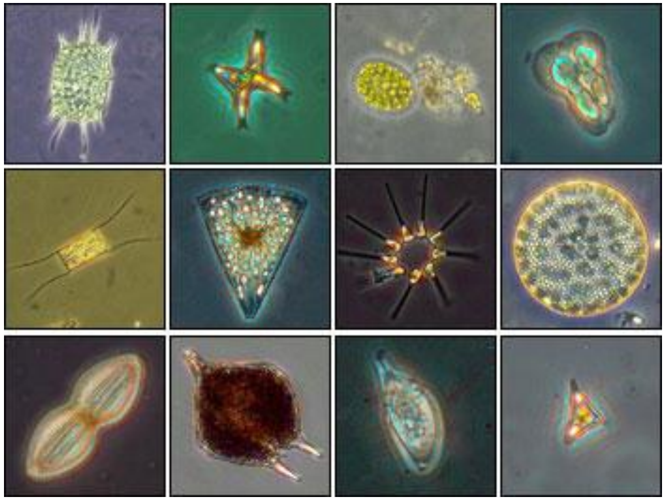
EBS 566/666 3/1/2010

Lecture 14: **Introduction to phytoplankton** (Ch.1, 2)

- Topics
  - Some general features of phytoplankton
  - Seasonal cycle of phytoplankton stocks
  - Sverdrup's critical depth hypothesis – the basics
  - Reconsidering Sverdrup's critical depth hypothesis

http://www.probalt.fi

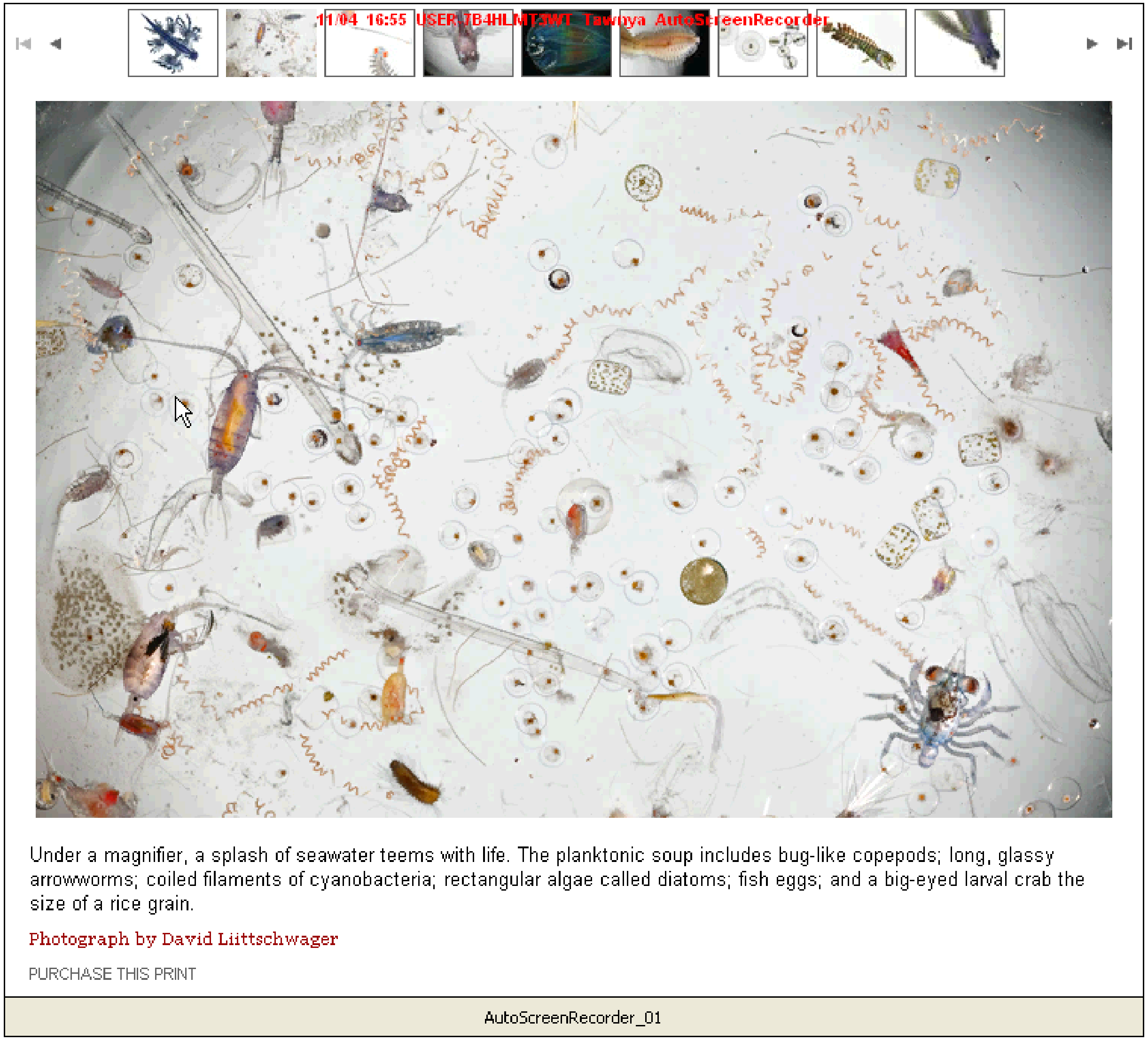


http://cmore.soest.hawaii.edu

What are phytoplankton?

- From the Greek ‘planktos’, meaning ‘drifter’ or ‘wanderer’
- Phyto- is the plant kind, zoo- is the animal kind
- Plankton can vary in size – cannot swim against a current (therefore, includes salps, jellies, etc.)
  - But many can migrate vertically
- Distributions are therefore closely connected with physical circulation and chemical composition of water masses
  - Partly because of advection and partly because of growth
- Can deduce distributions from remote sensing of chlorophyll *a* (common to all phytoplankton and plants)
  - Not as easy for zooplankton; starting to use other proxies
- **Holoplankton**: spend their entire lives as plankton
- **Meroplankton**: spend some portion of their lives as plankton (usually as larvae) and then adopt either a free-swimming lifestyle (nekton) or benthic existence

A drop of seawater



Under a magnifier, a splash of seawater teems with life. The planktonic soup includes bug-like copepods; long, glassy arrowworms; coiled filaments of cyanobacteria; rectangular algae called diatoms; fish eggs; and a big-eyed larval crab the size of a rice grain.

Photograph by David Liittschwager

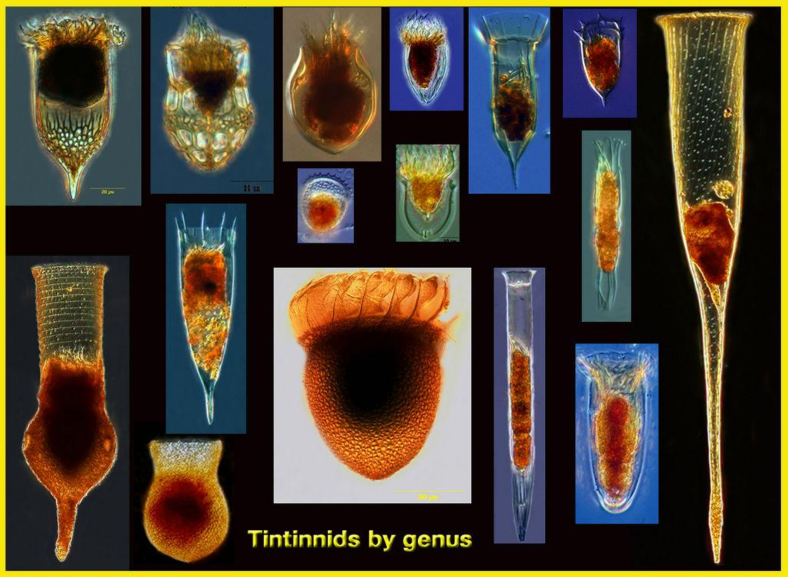
http://magma.nationalgeographic.com/ngm/2007-11/marine-miniatures/liittschwager-photography.html

Requirements for plant growth

Requirement	Land	Aquatic environment
Energy (radiation)		
Inorganic carbon		
Mineral nutrients		
Water		

Classification

- Size (Sieburth, 1978)
  - <0.2 µm – femtoplankton
  - 0.2-2 µm – picoplankton
  - 2-20 µm – nanoplankton
  - 20-200 µm – microplankton
  - 0.2-2 mm – mesoplankton
  - 2-20 mm – macroplankton
  - >20 mm - megaplankton
- Photosynthetic pigments
- Evolutionary relationships
- Functional groups



Size: why so small?

- Nutrients are limiting (dilute solution)
- Surface area: volume ratio is maximized by being small

  For a sphere:

  - SA = $4\pi r^2$; volume = $4/3 \pi r^3$
  - If r increases from 5 to 10 mm, then:
  - SA: 314 → 1256 mm^2 (4x increase in SA)
  - Vol: 500 → 4000 mm^3 (8x increase in vol)

Why so small?

- **Molecular diffusion** – rate of supply is limited by diffusion (Munk & Riley, 1952)
  - Turbulent shear occurs at scales larger than single cells
  - Kolmogoroff length scale (size of smallest turbulent eddy):
  - $L\nu = 2\pi(\nu^3/\varepsilon)^{1/4}$
- **Fick's Law of molecular diffusion**:
  - Flux (amount arriving/time) = $-AD\ \delta C/\delta x$

D is diffusion coefficient (specific to substance)

$\delta C/\delta x$ is the concentration gradient (away)

A = absorbing surface area

Blooms

- **Bloom** = a rapid multiplication of cells resulting in a dramatic increase in biomass (stock)-typically, >10^6 cells L^{-1}

- Standing stock is a balance between growth (bottom-up) and grazing (top-down) control

- Blooms occur with sufficient light and nutrients (therefore tightly coupled to physical and chemical processes)

Consequences of blooms

- Food web implications (sets how much growth and what type)
- Oxygen production/depletion
- Metal speciation (pH, ligand production)
- Harmful species (toxins)
- Light reduction/shading
- Temperature
- Carbon export
- Fouling/clogging of fish gills

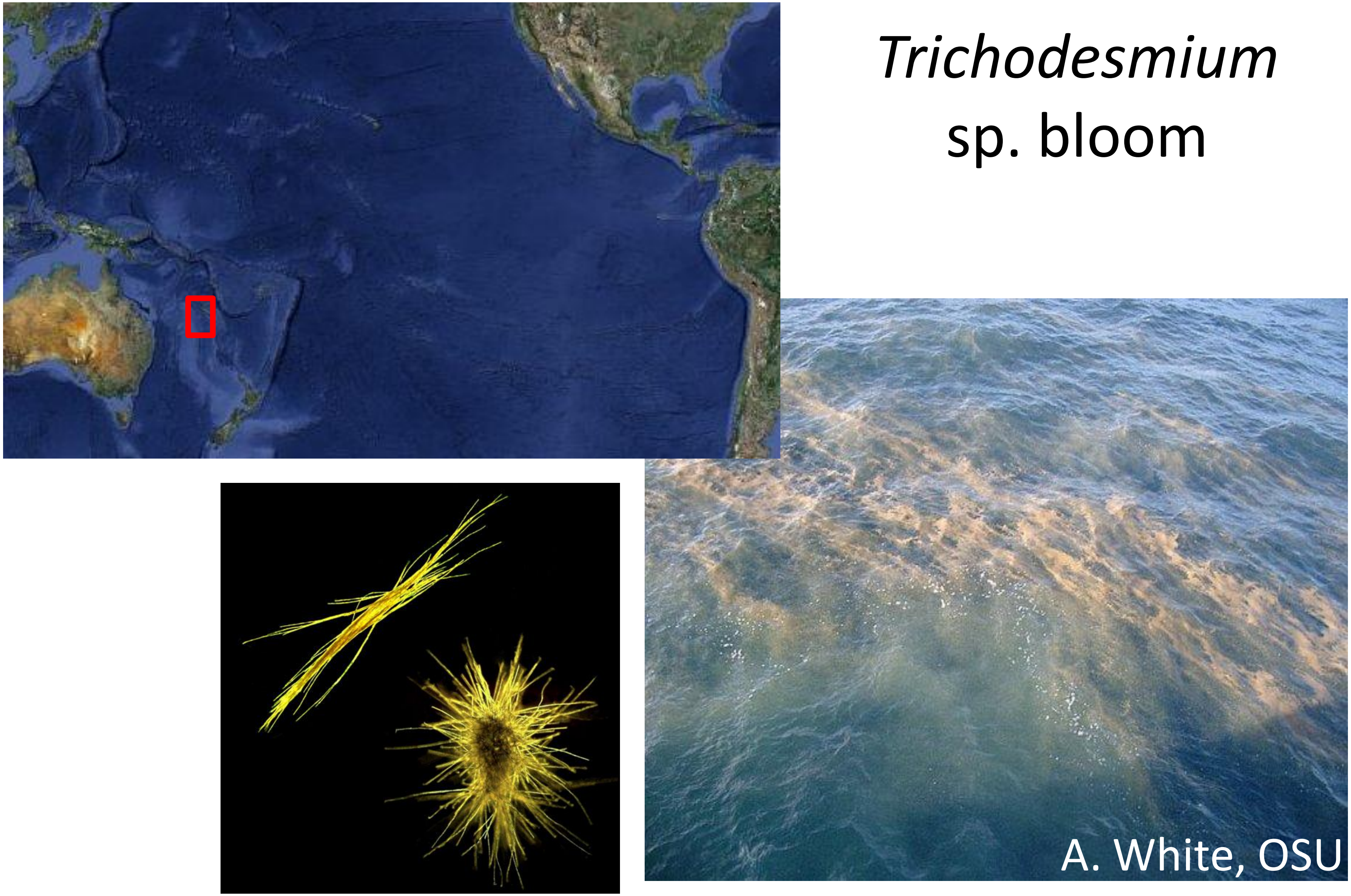
Algal blooms can be viewed by satellite remote sensing of chlorophyll *a*

www.enviswb.gov.in

Early on, knowledge of blooms was based on limited observations, generally close to marine laboratories (North Atlantic)

