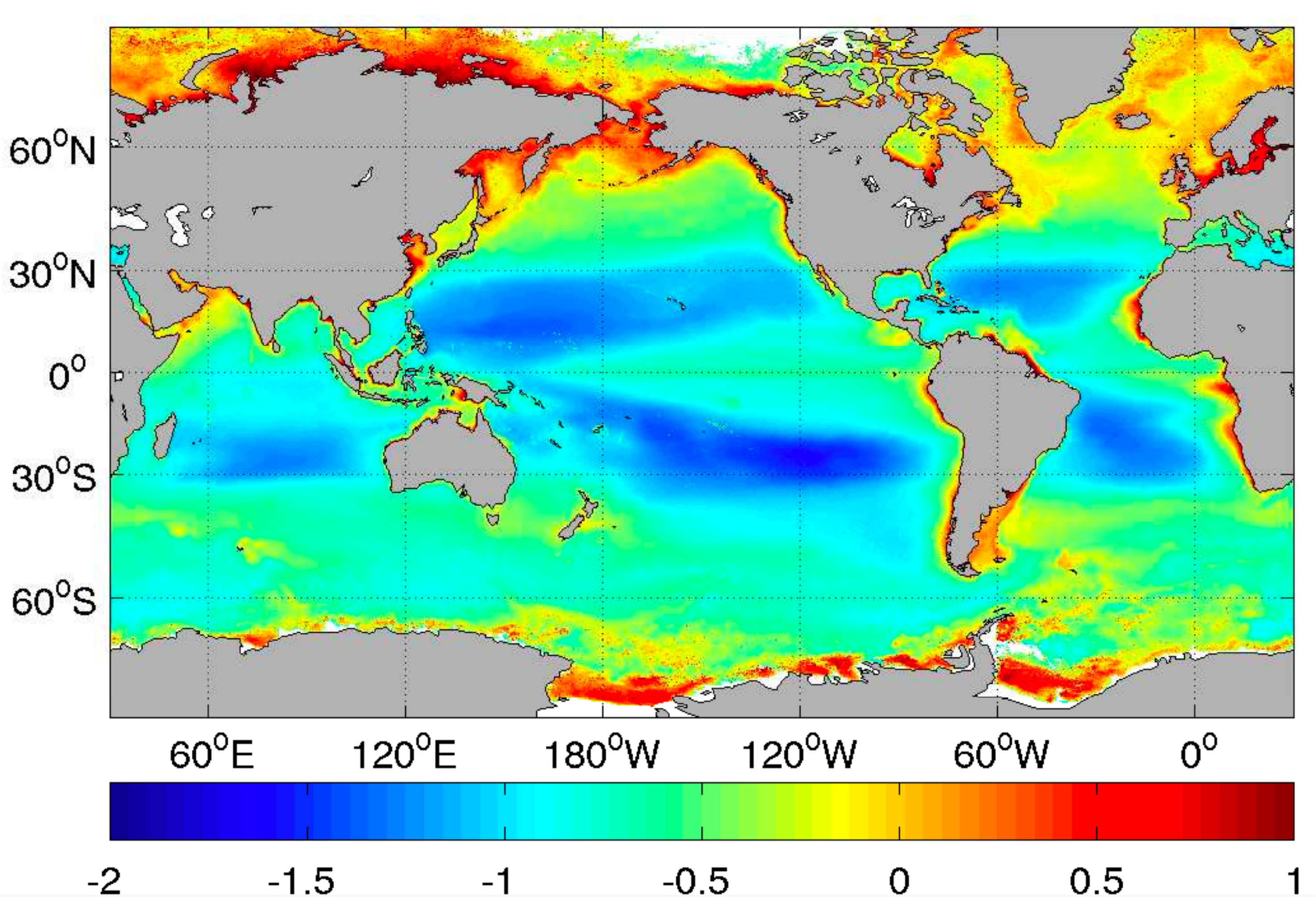
Life in the Surface Layer



Satellite-derived annual mean chlorophyll-a concentration, log(ChlA[mg/m^3]), the most widespread measurement of biological activity. The first-order interpretation is that this is integrated biomass in the euphotic zone, but this is a relative overestimate in polar regions because of pigmentation variety. There are positive correlations with DOC and PO_4 distributions, but interpretation is needed for other measures such as Net Primary Productivity (NPP).

Problems and Questions

- Resource scarcity

  How do they survive?

  - Physiological constraints and trade-offs
  - at the organism scale
- Competition and cooperation

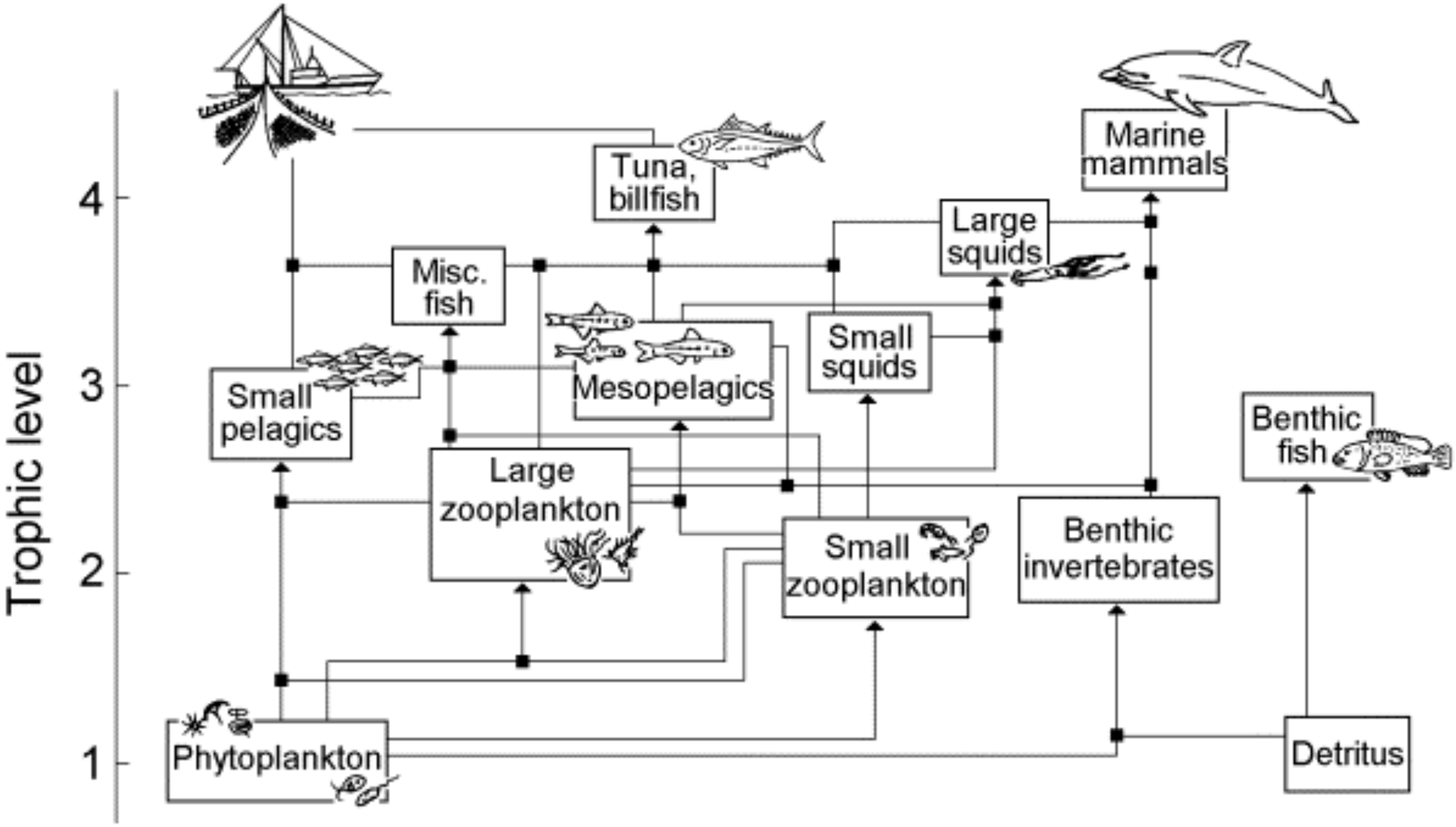
  How do they coexist?

  - Species diversity, plankton competition
  - at the population scale
- Complex environment

  How do they respond to and alter the environment?

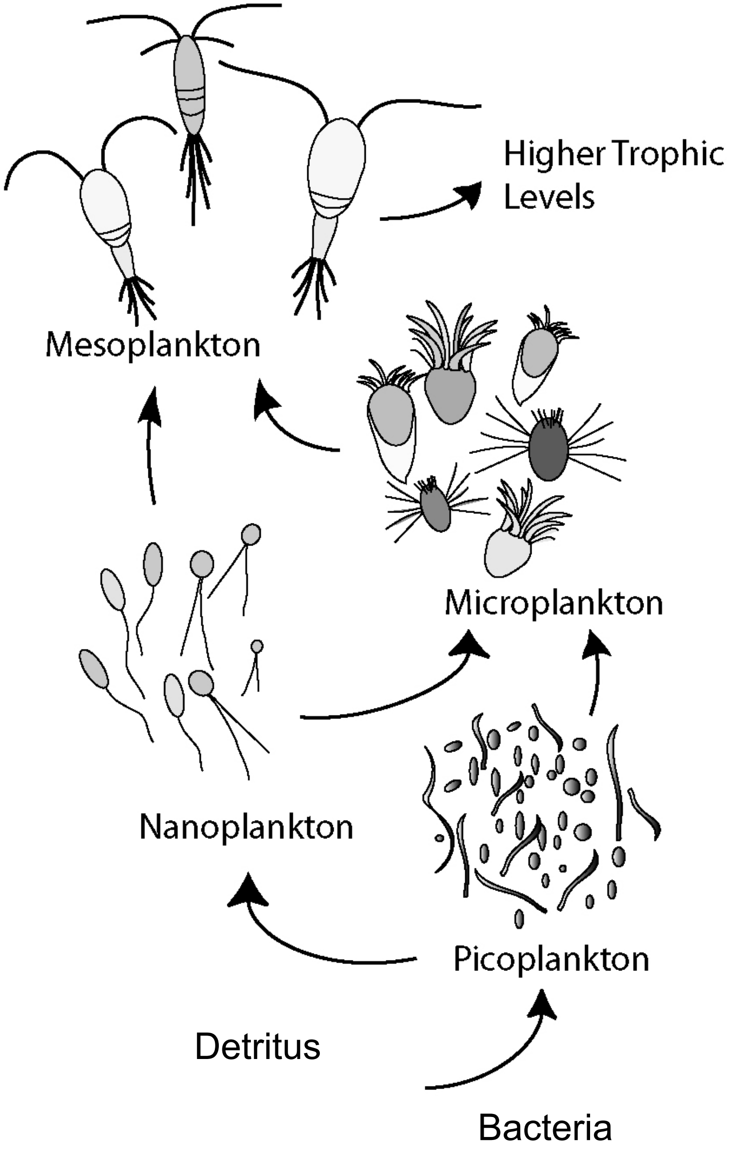
  - Rapid fluctuations, heterogeneous
  - Biological-chemical-physical interactions
  - at the regional - global scale

A typical ocean food web



Oceanic ecosystems are usually depicted in “food webs” as consisting mostly of animals. But most of the biomass and biogeochemical activity are in single-celled phytoplankton and microbes/bacteria (not even included here).

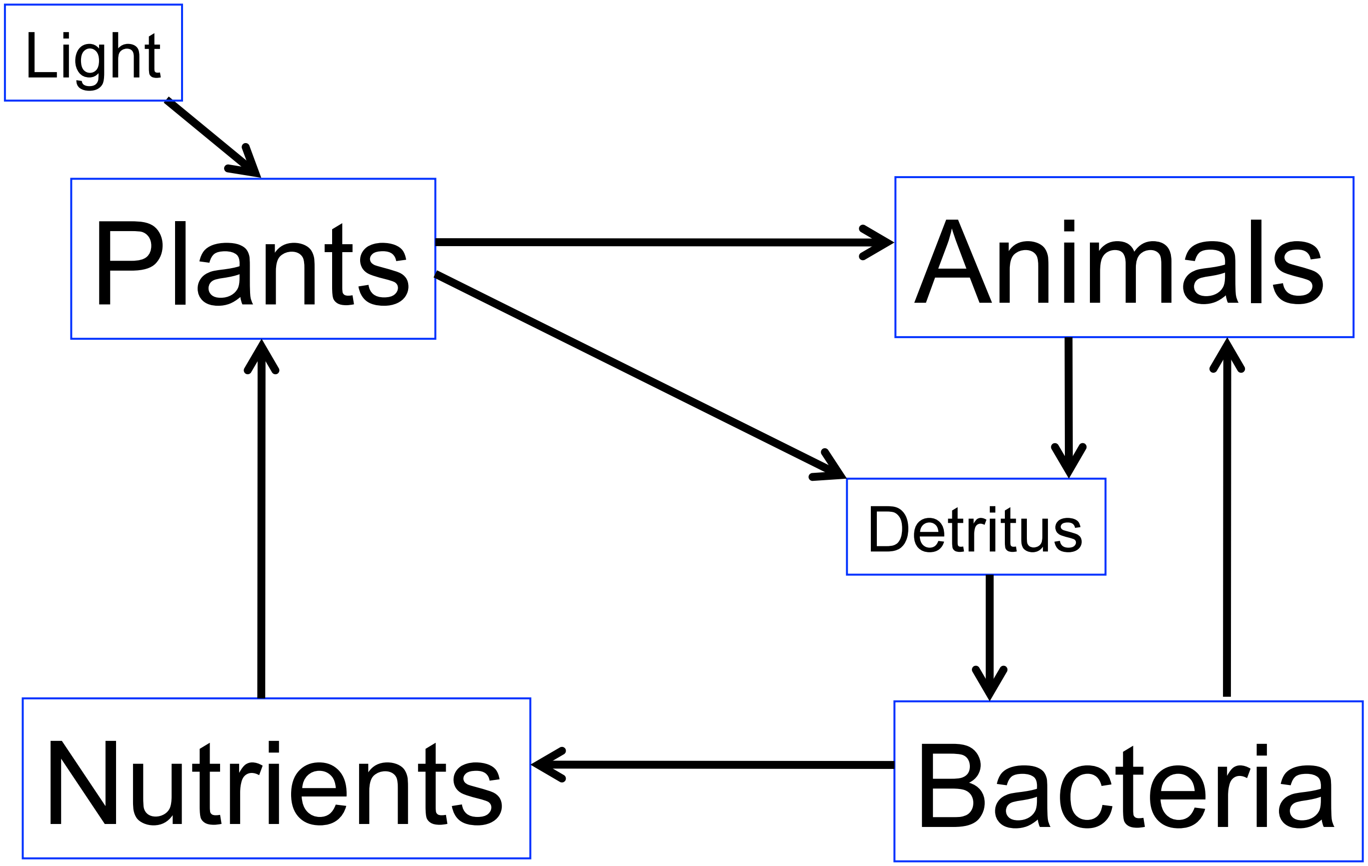
The “microbial loop” at the bottom of the food web



Marine microbes (single-celled bacteria and archaea) break down organic matter (detritus), fueling an alternate food web known as the “microbial loop”.

