:
Genomes to Biomes

University of Hawai'i
June 27, 2008

NSERC CRSNG

Office of Naval Research

Cellana

2008 HAWAI'I SUMMER COURSE ON MICROBIAL OCEANOGRAPHY

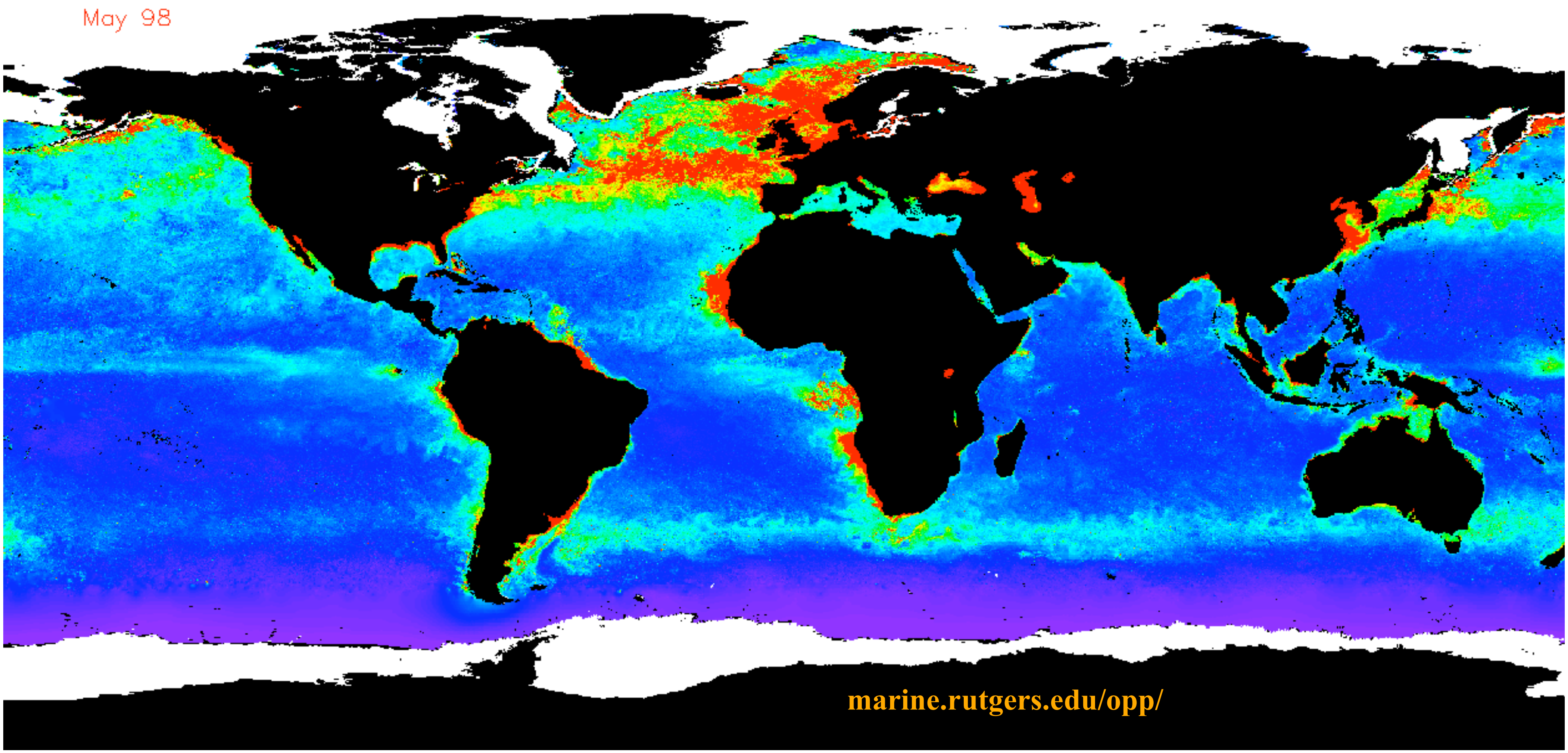
AGOURON INSTITUTE

Microbial Oceanography:
Genomes to Biomes

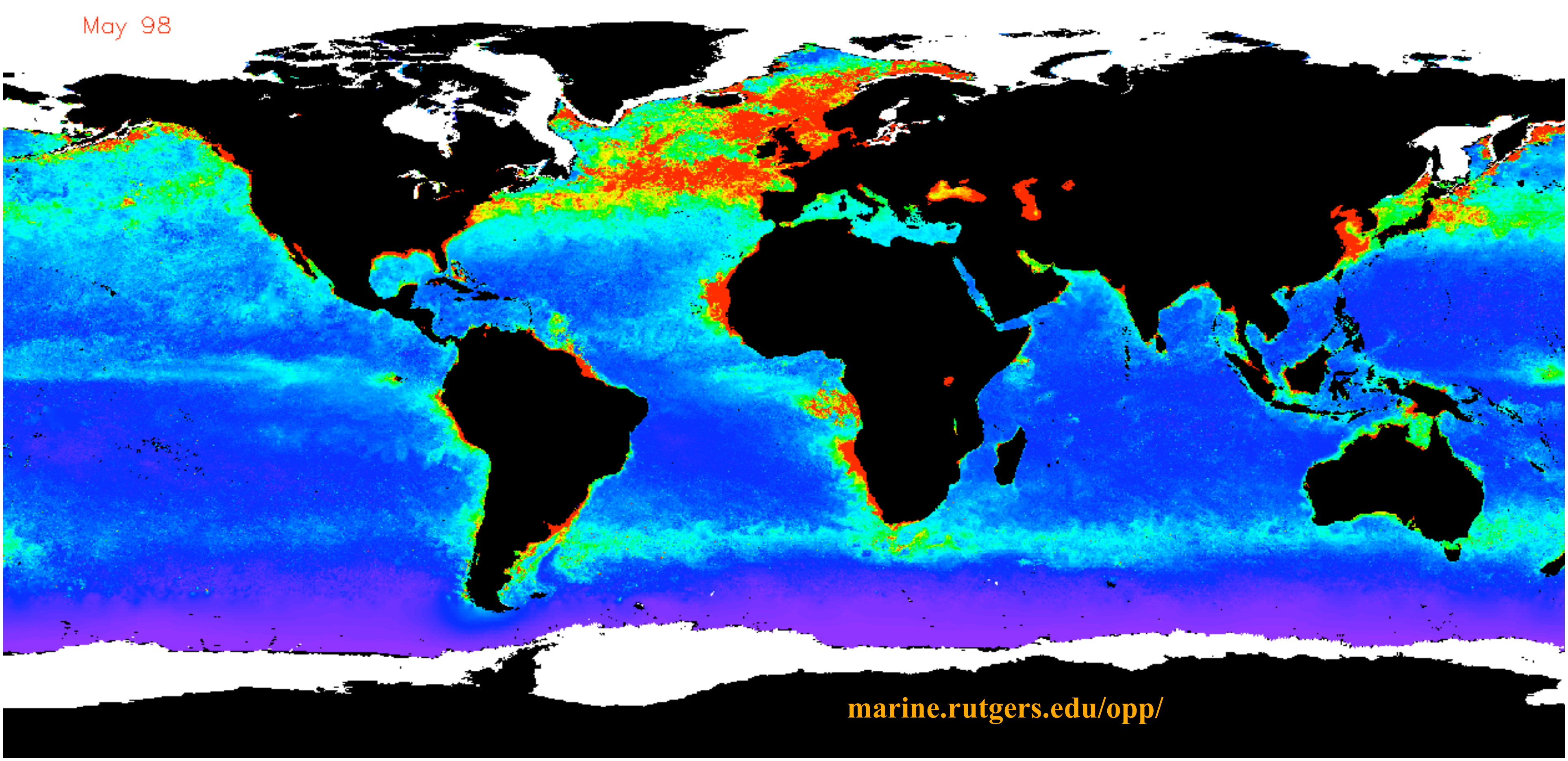
A laboratory-field training course at the University of Hawai'i at Mānoa

A principal goal of microbial oceanography

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



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

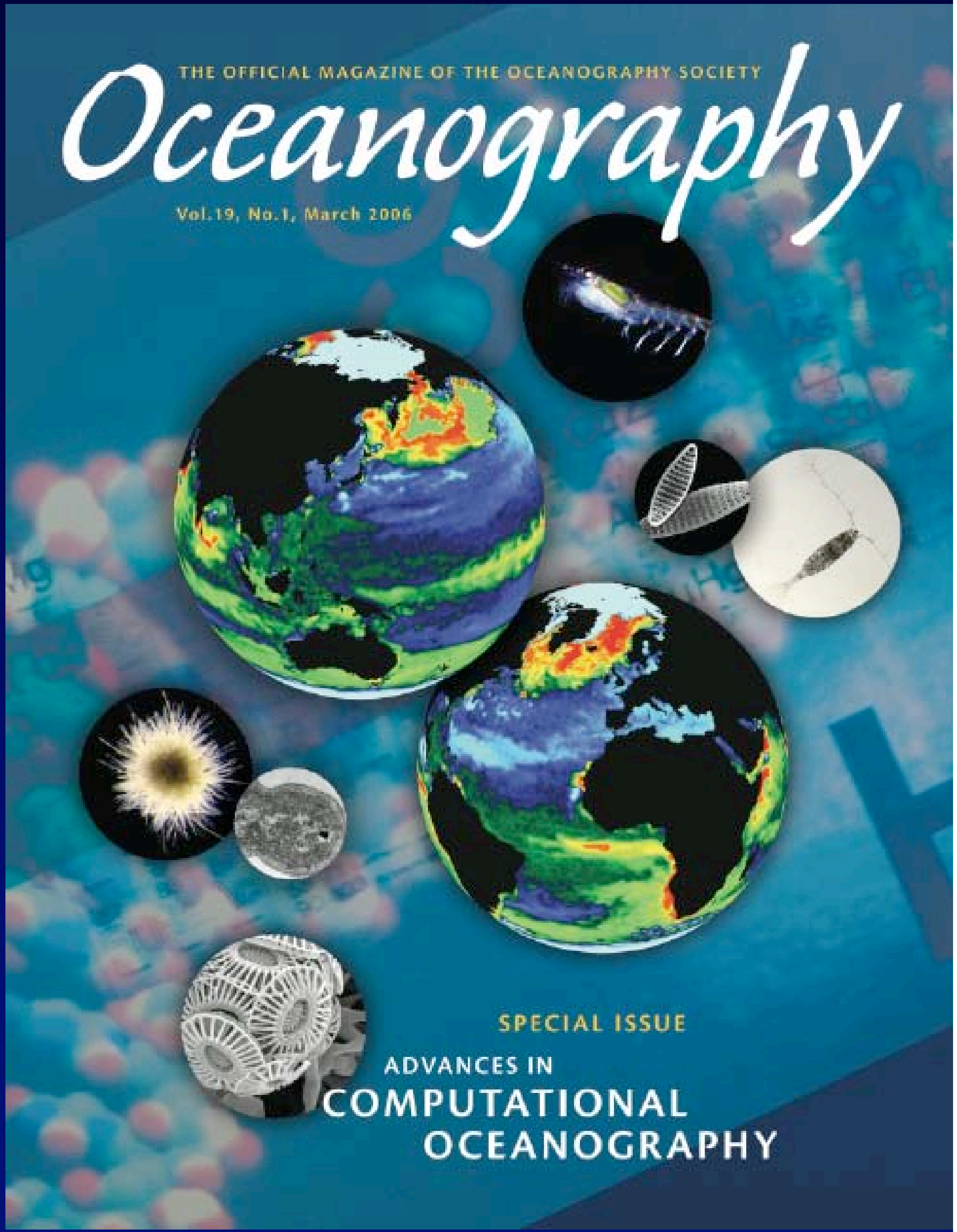


Key biogeochemical processes

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

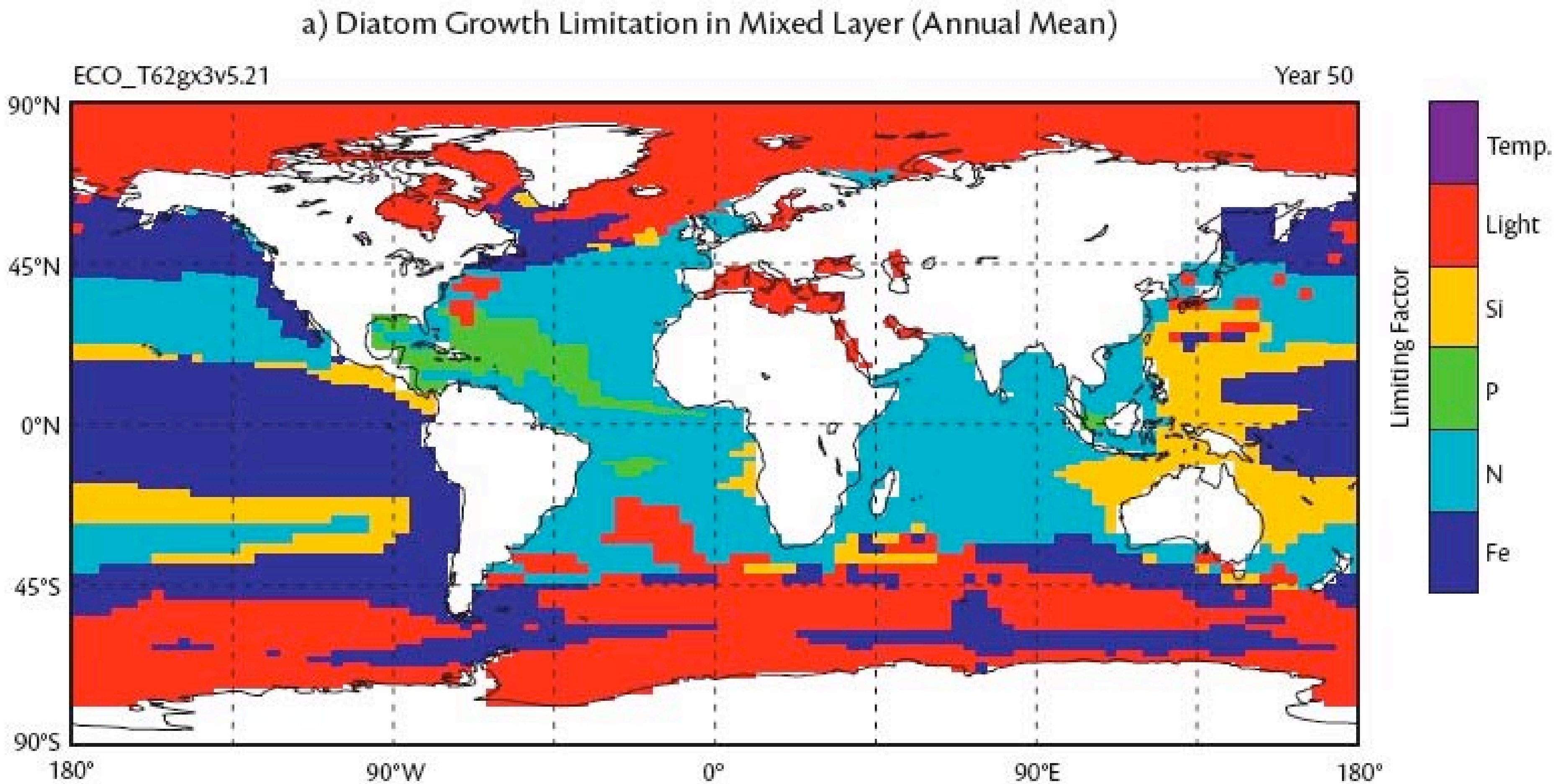
This can be achieved only through an integrated approach

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.



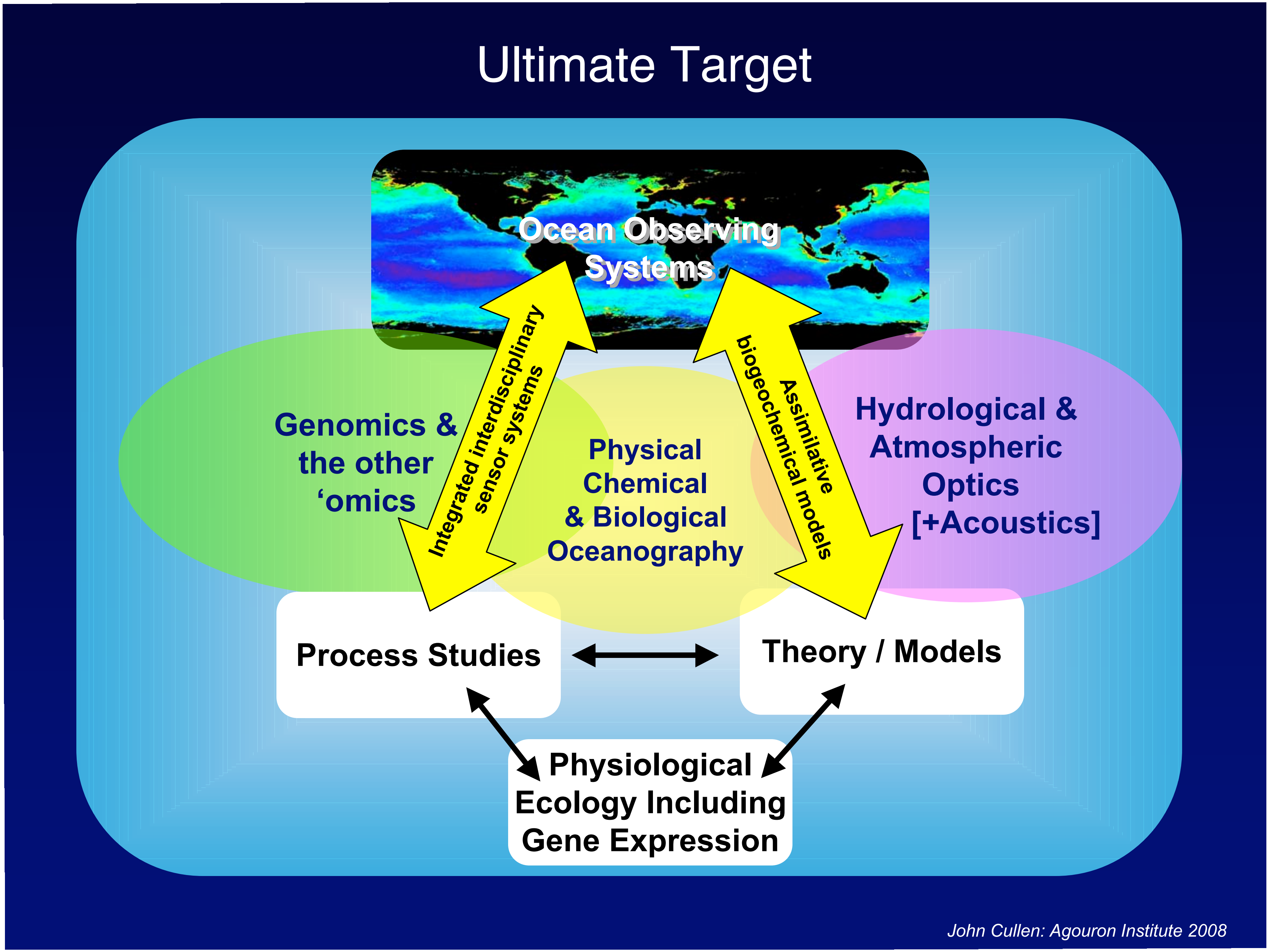
Rothstein et al., Oceanography Mag.

Arguably, this represents the state of the art



PARADIGM Global Biogeochemistry - Ecology - Circulation model (Doney and colleagues)

Rothstein et al. 2006 – Oceanography Magazine



Ultimate Target
Ocean Observing Systems
Integrated interdisciplinary sensor systems
Assimilative biogeochemical models
Genomics & the other ‘omics
Physical Chemical & Biological Oceanography
Hydrological & Atmospheric Optics [+Acoustics]
Process Studies
Theory / Models
Physiological Ecology Including Gene Expression
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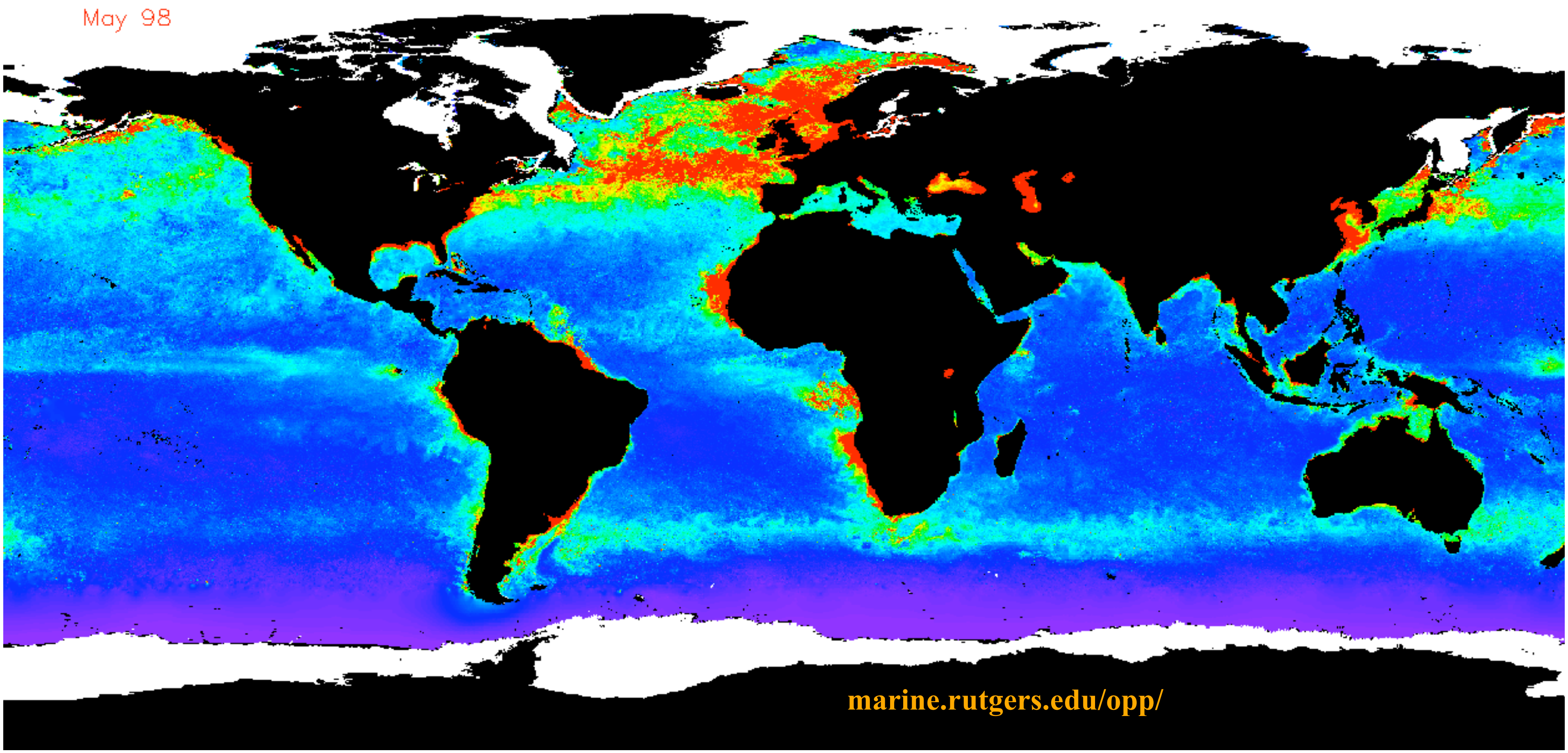
Biological oceanography and phytoplankton ecology