Goal was to understand when and why blooms occur

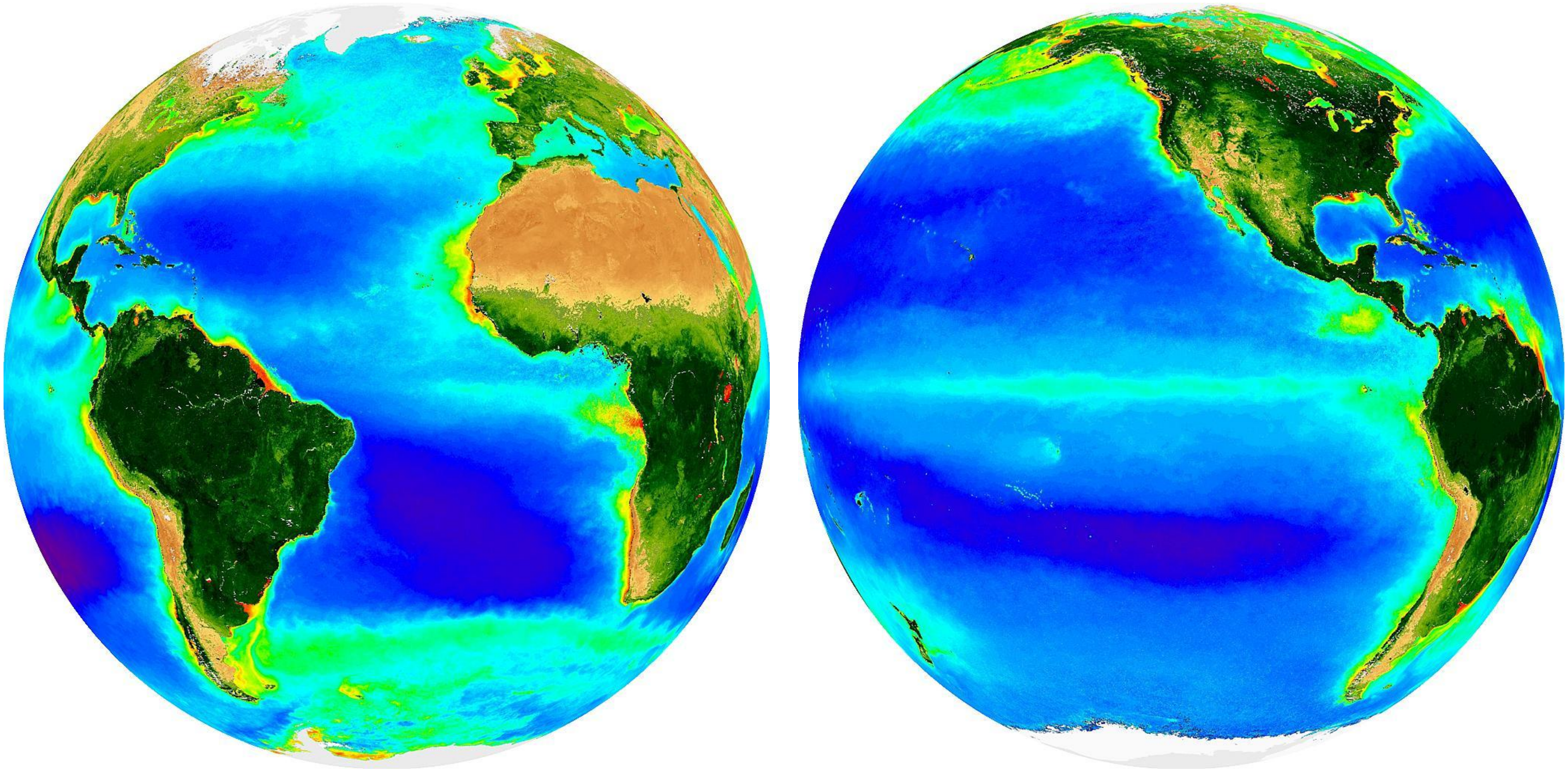
Trichodesmium sp. bloom



A. White, OSU

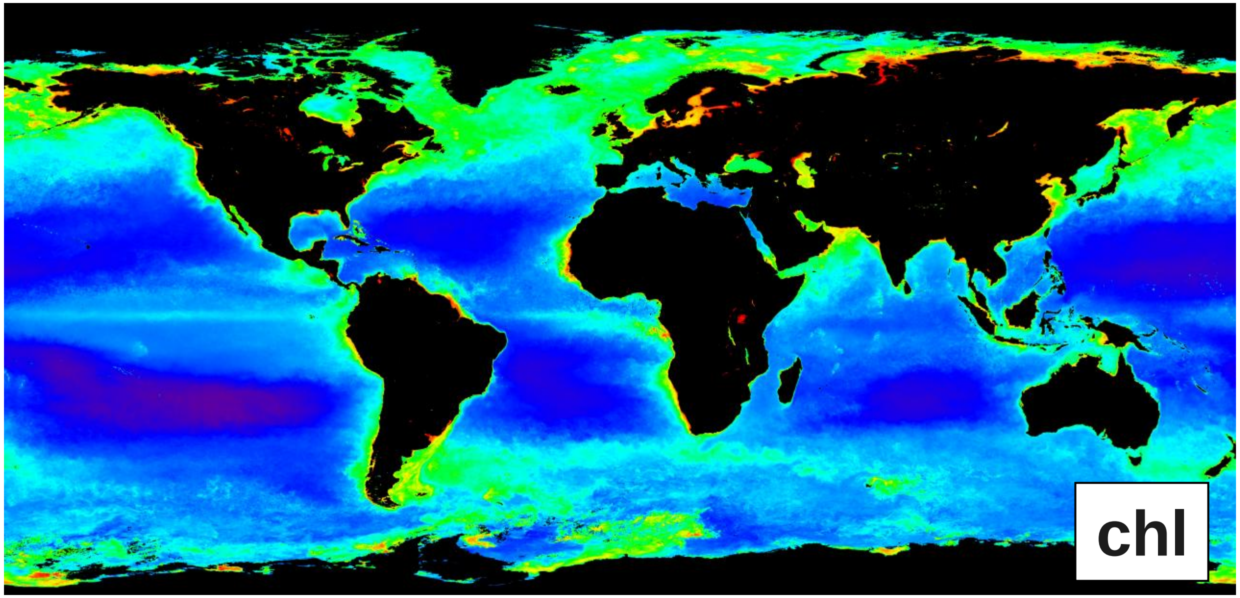
http://www.oceanleadership.org

Patterns observed in chl *a* distributions reflect oceanographic conditions

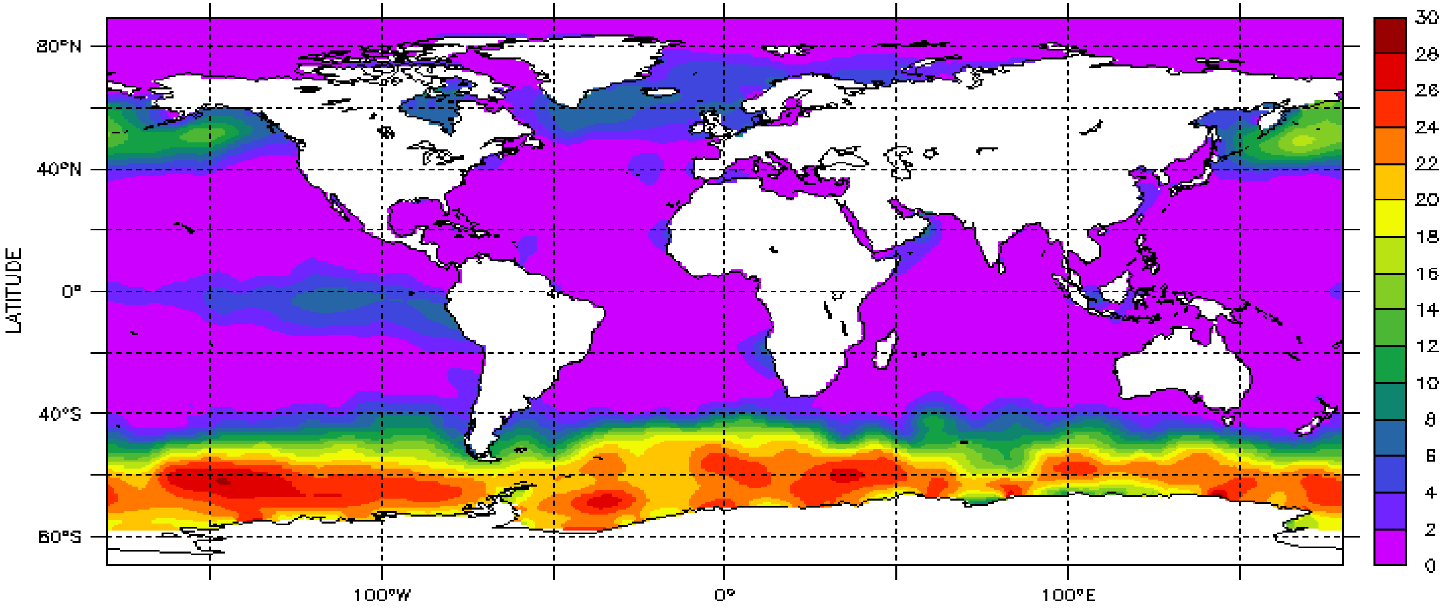


SeaWiFS (Sea-viewing Wide Field of View Sensor) satellite-derived chlorophyll

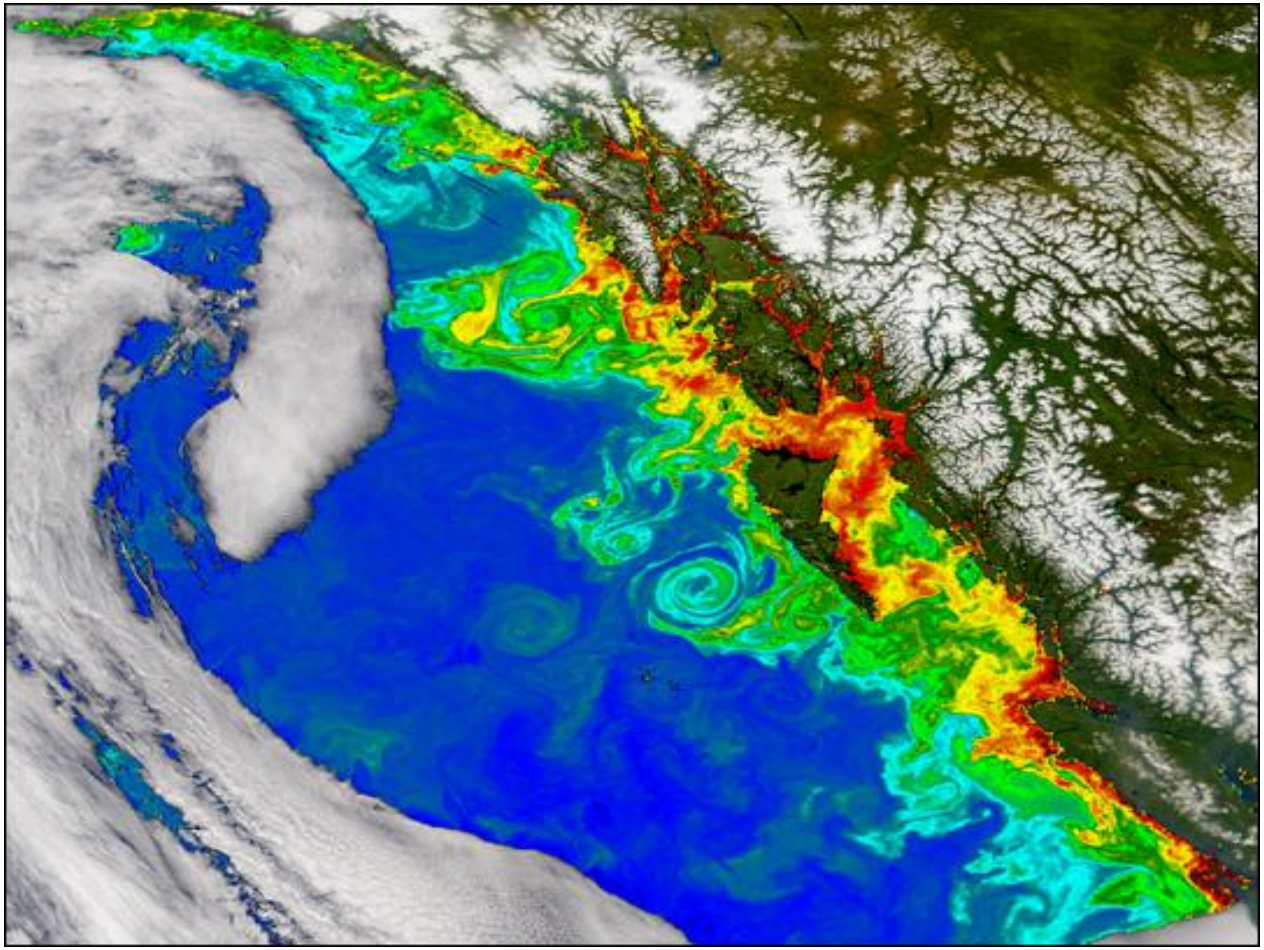
Based on light absorption



Based on in situ wet chemistry

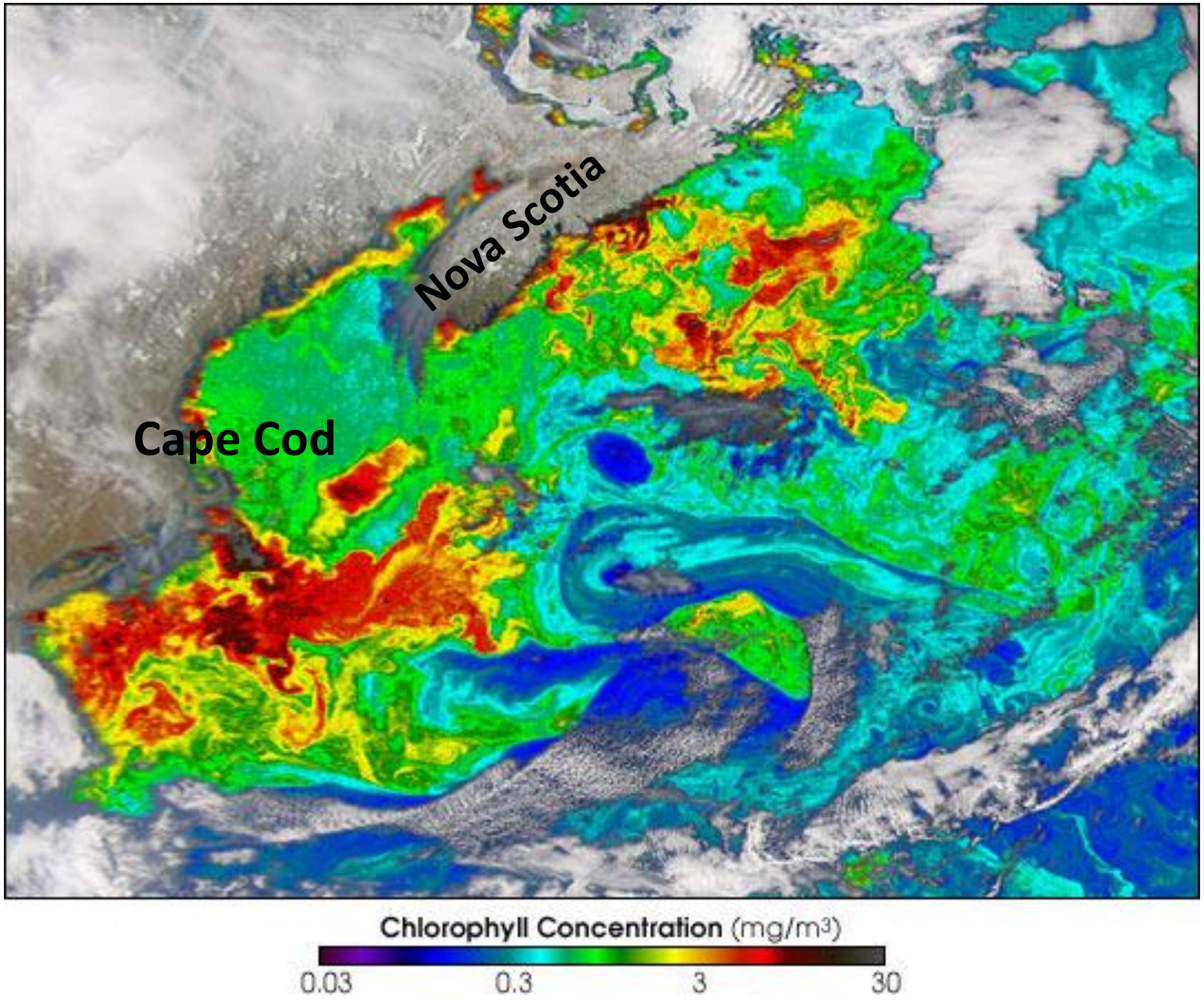


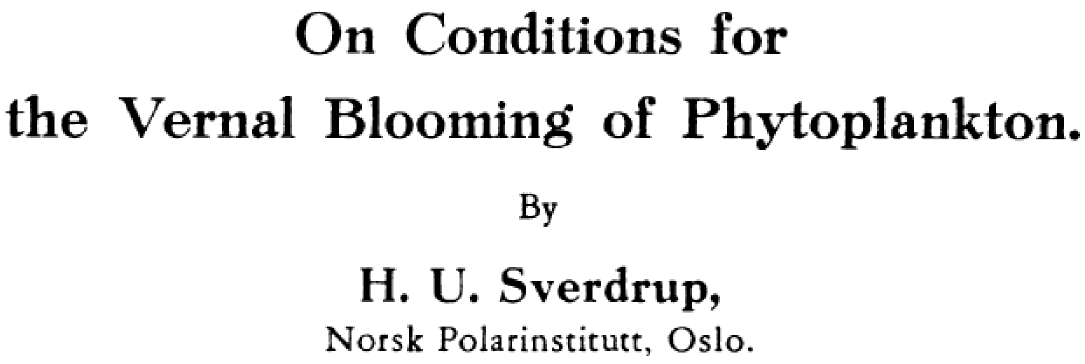
Nitrate (μM)



How much of what we see reflects in situ growth vs. advection?

The Spring Bloom, North Atlantic – what causes it?





On Conditions for the Vernal Blooming of Phytoplankton.

By

H. U. Sverdrup,
Norsk Polarinstitutt, Oslo.

1953

Google citation count: 561

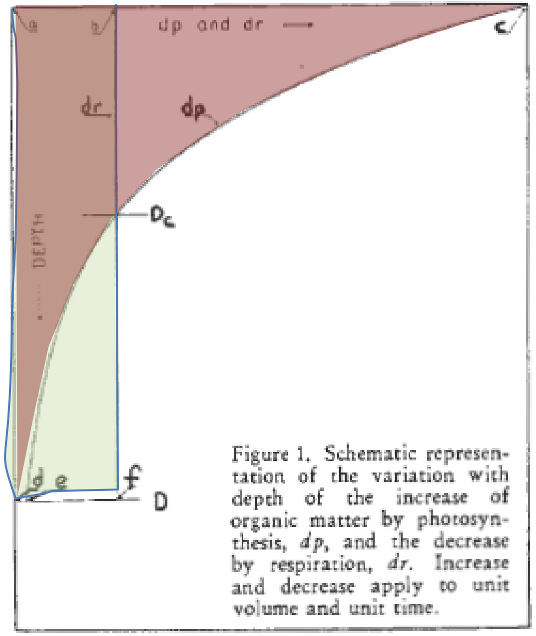
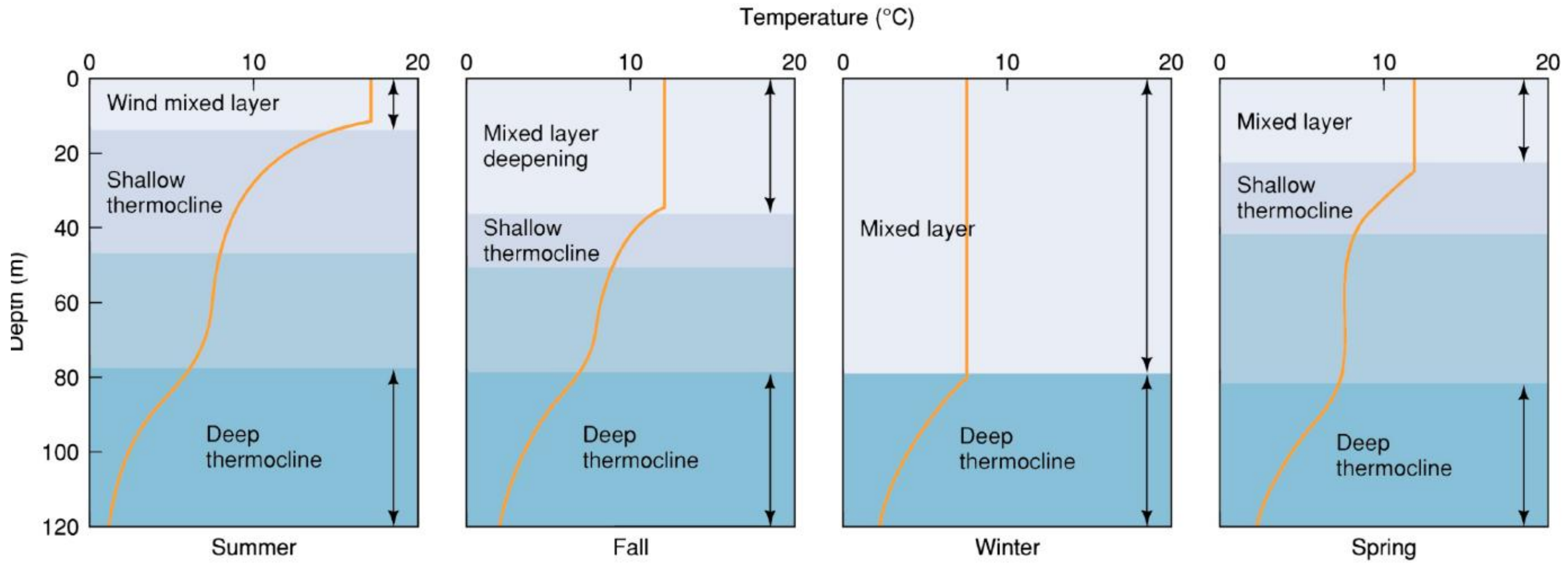


Figure 1. Schematic representation of the variation with depth of the increase of organic matter by photosynthesis, *dp*, and the decrease by respiration, *dr*. Increase and decrease apply to unit volume and unit time.

Net phytoplankton growth occurs when area acd > abdf

Evolution of seasonal thermocline depth



Permanent Thermocline: temperature gradient with depth that does not change. Wind mixing does not affect deep ocean due to permanent thermocline

Seasonal Thermocline: Surface heating during summer causes increased stratification in euphotic zone