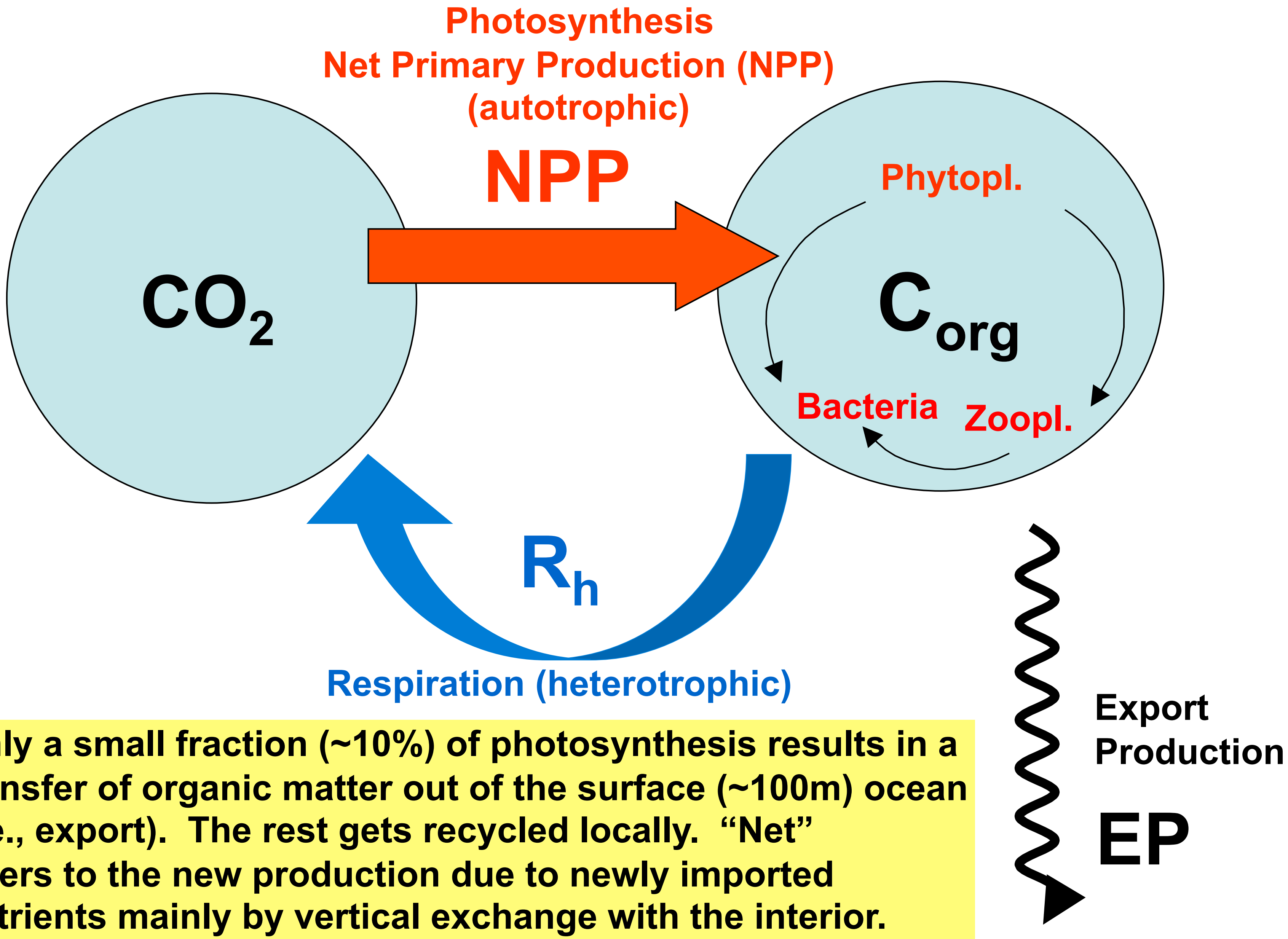
There are 100 million times more bacterial cells in the ocean than stars in the known universe, and probably 1 billion times more viruses (semi-alive).

A Simple View of the Ecosystem



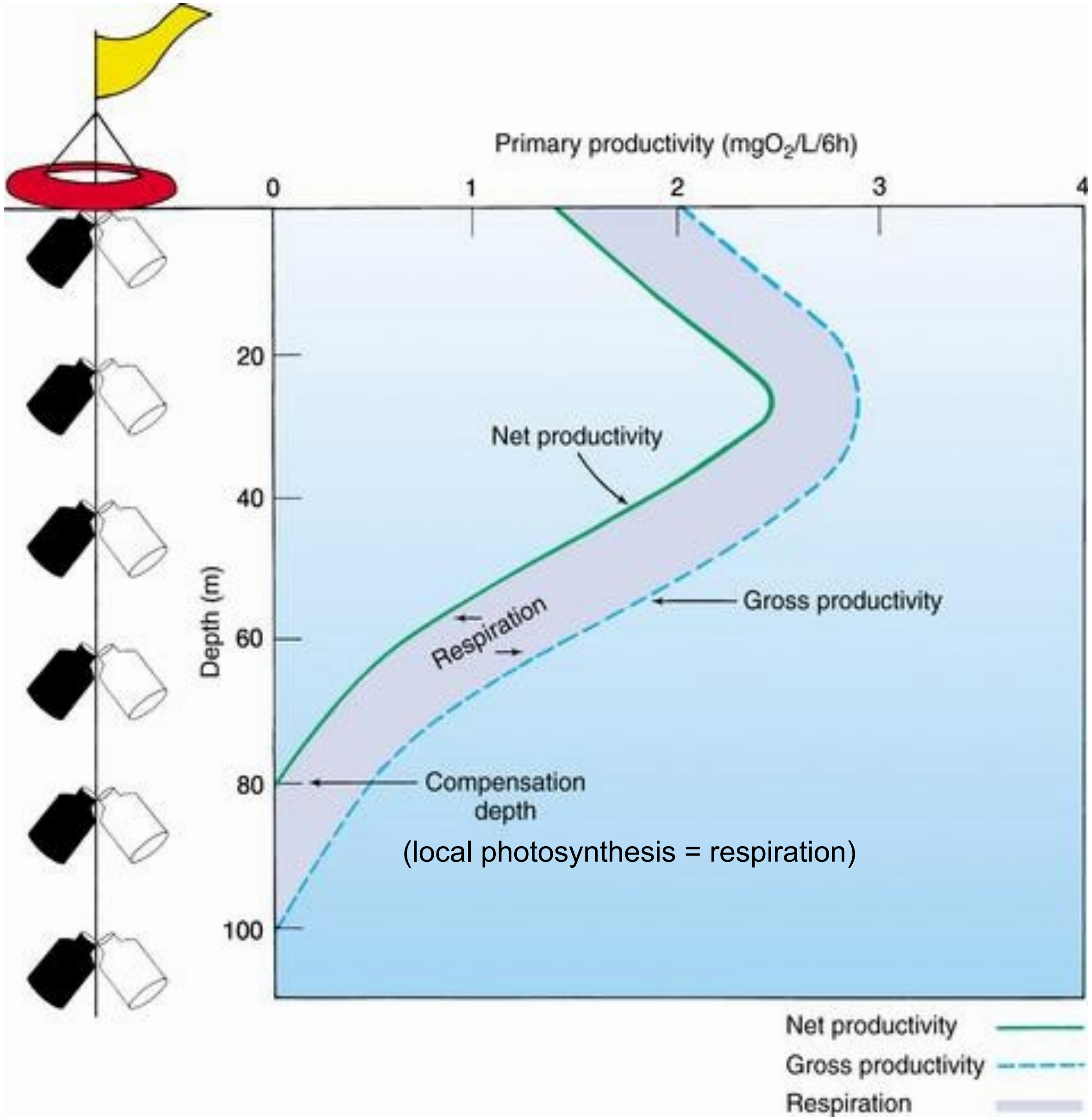
Resources for photosynthesis (nutrients, light) are used by plants, which are eaten by animals, both of which create detritus that are eaten by bacteria that return organic matter to its nutrient forms. The remineralization path is along the bottom.

Organic matter production (C perspective)



Only a small fraction (~10%) of photosynthesis results in a transfer of organic matter out of the surface (~100m) ocean (i.e., export). The rest gets recycled locally. “Net” refers to the new production due to newly imported nutrients mainly by vertical exchange with the interior.

Measuring Primary Productivity



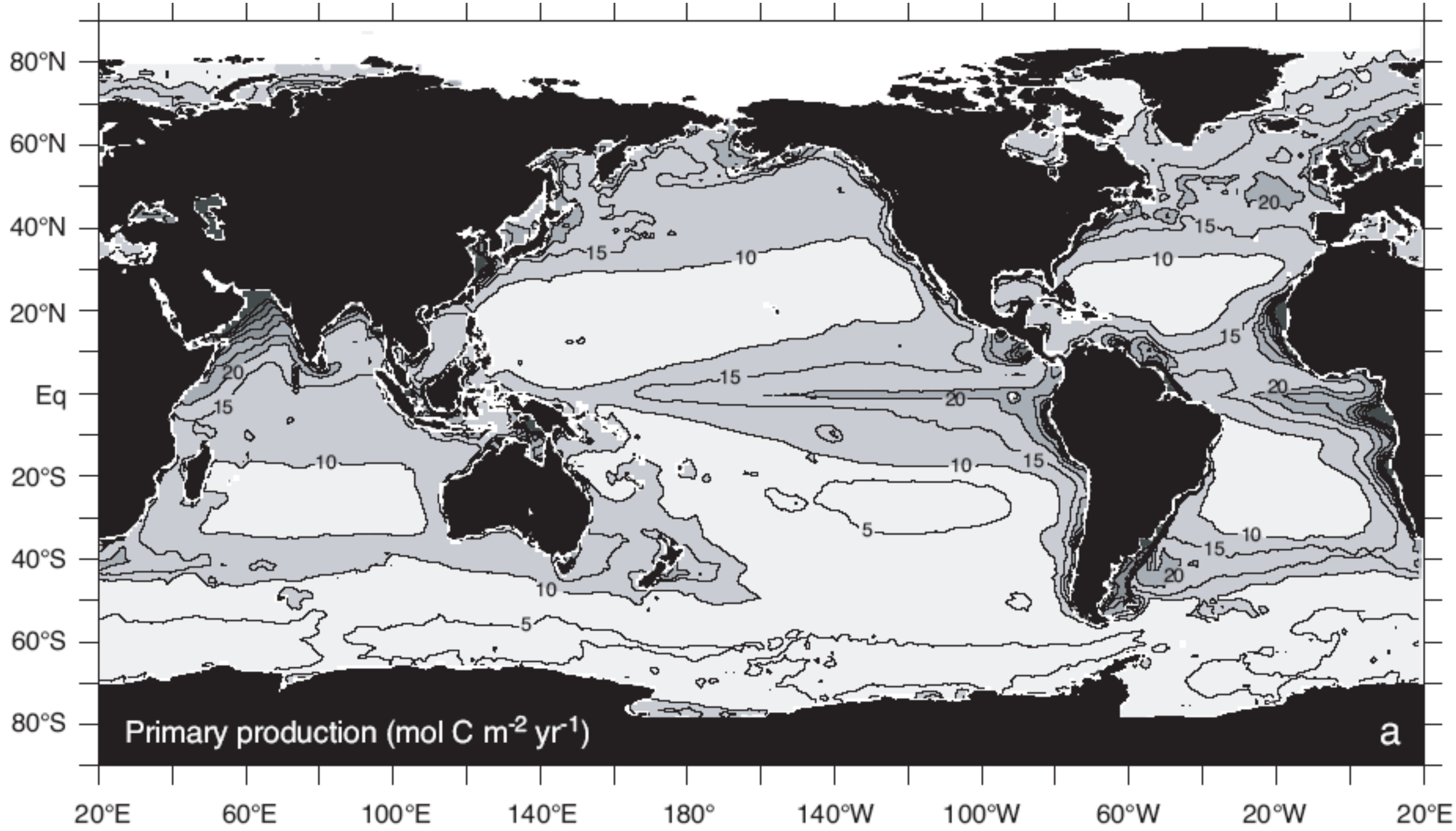
(local photosynthesis = respiration)

Methods of sample analysis:

1) Incubation with added ^{14}C-labeled CO_2.
2) Measure production/loss of O_2.
3) Subtract dark bottle (respiration) from light bottle (photosynthesis) rate to get NPP.

GPP = NPP + (autotrophic) respiration

Net Primary Production



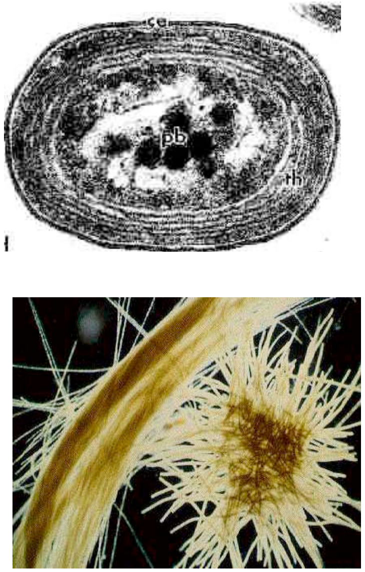
Vertically integrated NPP derived from several empirical algorithms applied to satellite chlorophyll. This pattern has broad similarities with DOC and ChlA patterns.

What are the factors that quantitatively determine the pattern?