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



An overview of established approaches to marine prediction

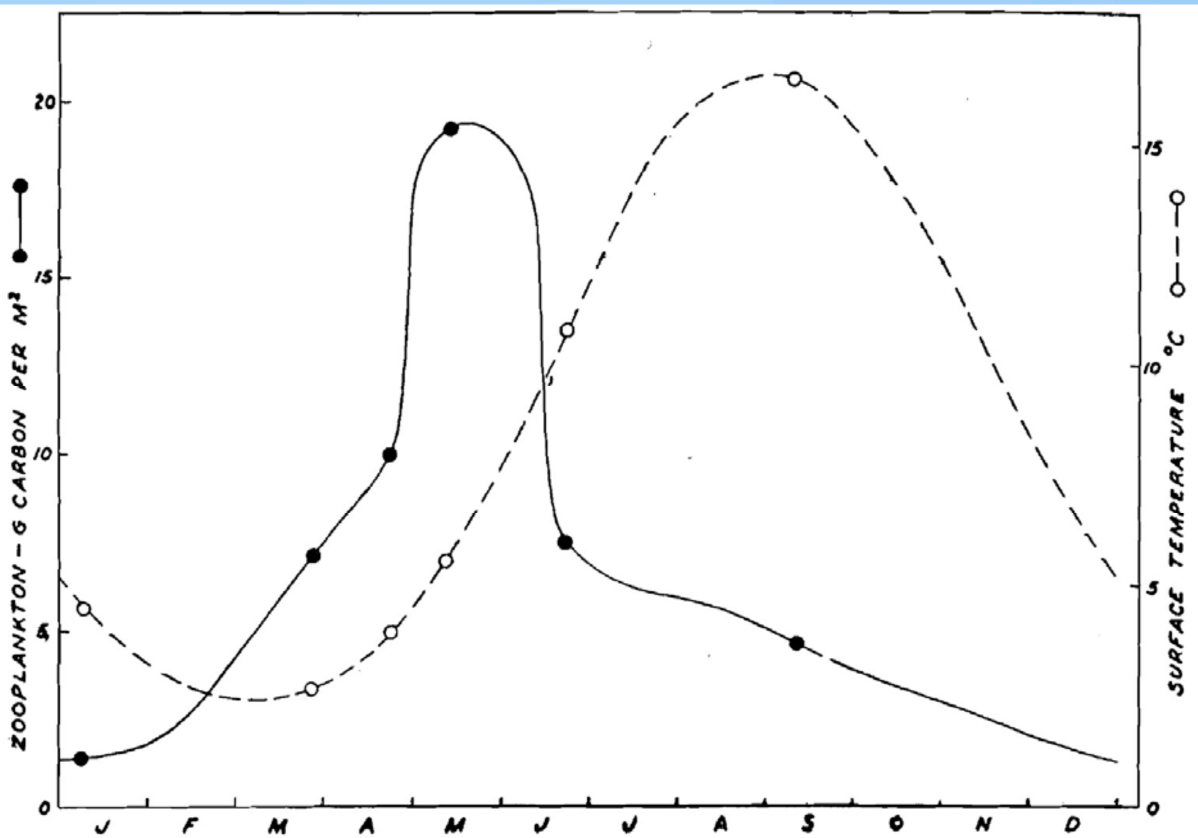
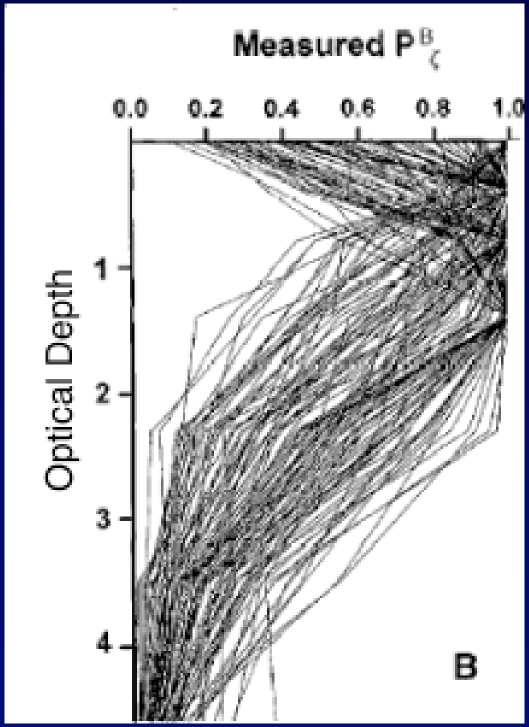
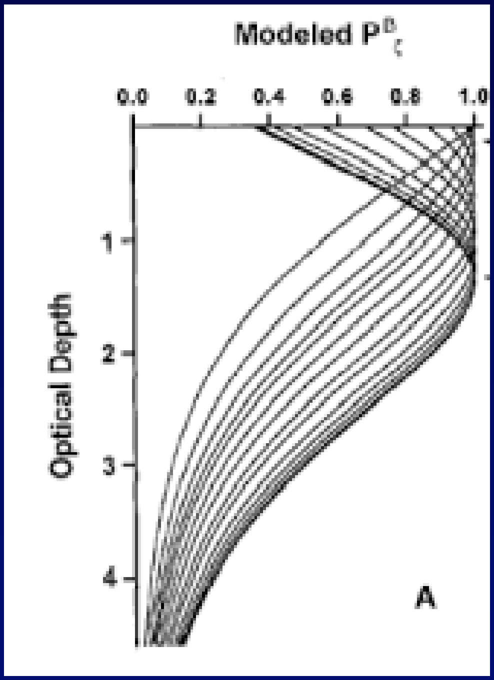


Figure 19. Solid line is the seasonal cycle of zooplankton. Measurements of zooplankton volume by the displacement method are treated by a conversion factor (wt. in g. = 12.5% × vol. in cc.) to derive a rough estimate of the carbon content. Dotted line is the mean surface temperature.

Gordon Riley

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





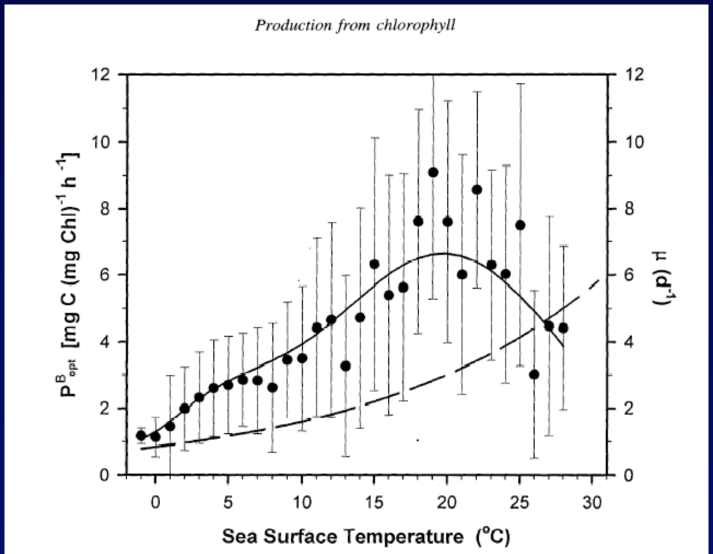


Fig. 7. Measured (●; ±SD) and modeled (——; Eq. 11) median value of the photoadaptive parameter, P^B_{opt}, as a function of sea surface temperature. Dashed curve indicates the theoretical maximum specific growth rate (μ; d^{-1}) of photoautotrophic unicellular algae described by Eppley (1972), which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

Behrenfeld and Falkowski 1997b L&O

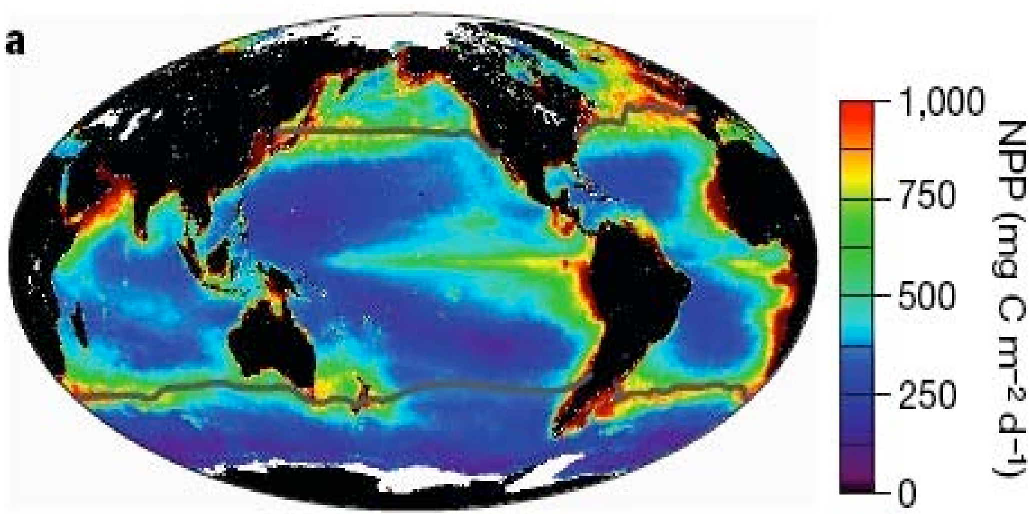
Modeling the pattern in the measurements — not necessarily primary productivity!

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

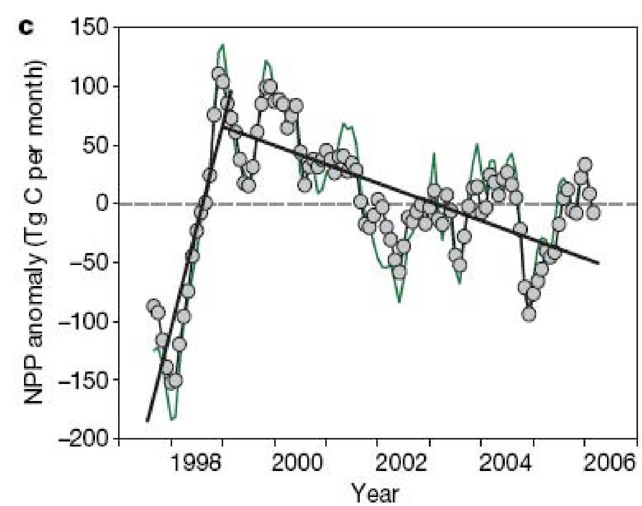
nature   Vol 444|7 December 2006|**doi:10.1038/nature05317**

Climate-driven trends in contemporary ocean productivity

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

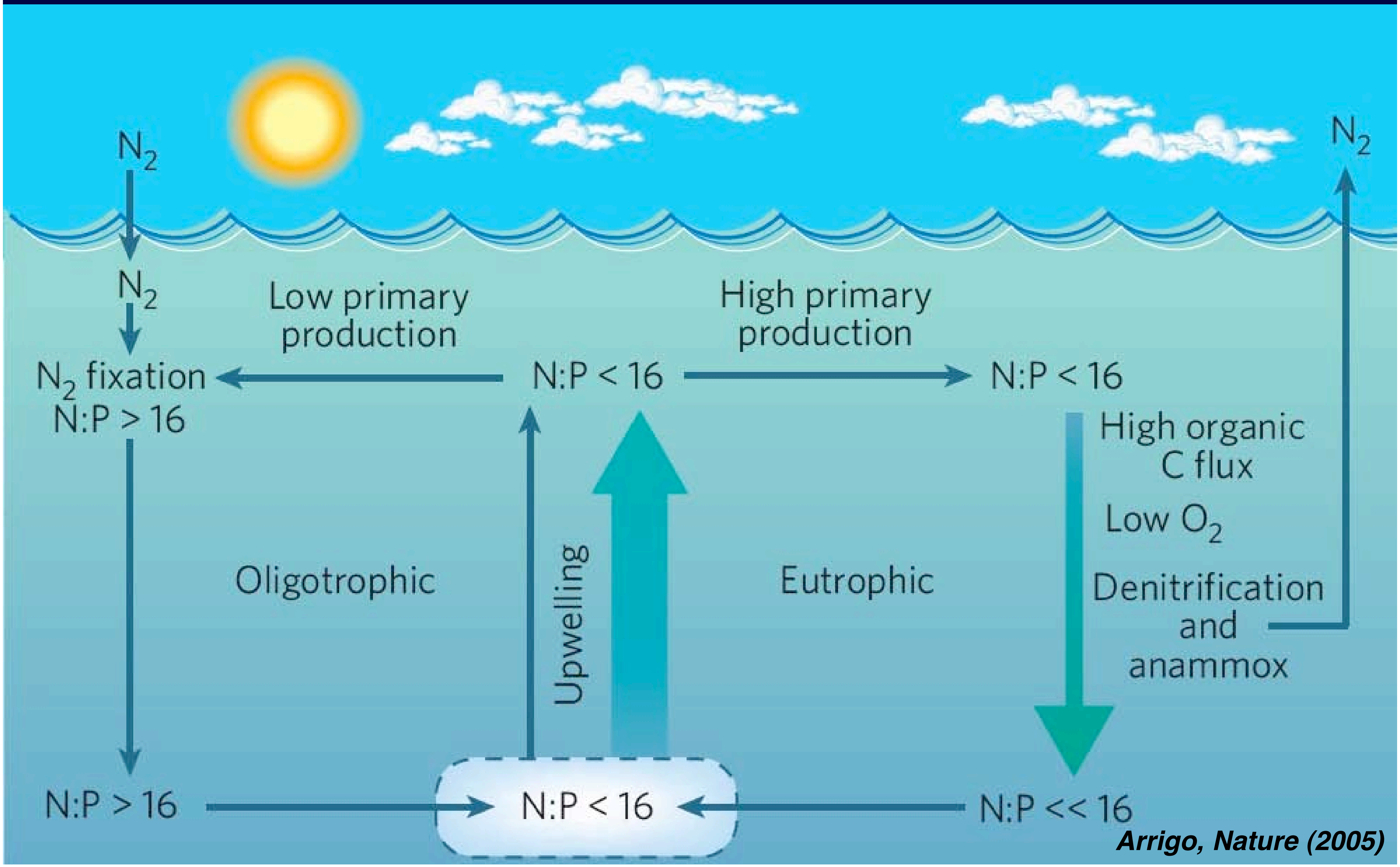


Inputs/Assumptions of the Productivity Model(s)



Validity of the Statistical Analysis

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



Arrigo, Nature (2005)

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

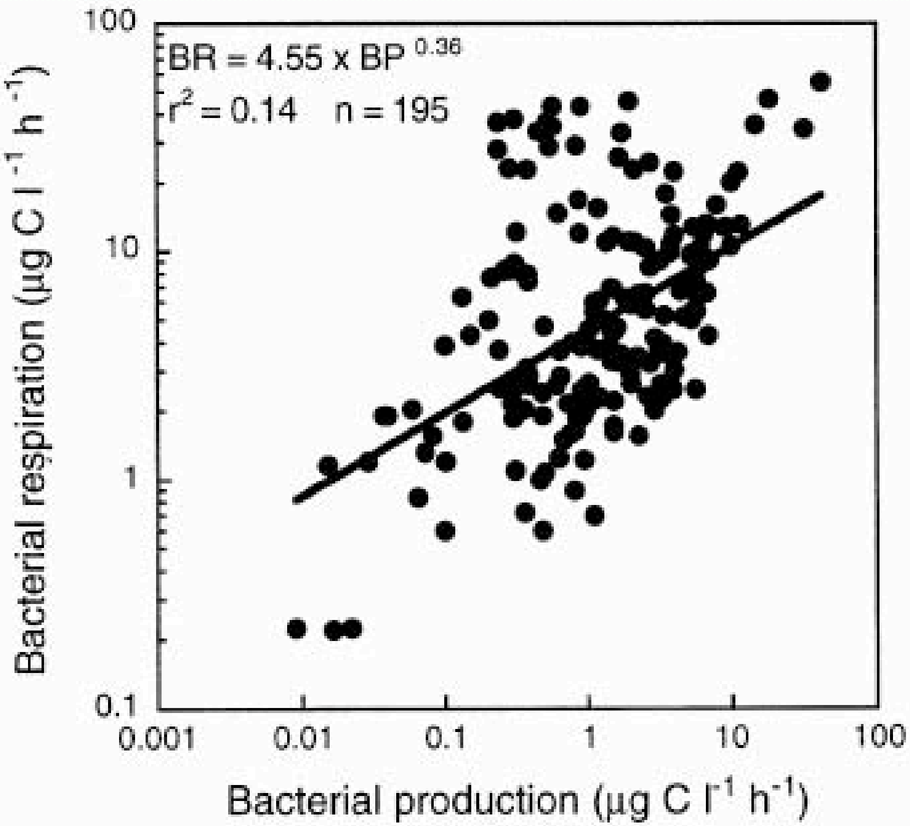


Figure 4. Bacterial respiration as a function of bacterial production in aquatic ecosystems. The data are paired observations of bacterial respiration (*BR*) and production (*BP*); the sources of these data appear in Table 1. The line is the least-squares fit to the log-transformed data.

del Giorgio and Cole (1999)

But predictions can be tested with appropriate observations

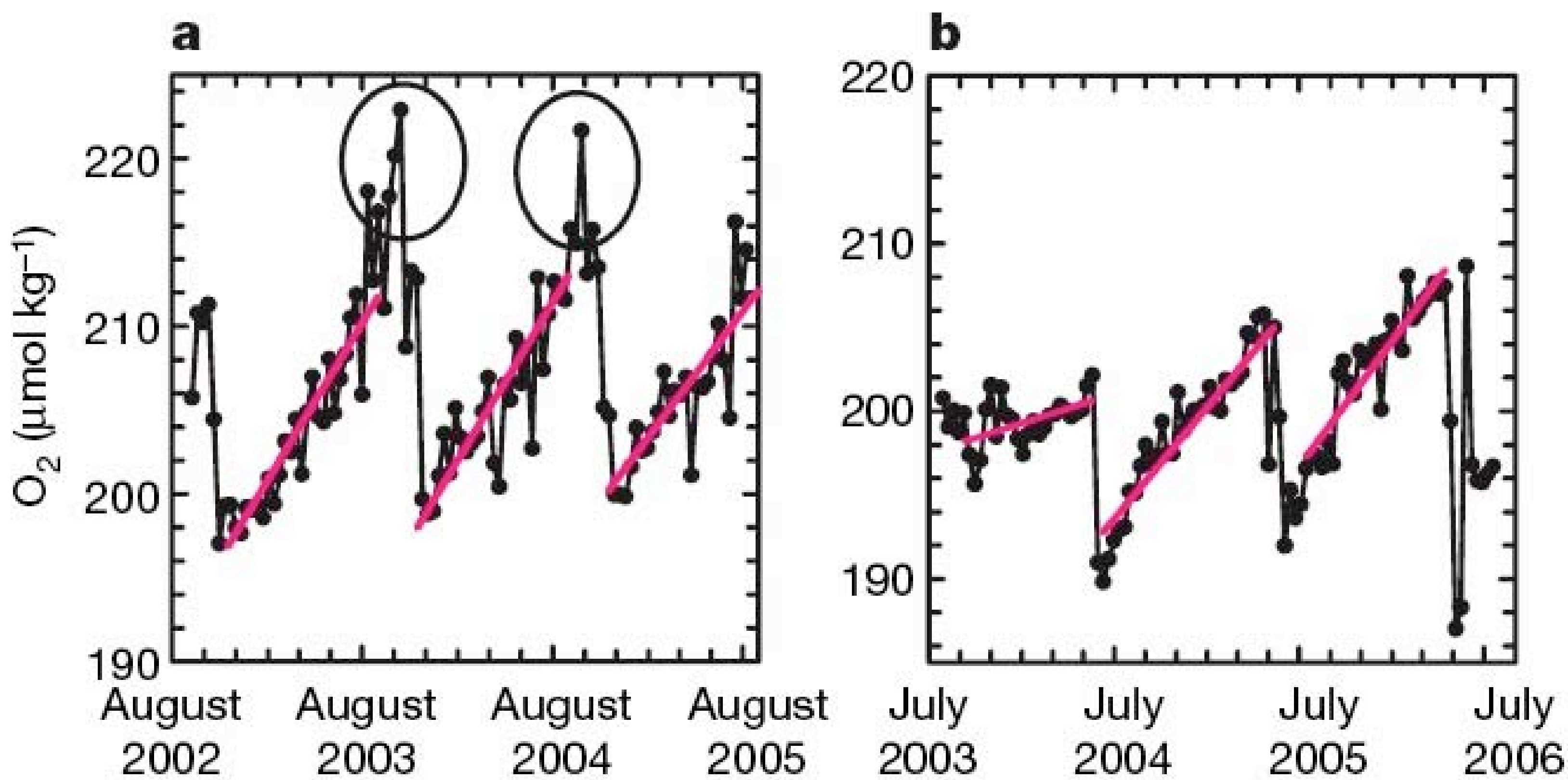
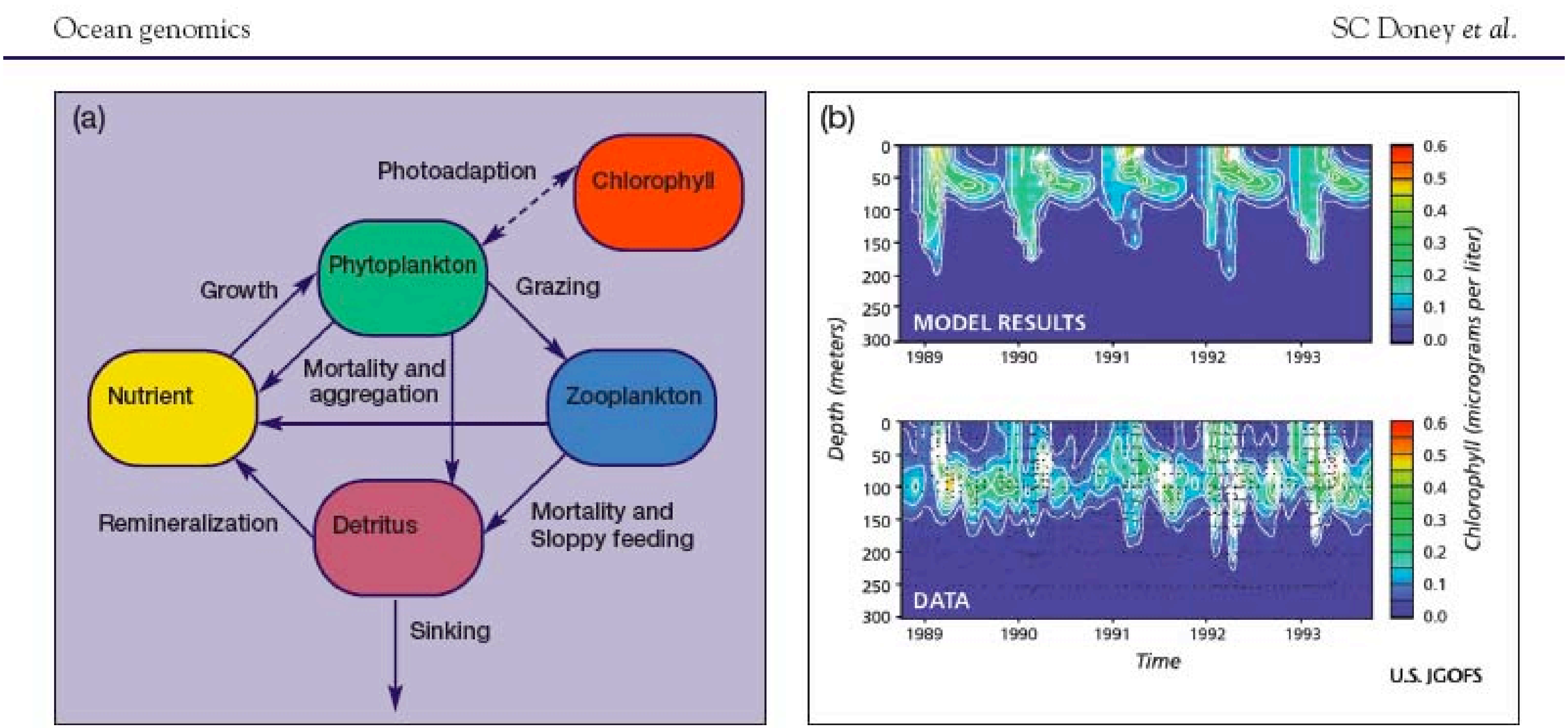


Figure 3 | Oxygen concentrations in the SOM versus time. Oxygen

Riser and Johnson Nature 2008

Approach #3: Prognostic models (quantitative, mechanistic, predictive models)



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

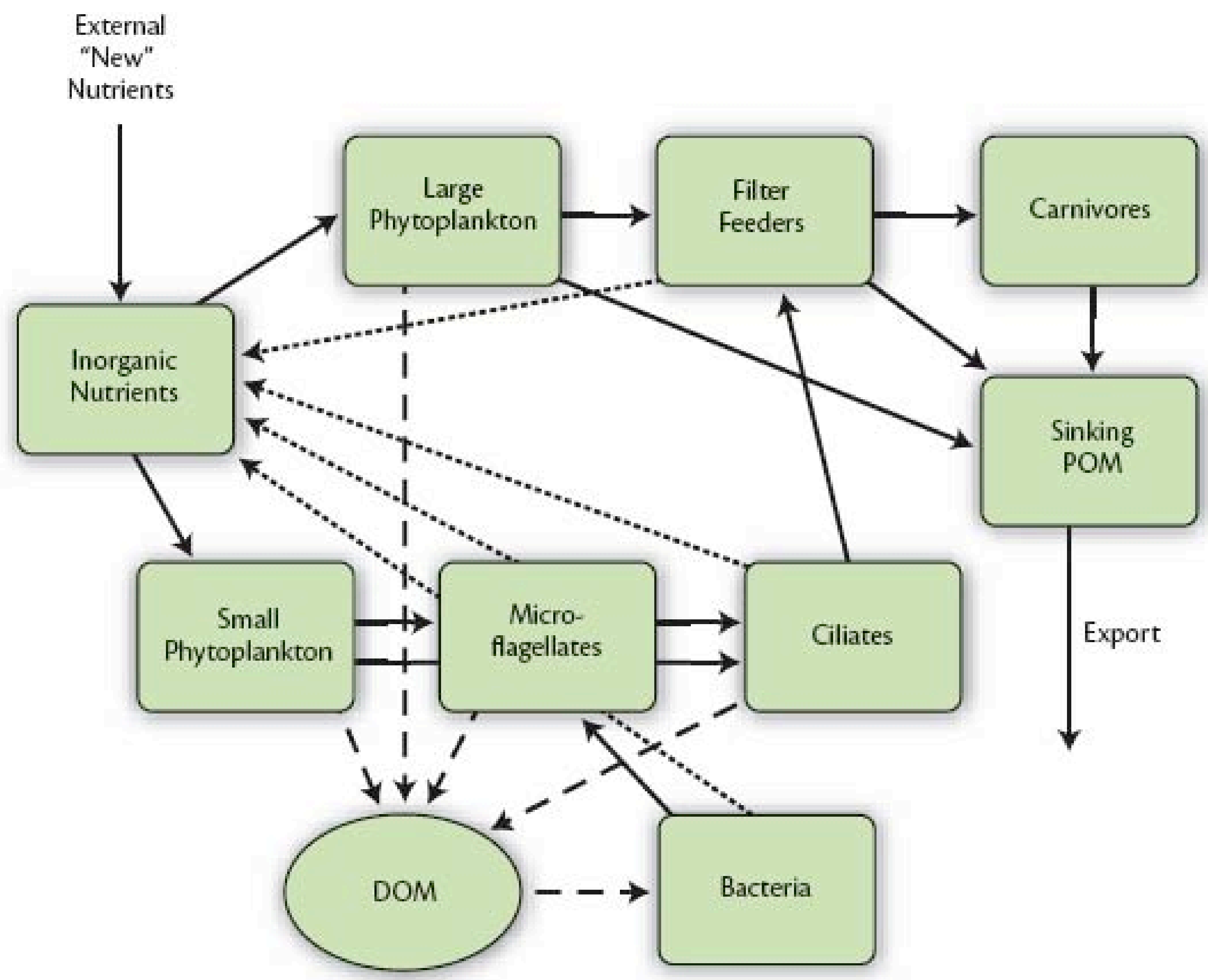


Figure 2. Oceanic plankton food web, after Laws et al. (2000). The upper pathway initiated by large phytoplankton contributes primarily to export from the upper ocean. The lower pathway starting with small phytoplankton results mainly in the recycling of nutrients. Solid arrows: flows of organisms and 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.