Stratification

- Layering of the ocean into depth “strata”
- Depends on density (ρ), with less dense layers on top of more dense layers
- Assessed in many ways; a common estimate for oceans is the Brunt-Väisälä buoyancy frequency (*N*), the frequency at which a vertically displaced parcel will oscillate within a statically stable environment

$$N = \sqrt{-\frac{g}{\rho}\frac{d\rho}{dz}}$$

- Mixed layer depth is commonly considered to be the depth at which a change of 0.125 units of sigma-t or sigma-θ (density anomaly) is observed (Millero et al., 1980)

Density anomaly

- Density of pure water: 1000 kg/m^3
- Density of seawater: 1022-1027 kg/m^3
- Easier to refer to density anomaly (referenced to fresh water)
- Density anomaly: Density – 1000 kg/m^3 = sigma-t (σ_t), the density anomaly that a water parcel would have if brought to the surface
- Potential density anomaly: refers to the density that the water parcel would have if it were brought to the surface, including the change in temperature that would occur due to the changes in pressure felt by the fluid as it moves to the surface (sigma-theta, σ_θ)

Mixing

Convective mixing

- Driven by heating and cooling
- Volume is a function of temperature and pressure [ρ (T, S, p)]

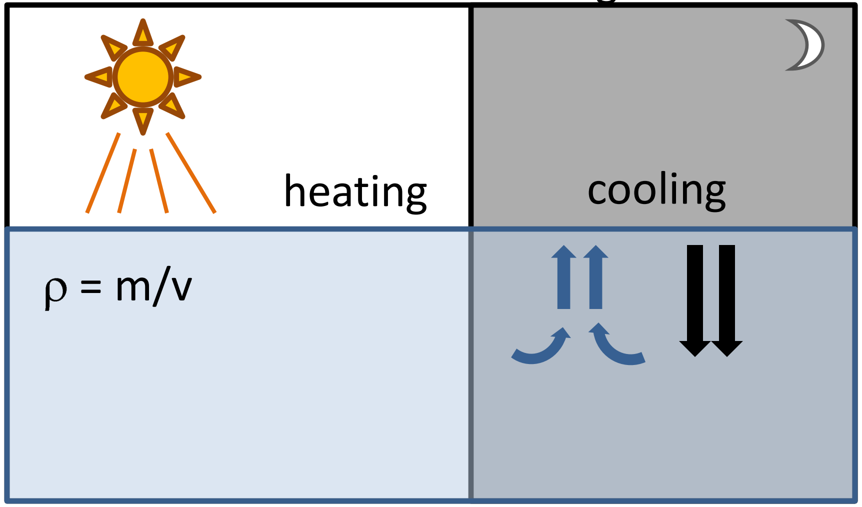
Wind-driven mixing

- Winds result from differences in pressure between sites (air travels from H→L pressure)
- Wind stress (T, or τ): horizontal force of wind on sea surface