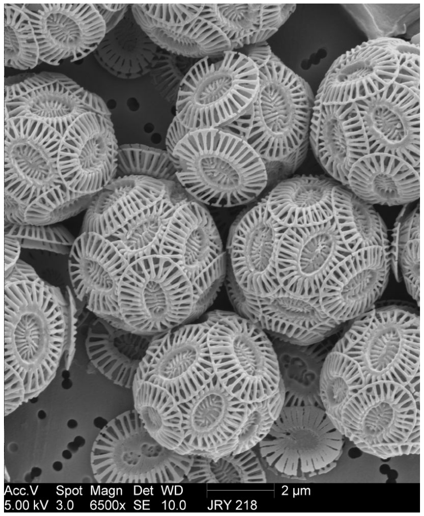
Phytoplankton: size and function

[plankton: drifting organisms]

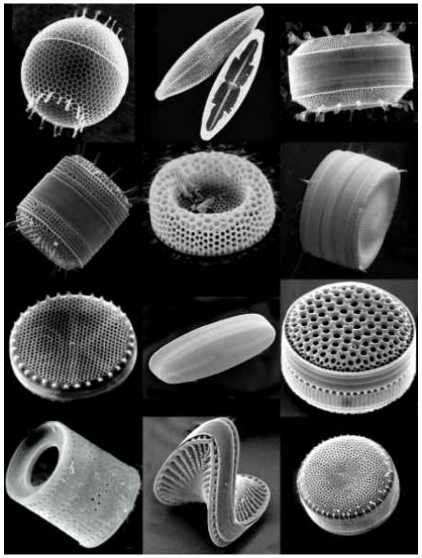
Over 20,000 species in 8 phyla



Cyanobacteria
~1 micron
No cell nucleus
Some fix Nitrogen



Coccolithophores
1-40 microns
Produce $CaCO_3$ shells
Paleo fossils
Produce DMS

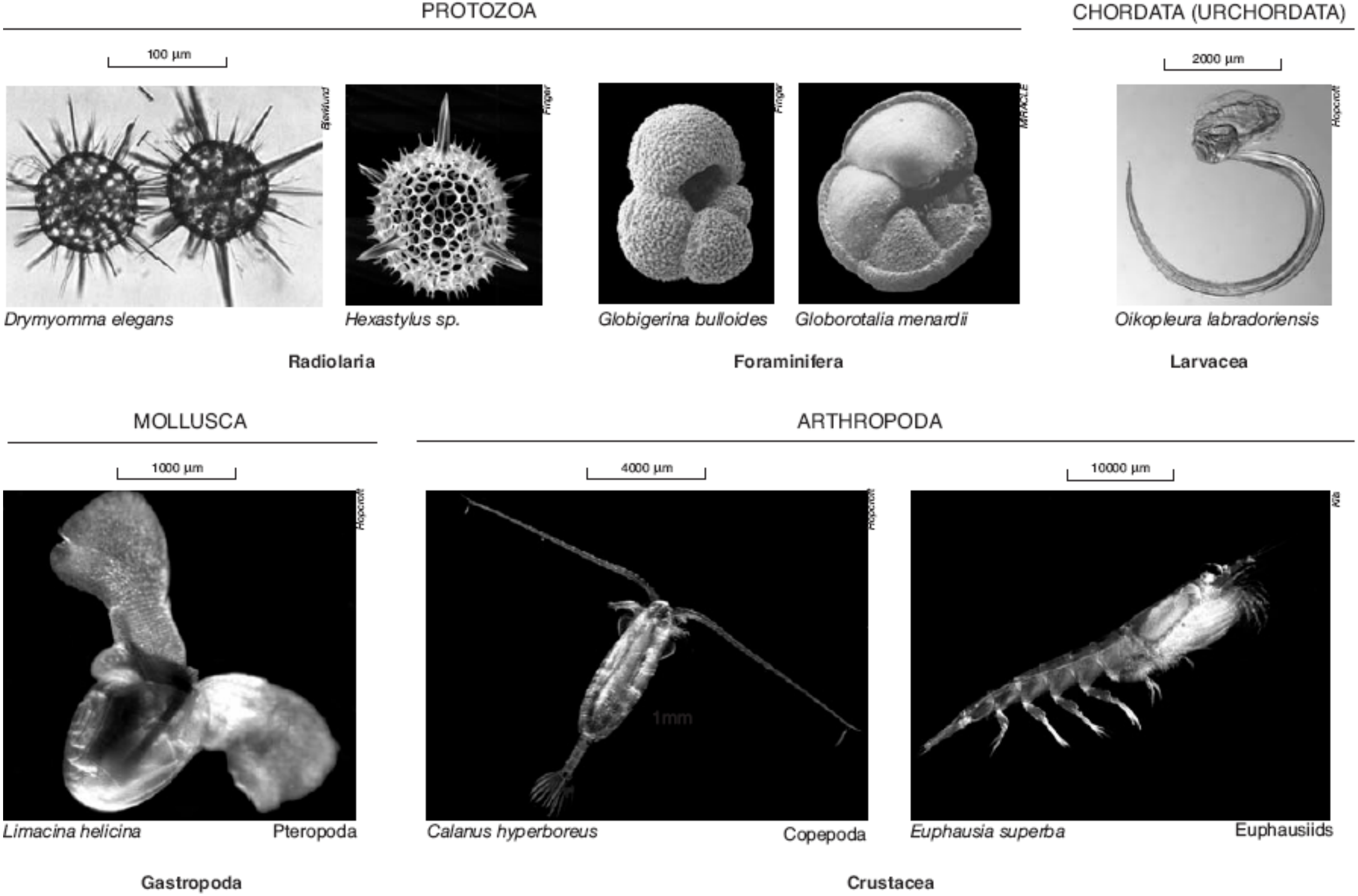


Diatoms
50-500 microns
Fast growing “bloomers”
Silicate shells (“frustule”)
Centric and Pennate forms

Dinoflagellates
10-2000 microns
Can be toxic in blooms
Capable of movement
n be heterotrophic

A few major plankton “functional groups” (comprised of many similarly behaving species) in increasing cell size, an important determinant of nutrient utilization, growth, mortality rates.

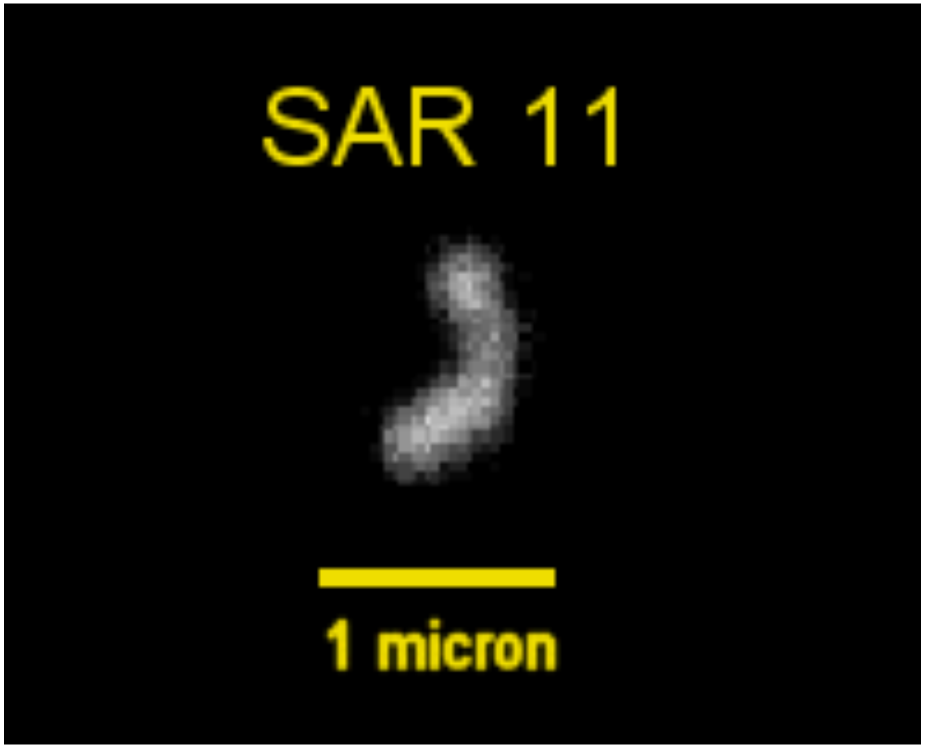
Zooplankton

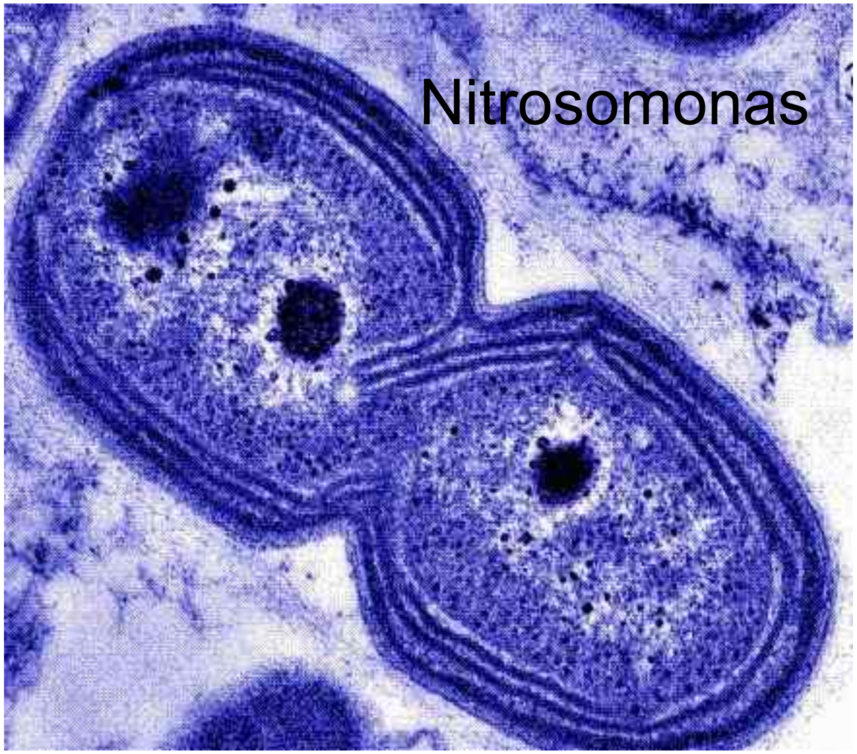


Zooplankton are the first step in secondary production, leading the way up the food web.

Bacteria

e.g., consumes DOC.;
oxidizes NH_4^+ to NO_3^- .

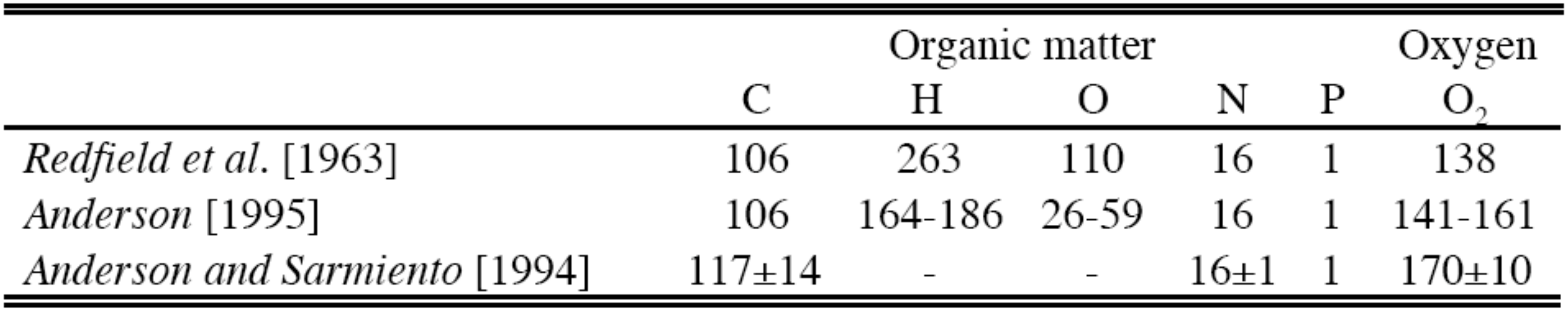




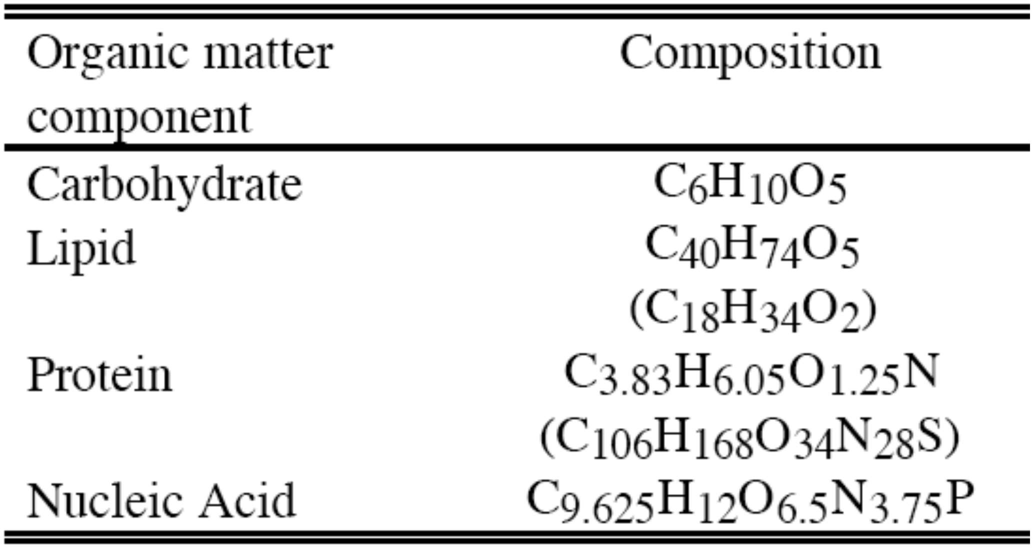
Extremely abundant: 10^{28} individual
bacteria cells vs. --> 10^{10} humans.

Composition of biomass

1) Major elements



	Organic matter					Oxygen
	C	H	O	N	P	O_2
Redfield et al. [1963]	106	263	110	16	1	138
Anderson [1995]	106	164-186	26-59	16	1	141-161
Anderson and Sarmiento [1994]	117±14	-	-	16±1	1	170±10



Organic matter component	Composition	
Carbohydrate	$C_6H_{10}O_5$	~55%
Lipid	$C_{40}H_{74}O_5$ $(C_{18}H_{34}O_2)$	~25%
Protein	$C_{3.83}H_{6.05}O_{1.25}N$ $(C_{106}H_{168}O_{34}N_{28}S)$	~15%
Nucleic Acid	$C_{9.625}H_{12}O_{6.5}N_{3.75}P$	~ 5%

Sarmiento and Gruber [2006]

Thus, for the Redfield ratio and equation of life to be approximately valid, there are robust composites over organisms, species, elements, and organic components.