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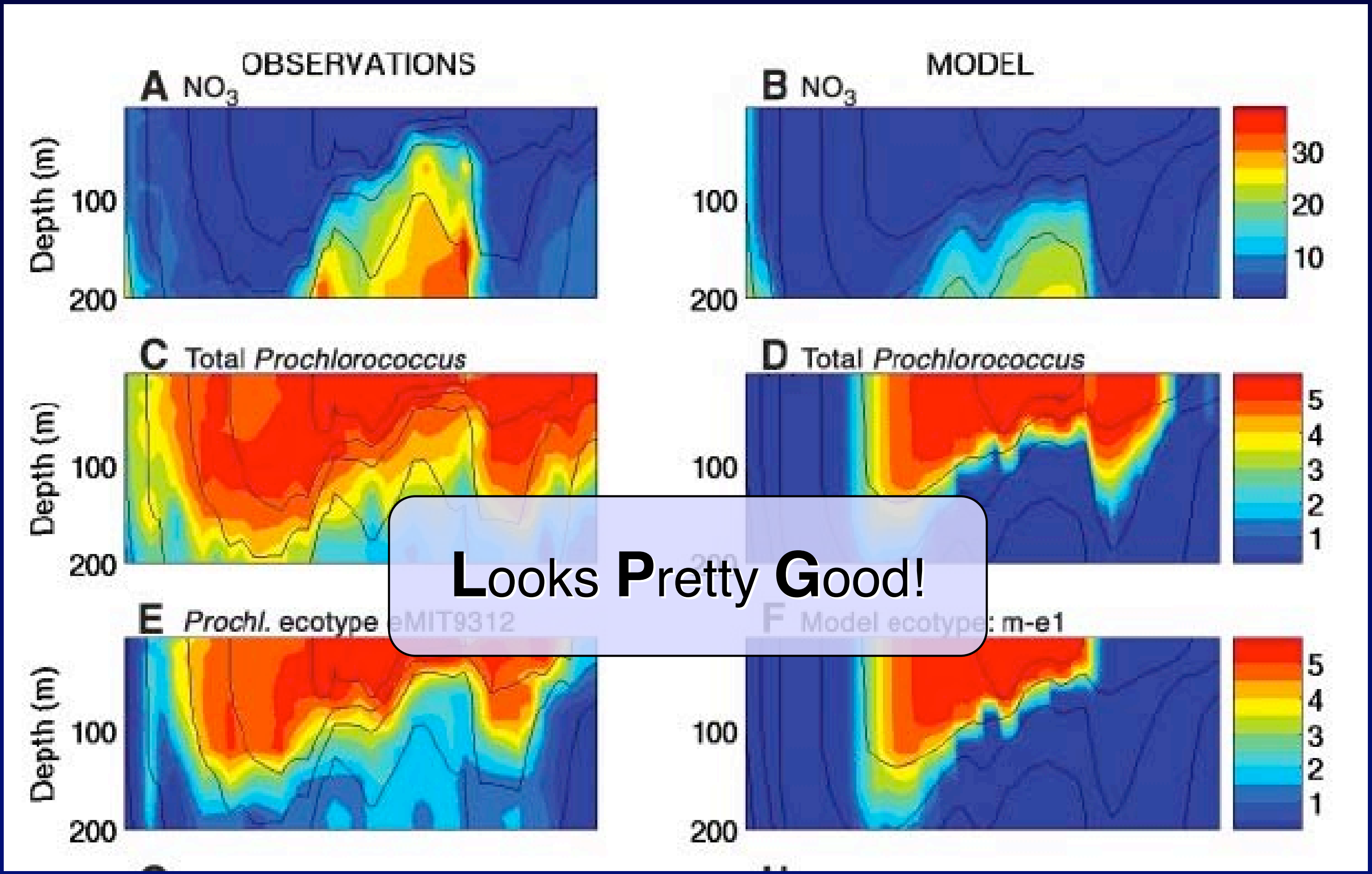
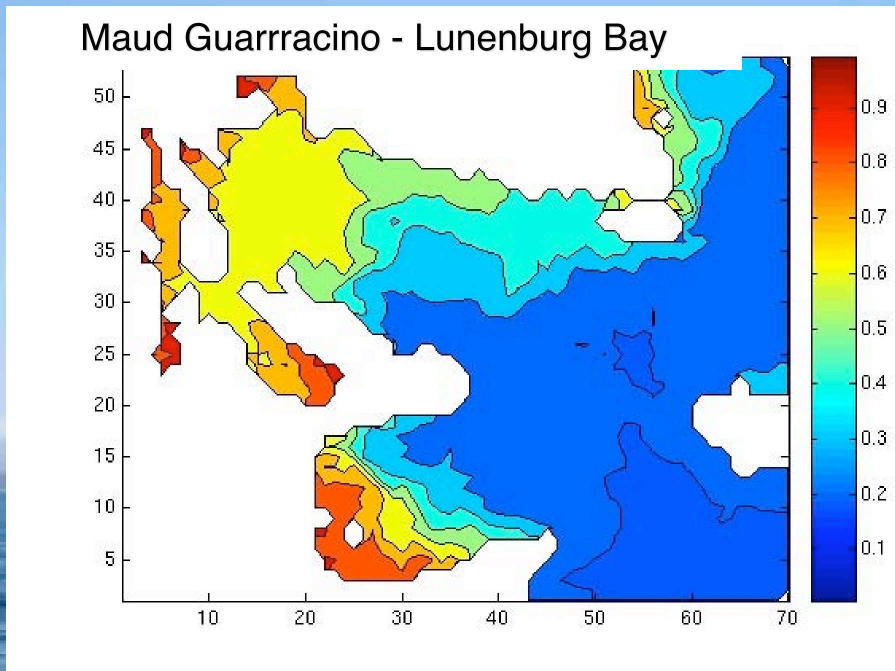
Conventionally tested by the "LPG" criterion — but that is changing

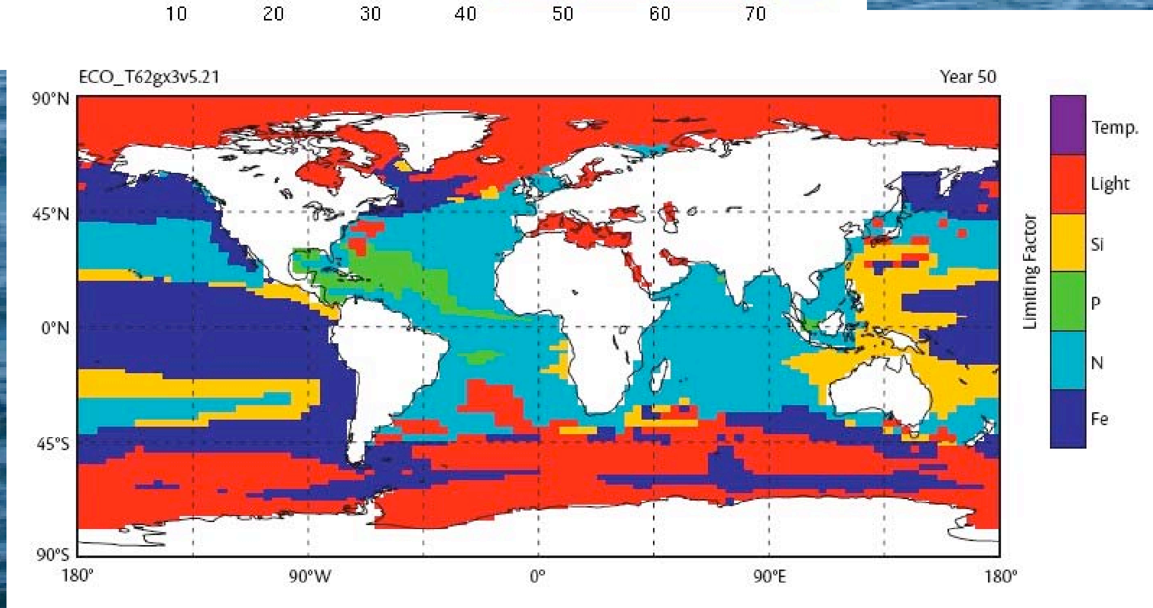


Follows, M. J., S. Dutkiewicz, S. Grant, and S. W. Chisholm. 2007. Emergent biogeography of microbial communities in a model ocean. Science 315: 1843-1846.

John Cullen: Agouron Institute 2008

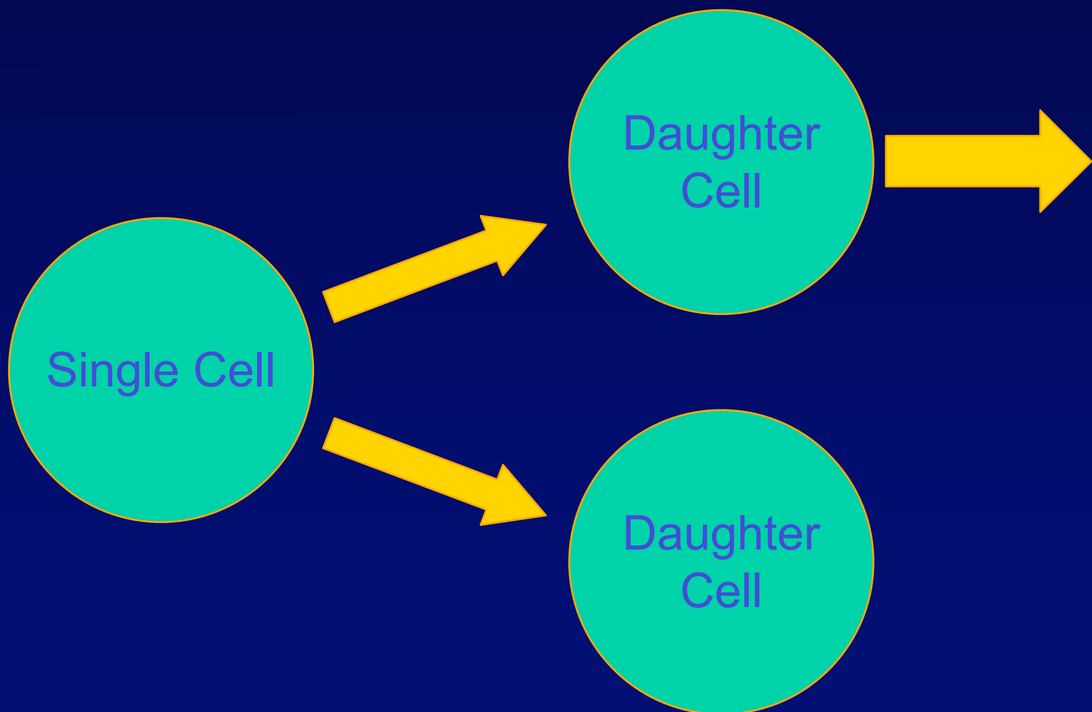
Approaches to Ecosystem Modeling





Fundamentally, ecosystem models should predict population dynamics

Growth



Loss

Accumulate (Bloom)

Be eaten

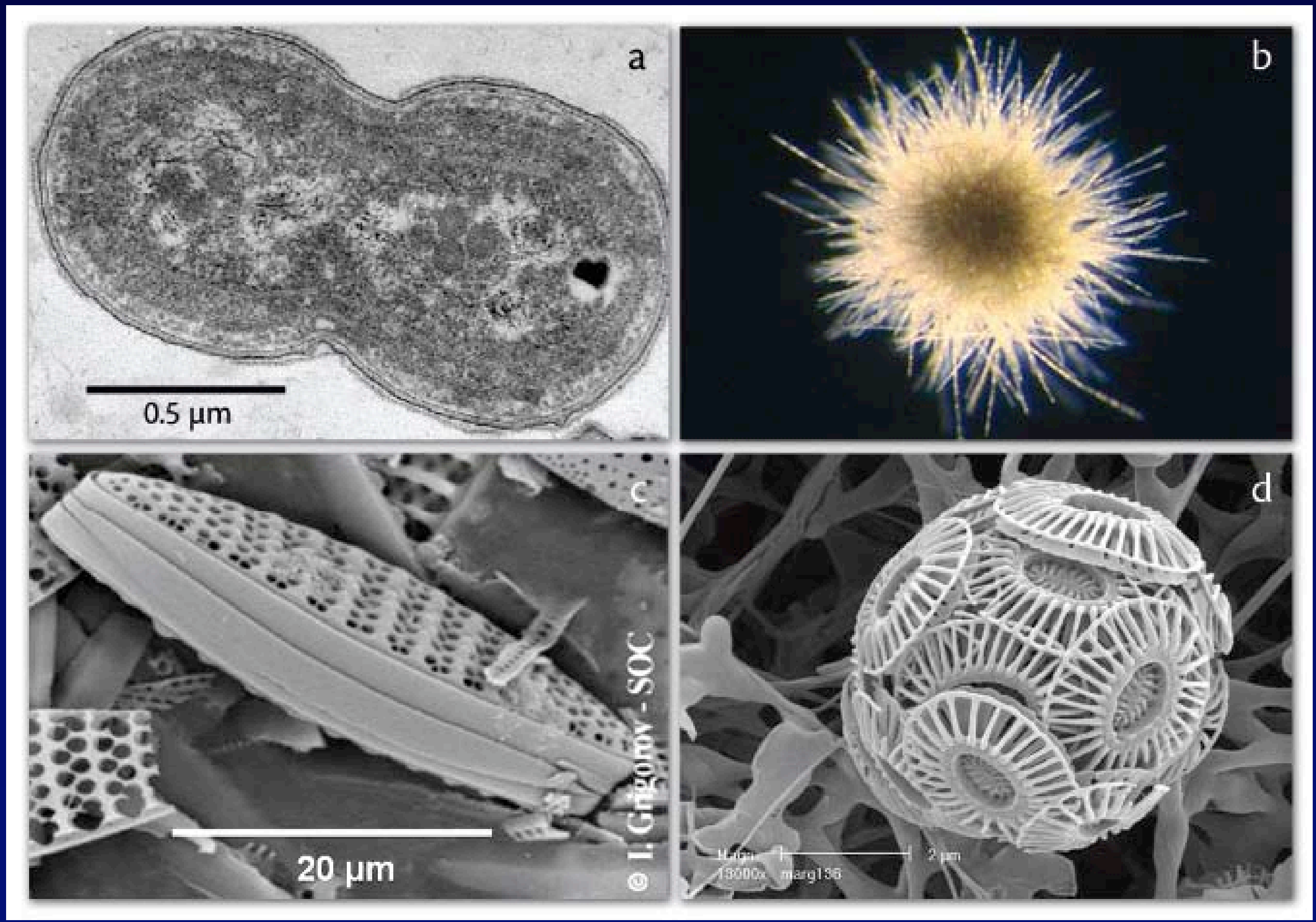
Blow up (viral lysis)

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



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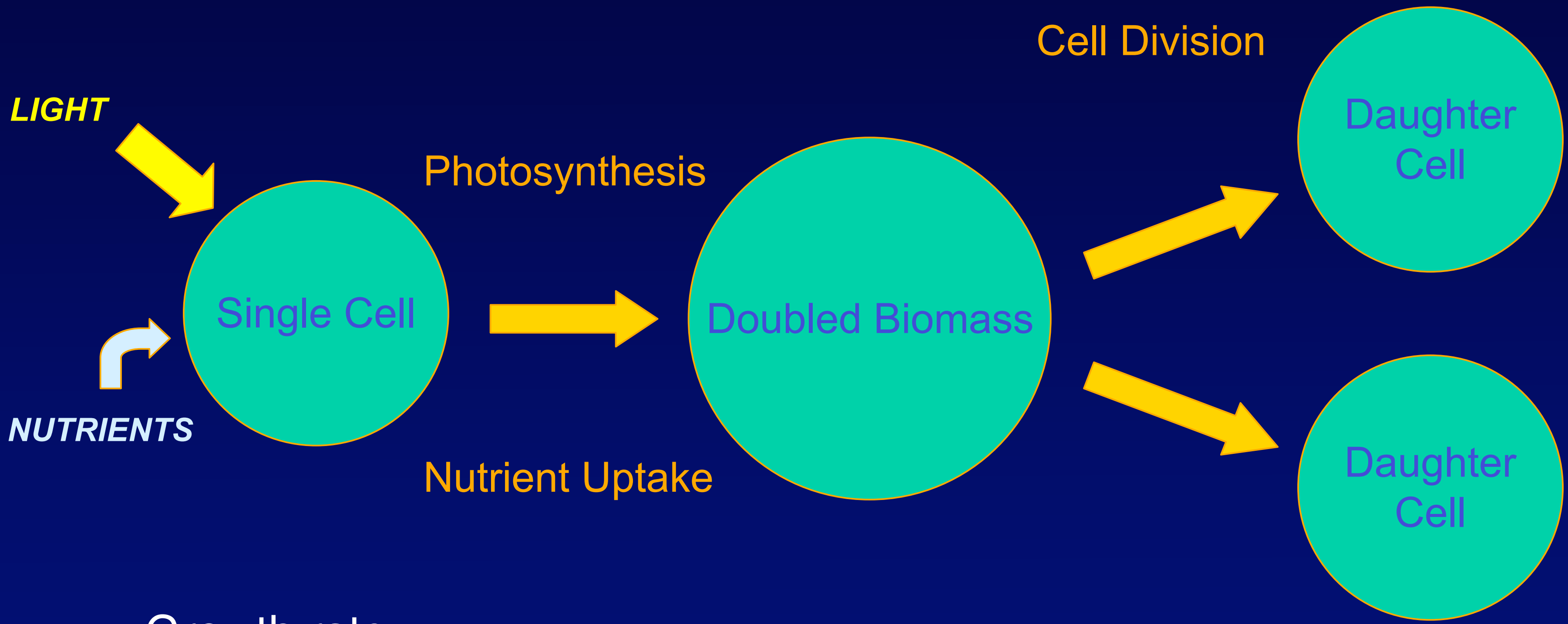
Essential Knowledge:

Environmental Influences on the Growth and Chemical Composition of Phytoplankton



Growth rate

Chemical composition

Biogeochemical transformations

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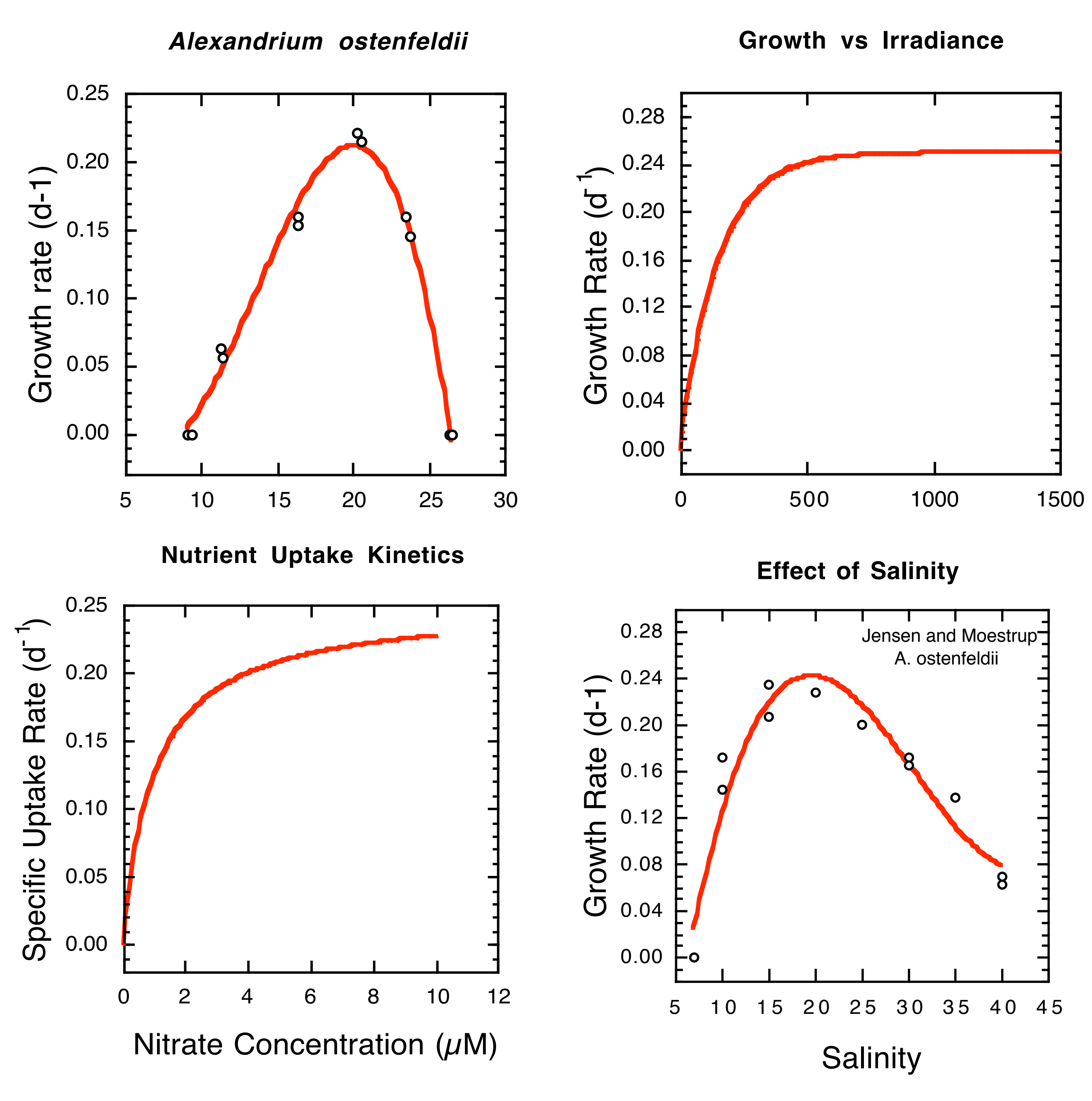
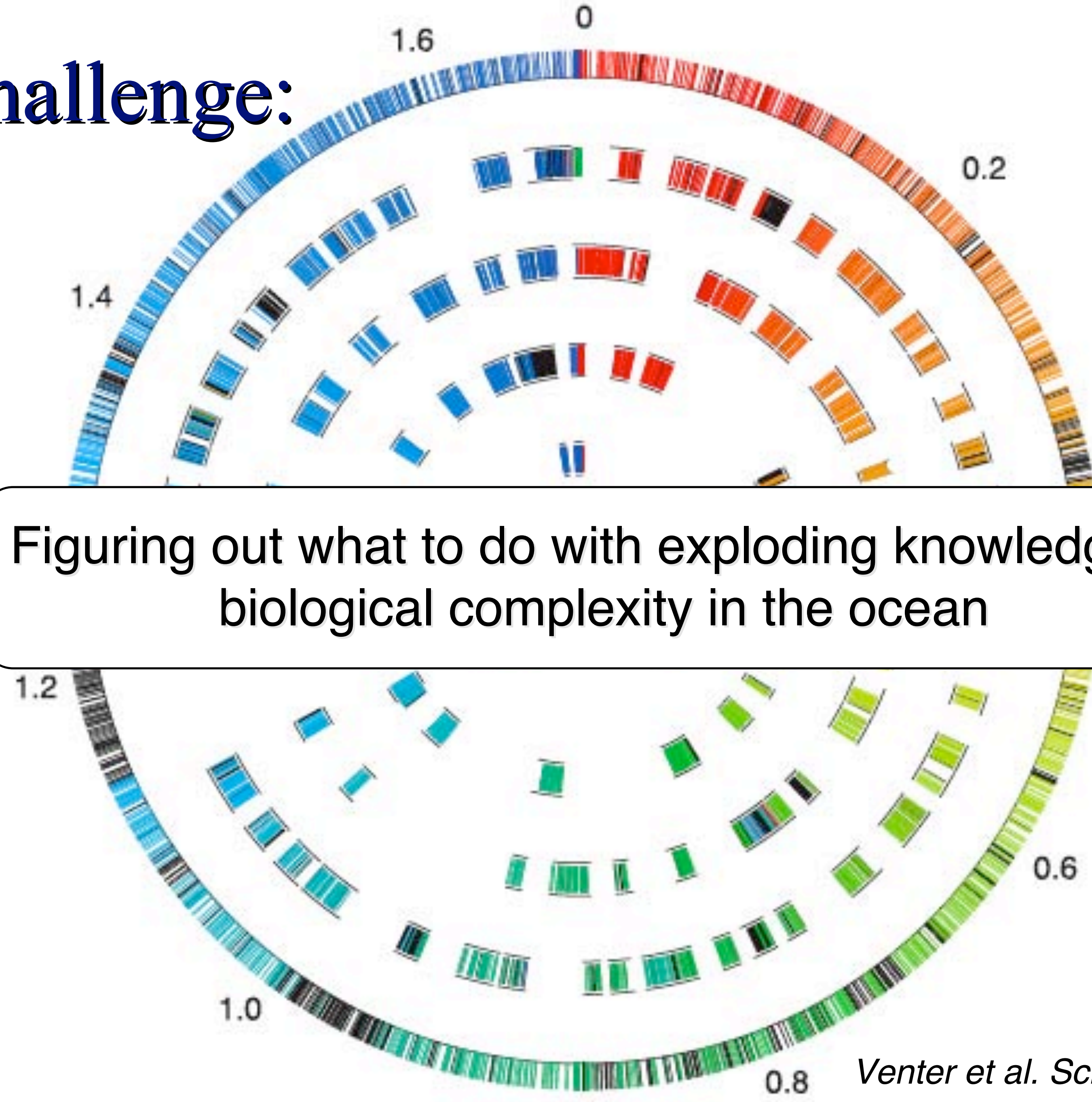
Critical to know the Environmental Influences on the Growth of Phytoplankton:

Temperature
Light
Daylength
Nutrients

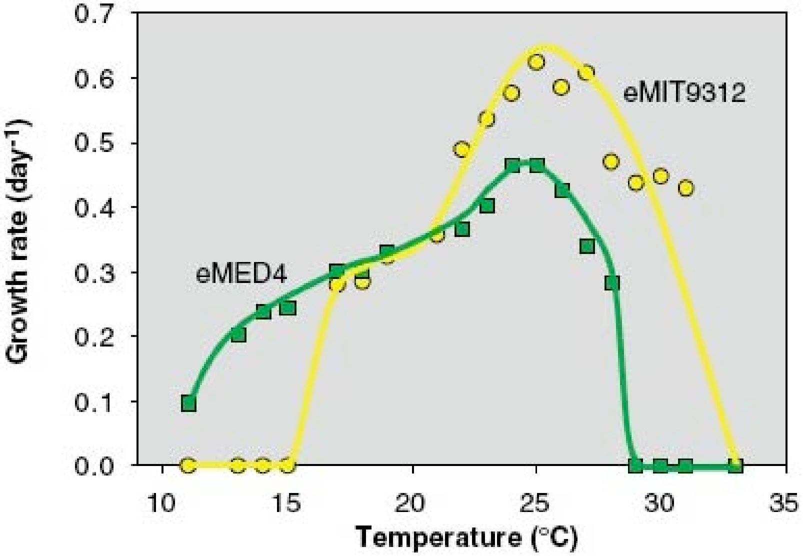


Challenge:



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

Venter et al. Science 2004

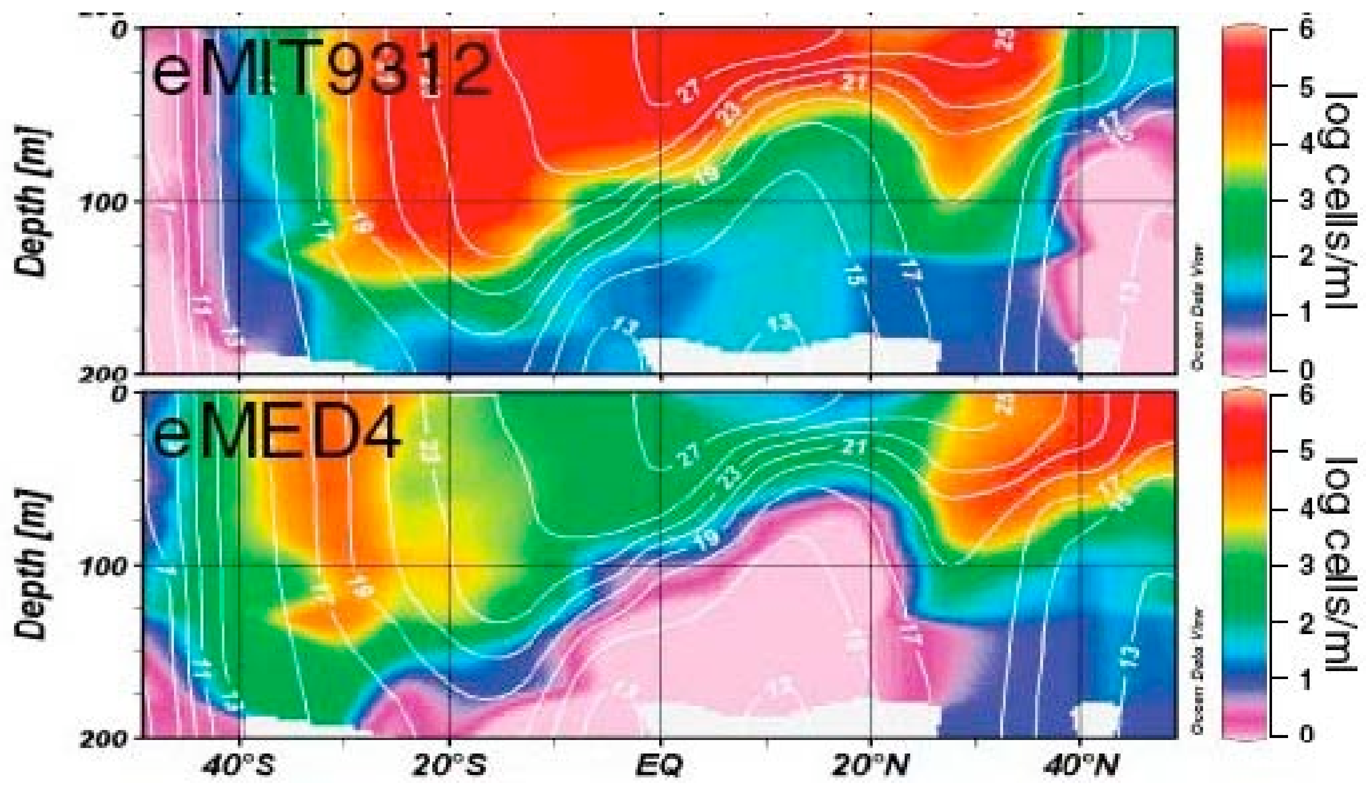


Growth *vs* Temperature

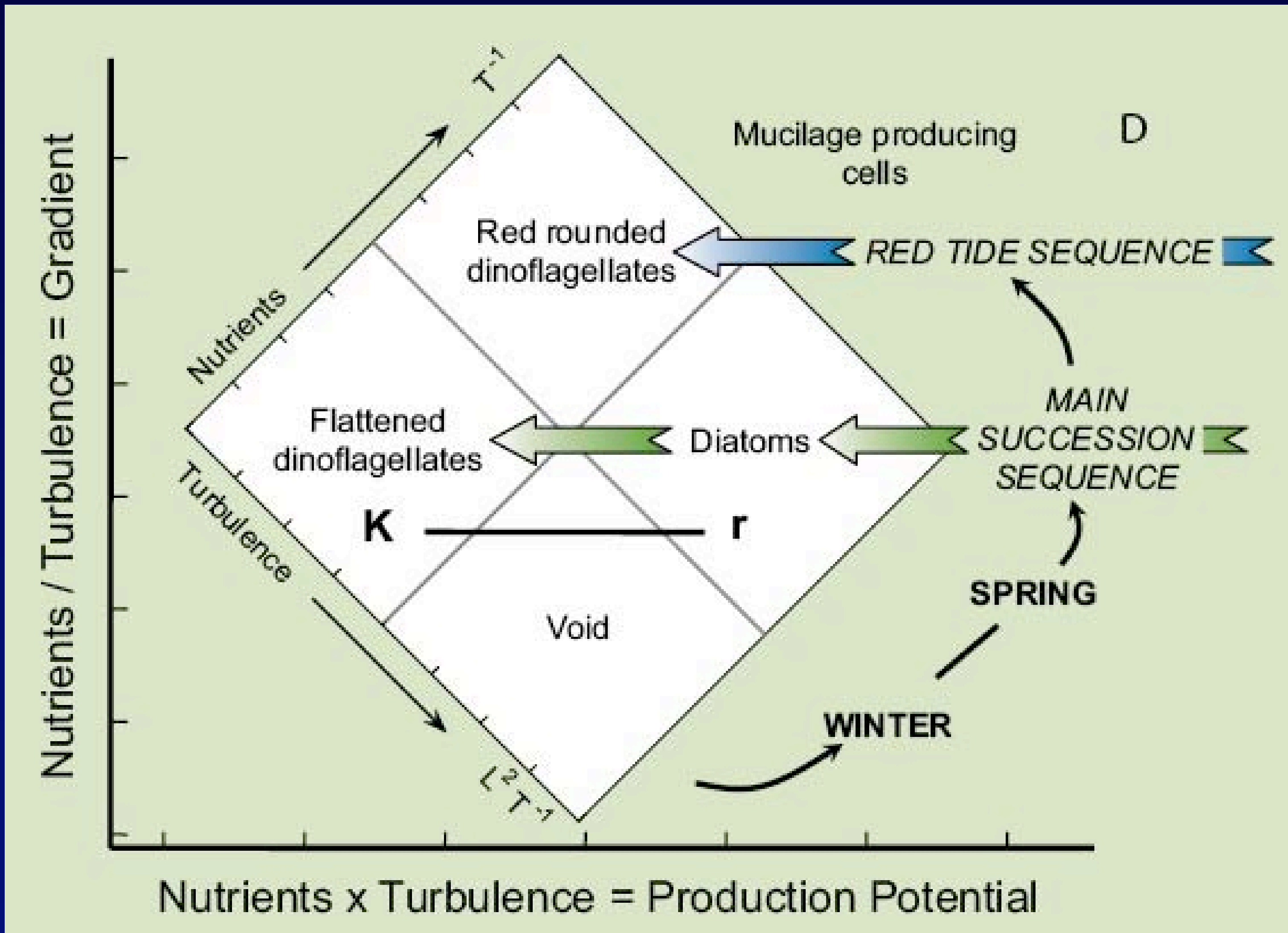
SCIENCE VOL 311 24 MARCH 2006 1737

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]†



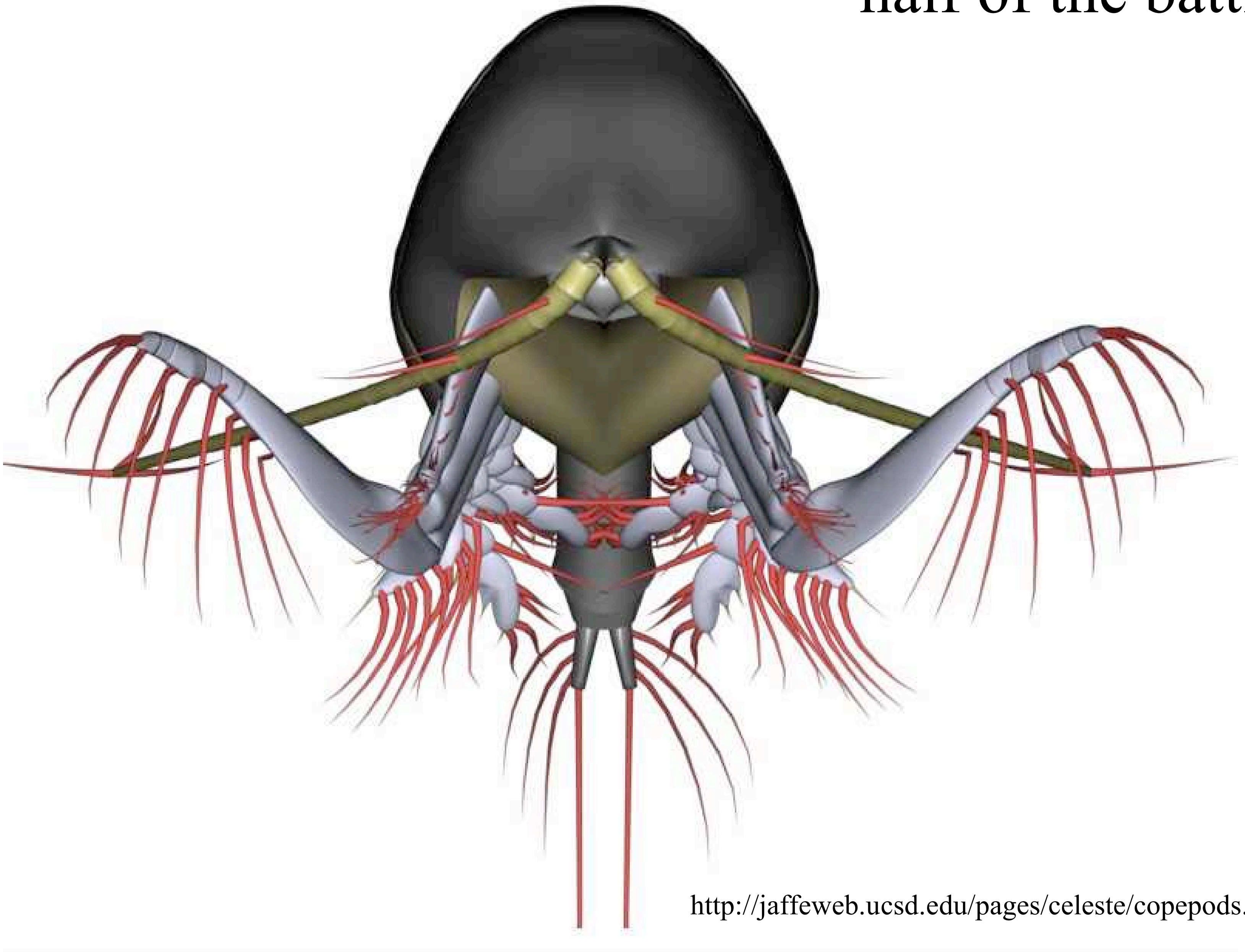
Many other things define the growth-niche of marine phytoplankton



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

John Cullen: Agouron Institute 2008

And cell division is only half of the battle!



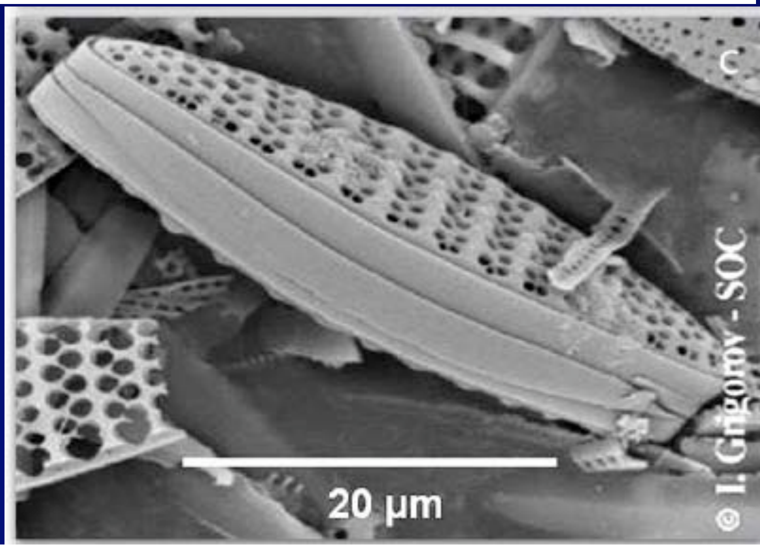
http://jaffeweb.ucsd.edu/pages/celeste/copepods.html

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



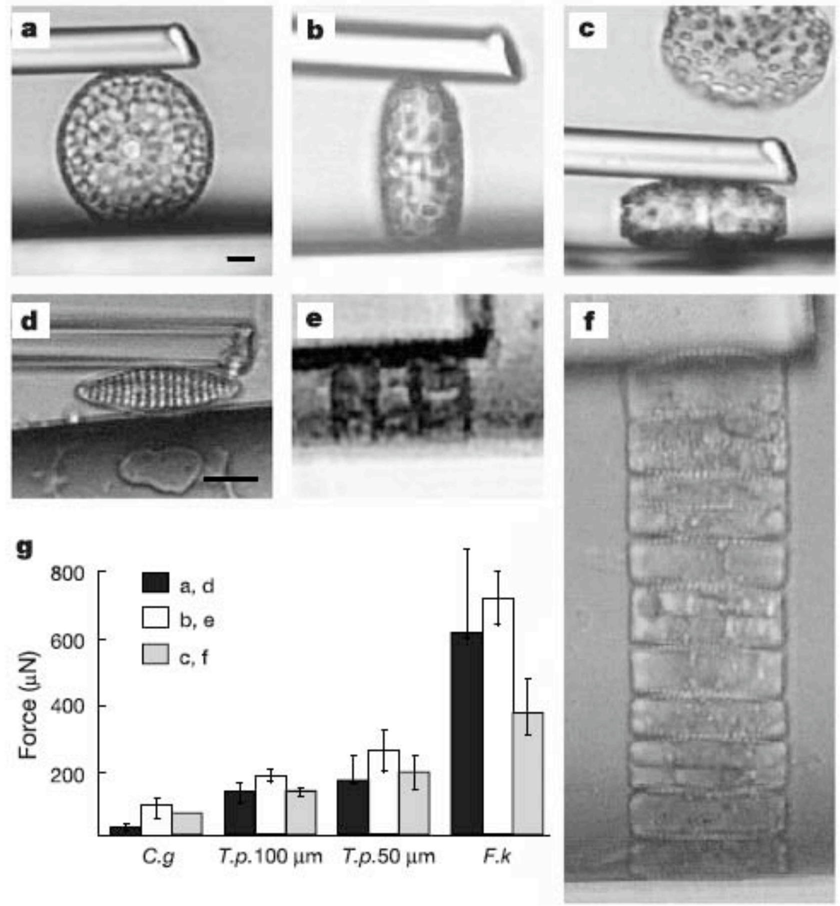
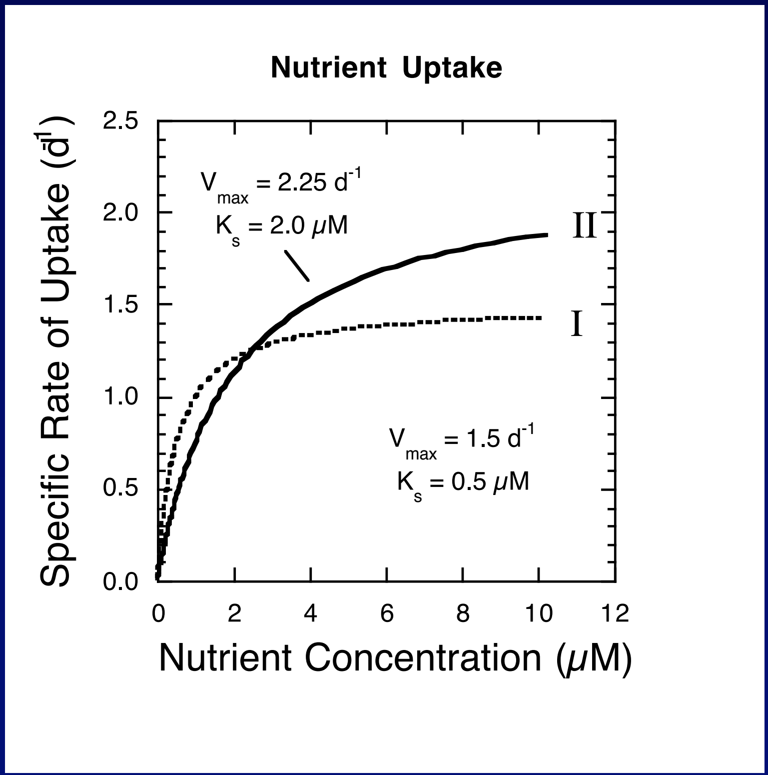


Figure 1 Glass needle tests: Live single cells of *T. punctigera* (**a**–**c**) and *F. kerguelensis* (**d**–**f**), in chains (**e**, **f**). Pressures applied along the girdle bands, (**a**, **d**), across the girdle bands (**b**, **e**), and across the centre of the valves (**c**, **f**). **g**, Forces 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.

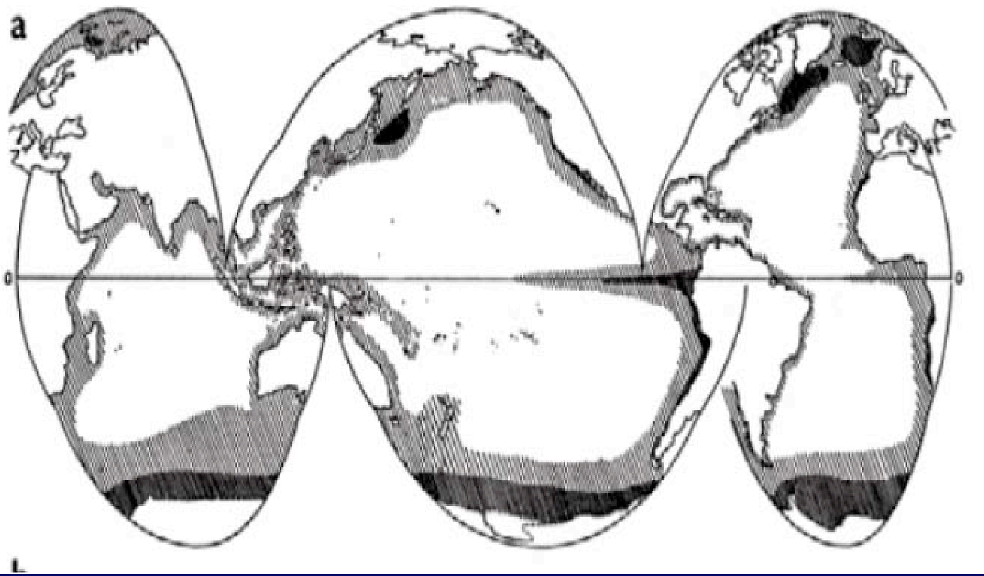
It's the gene, stupid!

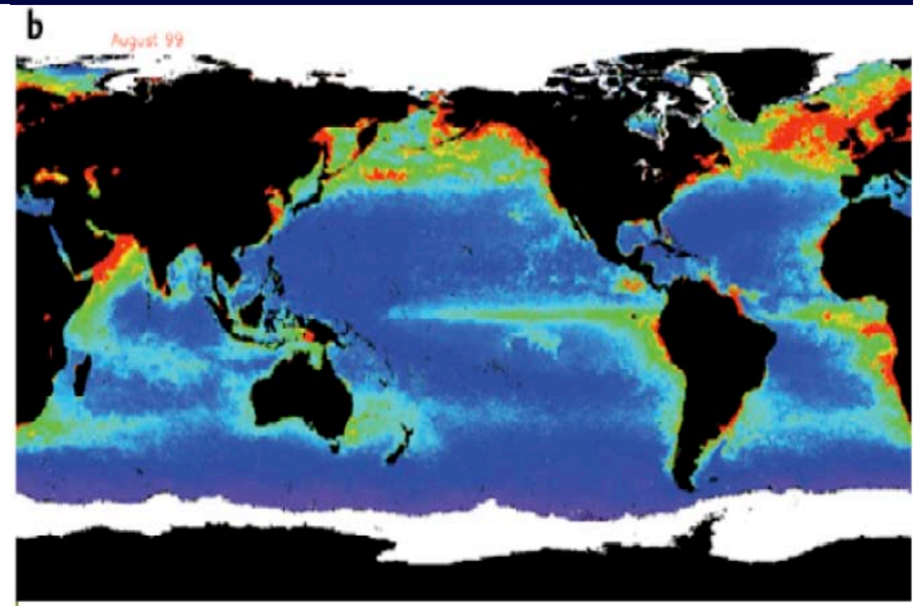
So rapid growth is not the only strategy for survival / selection



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

Top-down or bottom-up control?