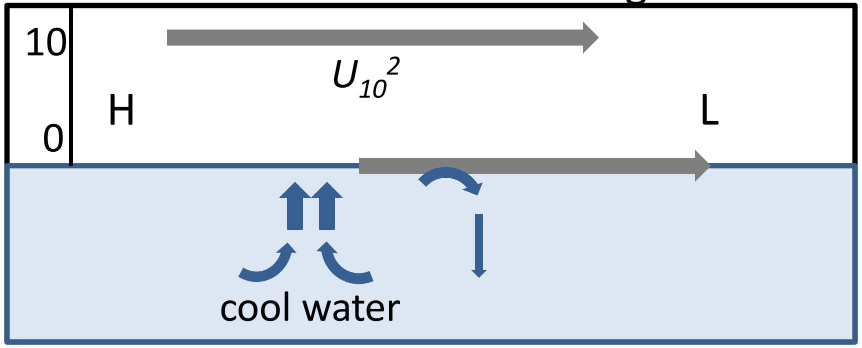
  $T = \rho_a C_D U_{10}^2$

  ρ_a is the density of air (1.3 kg m^{-3}), C_D is drag coefficient, U_{10} is wind speed at a height 10 m above the sea surface

Convective mixing

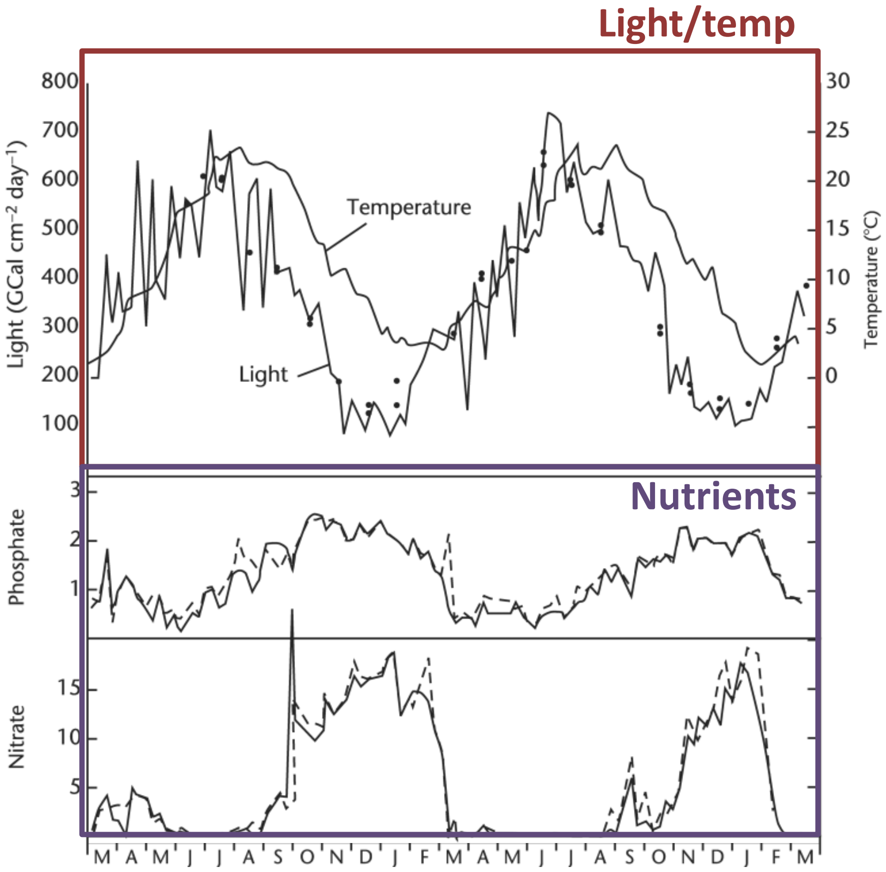


Wind-driven mixing

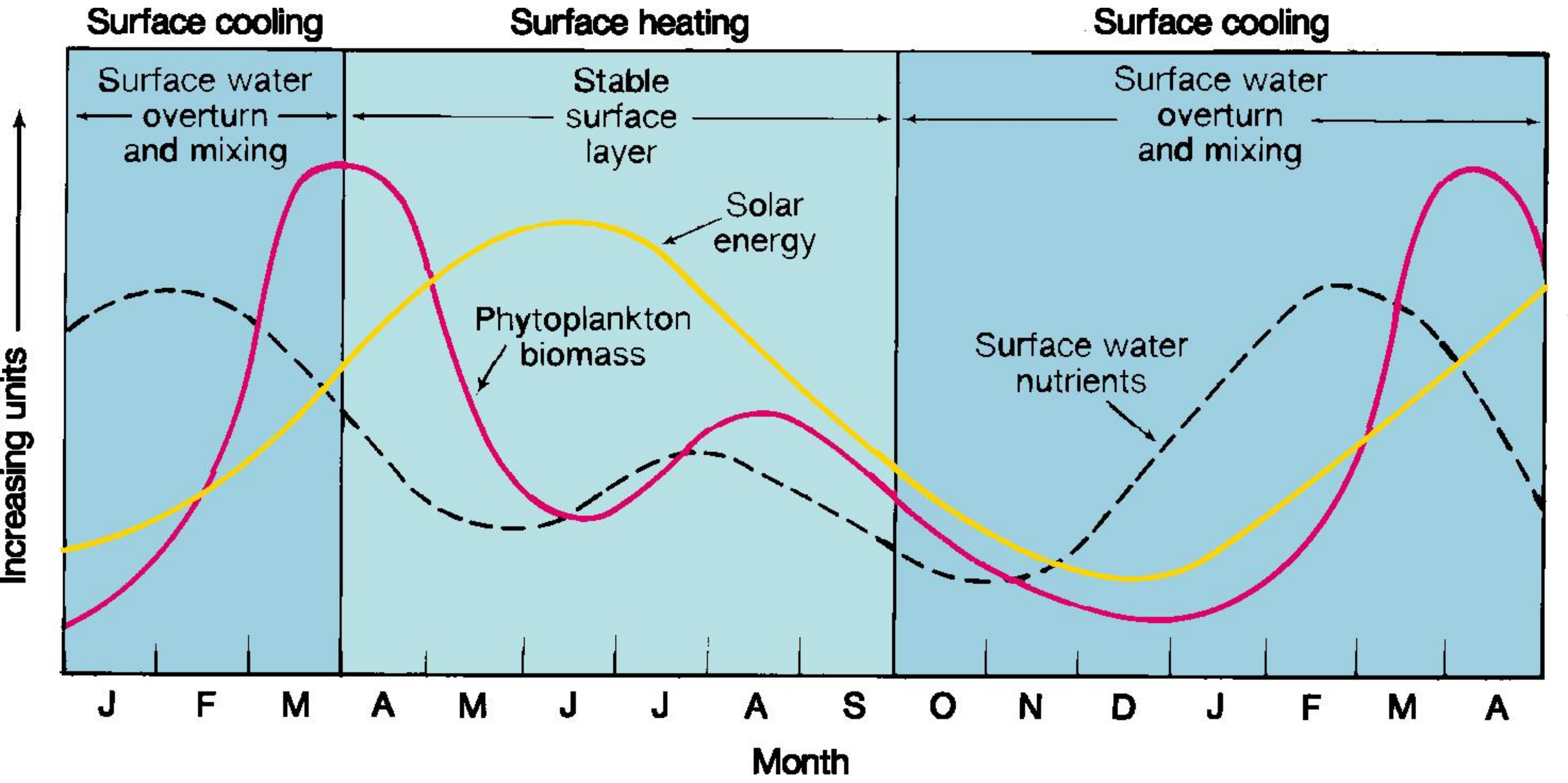


Critical Depth Theory

- CDT sought to explain the dramatic Spring Bloom observed each year in the North Atlantic Ocean
- Gran & Braarud (1935; Sverdrup, 1953)
- To support phytoplankton growth, need light and nutrients (carbon is plentiful)
    - Light and mixing and/or stratification (nutrients are implied)



Annual cycles of phytoplankton, nutrients, solar energy



- What is missing in this representation?

Critical Depth Theory (Sverdrup, 1953)

- P is phytoplankton stock
  - Photosynthesis (PS) depends on light, therefore P declines exponentially according to Beer's Law ($I_z = I_0 e^{-kz}$)
- Z is depth (m)
- Respiration (R) is invariant over depth
- Gross photosynthesis = total photosynthesis
- Net photosynthesis = total photosynthesis – respiration (OR community respiration)
- **Critical depth** = depth below which integrated photosynthesis < integrated respiration
- **Compensation depth** = depth at which photosynthesis = respiration (shallower than critical depth) PS – R = 0

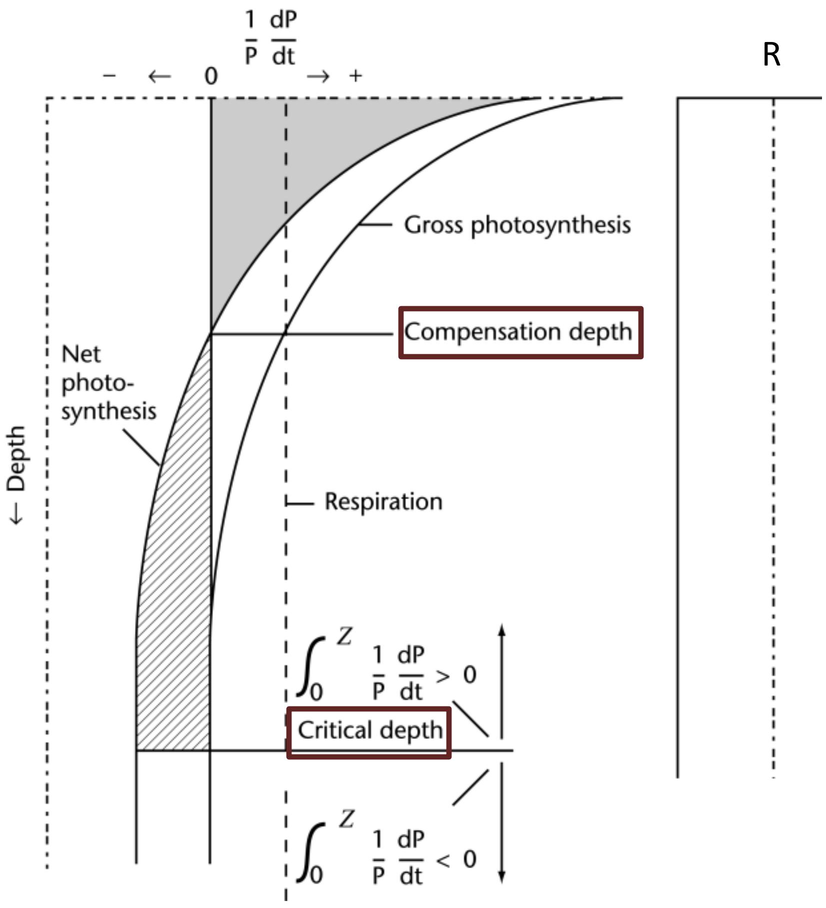
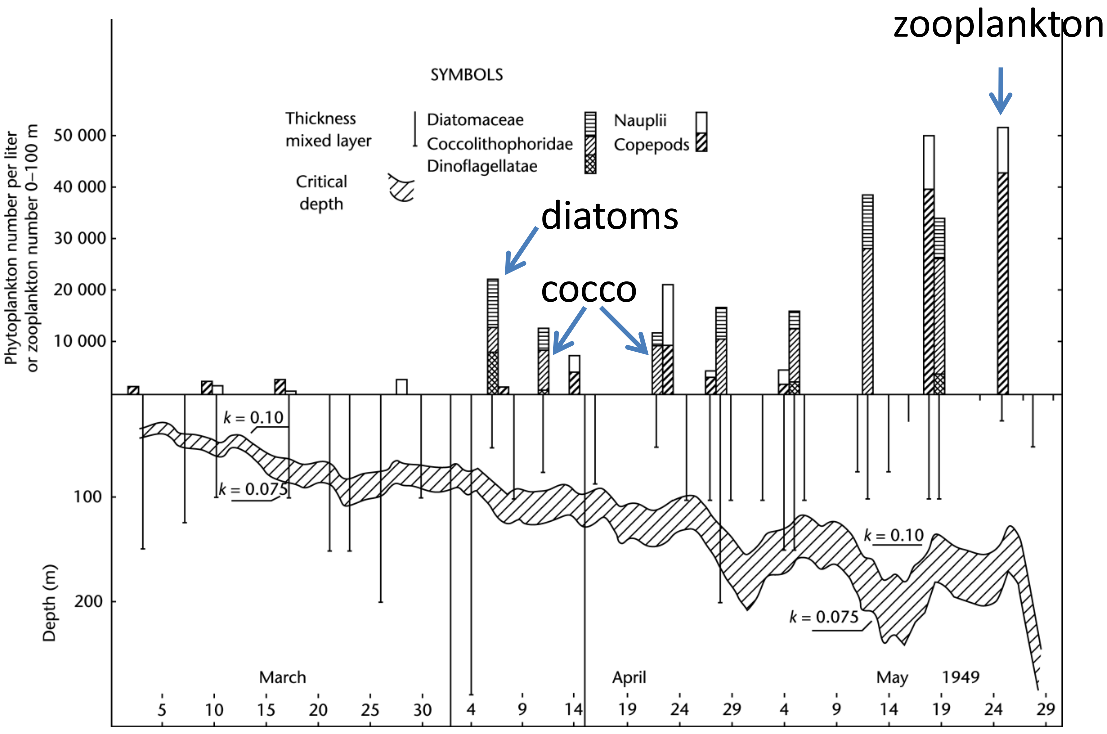