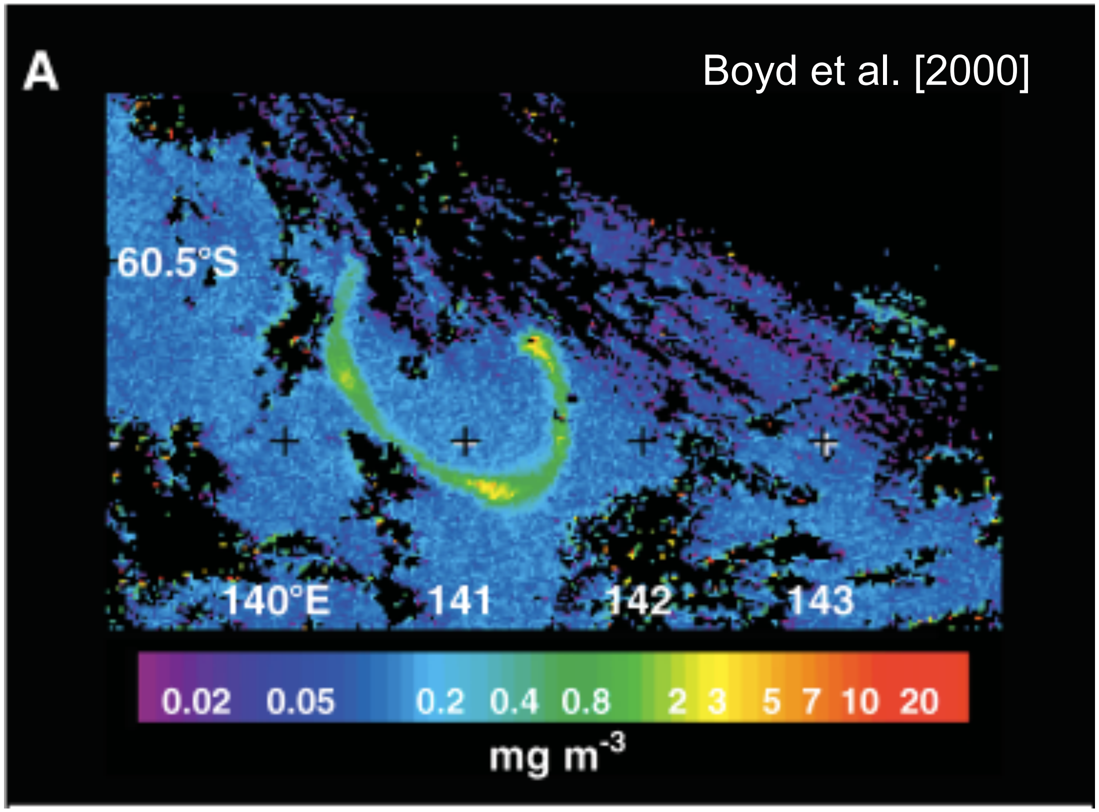
Composition of biomass

2) Minor elements

Metal elements are required “cofactors” for most enzymes to function: micronutrients.

e.g.,
Nitrate reductase [Fe],
Carbonic anhydrase [Zn]
Vitamin B12 [Co]

Many of the important ones are scarce in the surface ocean, as often are the macronutrients.



Boyd et al. [2000]

Satellite ChlA after deliberate iron fertilization
In the Southern Ocean.

Limits to Productivity

Change in phytoplankton biomass (P) = "Primary productivity" - Mortality

$$\frac{dP}{dt} = \mu P - M$$

$$\mu = \gamma(I) * \gamma(N) * V_{\max}(T)$$

Growth rate factors:

1) Light
2) Nutrients (N, P, Fe, Si, etc.)
3) Temperature

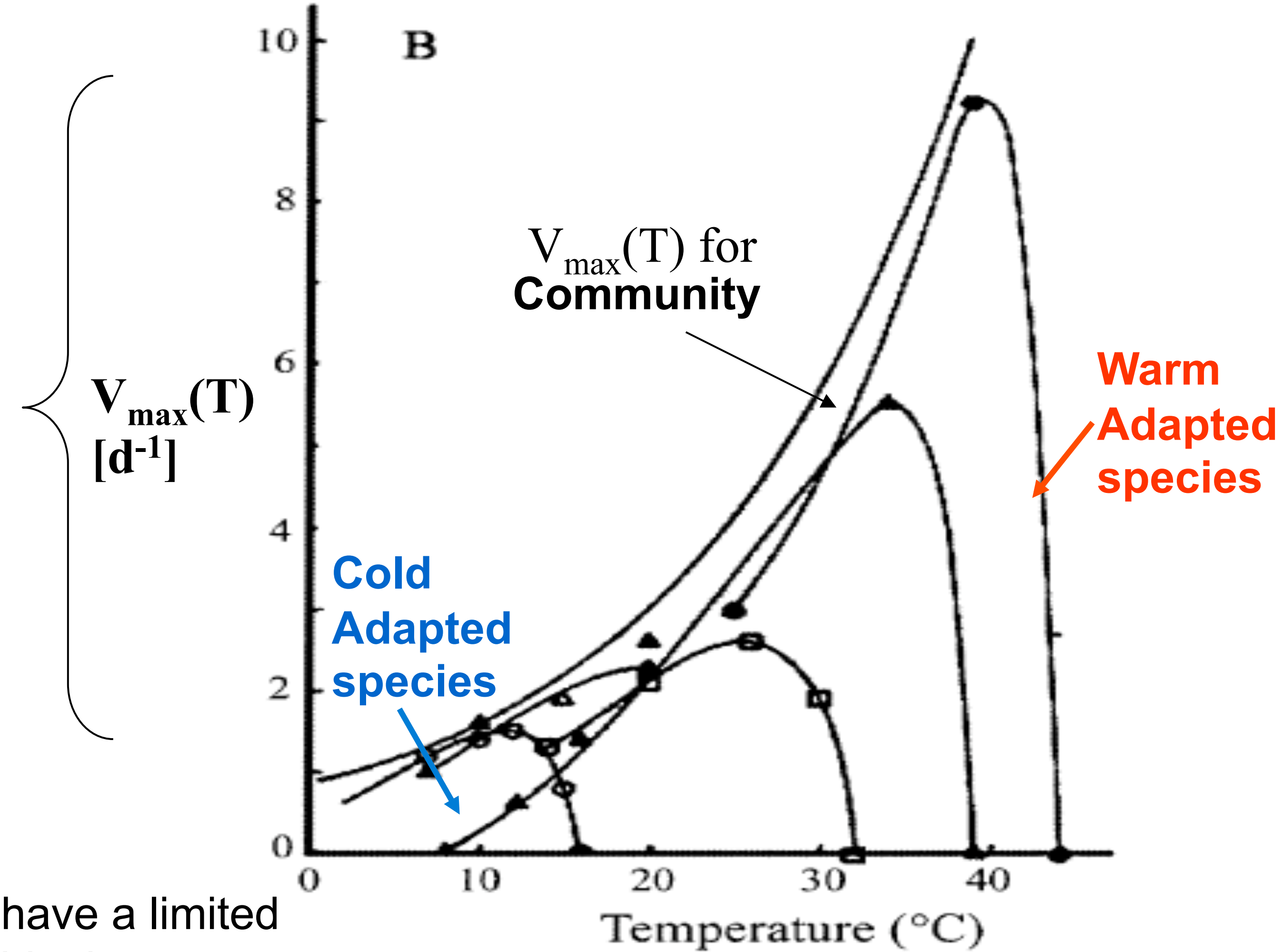
Mortality factors:

1) Zooplankton "grazing"
2) Viruses
3) Natural mortality

The strongest influences on productivity are environmental ("bottom-up"; e.g., nutrients) rather than biotic ("top-down"; e.g., grazing), as indicated by the strong correspondence between chlorophyll and physical/chemical ocean properties.
[But organismic biologists are fascinated by predator-prey relations.]

Growth Rate and Temperature

~ 5-fold increase from coldest to warmest T



$V_{max}(T)$ $[d^{-1}]$

$V_{max}(T)$ for **Community**

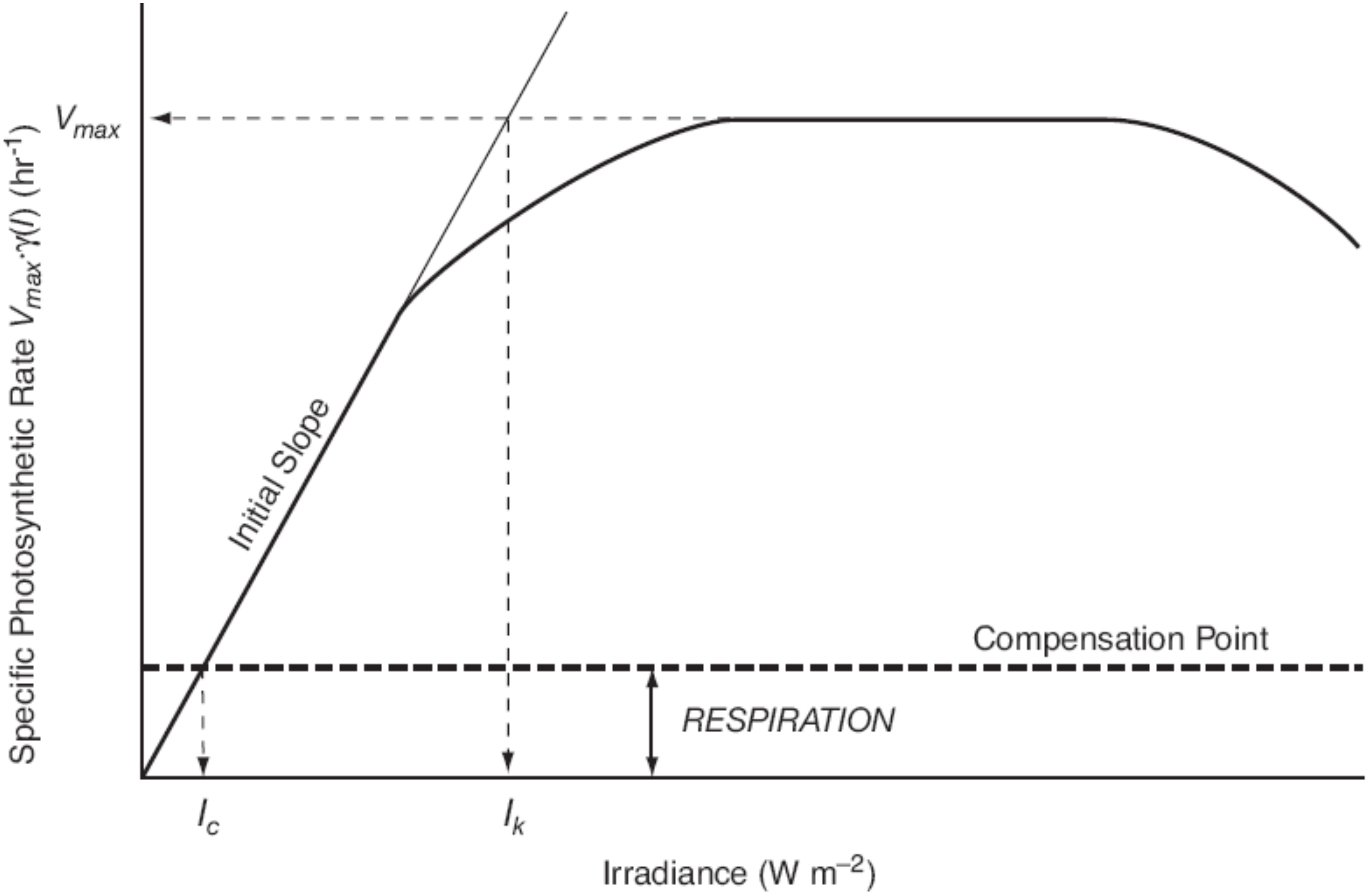
Warm Adapted species

Cold Adapted species

All plankton types have a limited range in T, and within the range Increased T usually favors growth from a population perspective.

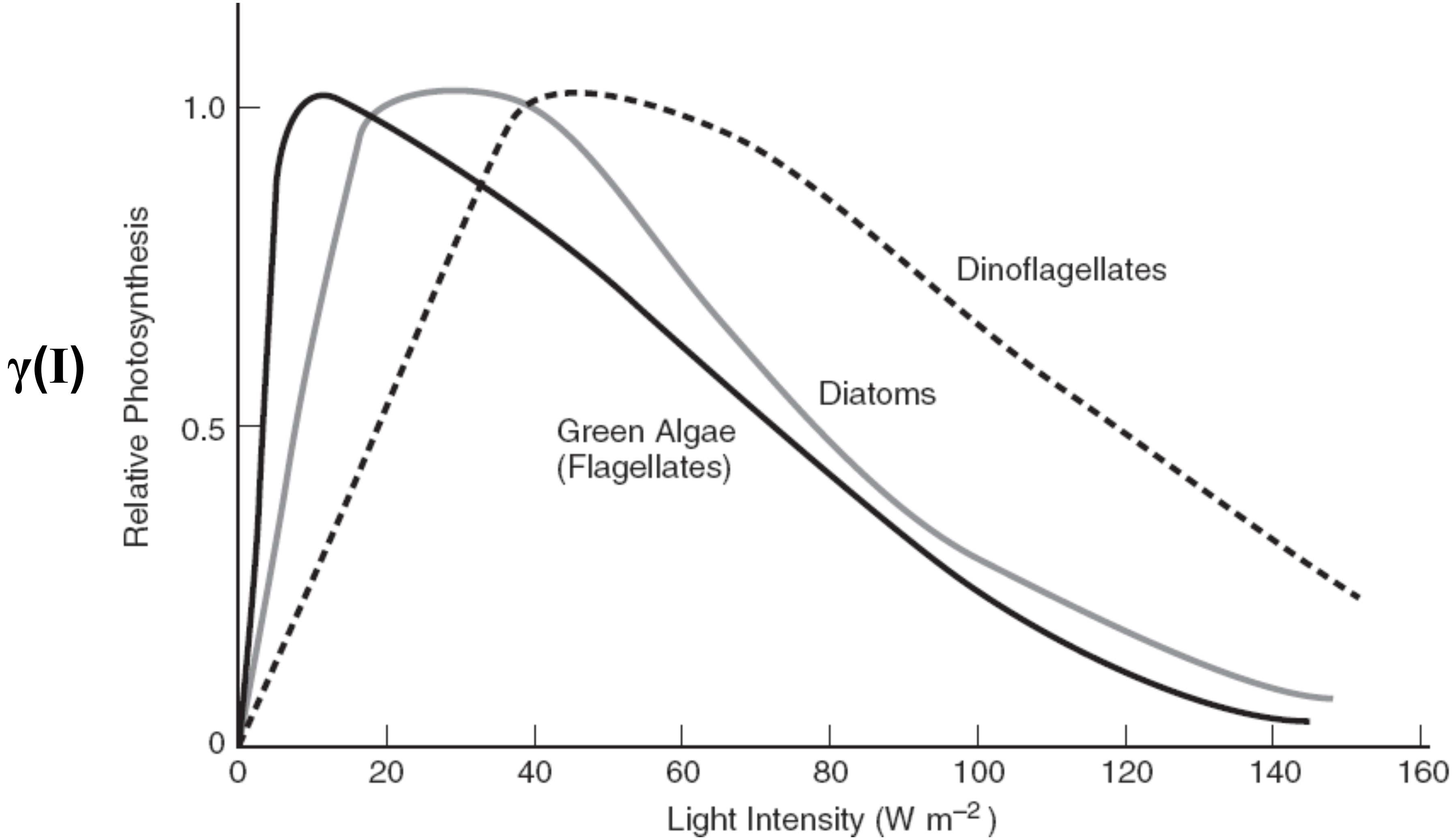
Eppley [1972]

Photosynthesis and Irradiance



Photosynthesis rate (growth rate of phytoplankton biomass, μ) versus irradiance. It initially increases, levels off, then declines due to cell damage. Background autotrophic respiration determines the “break-even” point for population viability, referred to as the compensation point with irradiance I_c.