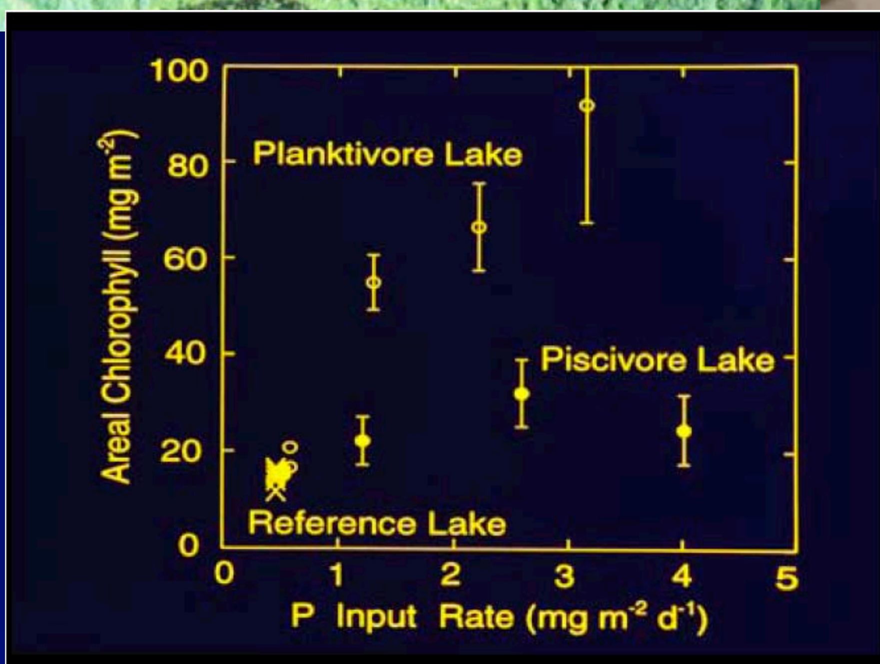


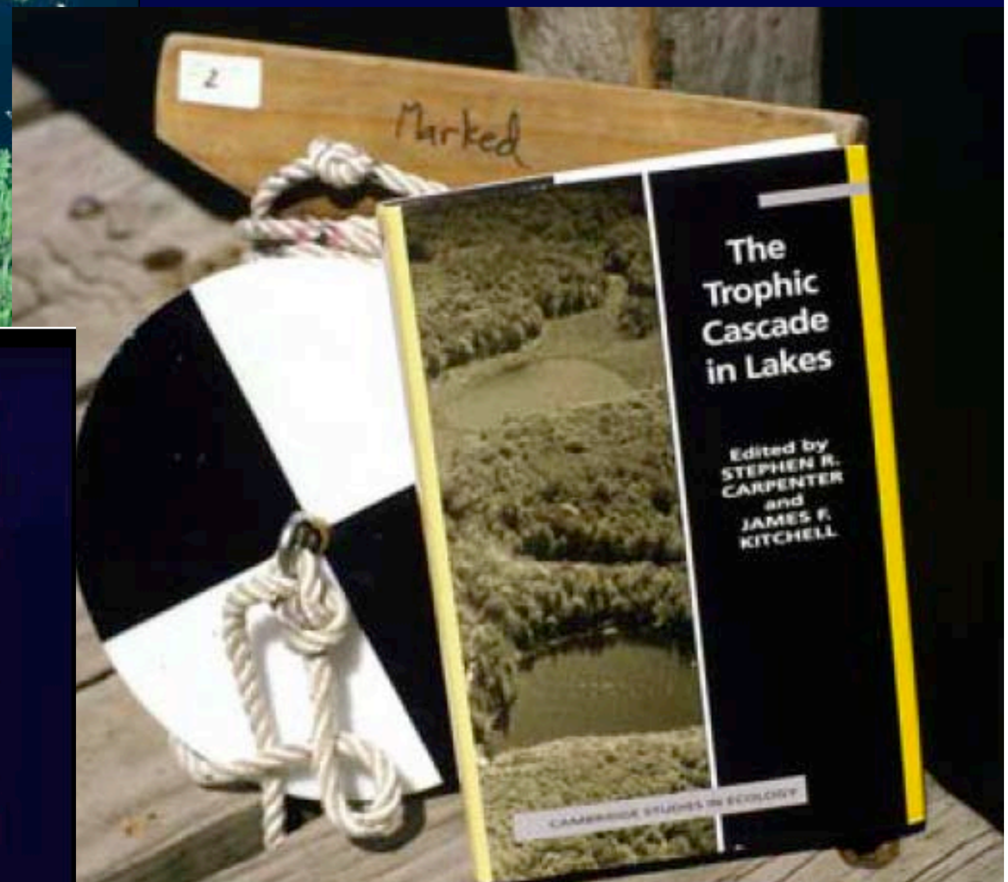
Sverdrup's (1955) map of productivity based on vertical convection, upwelling and turbulent diffusion

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

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

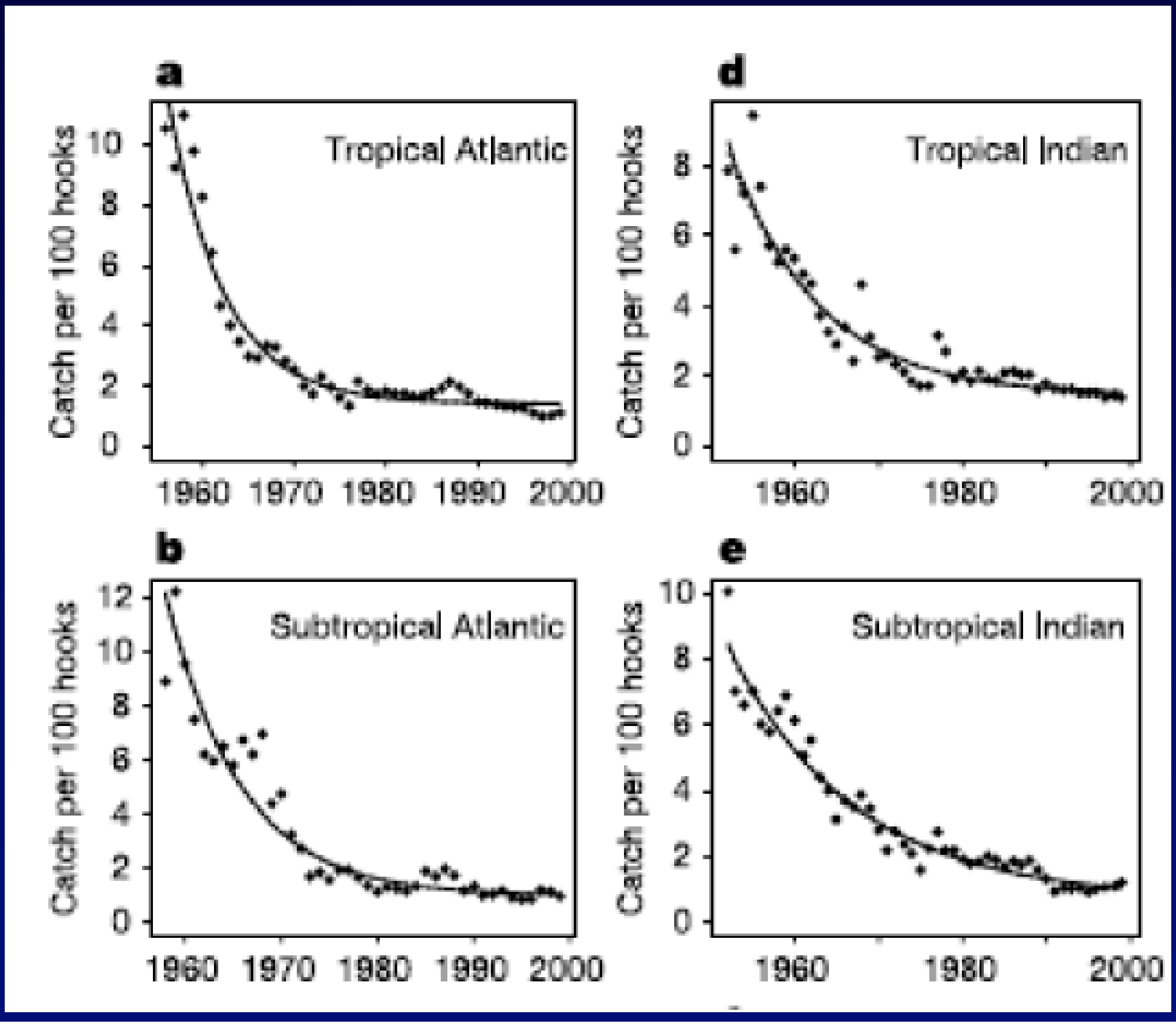
Top-down control





John Cullen: Agouron Institute 2008

Global test of the top-down hypothesis?



Decline of fish stocks since 1960

Myers and Worm Nature 2003

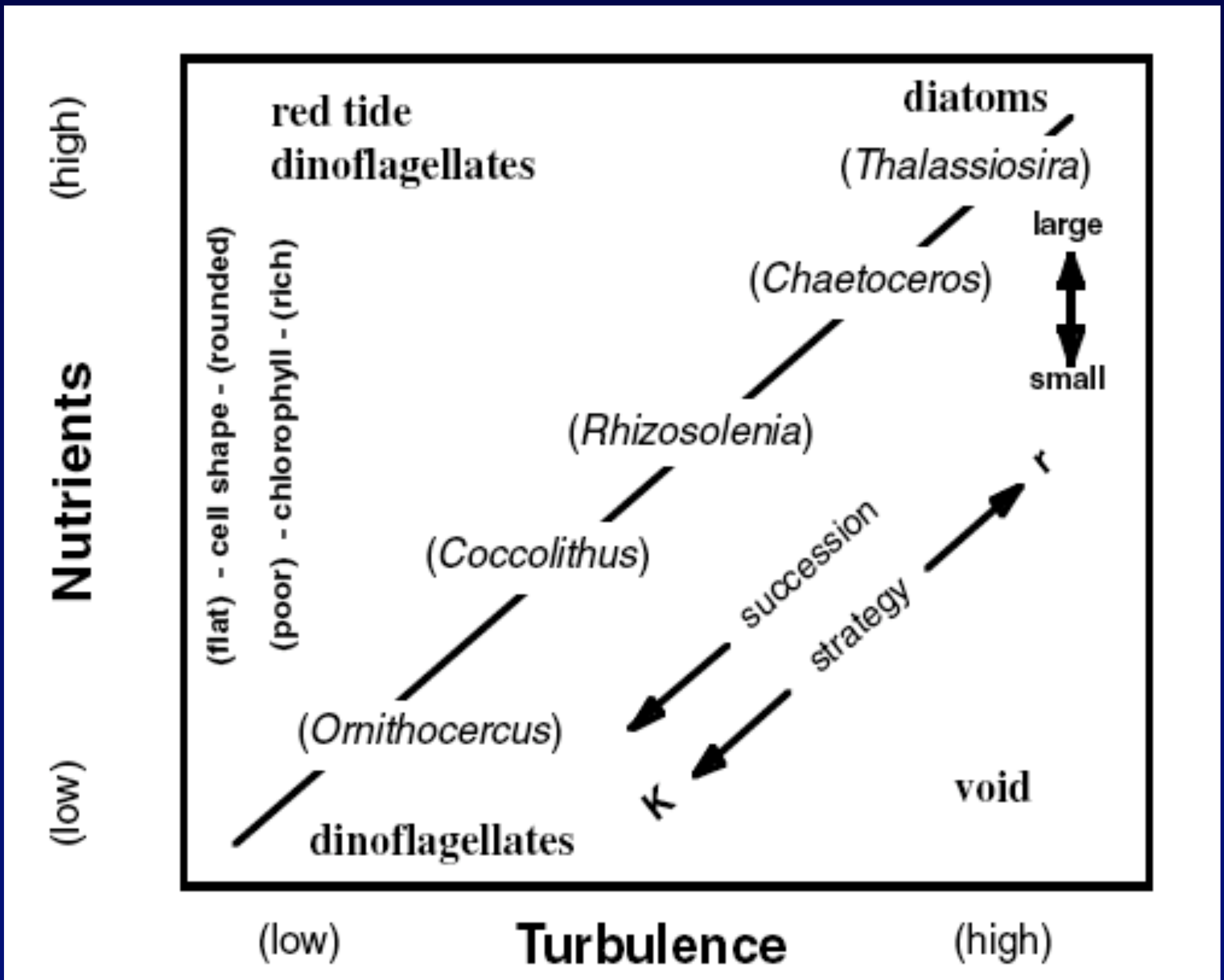
Bottom-up processes

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*)

A Tool for Making Sense of Physically Forced Ecosystem Dynamics:

Margalef's Mandala



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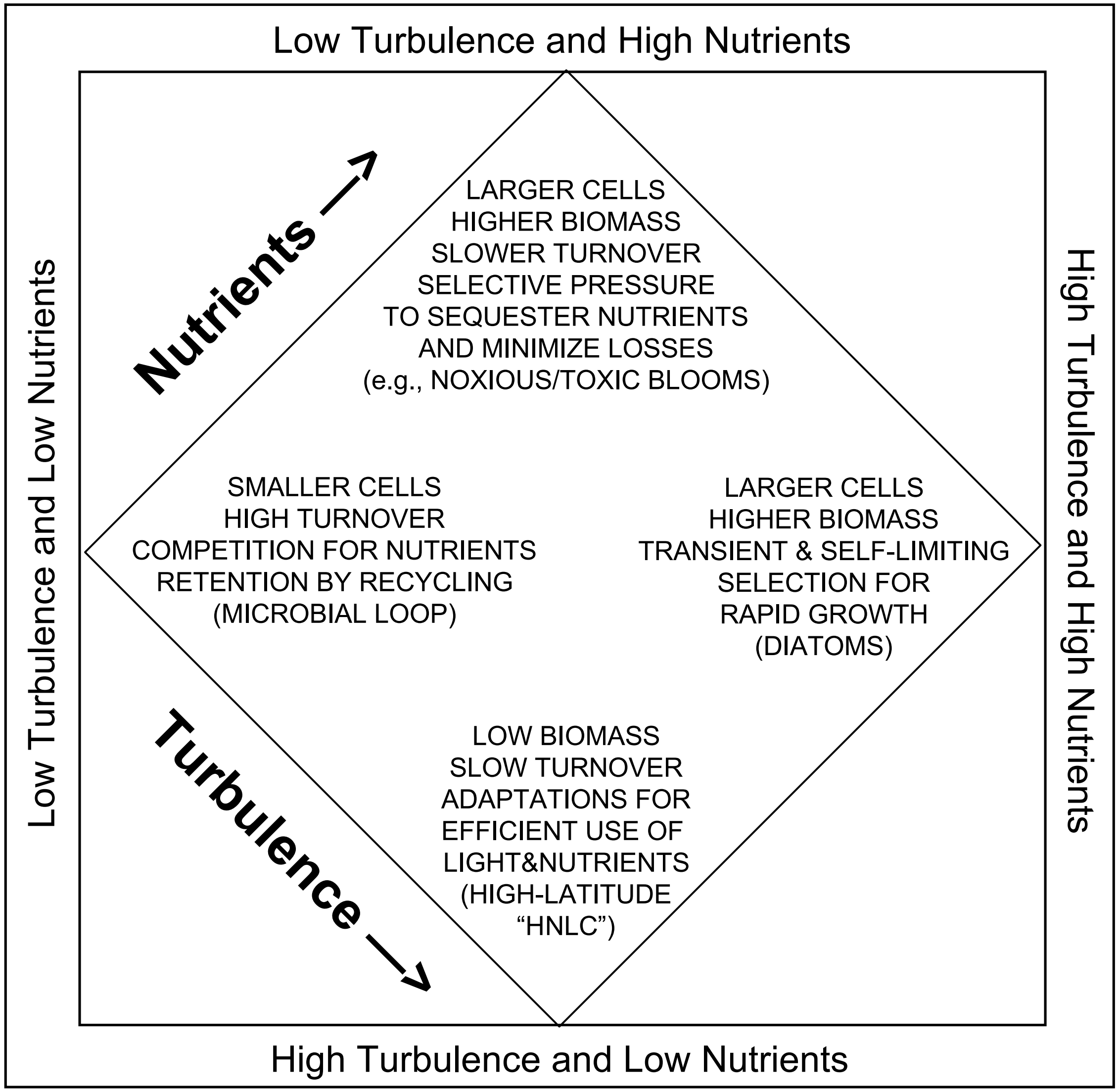
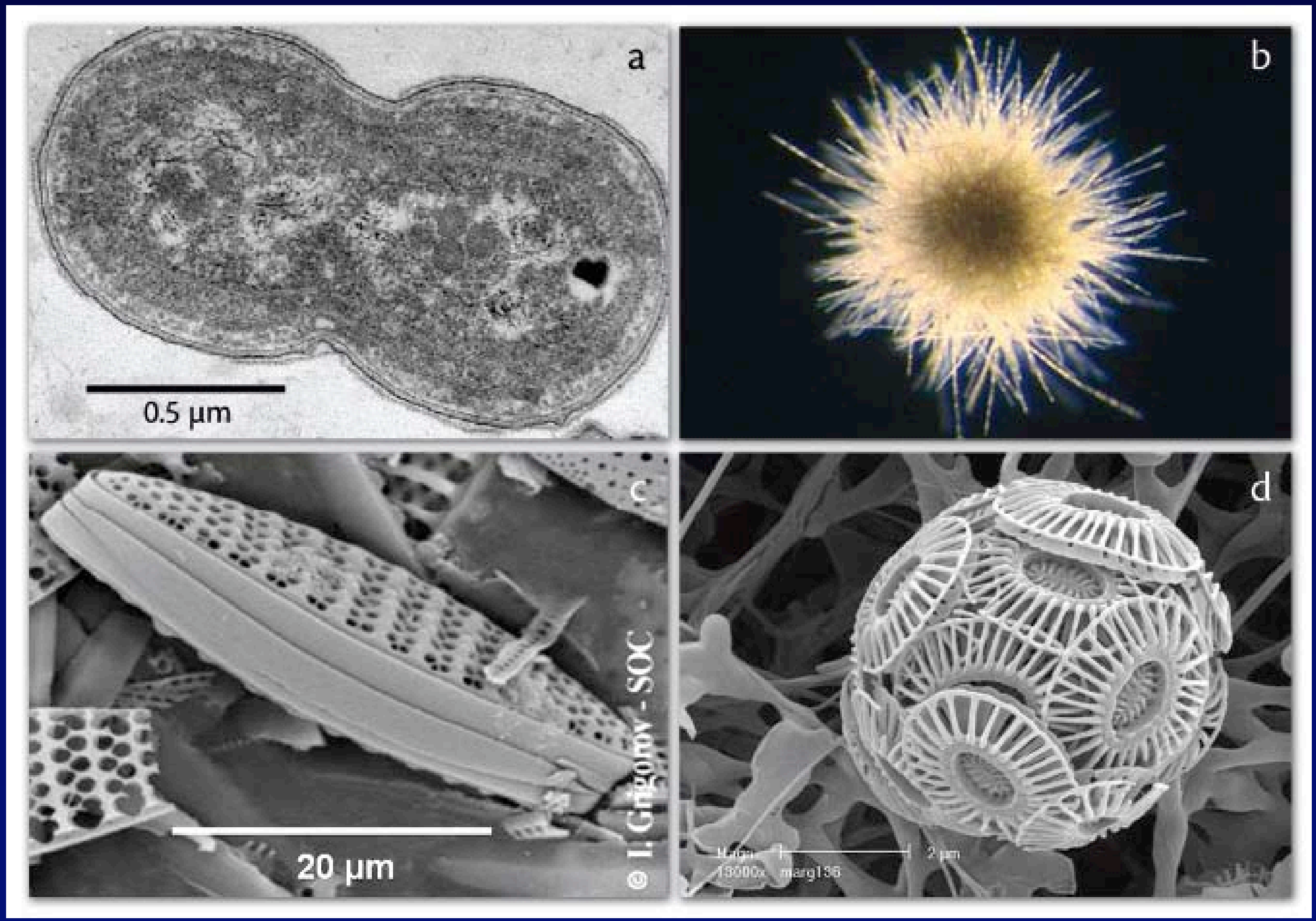
Event-Scale Forcing —>
<— Succession



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:

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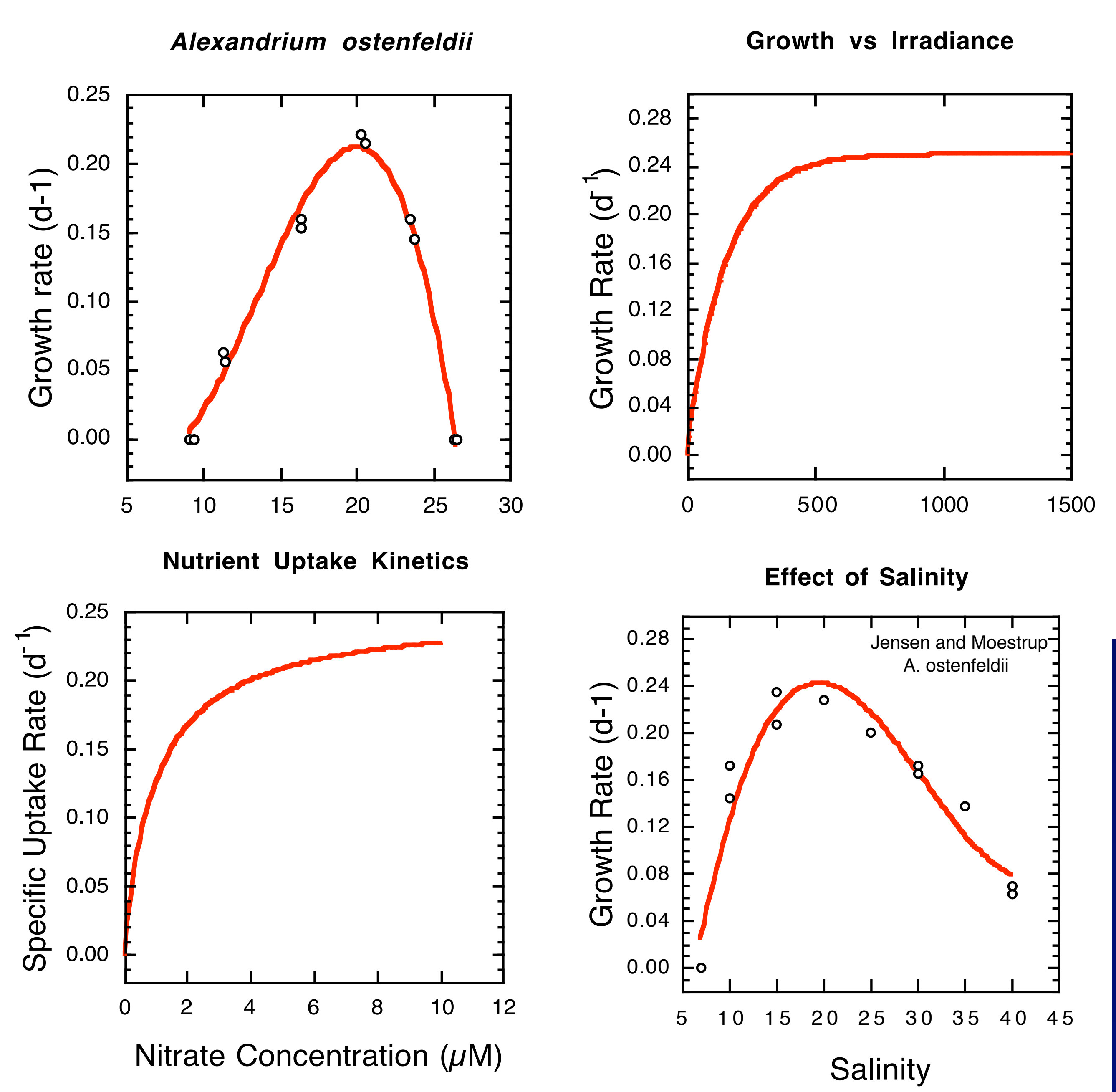
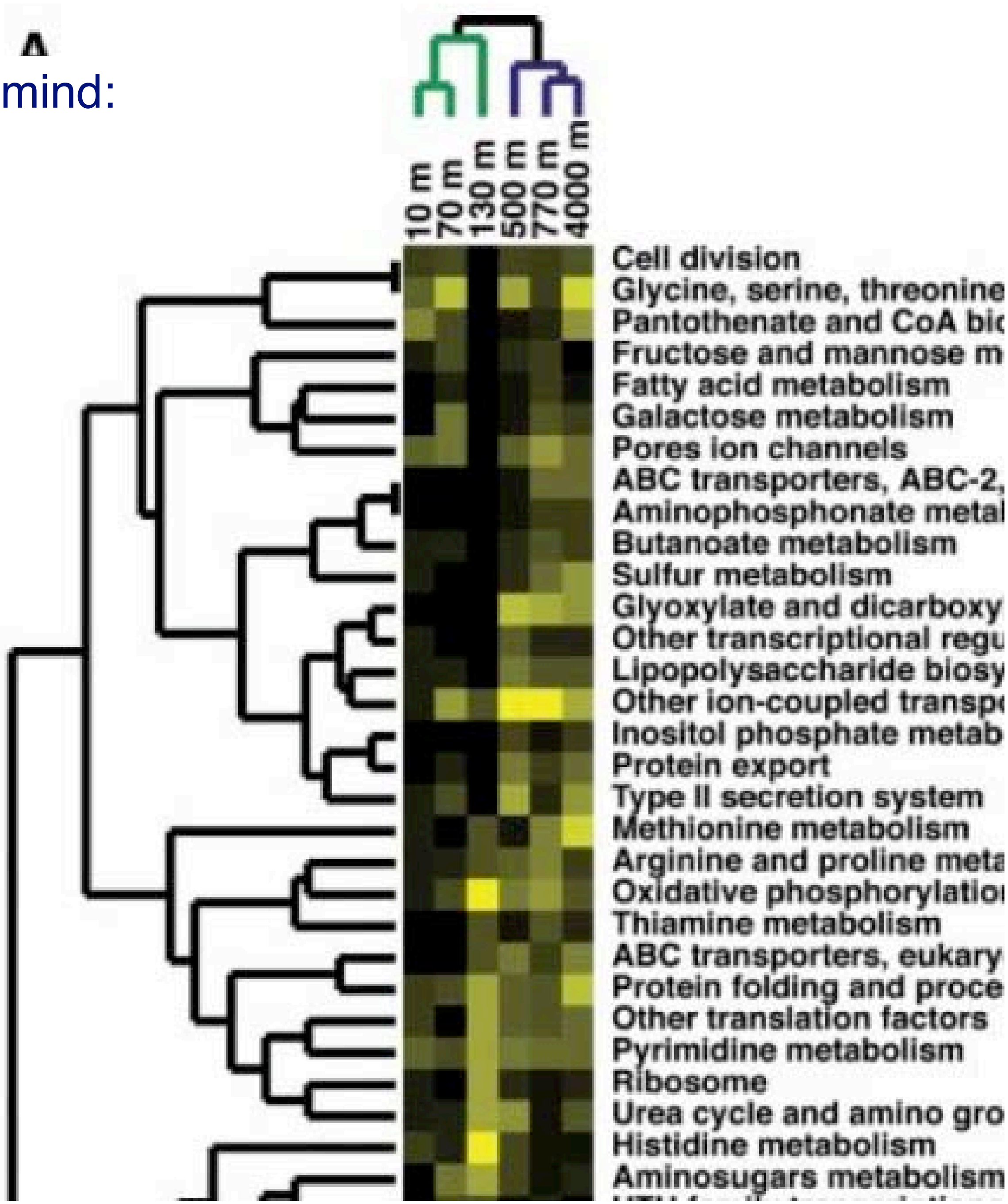


Keep in the back of your mind:

Surely, all this means something!