Fig. 1.3

Critical Depth Theory in the North Atlantic

- Critical depth **increases** and mixed layer depth **decreases** as solar energy increases from winter-spring-summer
- Bloom forms after seasonal thermocline established
- Succession from diatoms to coccolithophores and dinoflagellates
- Succession from phytoplankton to zooplankton



zooplankton

diatoms

cocco

Fig. 1.4

Underlying principles

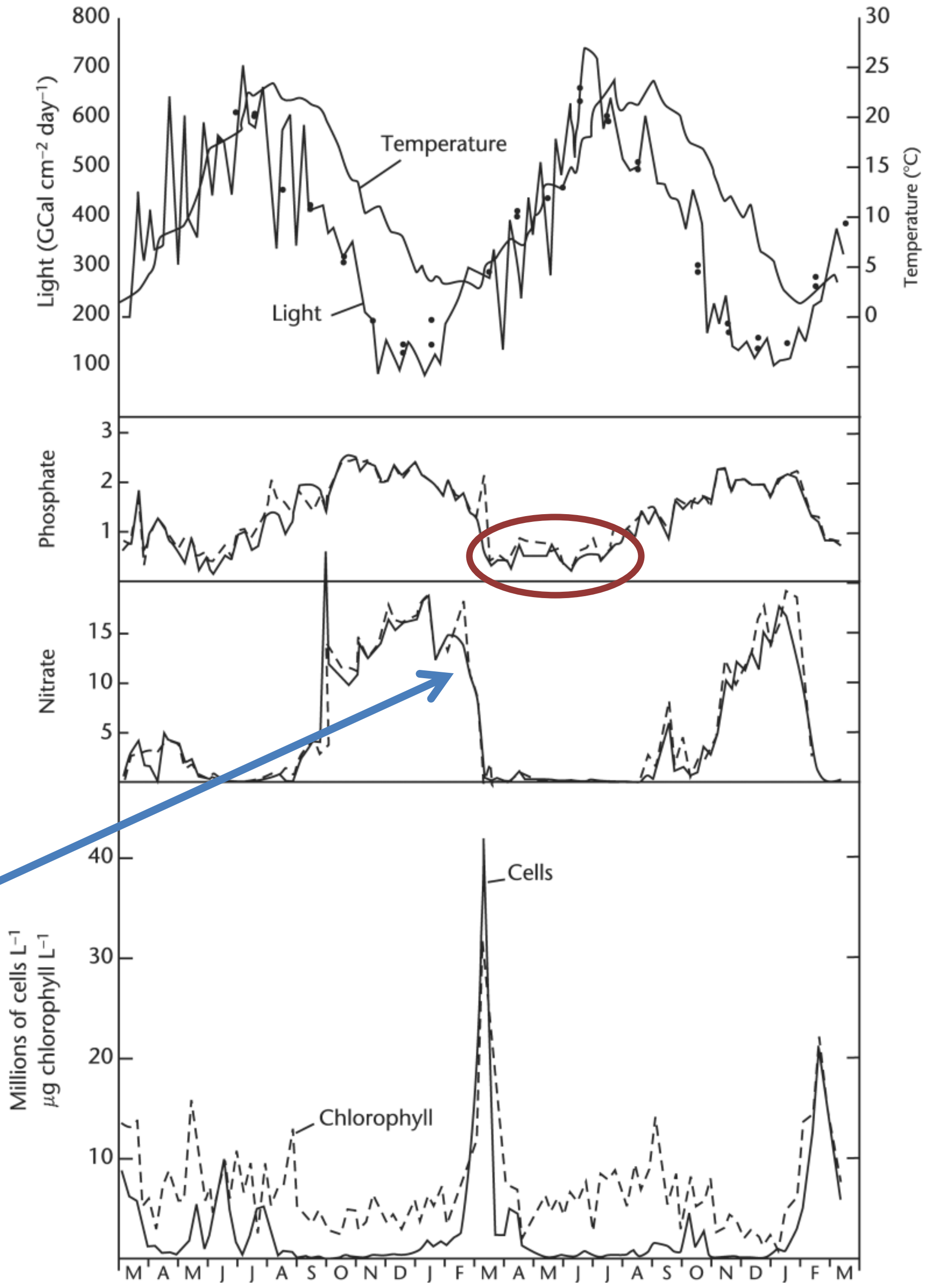
- Requirements for growth must be met
- Physics and biology are coupled
  - Annual cycle of establishment of stratification and erosion of mixed layer
  - Dynamics of mixing are important
- Several assumptions are made (today, much effort going into showing how these assumptions are violated)

7 assumptions of Critical Depth Theory

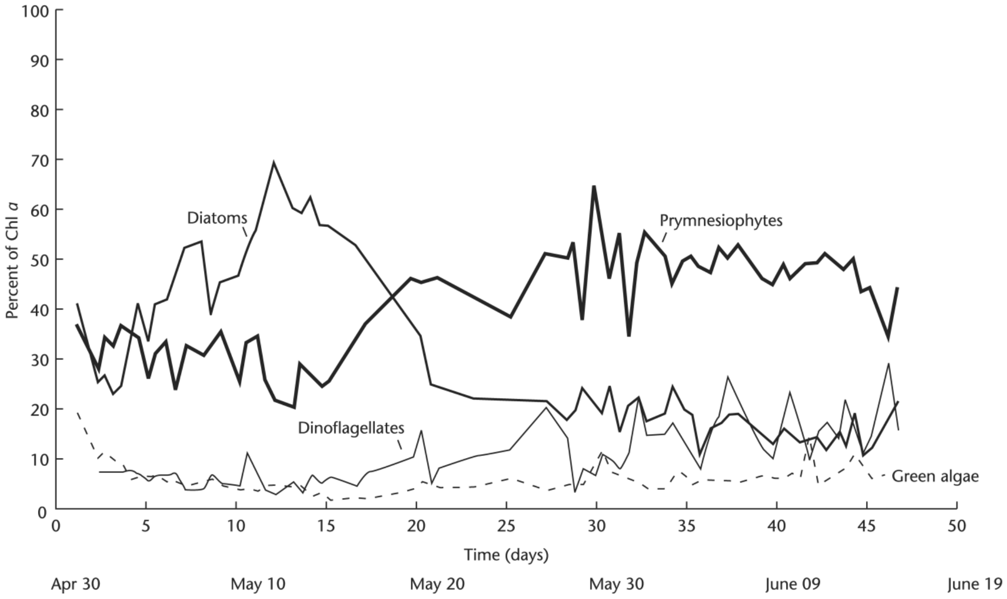
1. The mixed layer is thoroughly mixed
2. Plankton are evenly distributed by turbulent mixing
3. No nutrient limitation
4. light extinction coefficient (*k*) is constant throughout the euphotic zone
5. assume that the wavelengths of importance are between 420 and 560 nm, and that light energy at longer and shorter wavelengths is almost entirely absorbed in the first few meters
6. Primary production (production of organic matter) is proportional to available radiant energy
7. Energy, I_c, at the compensation depth (D_c) is known (D_c = depth at which PS = R)

General observations

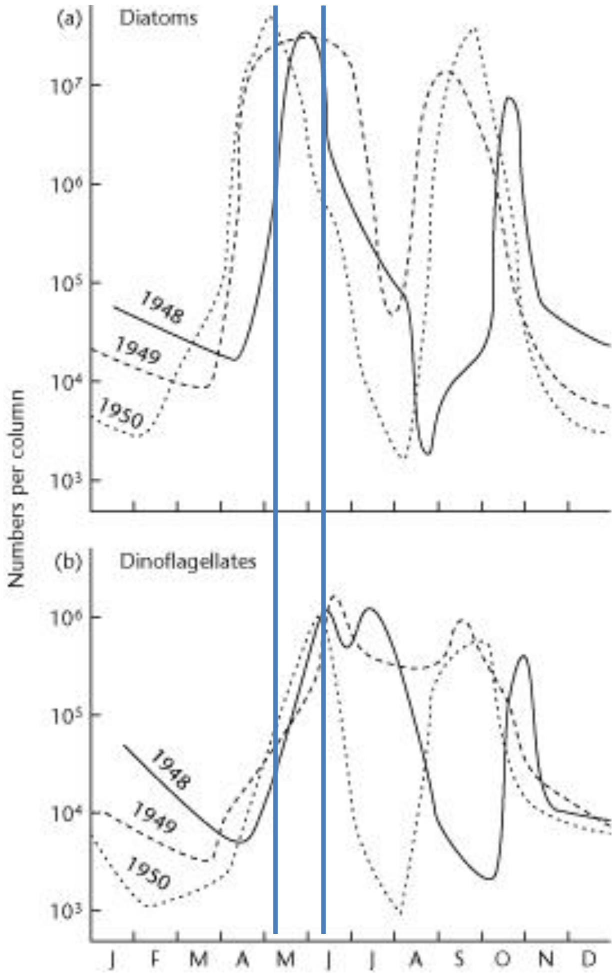
- As light increases, temperature increases
- Nitrate and phosphate are highest when temperature and light decline
- Nitrate depleted before phosphate in this case
- Blooms vary in timing (initiation) and magnitude