Light Adaptation



Phytoplankton also have an optimum light level, but it varies between species (like temperature). At a community/population level, more light is usually better.

Enzyme Kinetics: $\gamma(\mathbf{N})$

(Michaelis-Menten Model)

Enzymes are needed for nutrient assimilation, controlling productivity rates.

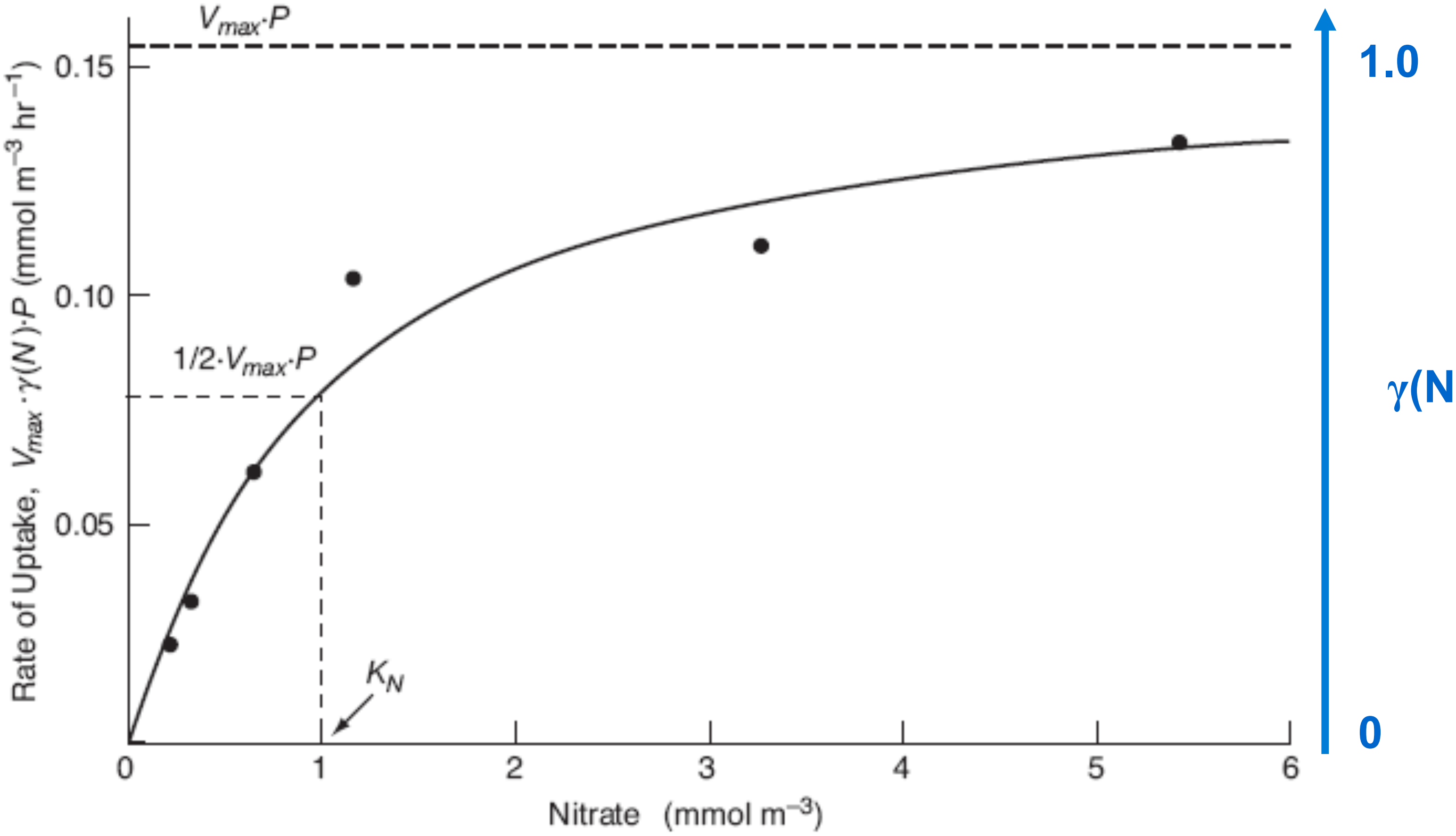
$$\mathrm{N} + \mathbf{E} \xrightarrow{k_1} \mathbf{E}\,{*}\mathrm{N} \xrightarrow{k_2} \mathbf{E} + \mathbf{P}$$

N = nutrient; E = enzyme; P = product; k = rate constant

$$\frac{dP}{dt} = V_{\max} \frac{N}{K_m + N} P = V_{\max}\, \gamma(N)\, P$$

$$K_m = \frac{k_2}{k_1} \quad , \qquad V_{\max} = k_2(E * N + E)$$

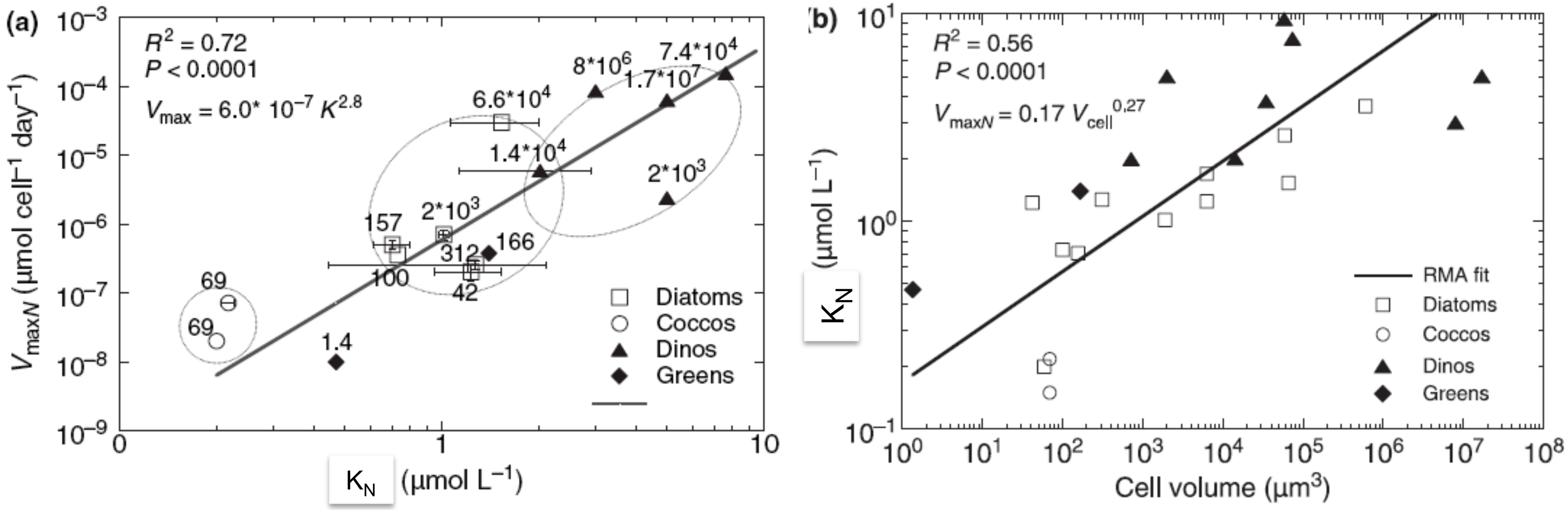
Nutrient Uptake



$$\gamma(N) = \frac{N}{N+K_N}$$

Phytoplankton growth will increase as nutrient concentrations increase, but will "level off" at a concentration determined by enzyme abundance.

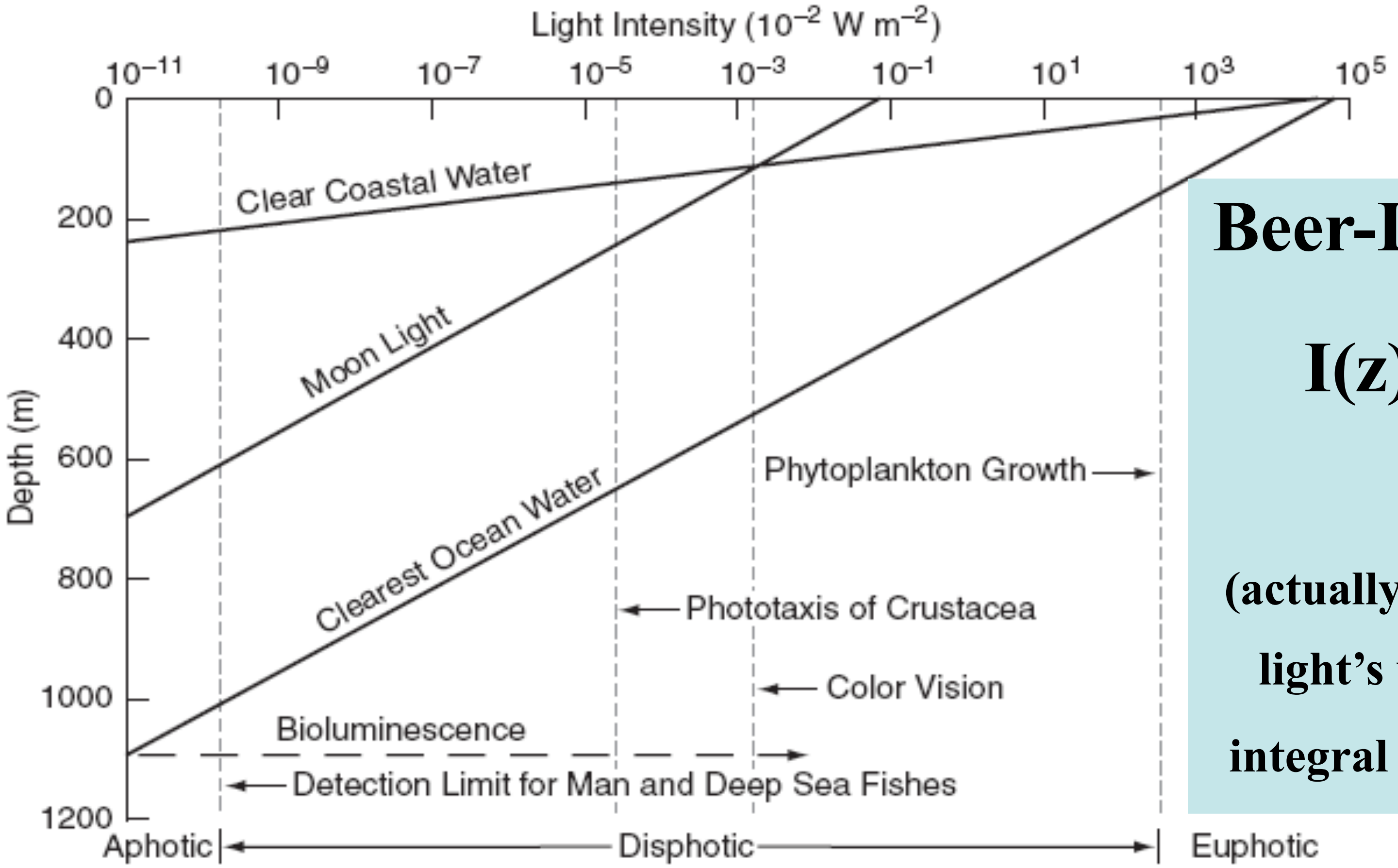
Plankton Size



Litchman et al. [2007]

Larger cells have a higher possible growth rate, but large cells tend to be more strongly limited at low nutrient concentrations.
Rate of nutrient acquisition goes up as R^2 (area), but metabolic demand increases as the volume (R^3).

Light Attenuation by Absoption



Beer-Lambert Law:

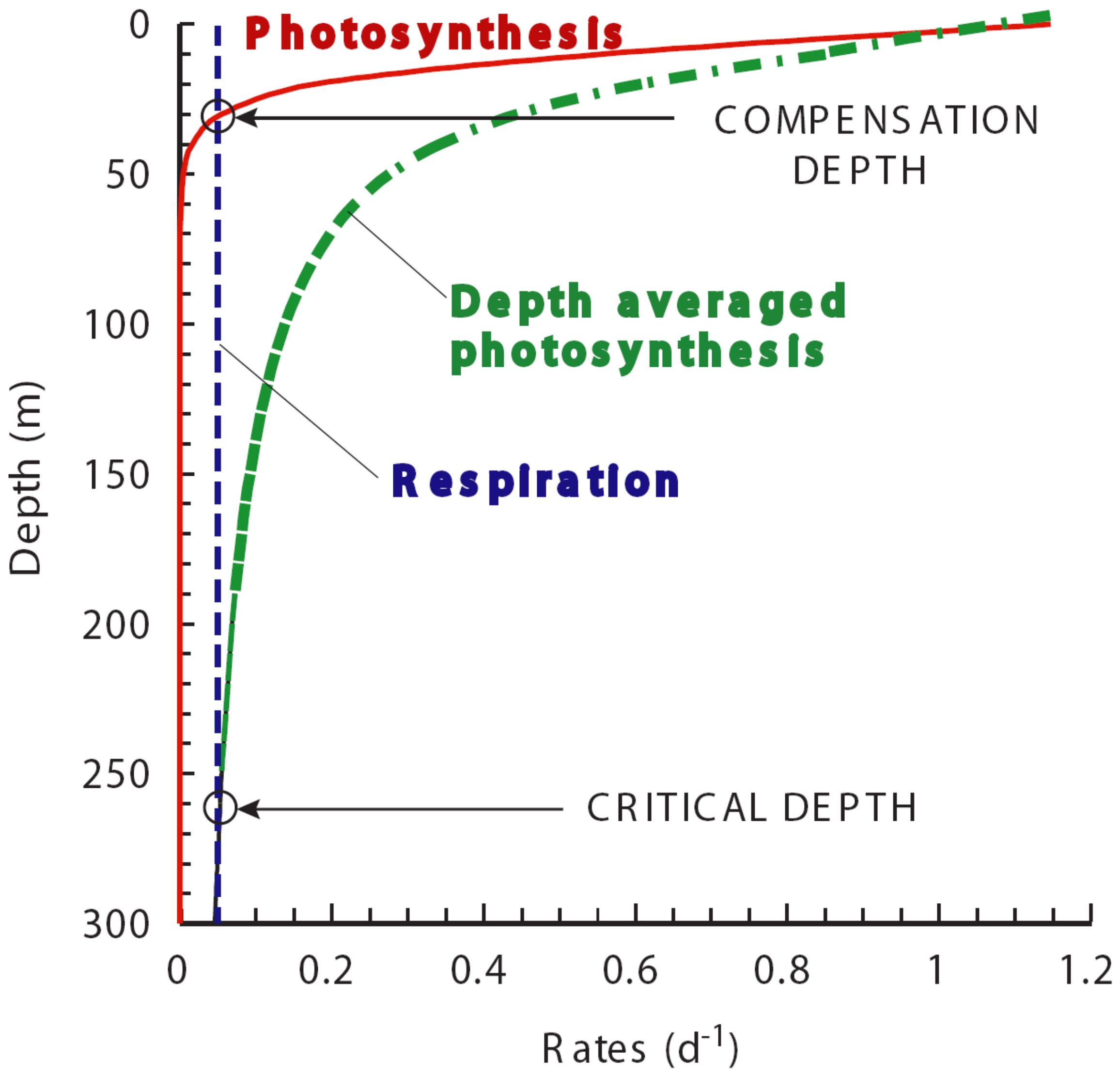
$$I(z) = I_o * e^{-kz}$$

k ~ 0.04/m

(actually a strong function of light's wavelength and an integral over the spectrum)

Light levels adequate for photosynthesis persist only to < 200 m, shallower in murkier water.