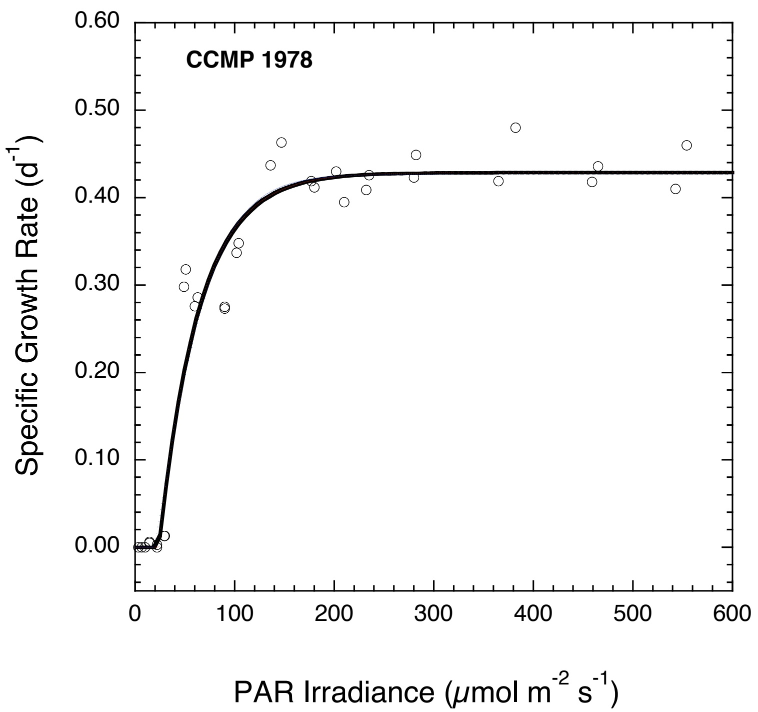


DeLong et al. Nature 2006

Ecosystem modeling ground zero:

Acclimated growth rate: genotypic

Cullen et al. in prep



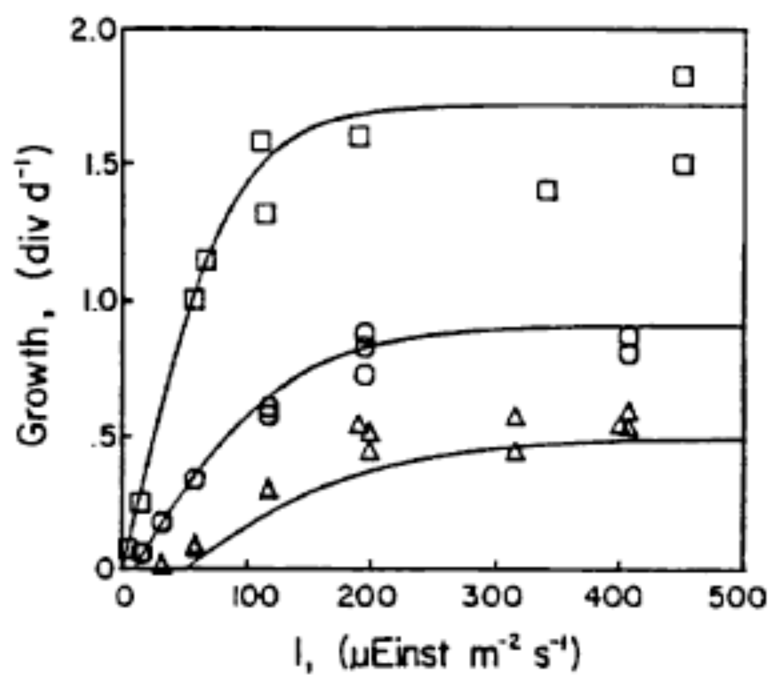
$$\mu(E) = (\mu_{max})(1 - e^{-(E-K_C)/(K_E - K_C)}) \quad \text{if } E > K_C$$

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

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

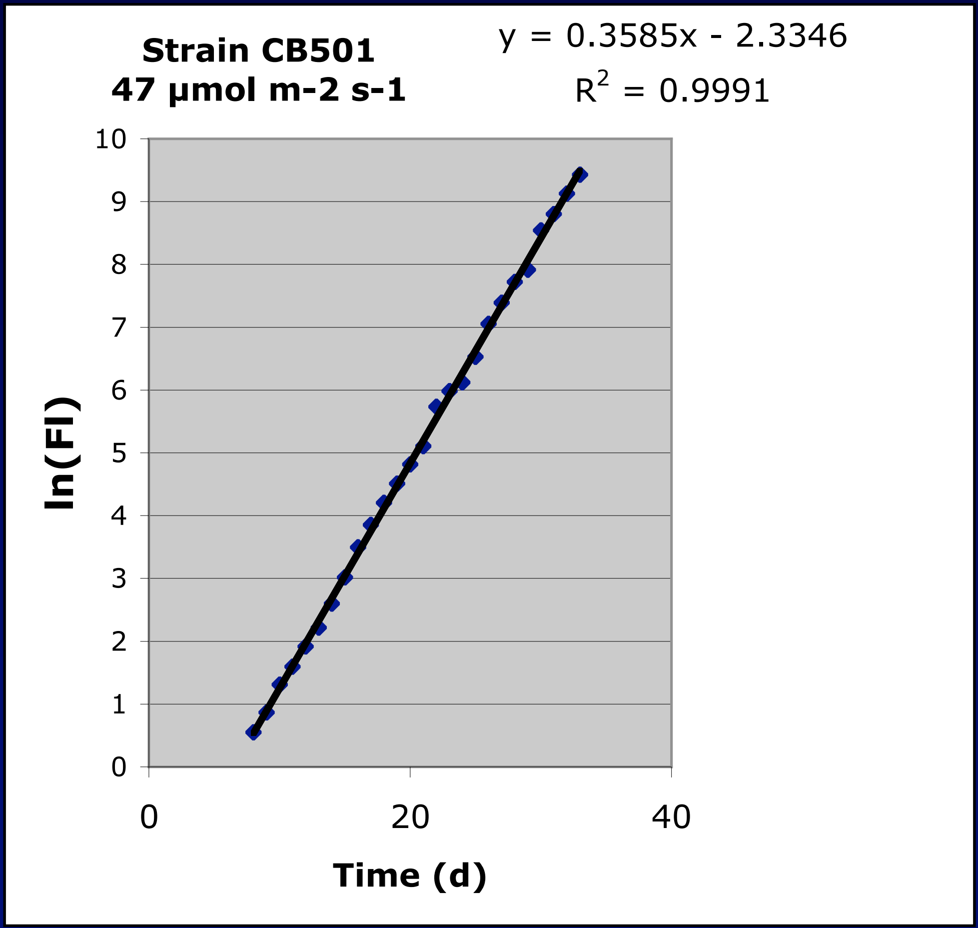
On the causes of interspecific differences in the growth–irradiance relationship for phytoplankton. Part I. A comparative study of the growth–irradiance relationship of three marine phytoplankton species: *Skeletonema costatum*, *Olisthodiscus luteus* and *Gonyaulax tamarensis*

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

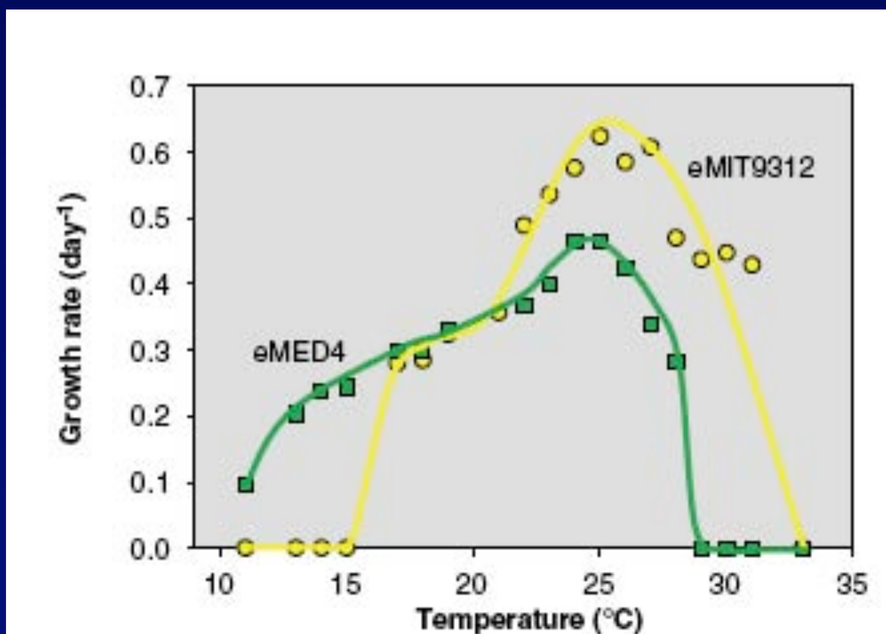
Growth determined using the method of Brand and Guillard

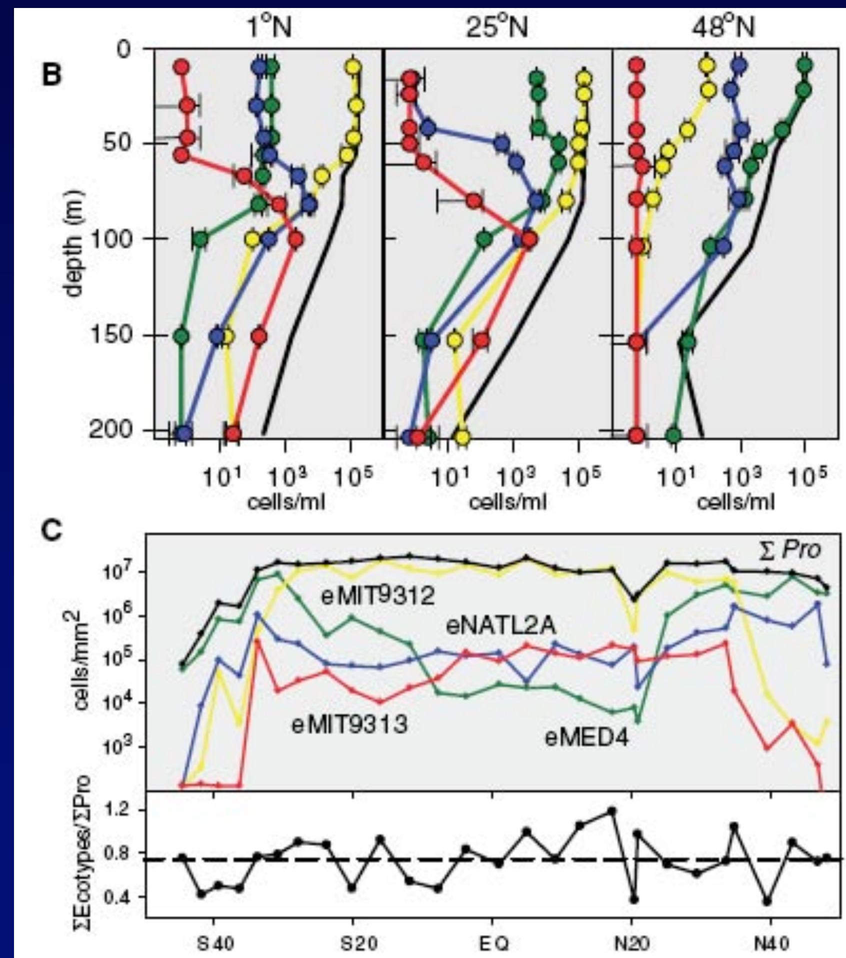
Brand, L. E. and Guillard, R. R. L. (1981). A method for the rapid and precise determination of acclimated phytoplankton reproduction rates. *J. Plankton Res.* 3: 191-201.

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]†





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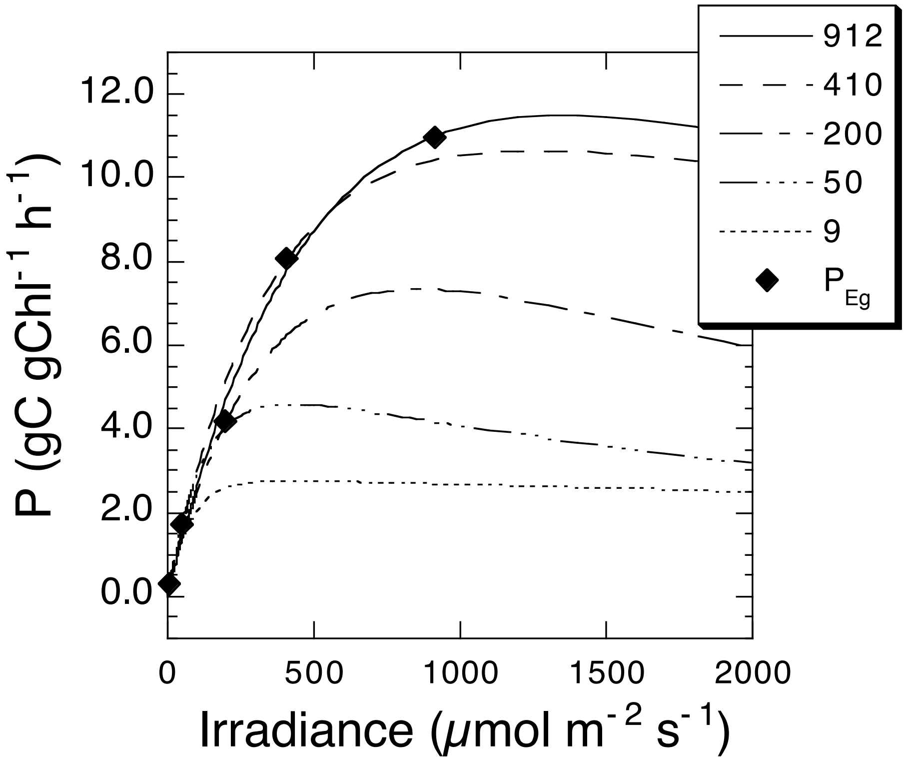
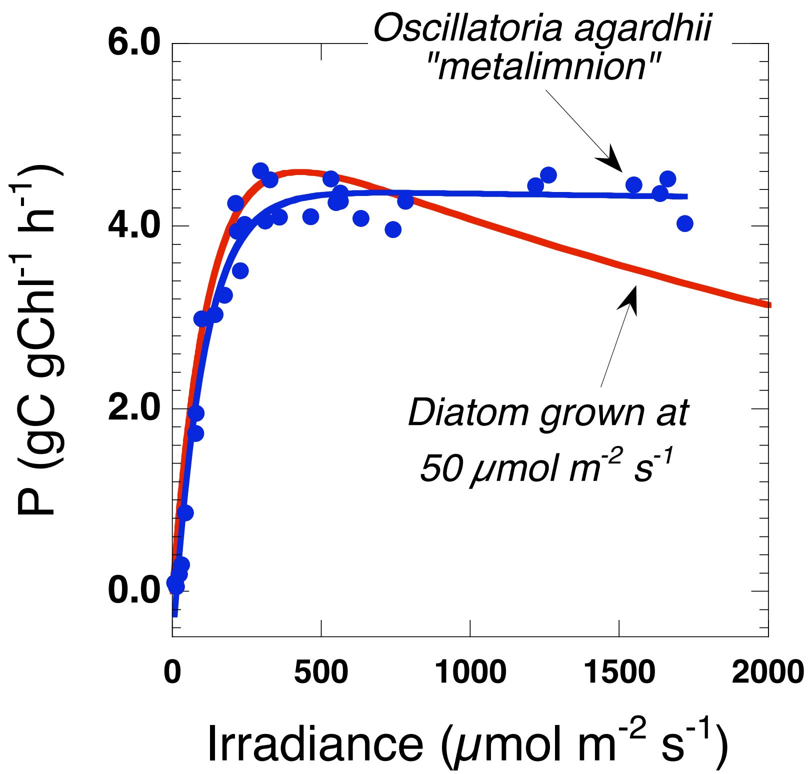
Photosynthesis vs Irradiance: phenotypic

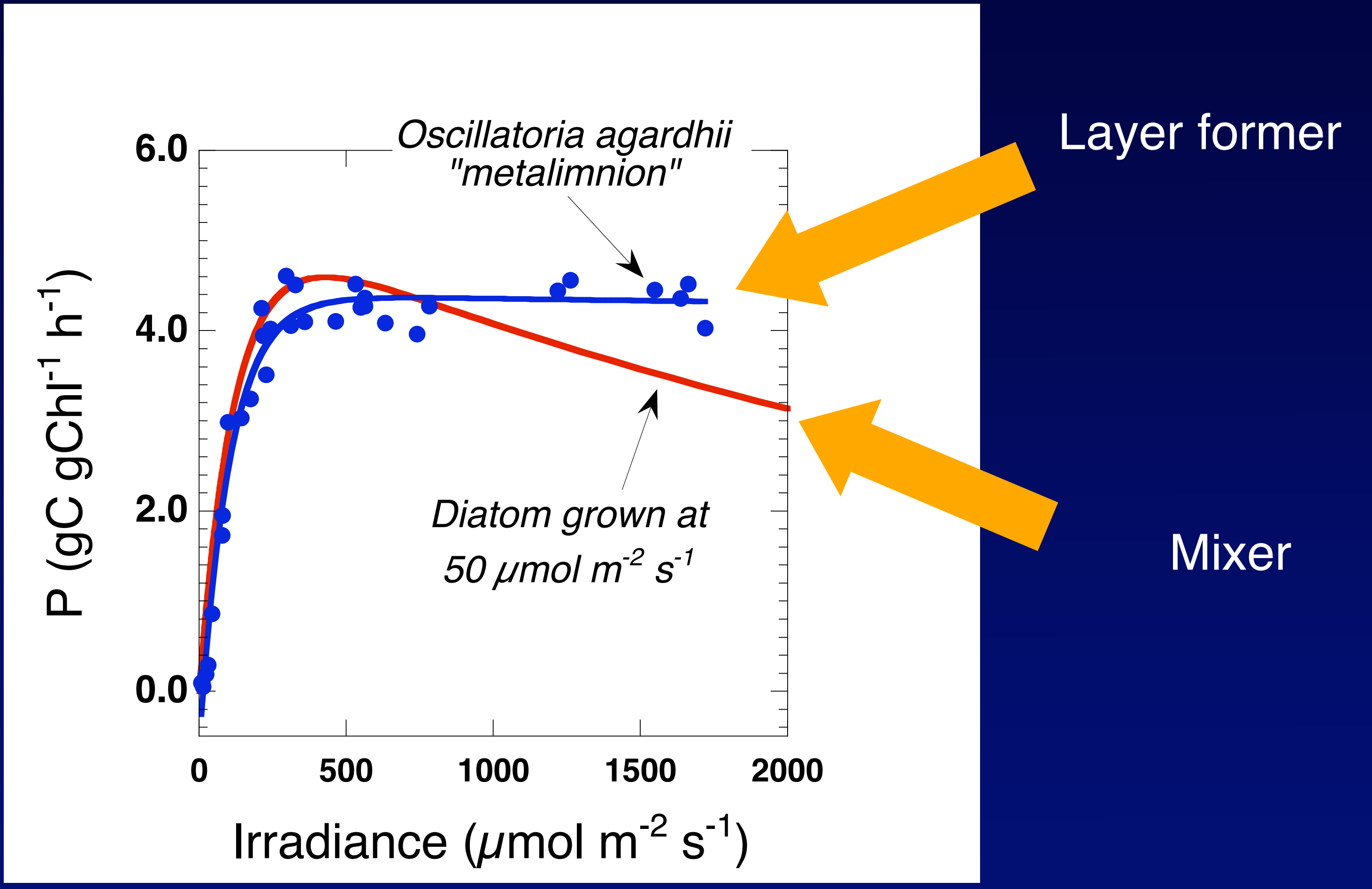




Species develop different functions through ***acclimation***

John Cullen: Agouron Institute 2008

Photosynthesis vs Irradiance: phenotypic



Strategies to respond to environmental variability are adaptations

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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

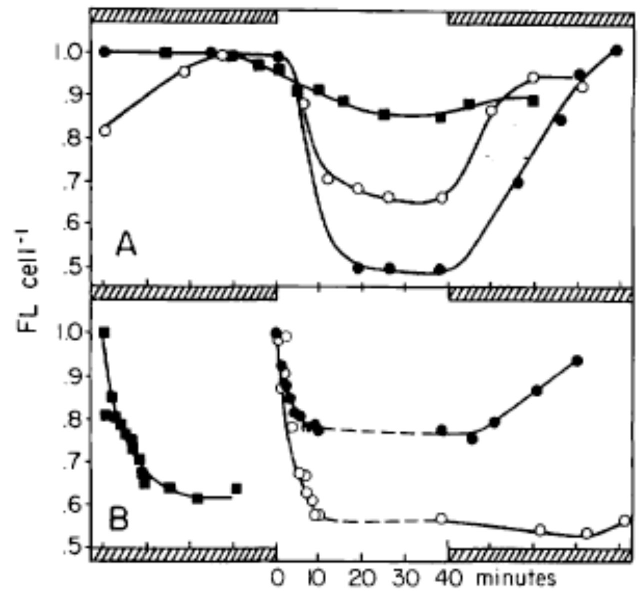


Fig. 5. *Thalassiosira pseudonana and T. oceanica*. Short-term changes of *in vivo* fluorescence per cell normalized to the highest observed value in each experiment. (A) *T. pseudonana* at 600 (○) or 800 µmol m^{-2} s^{-1} (●) exposed to 2800, and then to 600 or 800 µmol m^{-2} s^{-1} and *T. oceanica*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