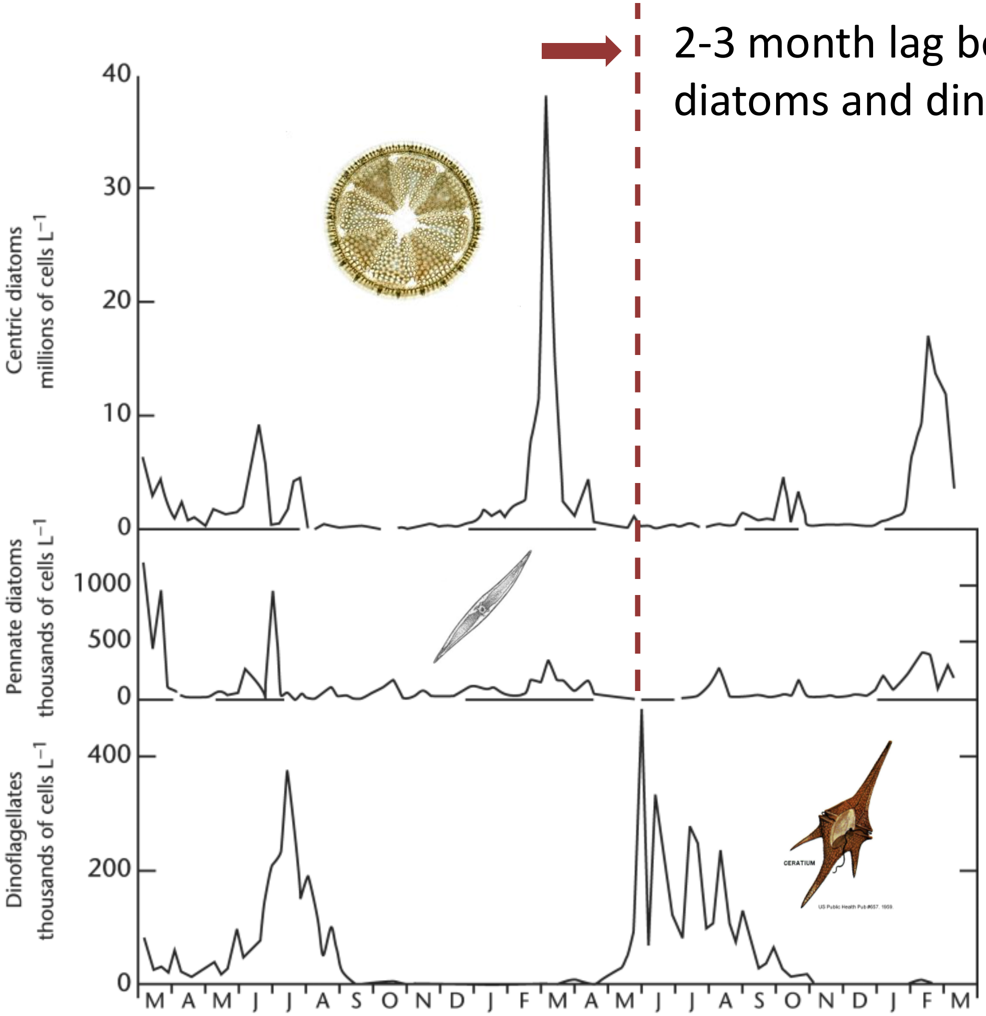
Species successions are often observed



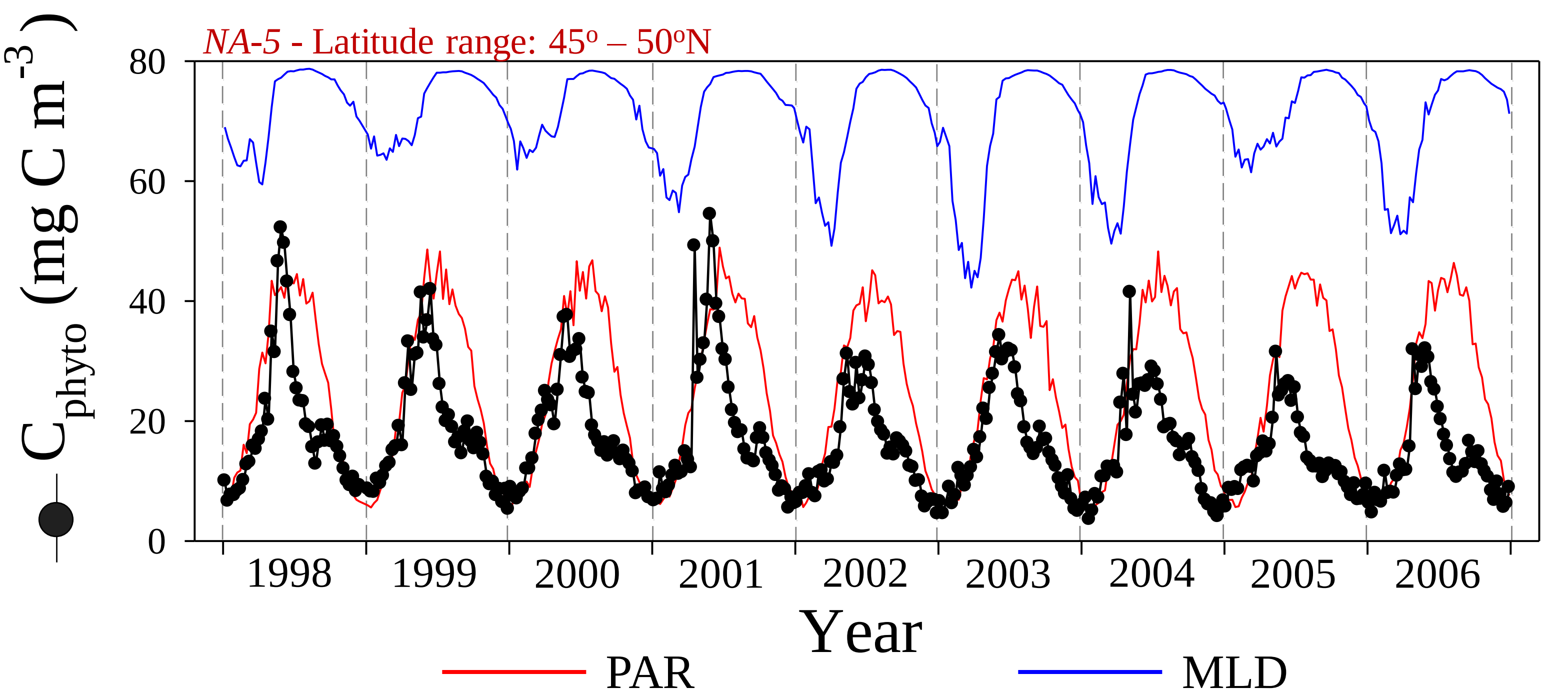
As diatoms decline, prymnesiophytes increase



As diatoms decline, dinoflagellates increase

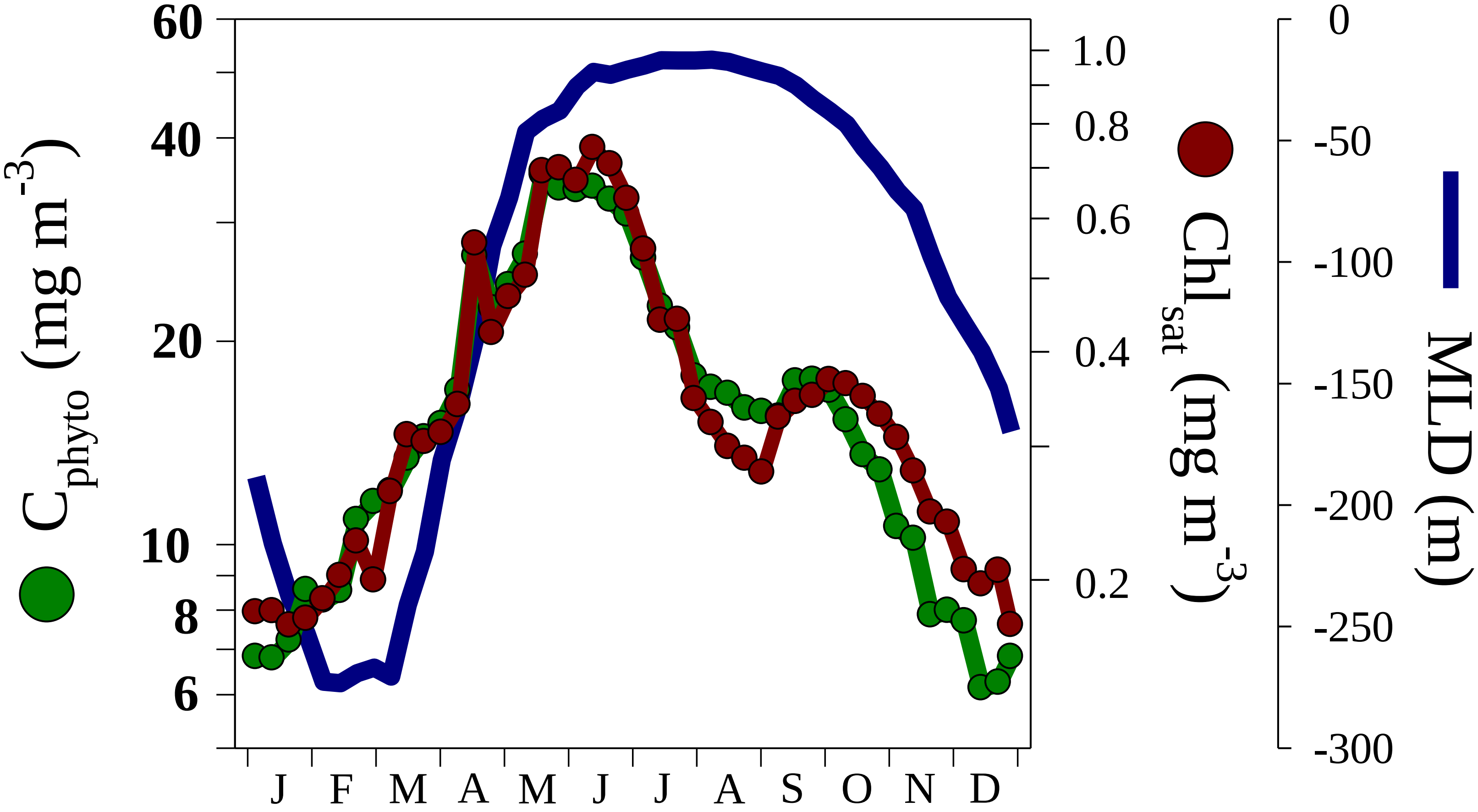


2-3 month lag between centric diatoms and dinoflagellates

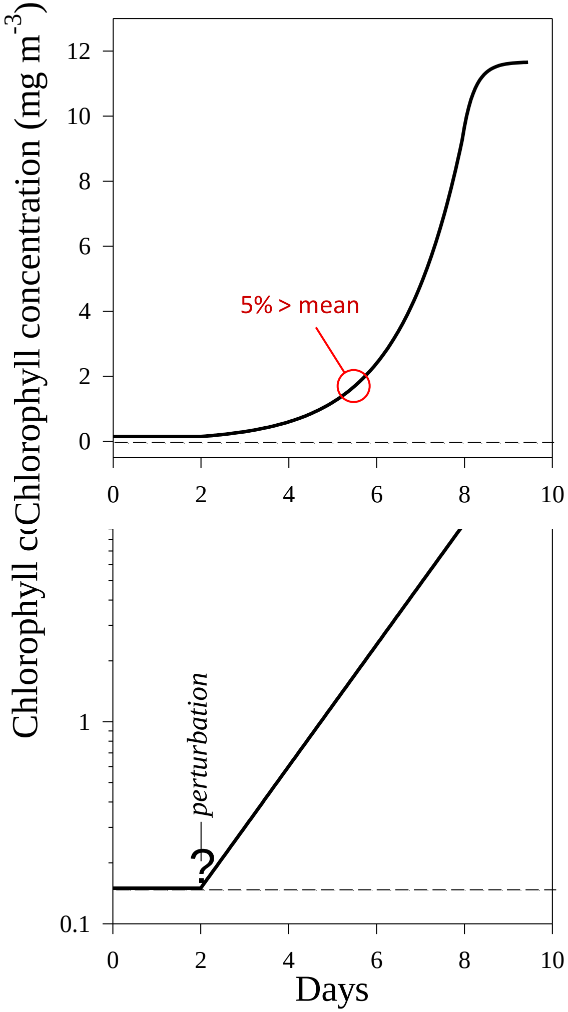


- peak biomass occurs in spring
- coincident with rising PAR and shoaling MLD
- also associated with rapid rise in primary production

Conclusion: phytoplankton in the North Atlantic exhibit a repeated vernal bloom caused by increased primary production and growth associated with rising light and shallowing mixed layers – *aka, Sverdrup*



M. Behrenfeld lecture, *'Abandoning Sverdrup'*



- To understand what causes a bloom, it is necessary to first identify *when* a bloom started

- The start of a bloom *cannot* be defined by biomass - e.g., when biomass X mg m^{-3} or Y% above annual median

- Using biomass can lead to the wrong start date and *association* of bloom initiation with the wrong environmental forcing

- Bloom initiation implies a *change in the rate* of growth – for Sverdrup it was the beginning of positive net growth

$$\text{Net growth rate} = r = \frac{\ln(C_1/C_0)}{t_1 - t_0} = \text{slope of log plot}$$

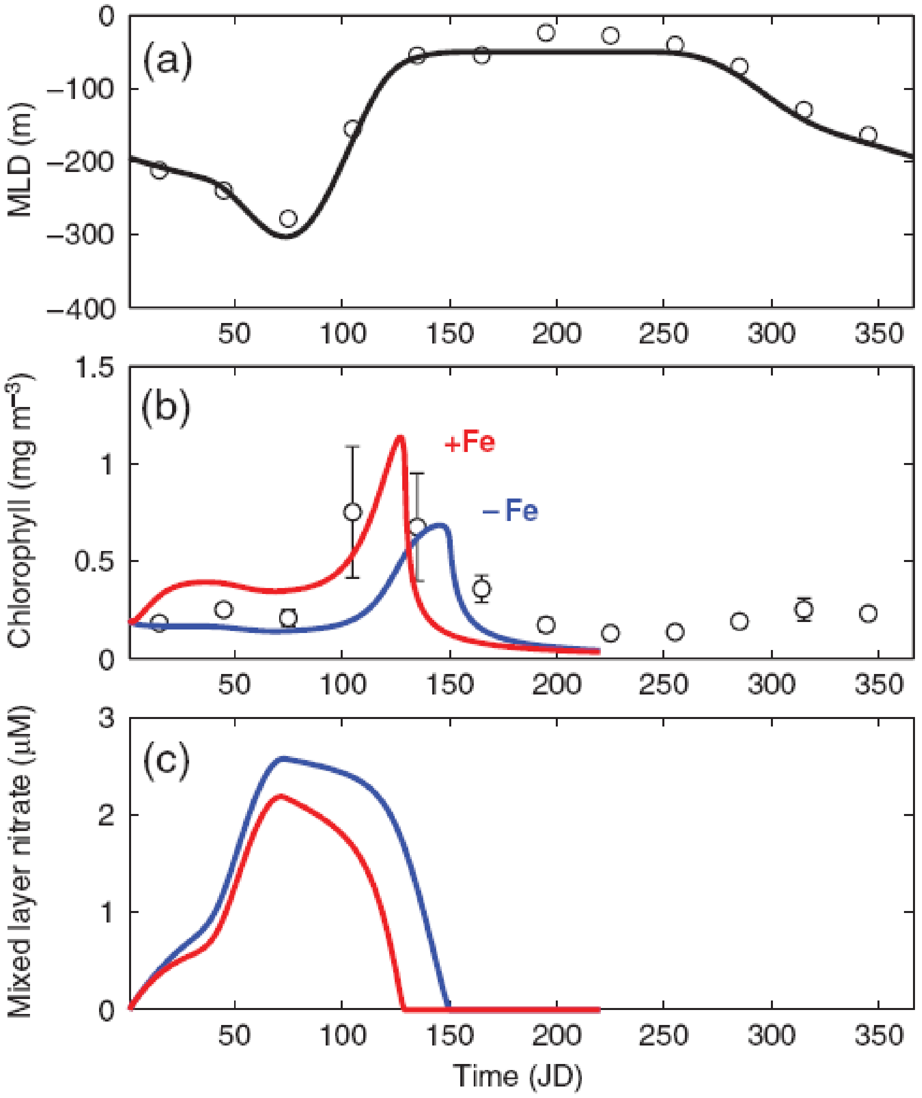
Abandoning Sverdrup

- The North Atlantic bloom does not begin in the spring
- Net exponential growth begins mid-winter
- Shift from negative to positive biomass changes coincides with the cessation of mixed layer deepening
- Net growth rates are, on average, comparable from winter through spring
- Net growth rates do not reflect changes in incident light, photosynthetic rate, or gross growth rate (μ)

Can we dismiss the critical depth hypothesis?