Photosynthesis in Motion



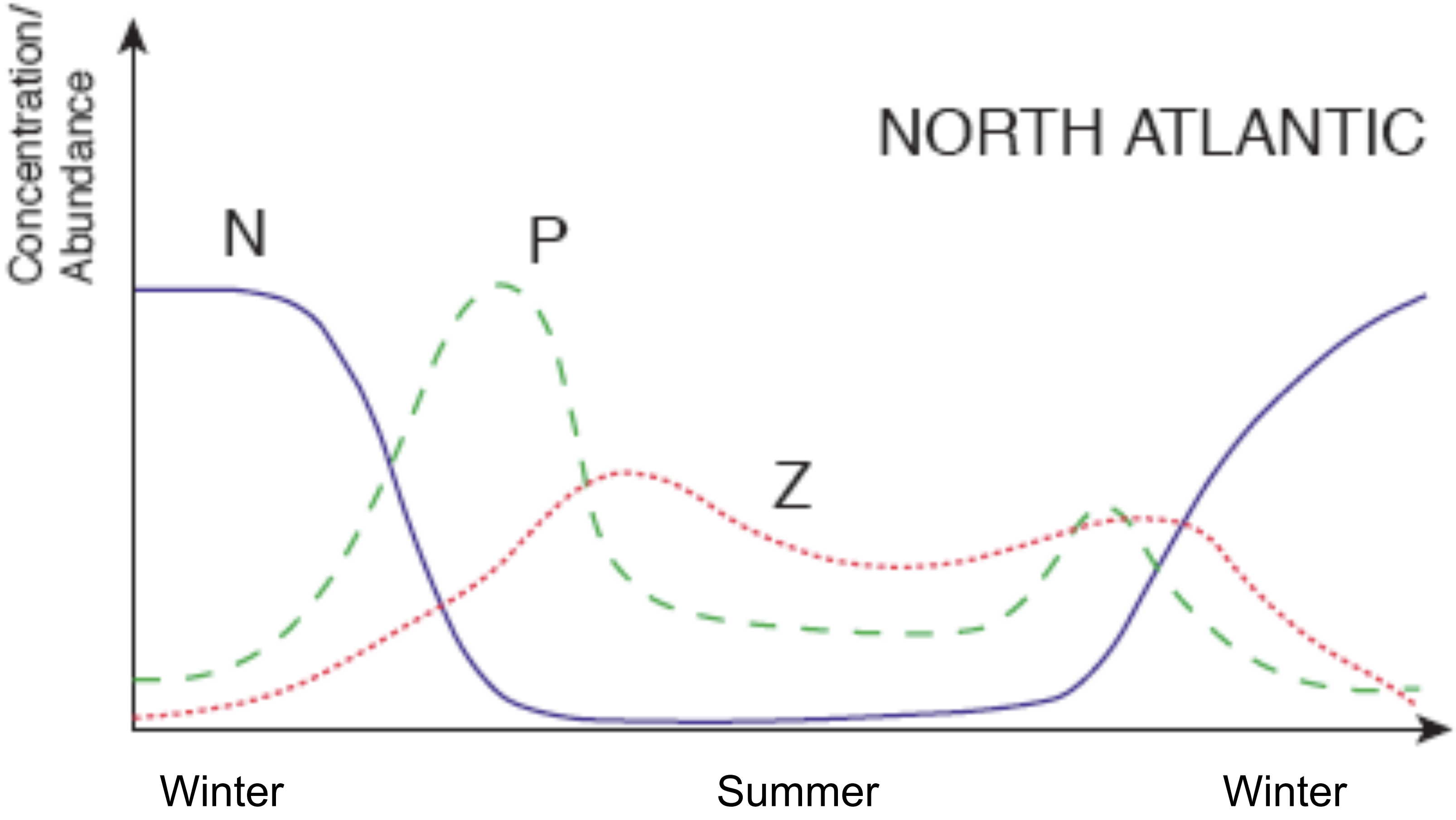
Compensation: local respiration matches light-limited production.

Critical: vertically averaged respiration matches production.

In regions of deep winter mixing, the condition for a plankton "bloom" is that the mixed layer depth must be shallower than the critical depth. (H. Sverdrup, 1949)

The nutrient-light trade-off

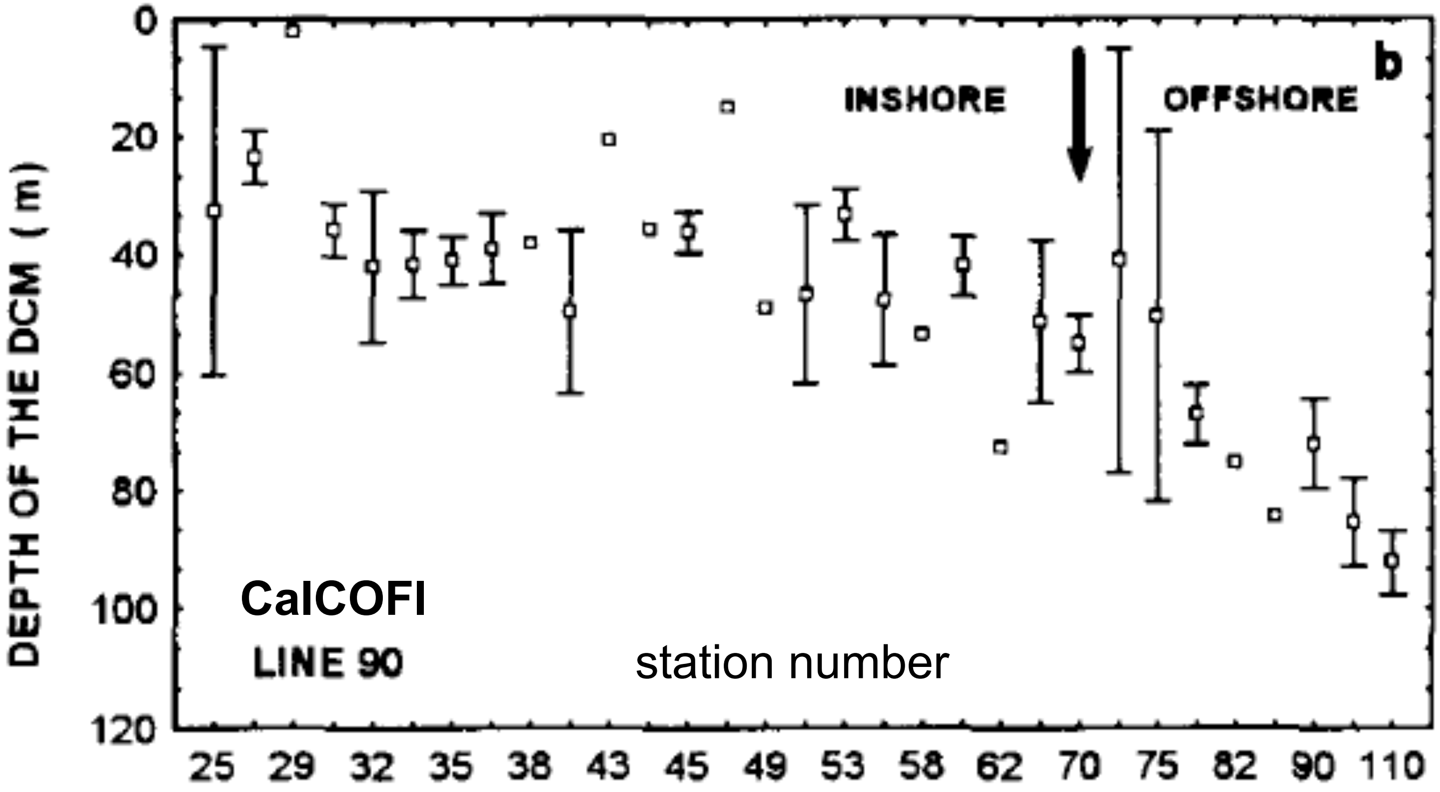
1) Seasonal



Nutrient and light availability are not in phase, and there are time lags between N, P, and Z. Note There are two blooms where N and light coincide in this high-latitude type of seasonal cycle.

The Nutrient-Light Trade-off

2) Depth



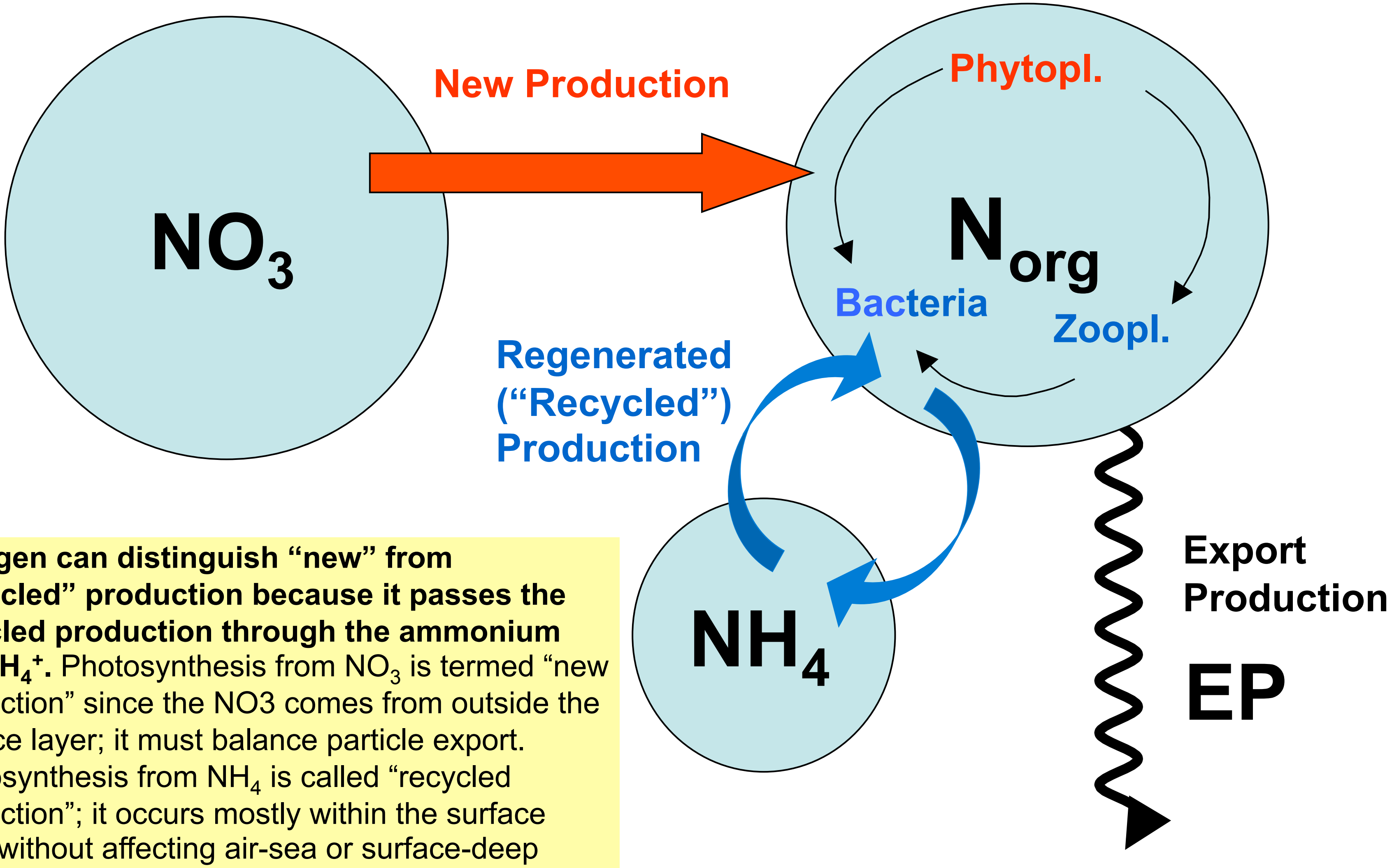
Millan-Nunez et al. [1996]

DCM = depth of the maximum in ChlA.

CalCOFI = California Cooperative Oceanic Fisheries Investigation (since 1949)

In many oceanic regions, the highest concentration of chlorophyll is found many meters below the ocean surface, where light intensity is already greatly attenuated but nutrients are more abundant. DCM is deeper in clearer water farther offshore.

New and Regenerated Production (N perspective)



NO_3

New Production

N_{org}

Phytopl.

Zoopl.