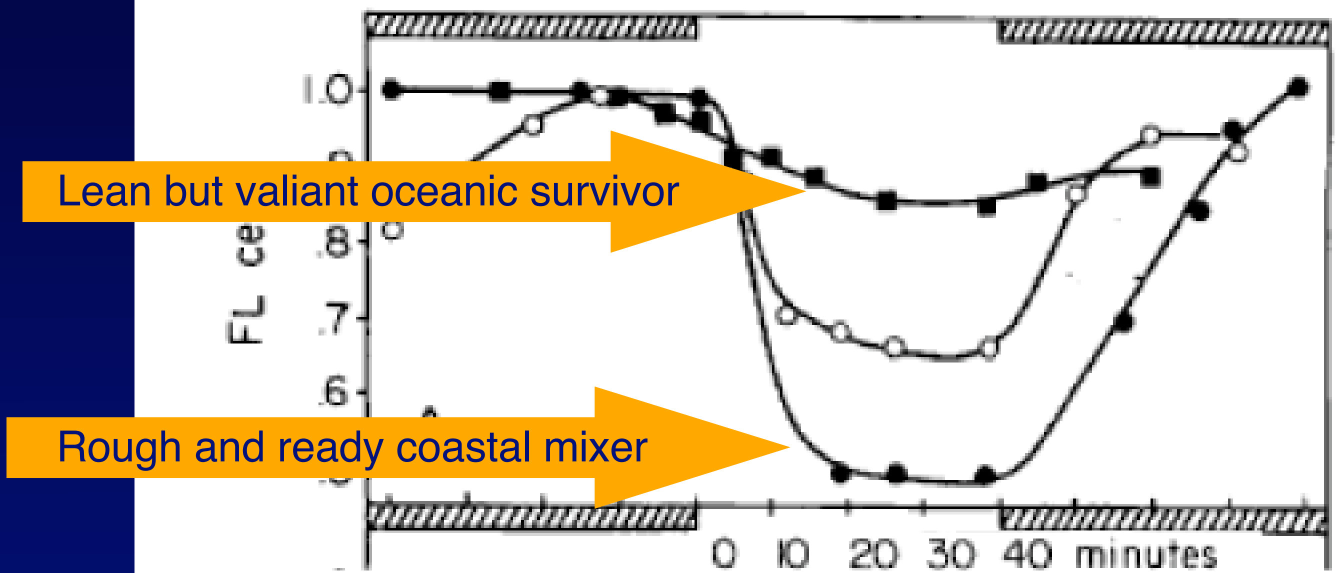
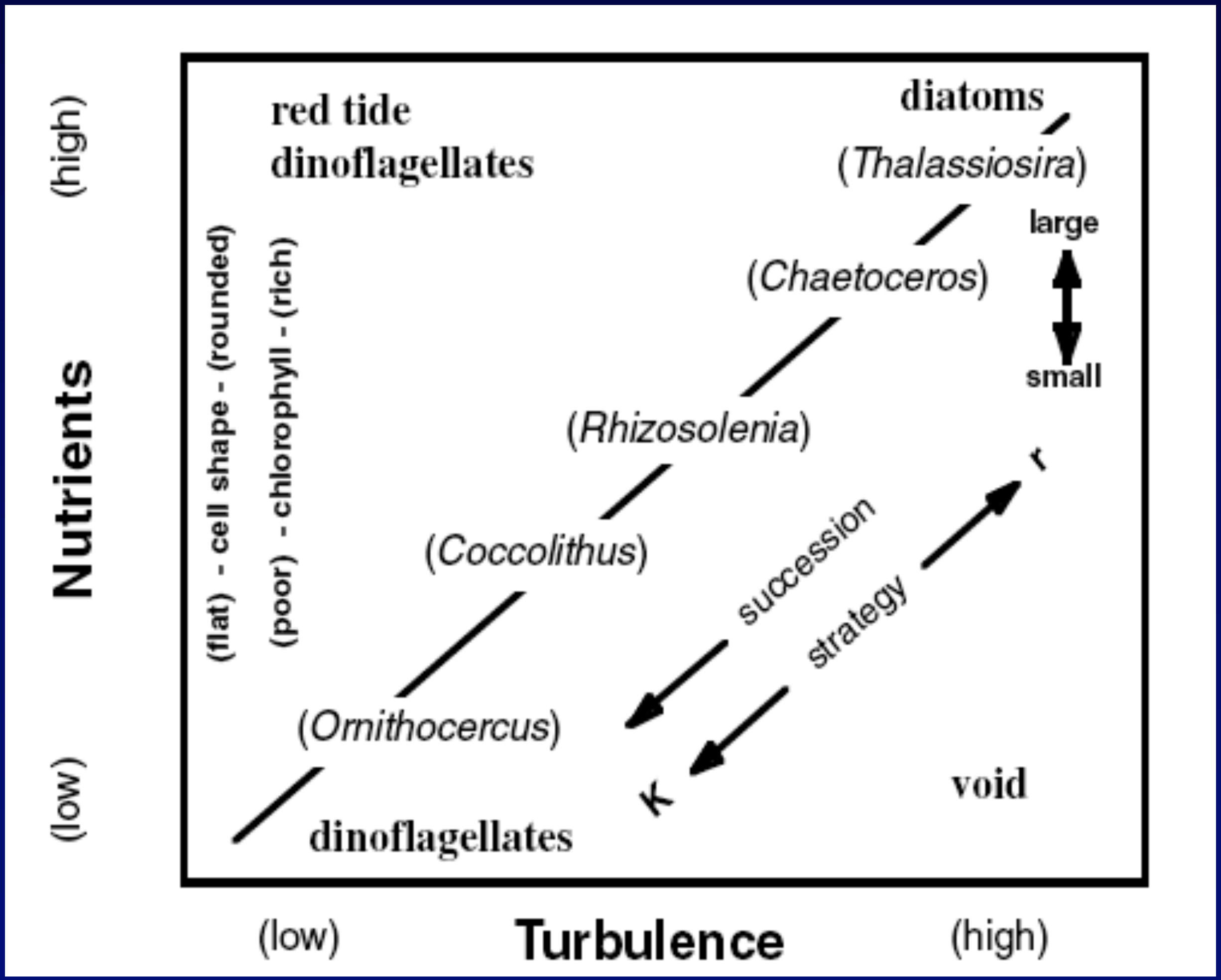


Fig. 5. *Thalassiosira pseudonana and T. oceanica*. Short-term changes of *in vivo* fluorescence per cell normalized to the highest observed value in each experiment. (A) *T. pseudonana* at 600 (○) or 800 μmol m^{-2} s^{-1} (●) exposed to 2800, and then to 600 or 800 μmol m^{-2} s^{-1} and *T. oceanica*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

Niches abound!



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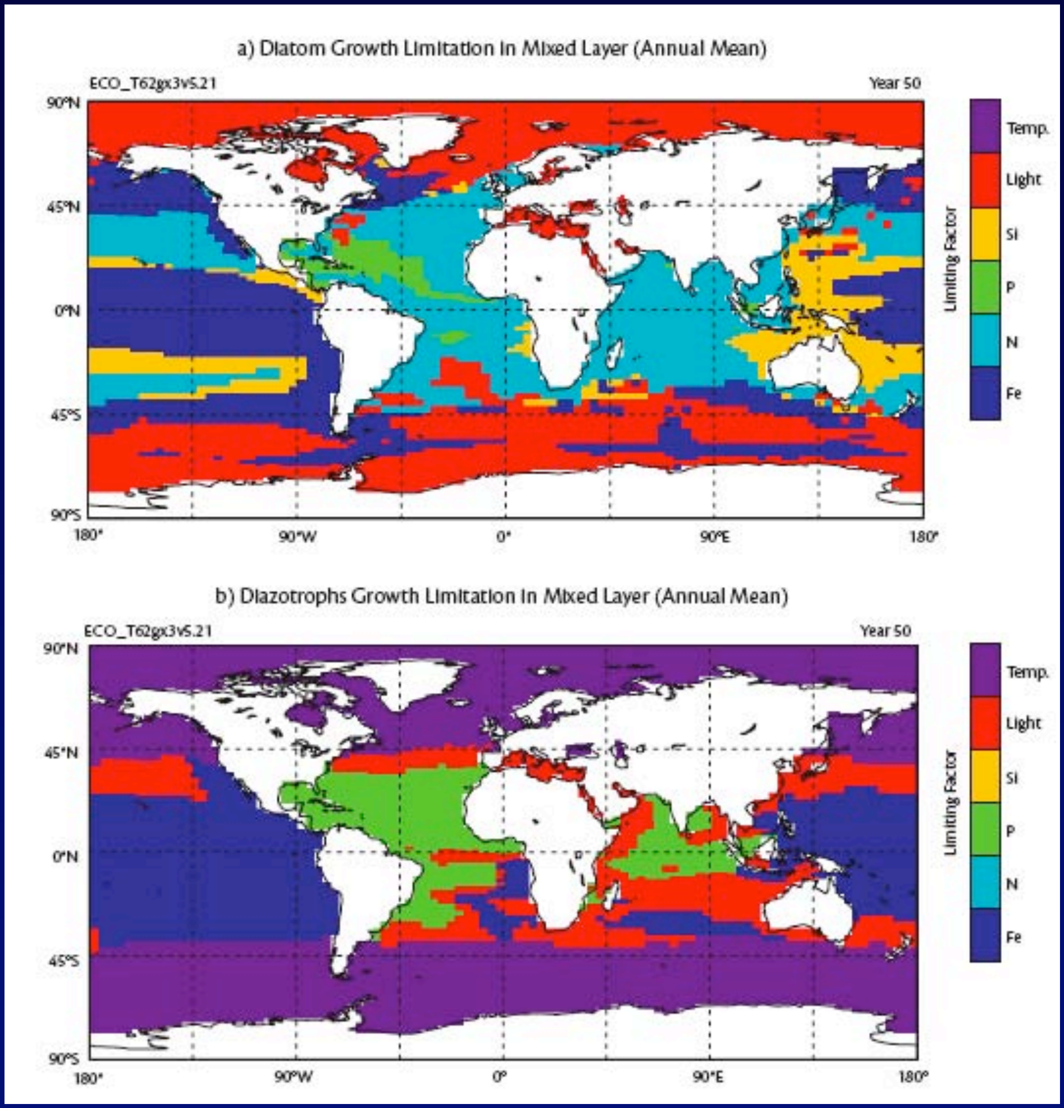
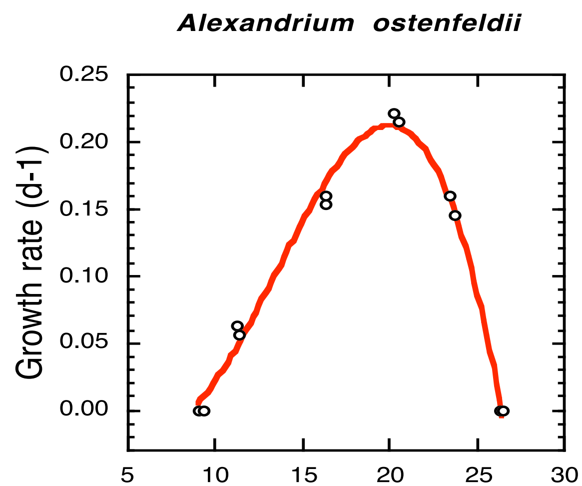
But what about quantitative prediction?

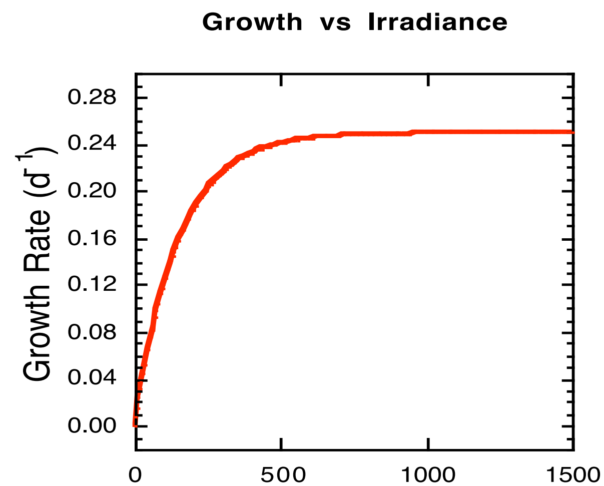


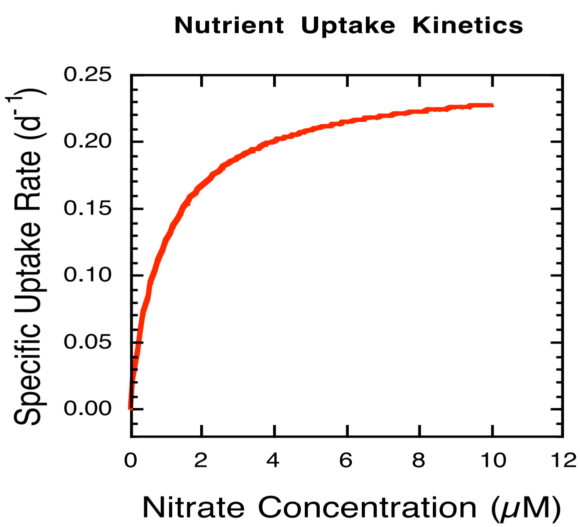
Rothstein et al. Oceanography Mag. 2006

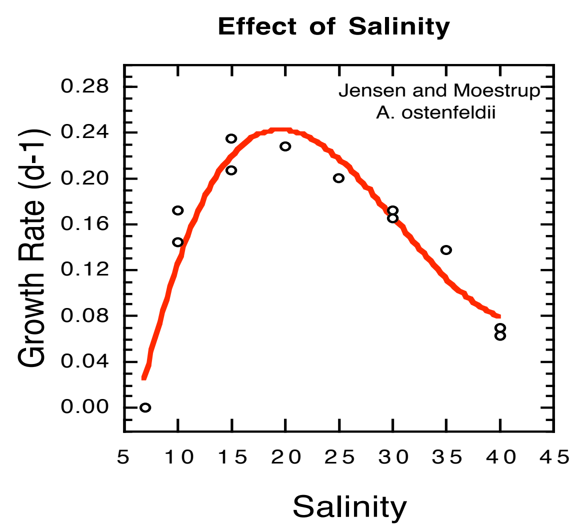
John Cullen: Agouron Institute 2008

Growth must be described as a function of environmental conditions

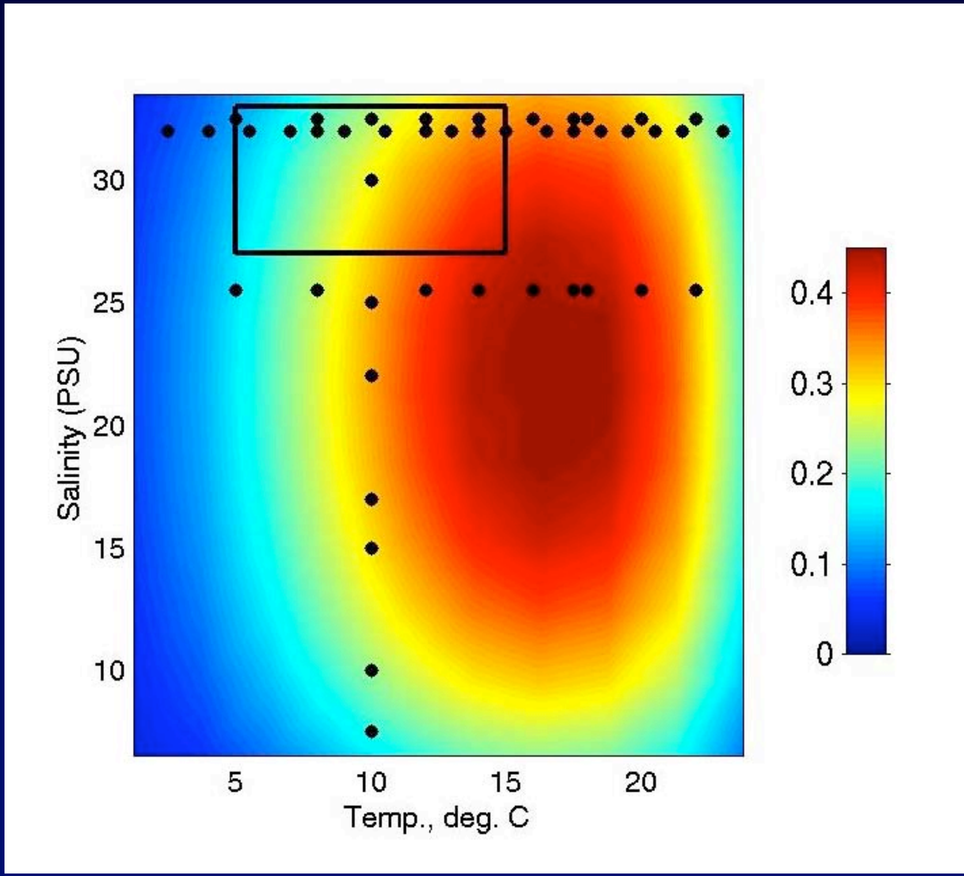








Functions can be Developed



McGillicuddy, Stock, Anderson, and Signell WHOI

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

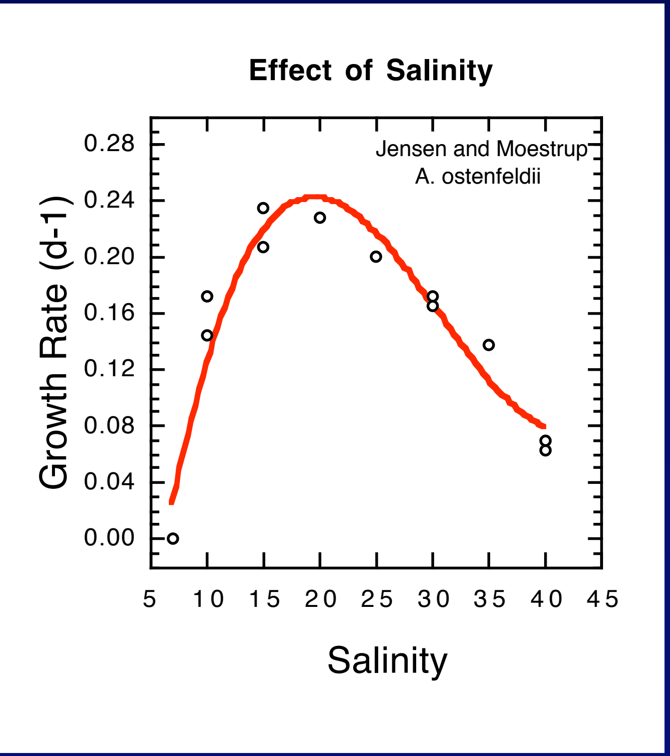
(Daylength, Irradiance, Temperature, Nutrients)

…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



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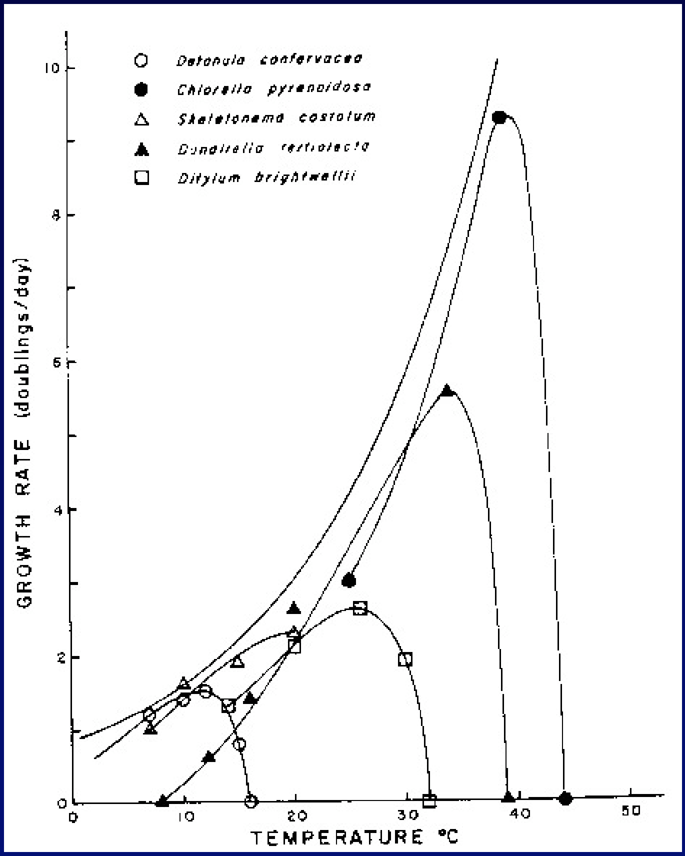
Summary: μ as a function of environmental conditions

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.

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

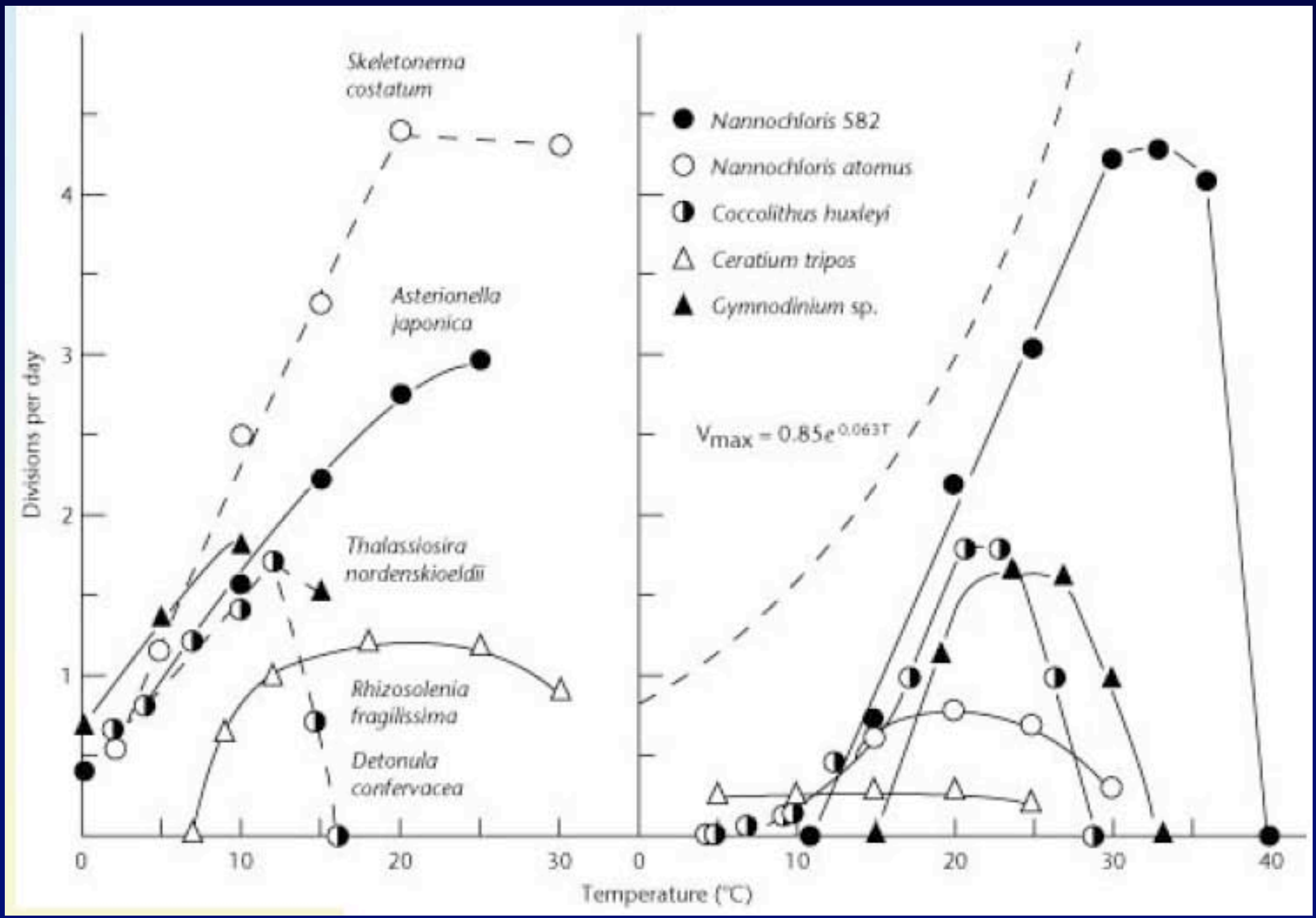
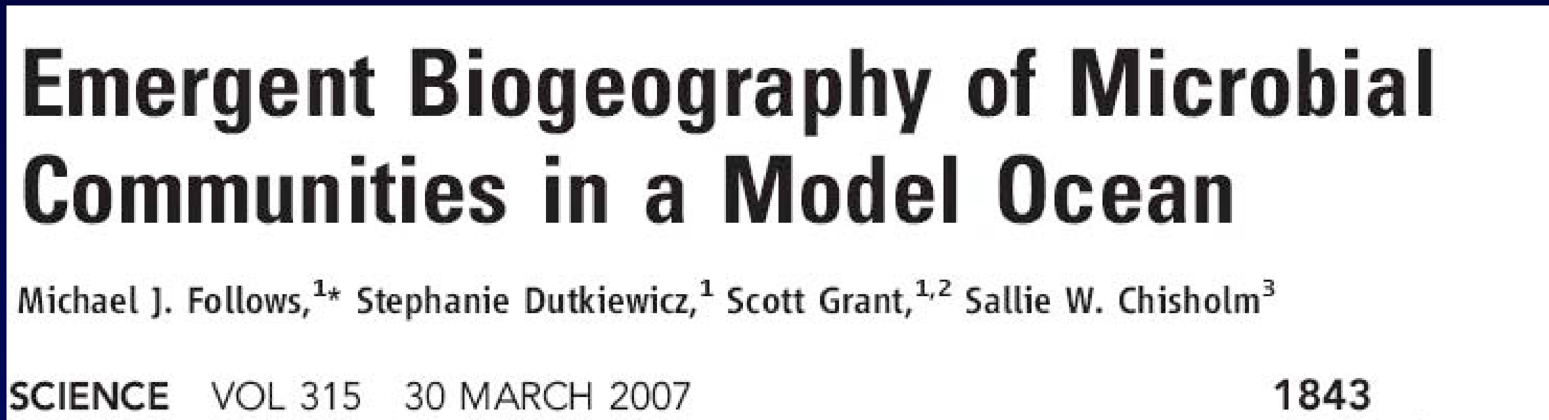
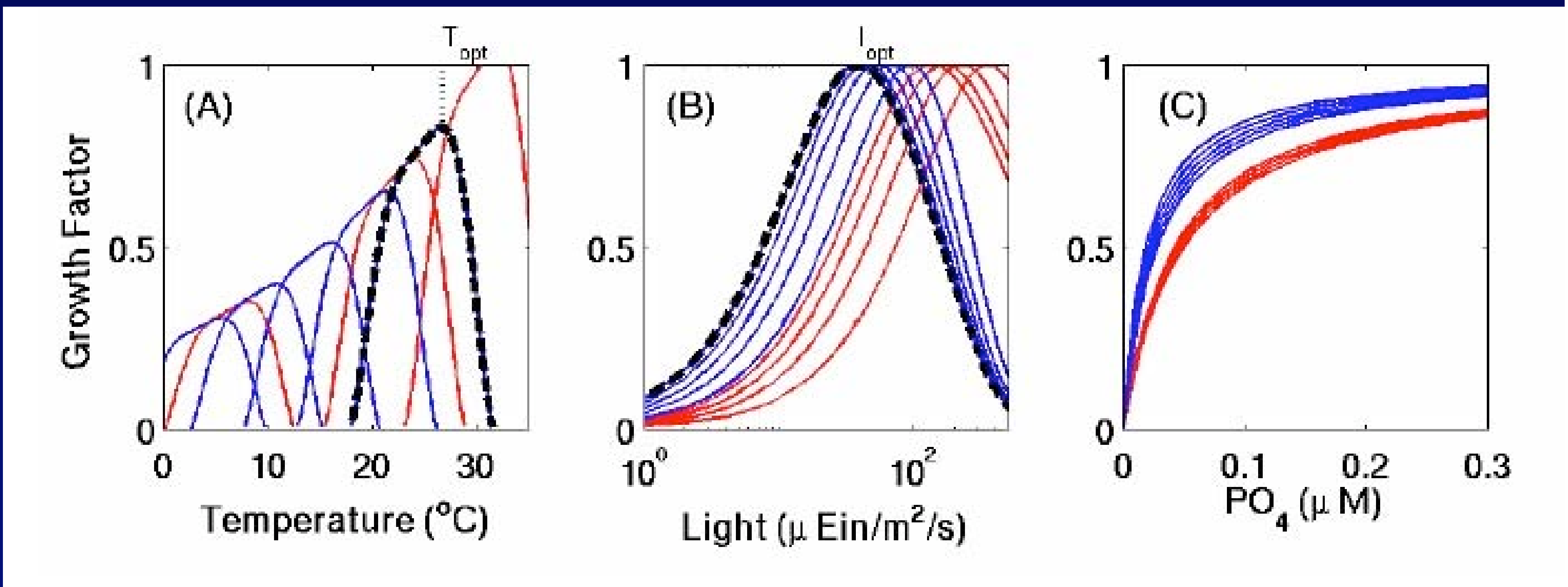