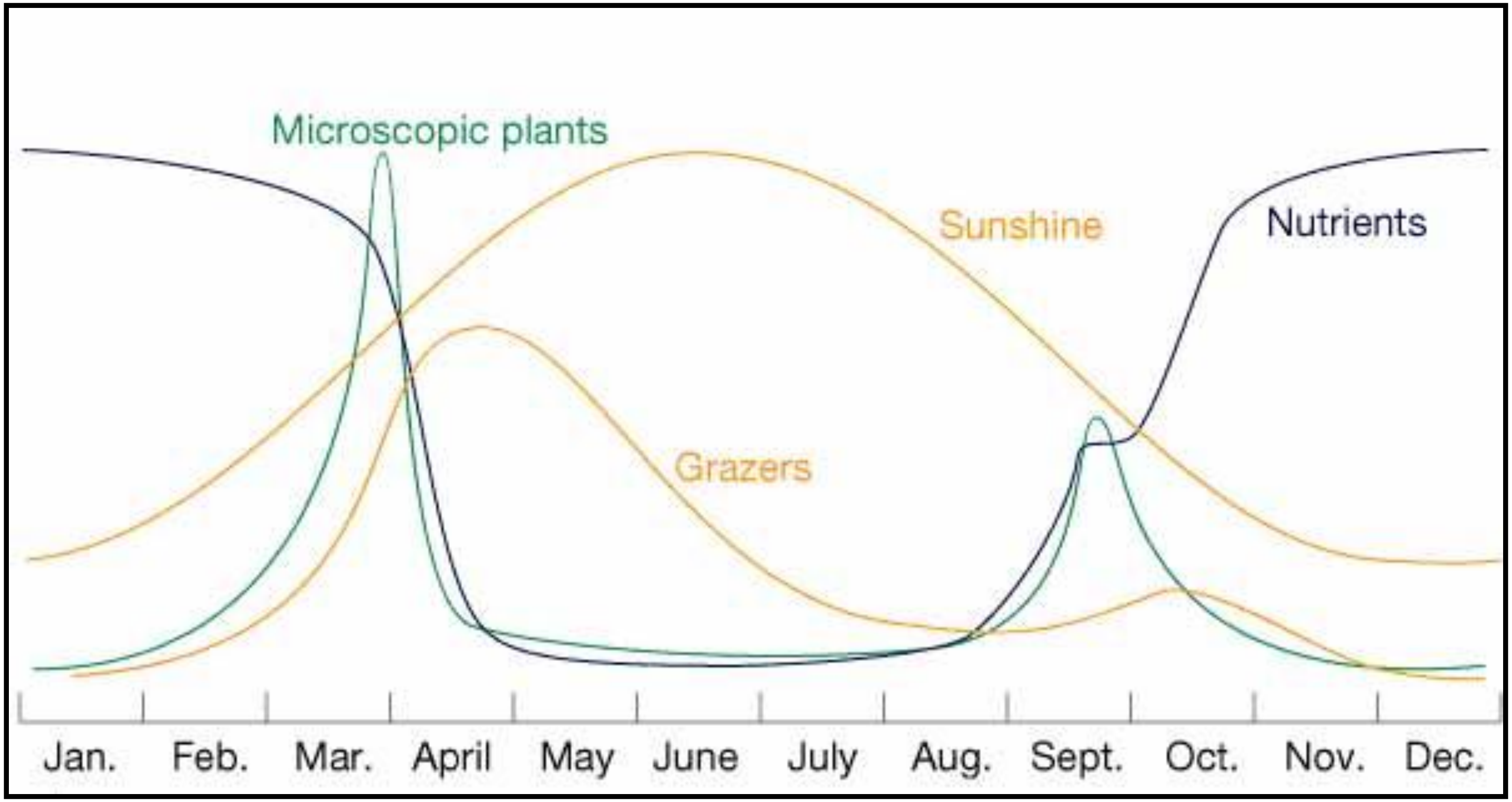
M. Behrenfeld lecture ‘*Abandoning Sverdrup*’

Numerical model demonstrating the potential influence of iron availability on spring bloom magnitude, timing and progression at 42^{o}N, 42^{o}W



Moore et al., 2006

Adding grazers



What about dilution?

- Population specific net growth rates (r) can be calculated from changes in phytoplankton concentration, C (m^{-3}) as long as the mixed layer is either shoaling or not deepening

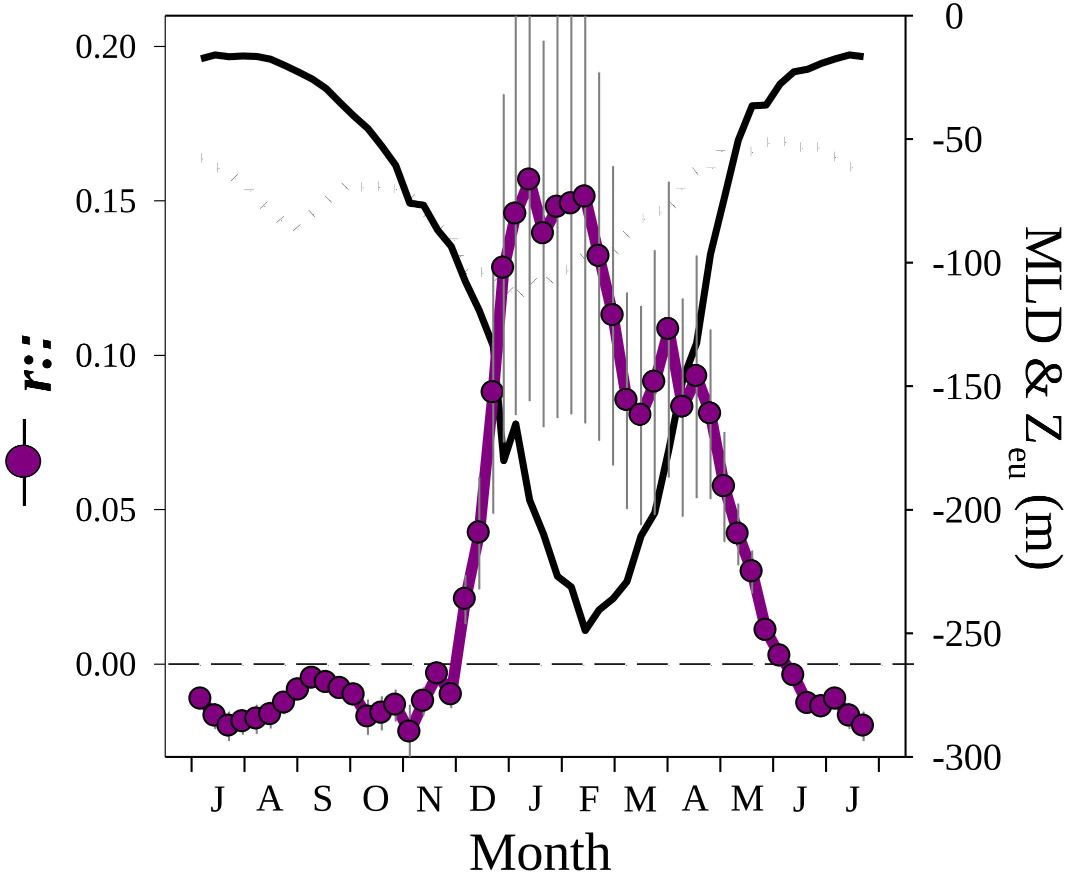
$$r = \frac{\ln(C_1/C_0)}{t_1 - t_0}$$

- The influence of **dilution** must be considered when the mixed layer is deepening

$$r = \frac{\ln[(C_1 \quad MLD_1) /[(C_0 \quad MLD_0)]}{t_1 - t_0}$$

- A dilution correction should be considered when assessing growth rates during mixed layer deepening

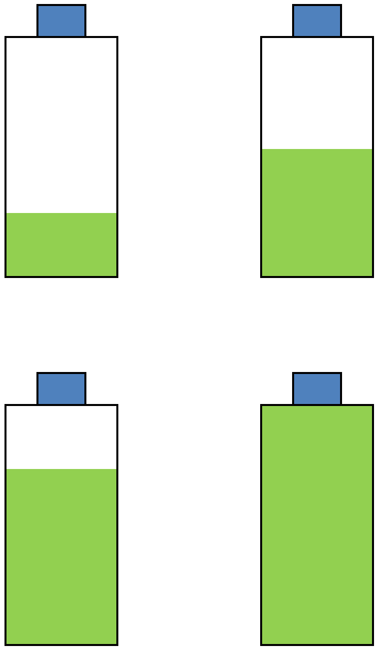
M. Behrenfeld lecture, *'Abandoning Sverdrup'*

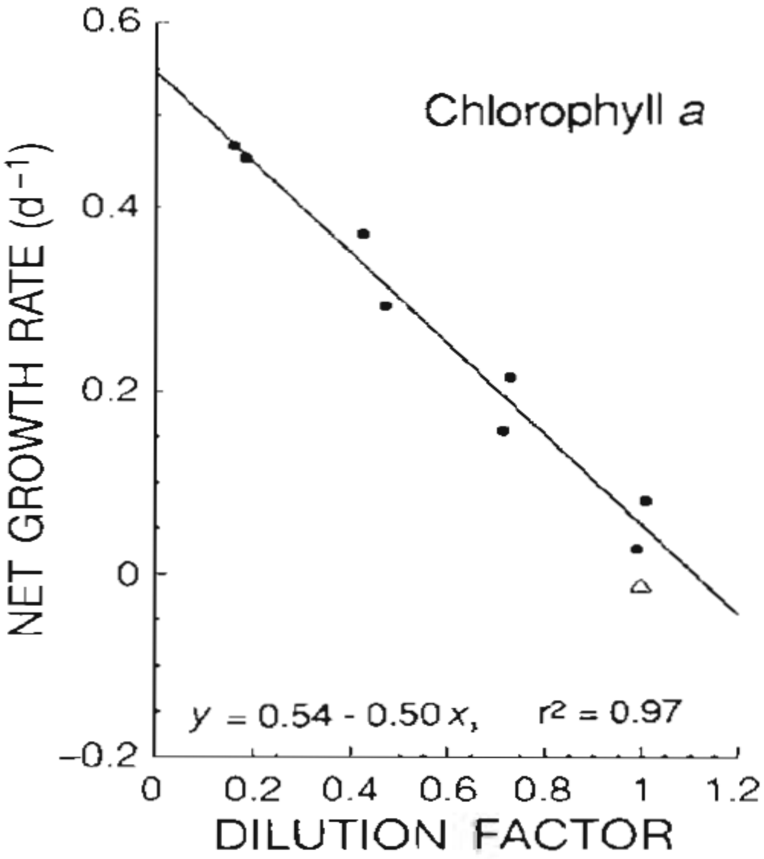


- The ‘vernal’ bloom appears to be an event initiated in late fall
- Triggering of the bloom appears to be associated with mixed layer deepening (not shoaling)

How is this possible? Why the mid-winter decrease in *r* ?

A word about dilution





Landry & Hassett 1982 Mar. Biol. 67, 283-288
Landry et al. 1995 Mar. Ecol. Prog. Ser. 120, 53-63

The ‘Grand Dilution Hypothesis’

- As a replacement for the Critical Depth Hypothesis, it is proposed that the north Atlantic bloom is a consequence of a massive scale ‘dilution experiment’

- Mixed layer deepening causes a slight decoupling between phytoplankton growth and losses (grazing, mostly)

- The ‘decoupling’ increases so long as the mixed layer continues to deepen

- Mixed layer shoaling drives a ‘re-coupling’ of phytoplankton growth and losses (grazing)

- While spring shoaling and increasing light favor enhanced photosynthesis and growth, they also favor heavier grazing losses

On Conditions for the Vernal Blooming of Phytoplankton.

- Sverdrup's 1953 paper was a formalization of the 'critical depth' concept originally proposed by Gran and Braarud in 1935*

- The critical depth hypothesis attempts to explain what initiates a vernal bloom, not what controls the magnitude of a bloom

- A bloom is an increase in biomass, not photosynthetic rate

- The hypothesis states that a bloom begins when the mixed layer shoals to a depth above the critical depth horizon where production (P) > respiration (R)

- R = grazing + sinking + phytoplankton respiration + all other losses

- R is assumed constant

- Inverse of Sverdrup: prior to crossing the critical depth criterion, net growth is negligible or negative

* Gran & Braarud. 1935. *J. Biol. Board Can.* **1 (5),** 279-467

On Conditions for the Vernal Blooming of Phytoplankton.

- Sverdrup: net growth can be independent of gross production under heavy grazing

- Sverdrup: the ‘bloom’ observed 2 days after “the depth of the mixed layer was for the first time smaller than the critical depth” likely reflected **advection** not rapid local growth

- Sverdrup: the first increase in biomass occurred before stratification

- Sverdrup: “It is therefore not advisable to place too great emphasis on the agreement between theory and [the Weather Ship ‘M’] observations”

(occurrence of blooms in the absence of stratification is not uncommon)

* e.g., Townsend et al. 1992. *Nature* **360,** 59-62

How do we explain the Spring Bloom?