Bacteria

Regenerated (“Recycled”) Production

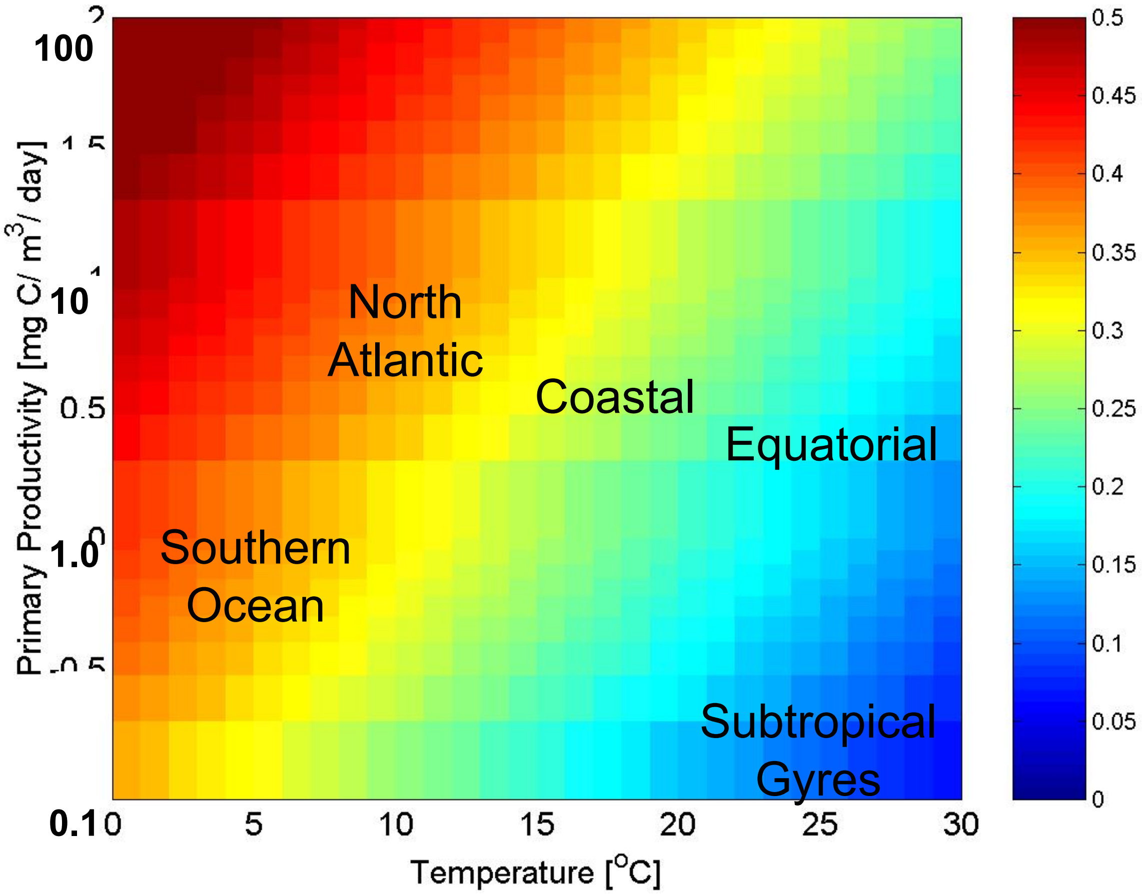
NH_4

Export Production

EP

Nitrogen can distinguish “new” from “recycled” production because it passes the recycled production through the ammonium ion NH_4^+. Photosynthesis from NO_3 is termed “new production” since the NO3 comes from outside the surface layer; it must balance particle export. Photosynthesis from NH_4 is called “recycled production”; it occurs mostly within the surface layer without affecting air-sea or surface-deep exchange.

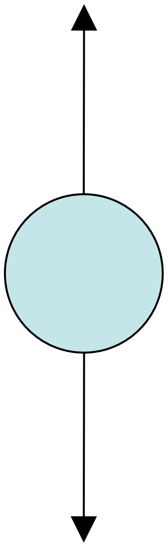
Particle Export Ratio (f-ratio)



Empirically derived effect of temperature and Net Primary Productivity on the f-ratio (the *fraction* of productivity that gets exported), and approximate values for some large ocean regions.

Plankton Size and Fall Speed

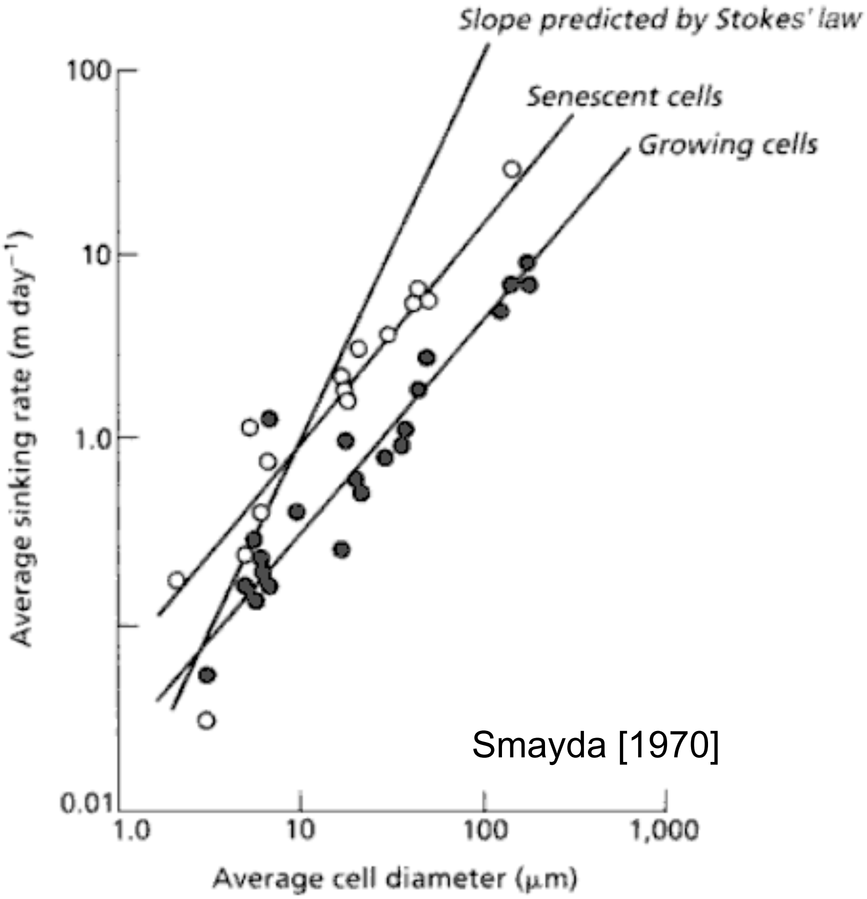
$$F_d = 6\pi\mu R w$$



Drag Force

Gravity Force

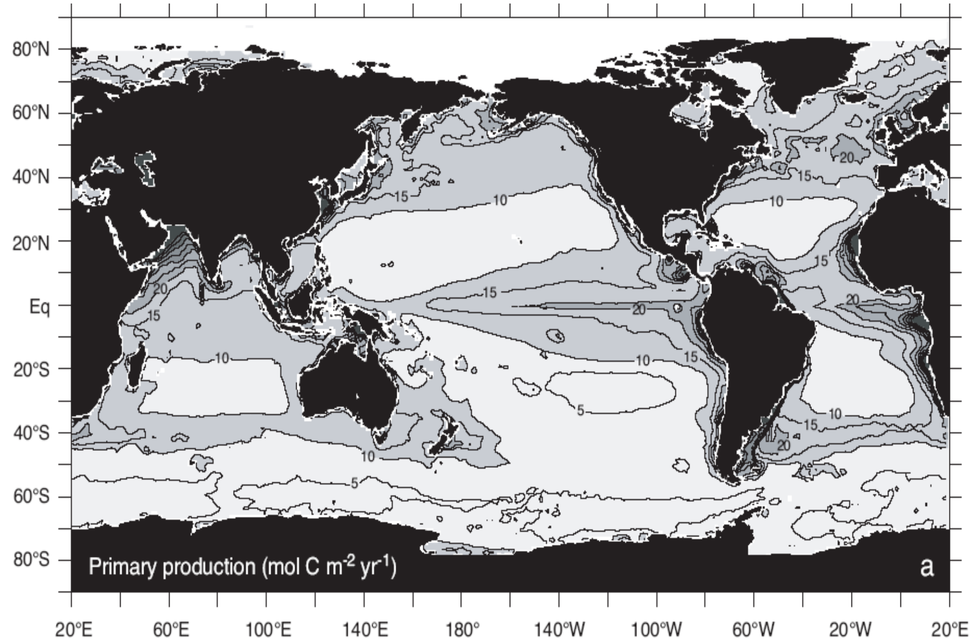
$$F_g = \rho' g \,(4\pi R^3 \;/ 3)$$

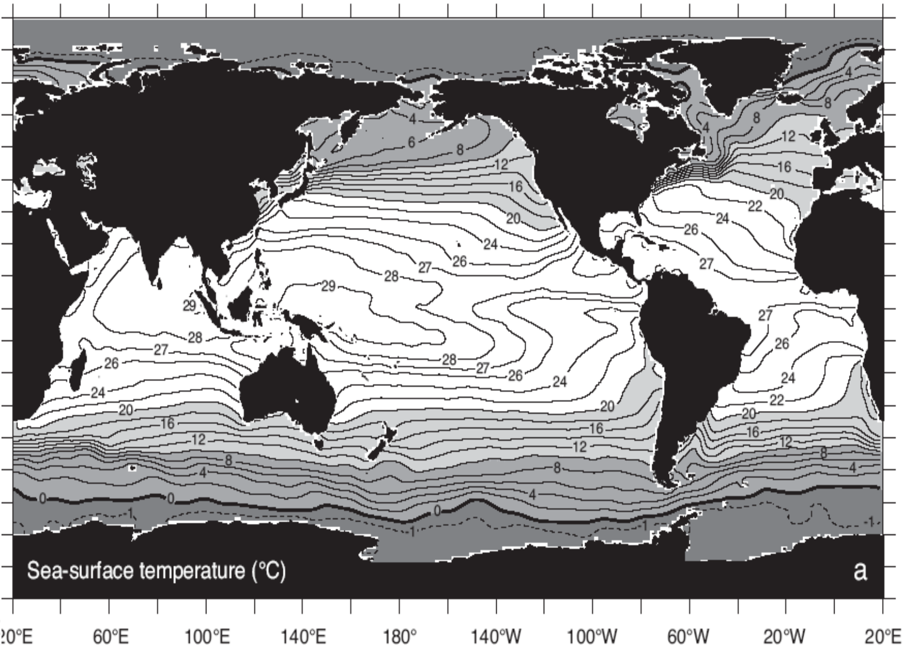


Smayda [1970]

Terminal velocity of a small and slowly falling (Re<1) sphere is proportional to $w \sim R^2$ (Stokes' Law; viscous flow). Bigger particles fall faster. Actual plankton fall speeds are $w \sim R^{1.2}$, for reasons that are not fully explained but are due to particle shape complexity.