Figure from C.B. Miller, "Biological Oceanography" after Smayda, 1976

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

A novel approach





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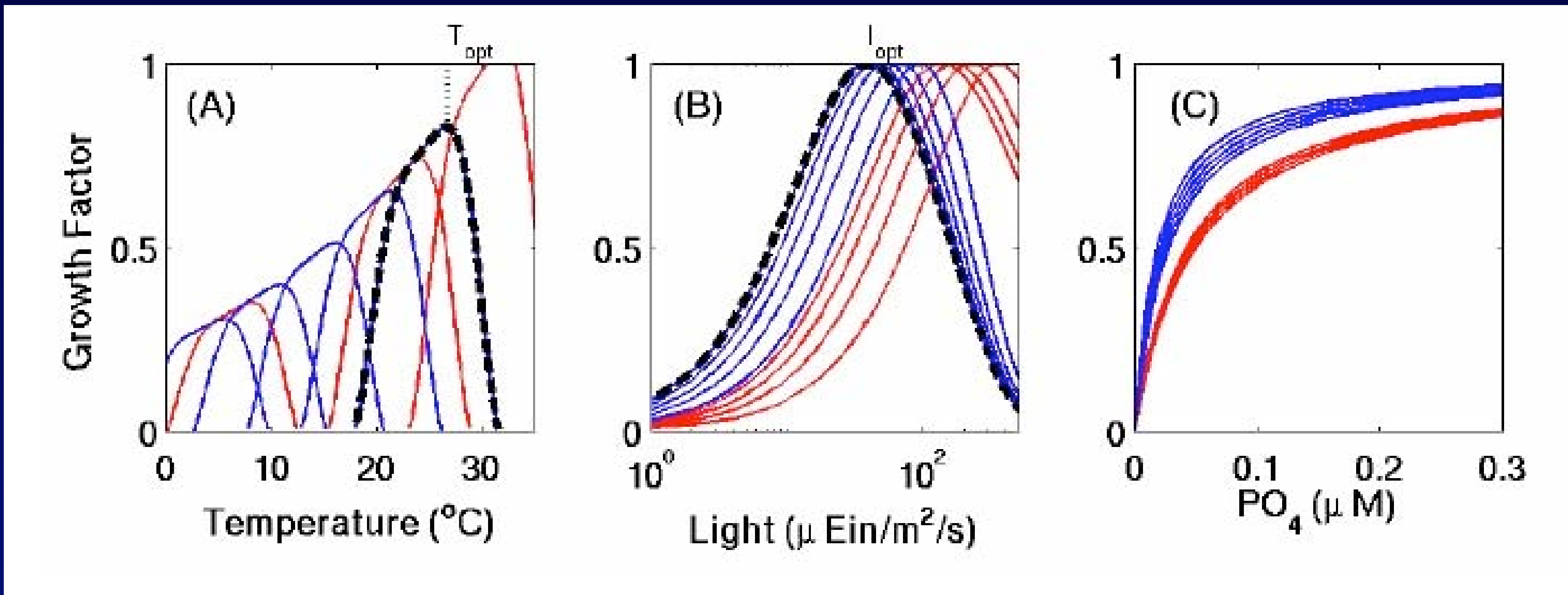
Everything (well, a lot of things) is everywhere and the environment selects



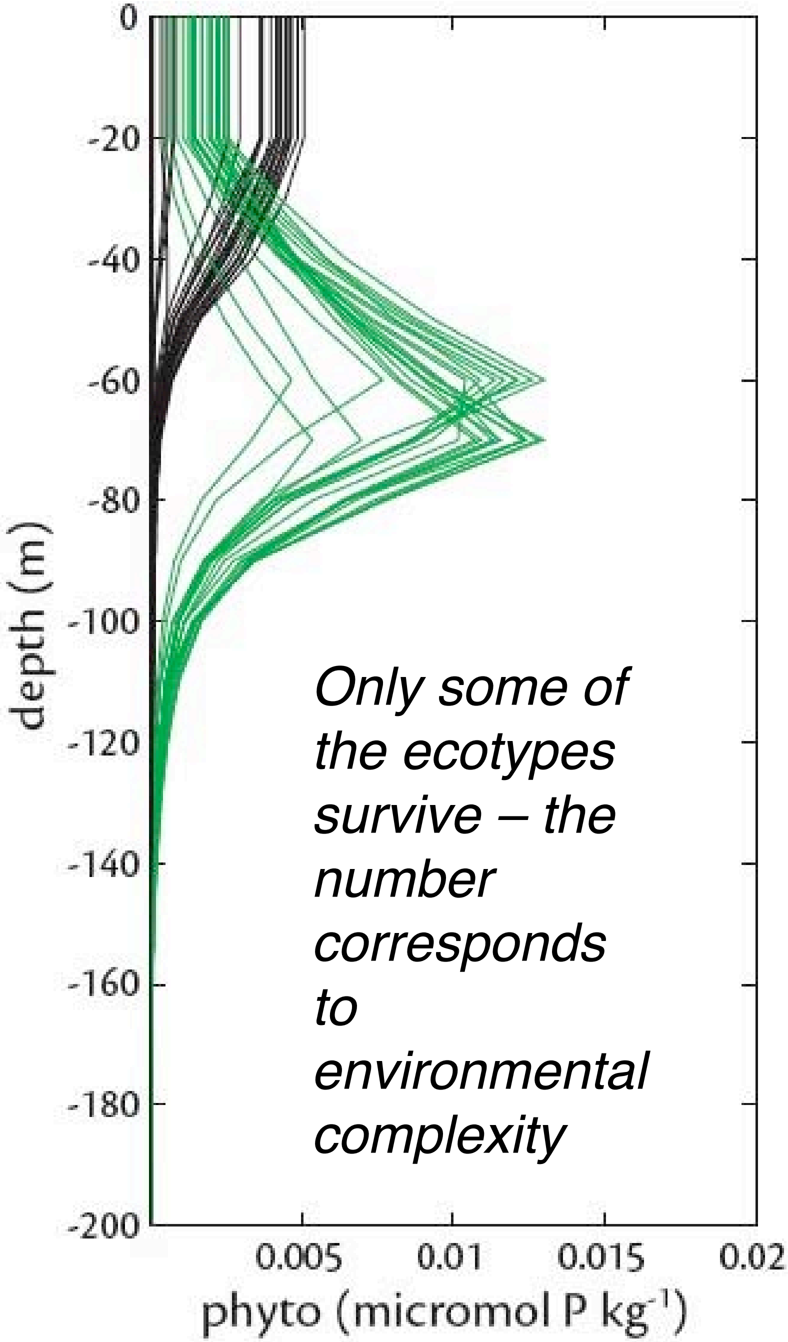
Emergent Biogeography of Microbial Communities in a Model Ocean

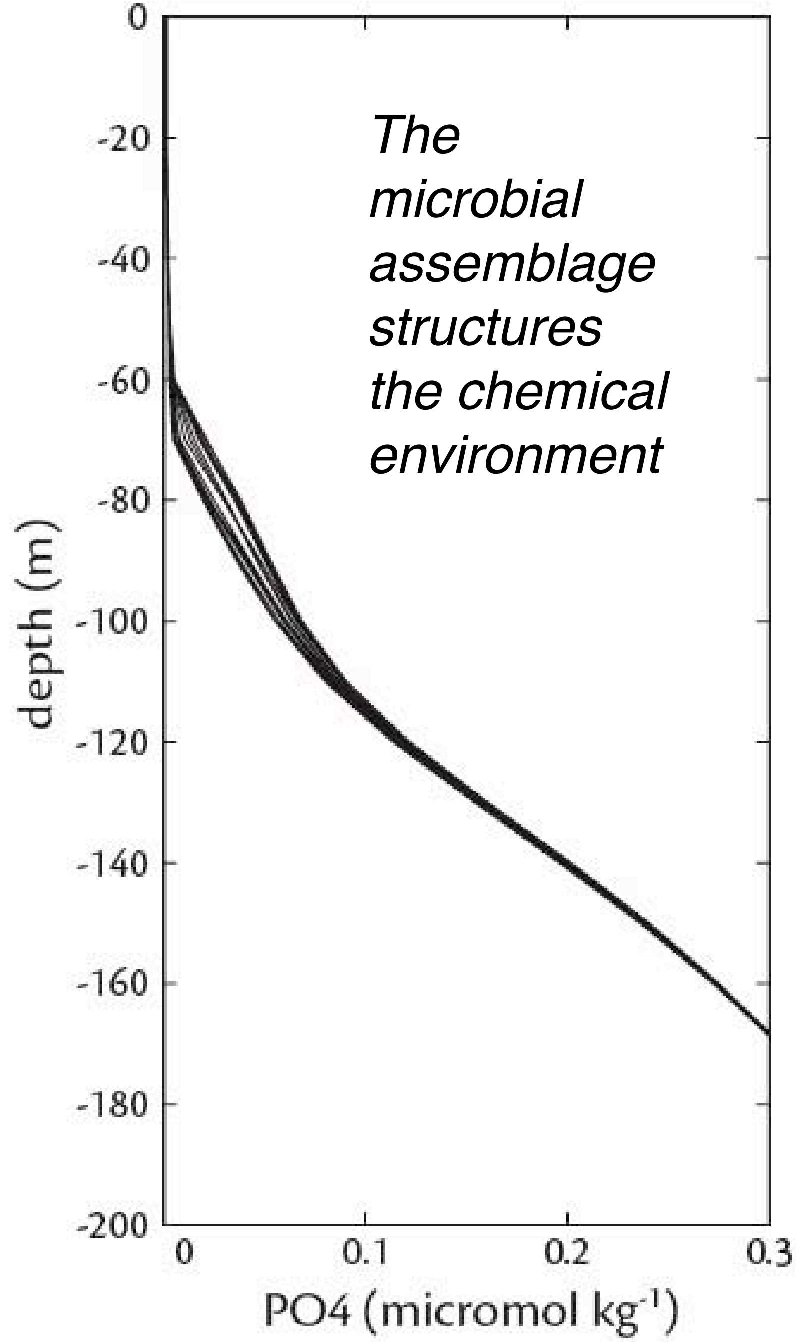
Michael J. Follows,[1]* Stephanie Dutkiewicz,[1] Scott Grant,[1,2] Sallie W. Chisholm[3]

SCIENCE VOL 315 30 MARCH 2007 1843

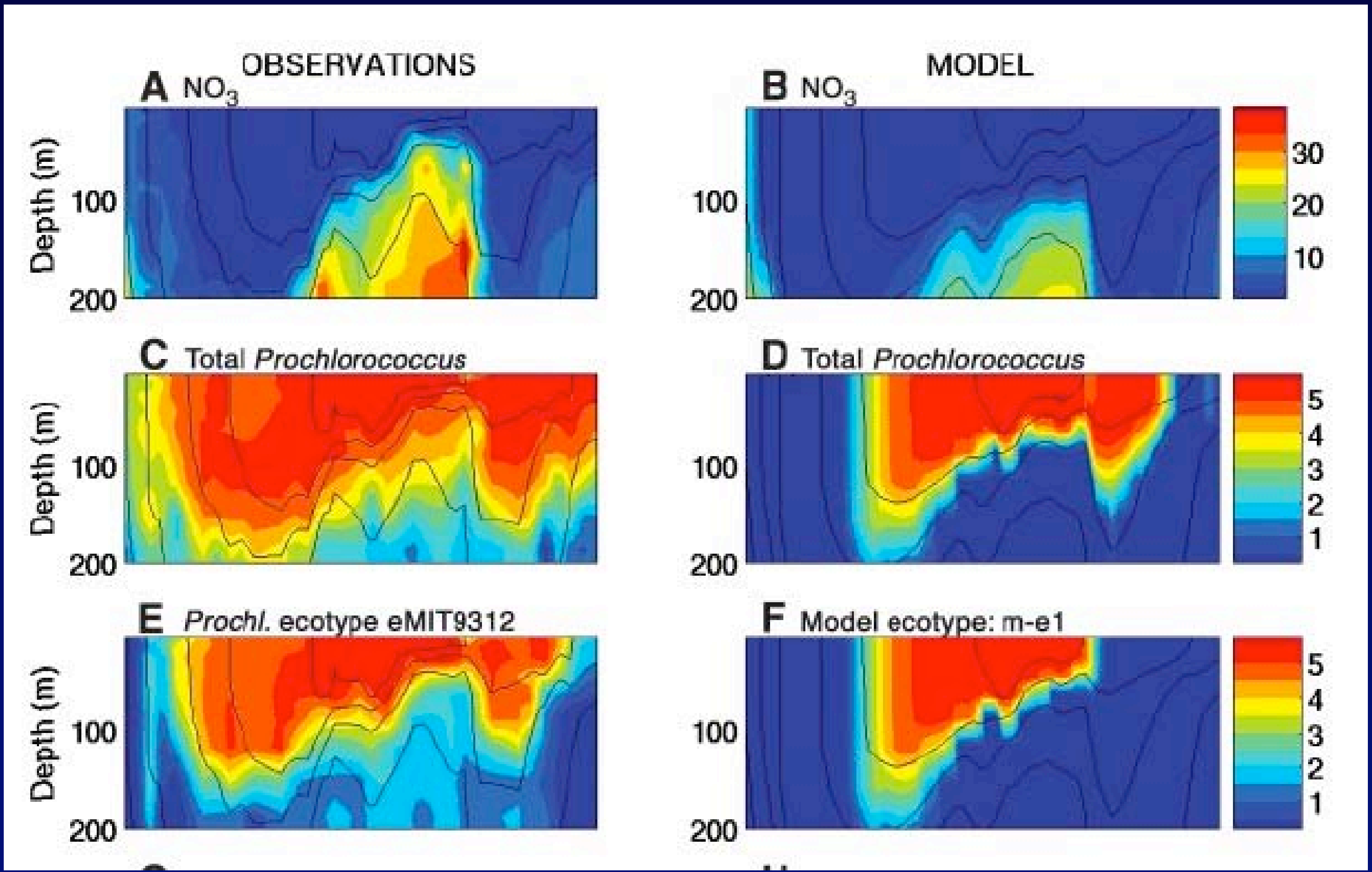
Natural selection *in silico*

Rothstein et al. 2006





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



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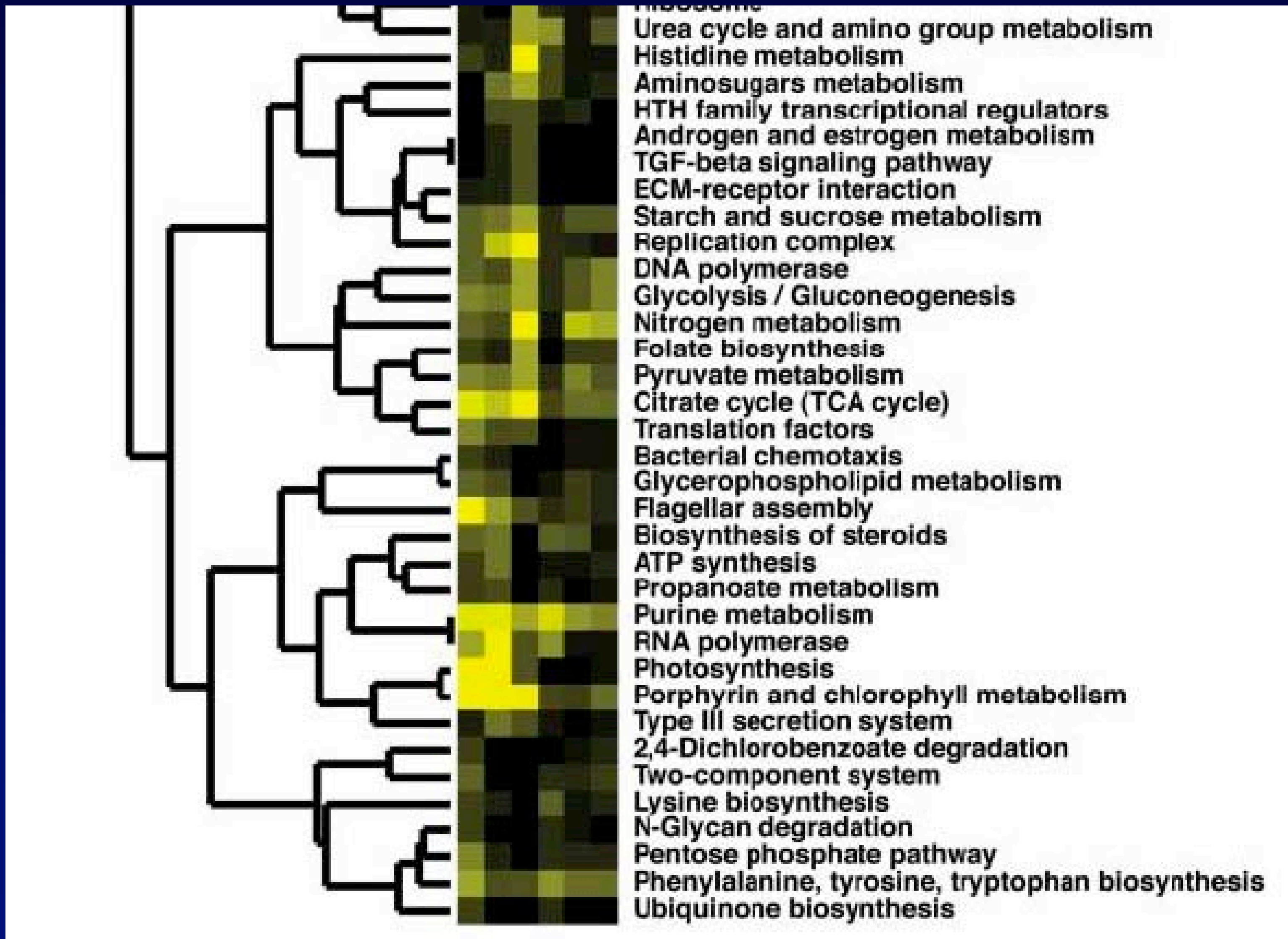
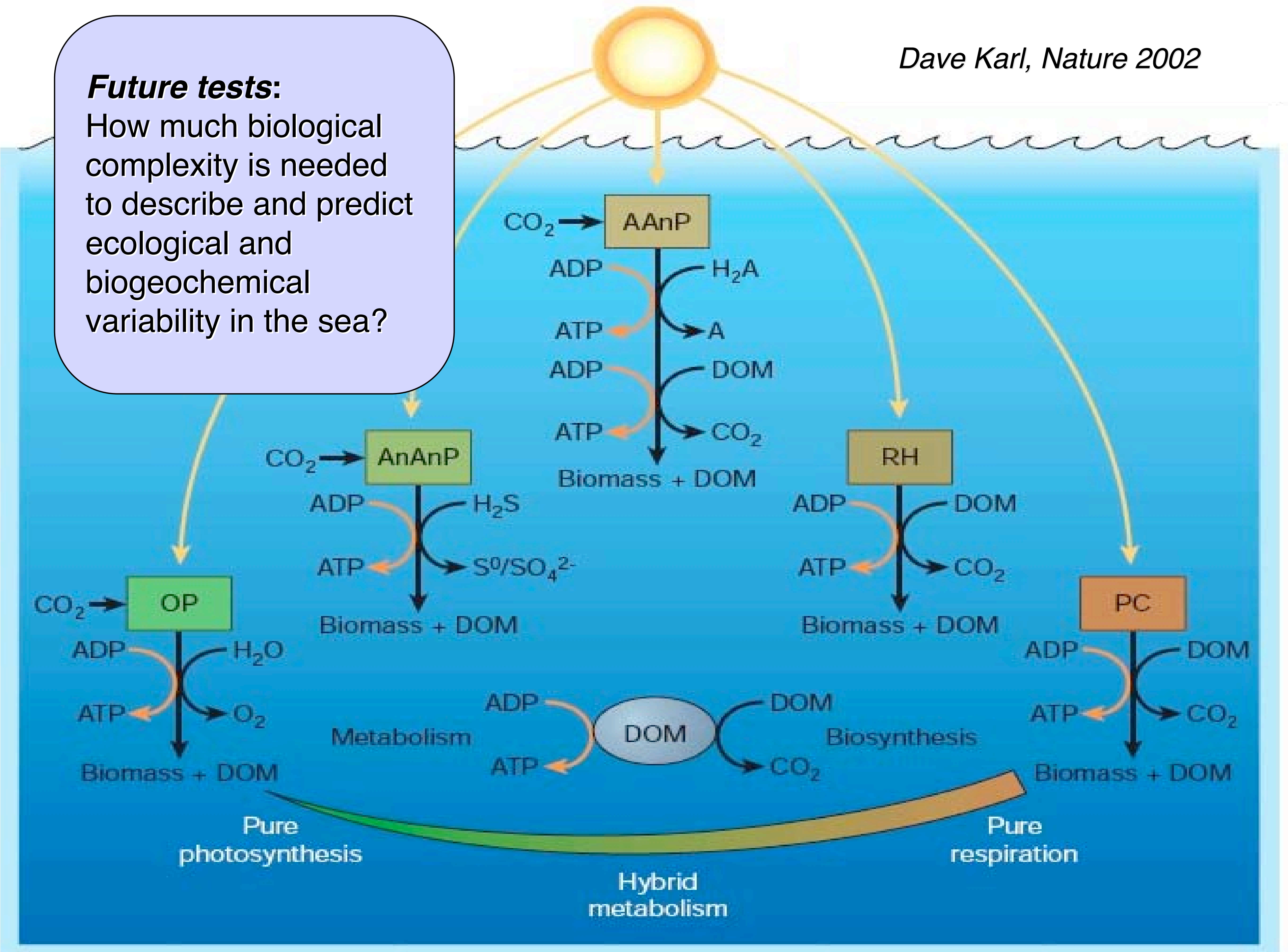
Future steps:
Assembly and natural selection of microbial communities guided by metagenomics



John Cullen: Agouron Institute 2008

Dave Karl, Nature 2002

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



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!