- The critical depth hypothesis is found wanting

- A Grand Dilution Hypothesis is suggested, but is not the only potential explanation (aggregation, temperature effects, sinking….?)

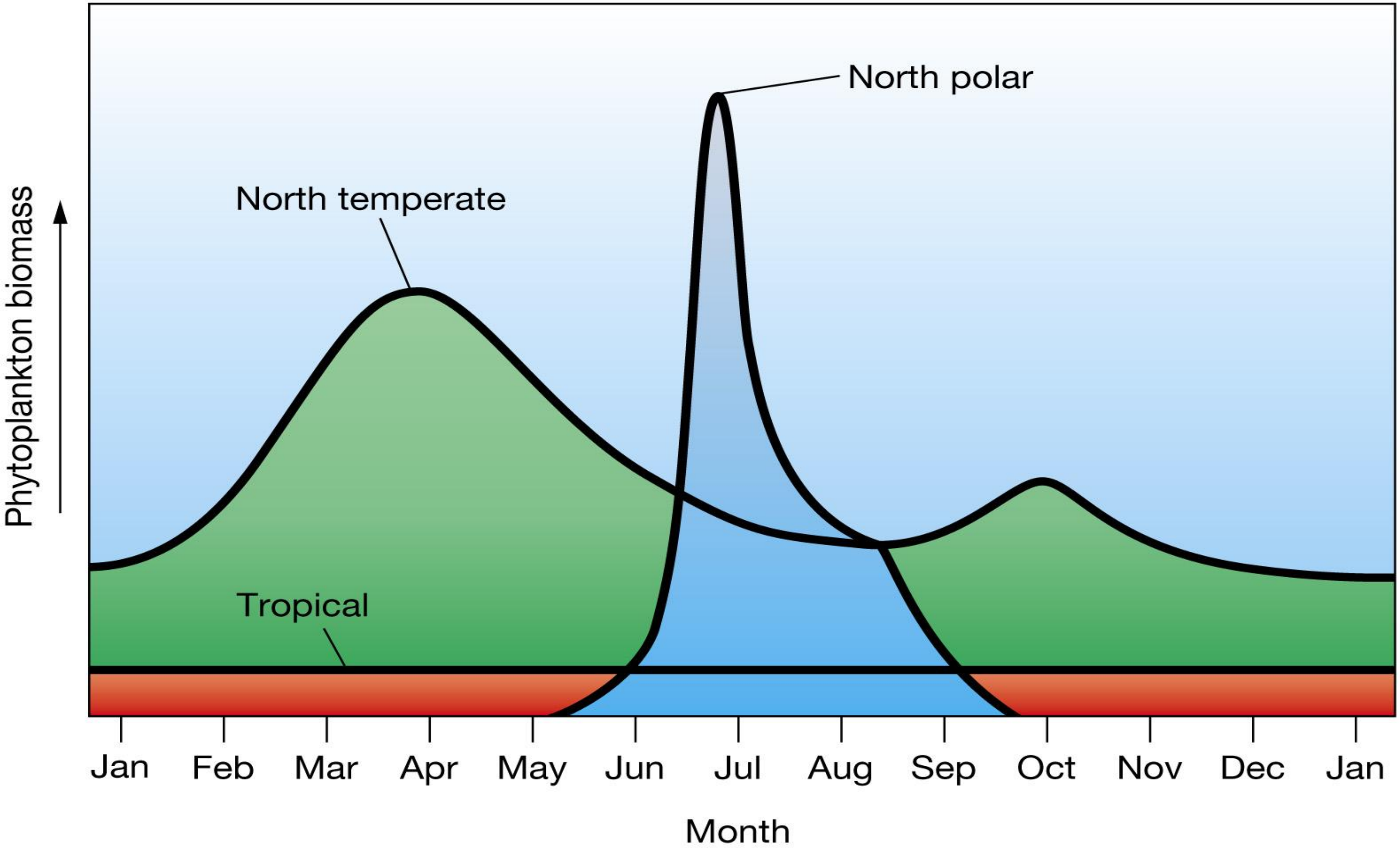
- Dilution Hypothesis accommodates blooms without stratification

- Climate change effects on North Atlantic (and other) blooms may be very much different for a ‘Critical Depth’ concept of blooms and a ‘Dilution’ concept of blooms

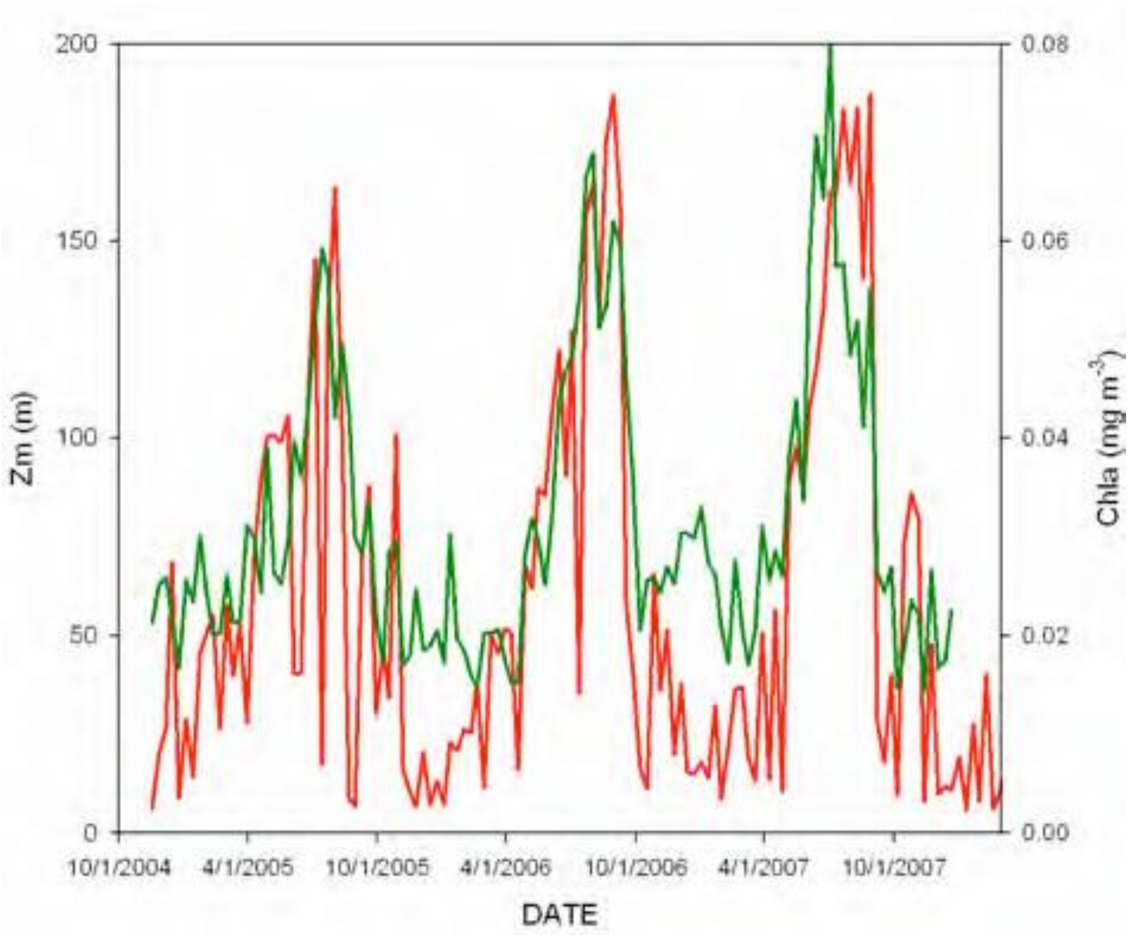
Alternatives to Spring Bloom

- Polar and tropical seas
- Shallow water case: stratification not important for bloom initiation, only light is important
- Estuaries (Cloern and Jassby 2008, 2009)
- Extremely oligotrophic regions
- Iron limitation (e.g. subarctic North Pacific)
  - But also applies to spring bloom!
- Grazing regime
- Upwelling systems (coastal, equatorial)

Global comparison of phytoplankton biomass

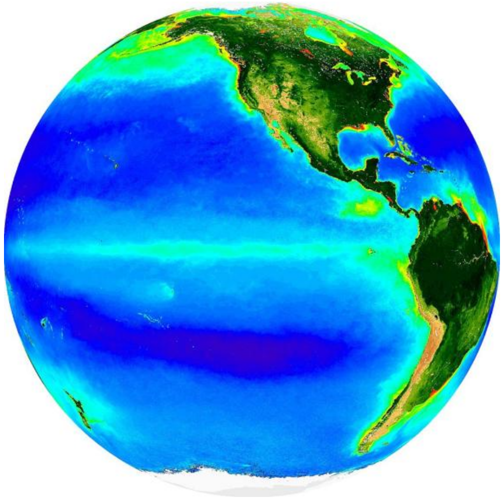


In South Pacific Gyre, chl *a* is highest in winter compared to summer

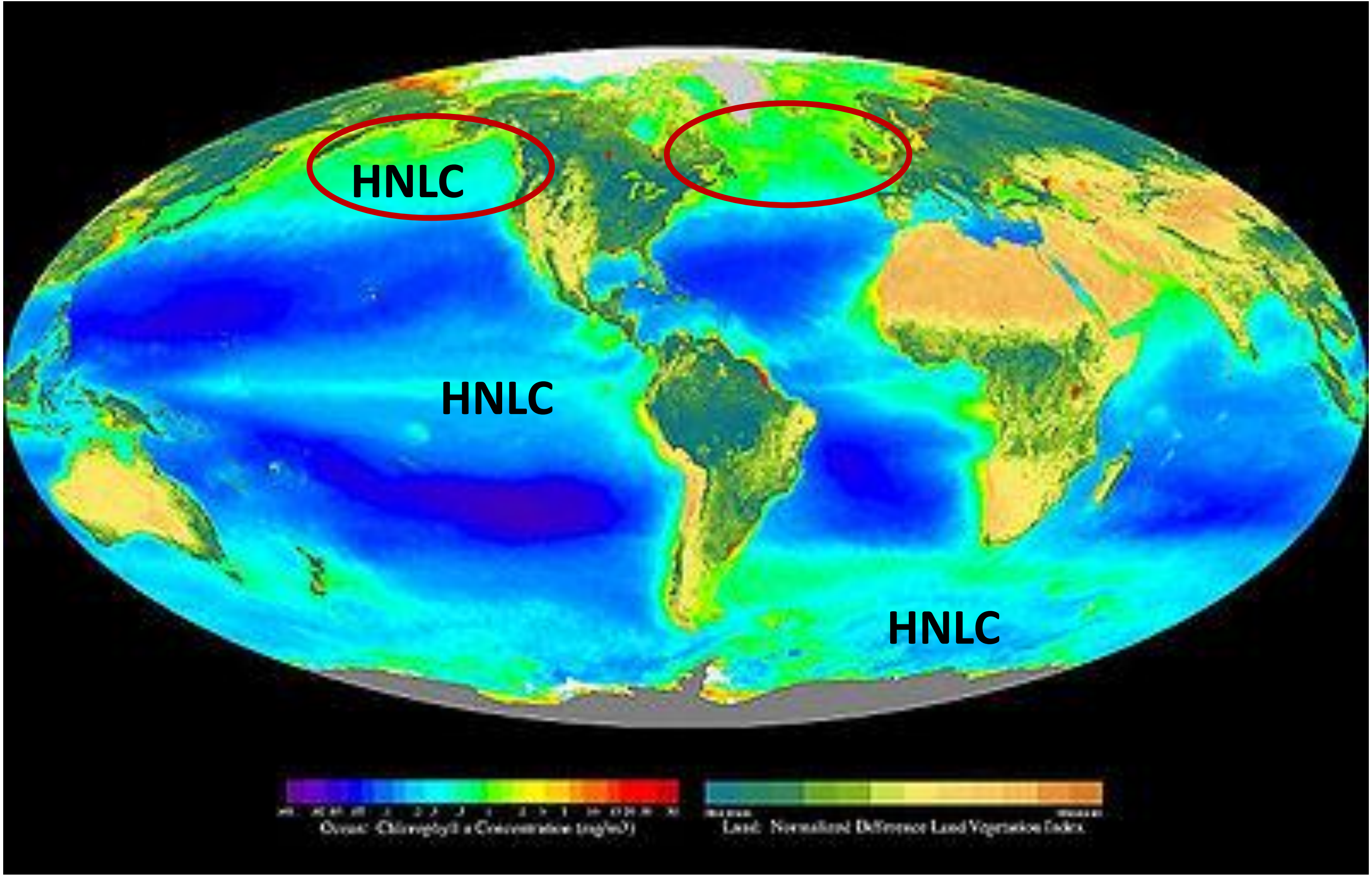


Claustre, unpubl.

Green = chl a
Red = mixed layer depth (determined from Argo float)



Annually averaged chl *a*



Fate of bloom phytoplankton

- Shallow decomposition (→ microbial loop, regeneration)
- Export
  - To deep ocean
  - Burial in sediments (→ sedimentary record)
- Grazing
  - Mesozooplankton
  - Microzooplankton
  - Excretion → regenerated nutrients