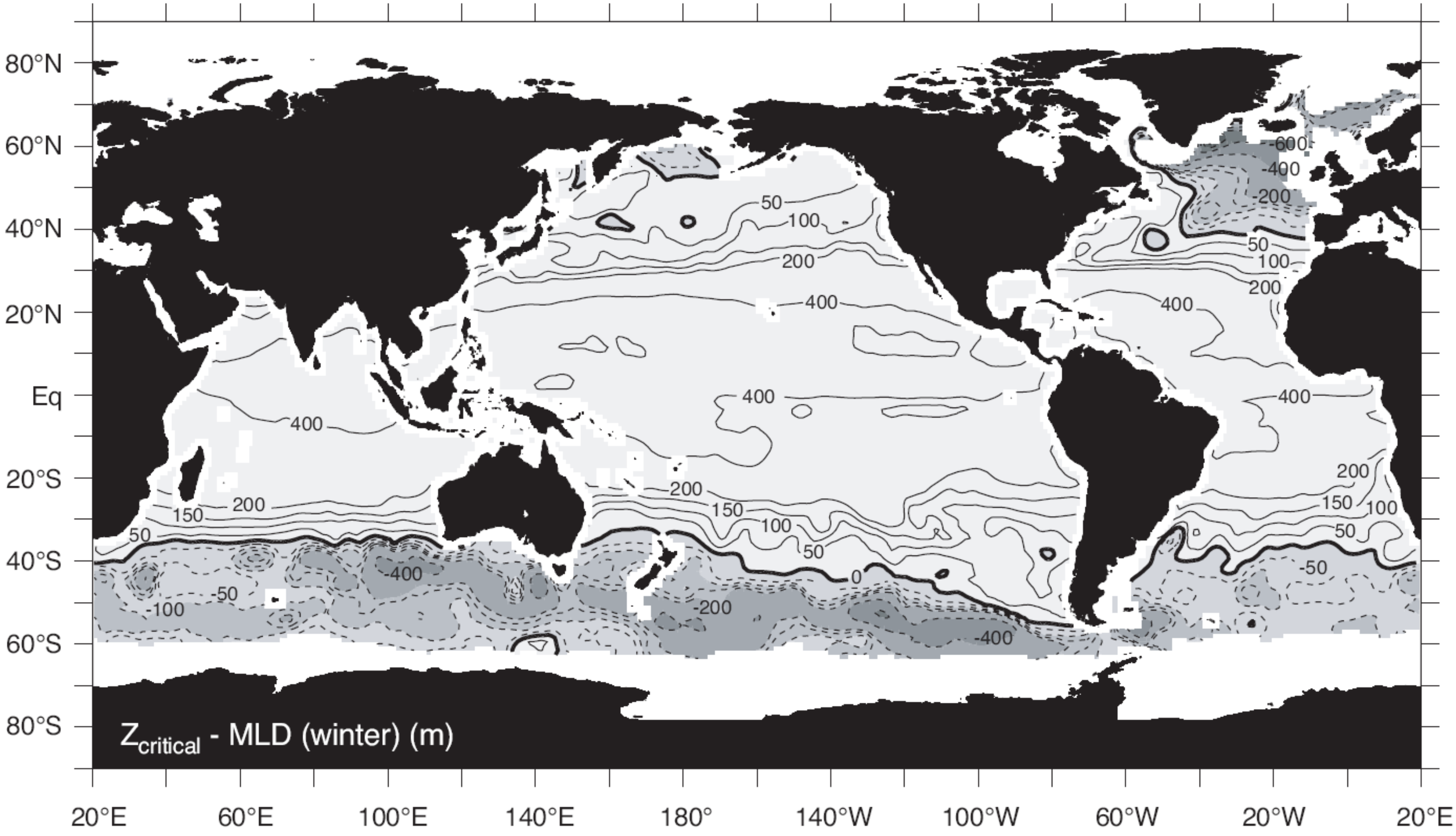
NPP vs SST





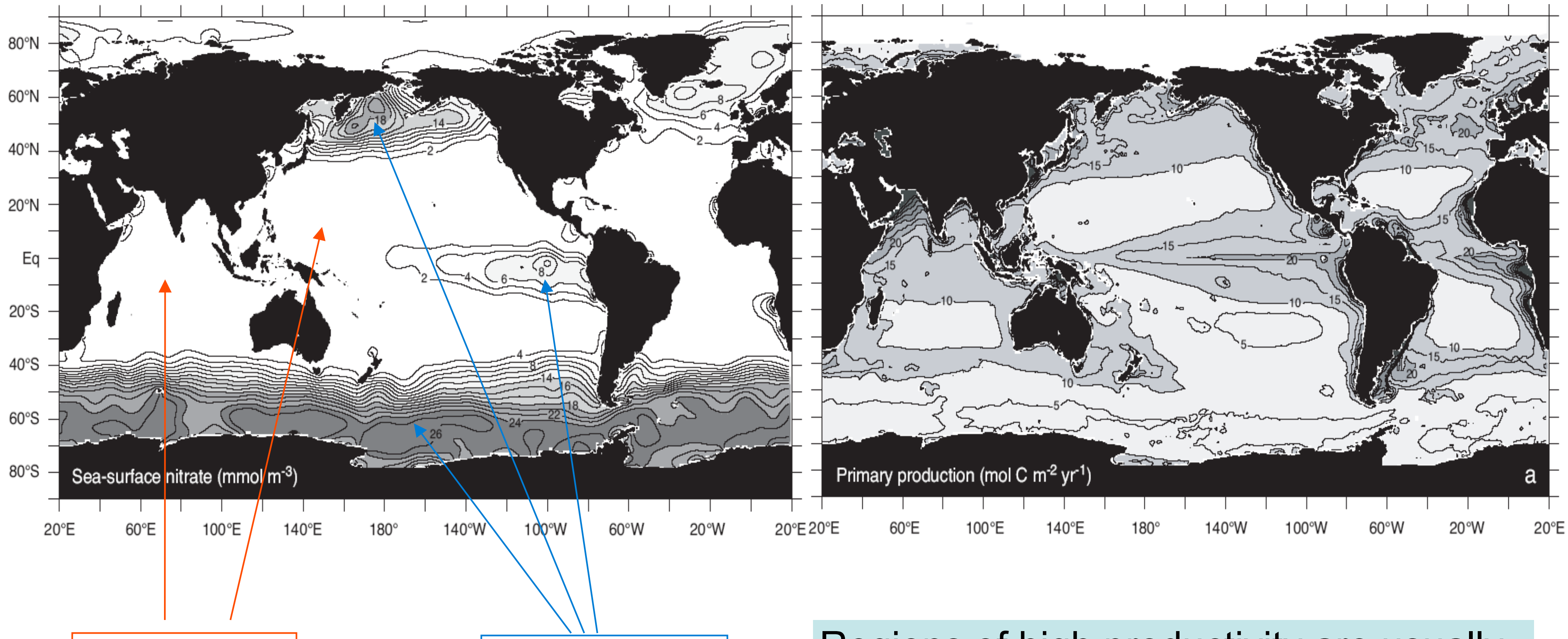
Plankton growth rate increases with temperature, but large-scale patterns of productivity are not positively correlated to SST.

Seasonal light limitation



Light is always limiting in the polar winter, can be limiting in mid-latitudes even in summer, but is not limiting in low latitudes. Negative values indicate that MLD > critical depth => life is not viable.

Nutrient Limitation



$[NO_3] << K_N$

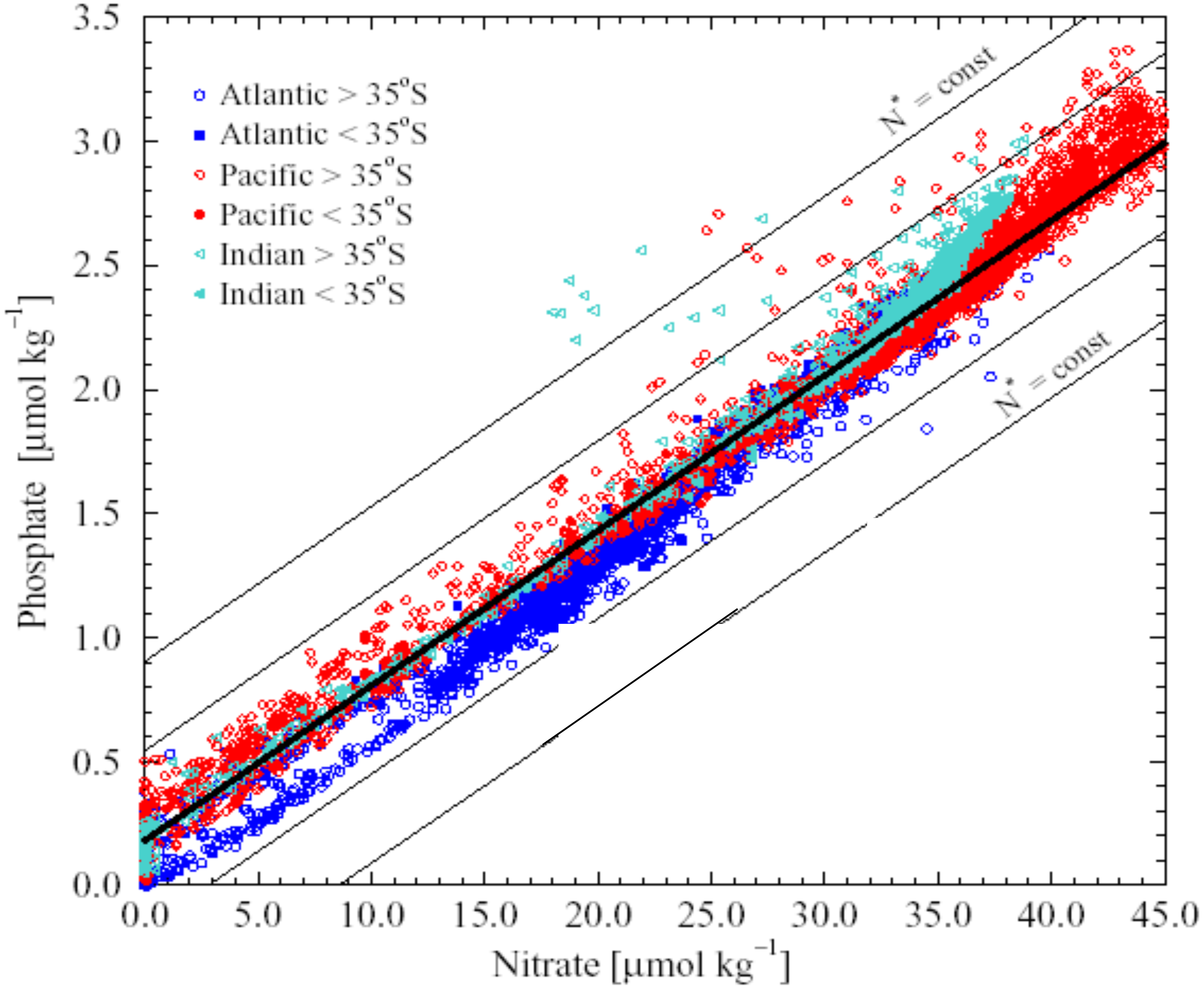
$\gamma(N) << 1$

$[NO_3] >> K_N$

$\gamma(N) \approx 1$

Regions of high productivity are usually associated with high surface nutrient concentrations, but there are prominent exceptions (e.g., Arabian Sea, Eastern Tropical Atlantic).

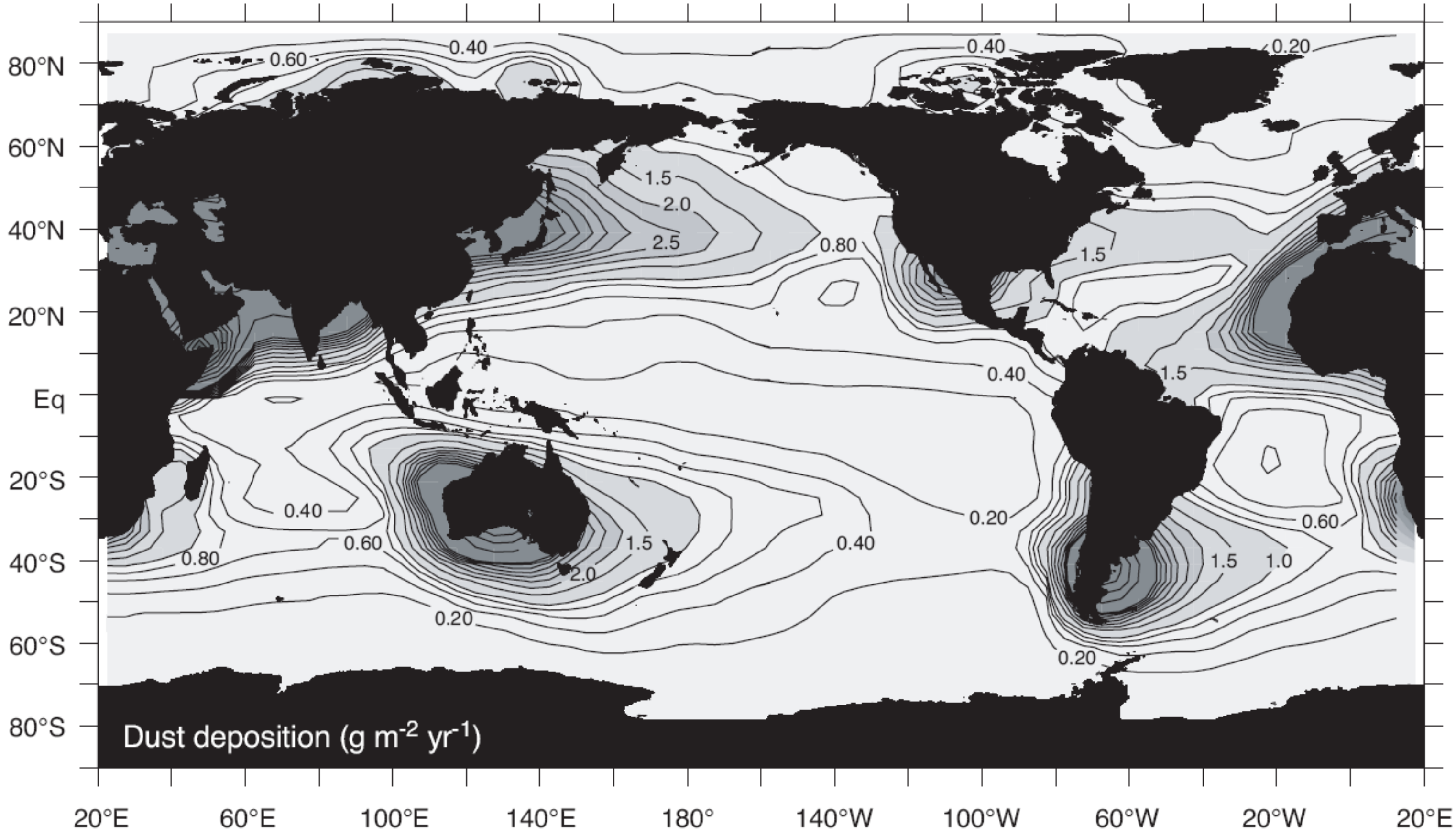
Nutrient Limitation



The major nutrients N (Nitrate) and P (Phosphate) co-vary at the Redfield Ratio of 16:1 in plankton, but their seawater concentrations are in a lower ratio (<15:1), implying that N is the more limiting nutrient. At the lowest levels, N disappears entirely while some P remains.

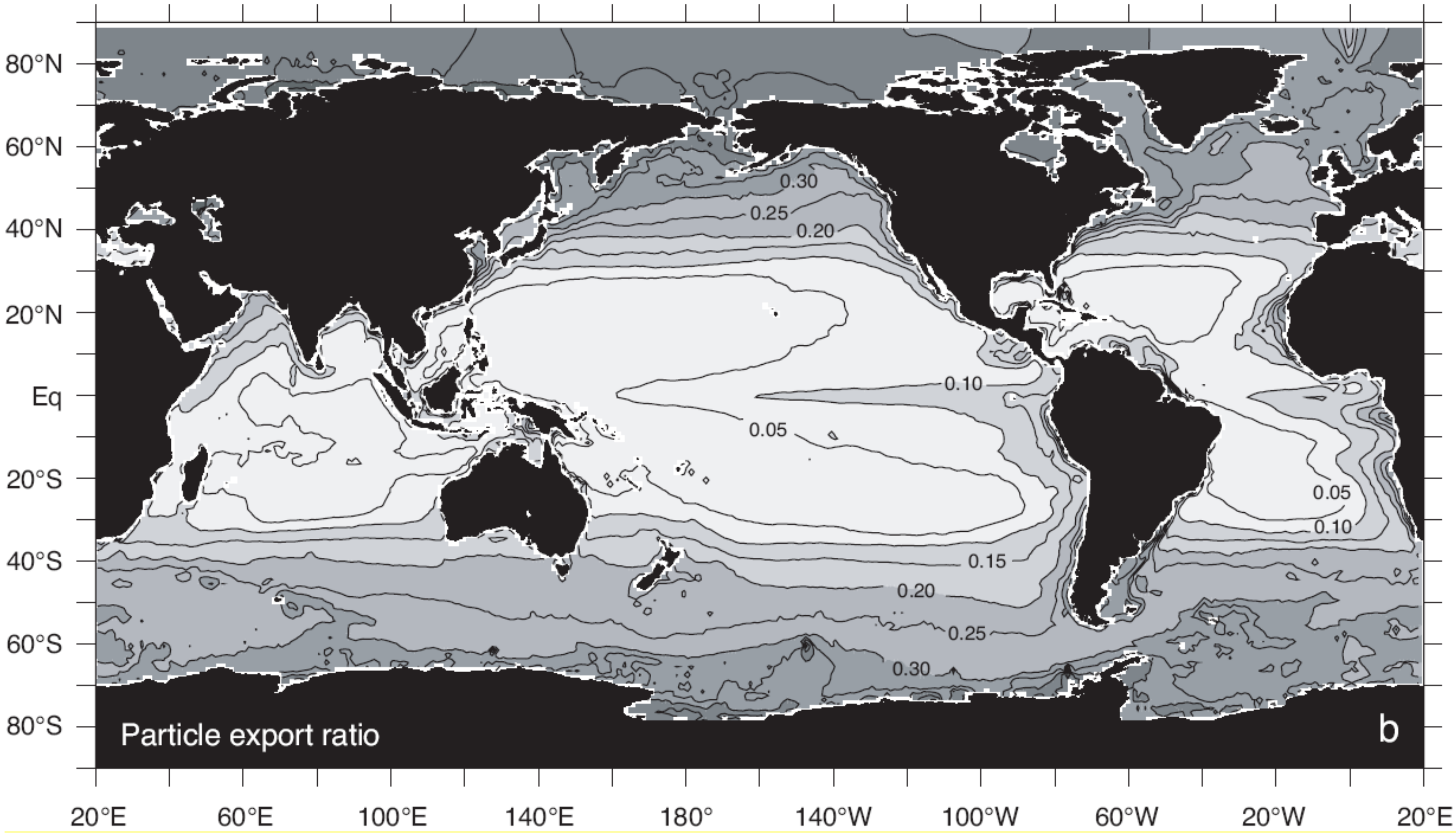
(This is a repeated slide.)

Micronutrient Limitation



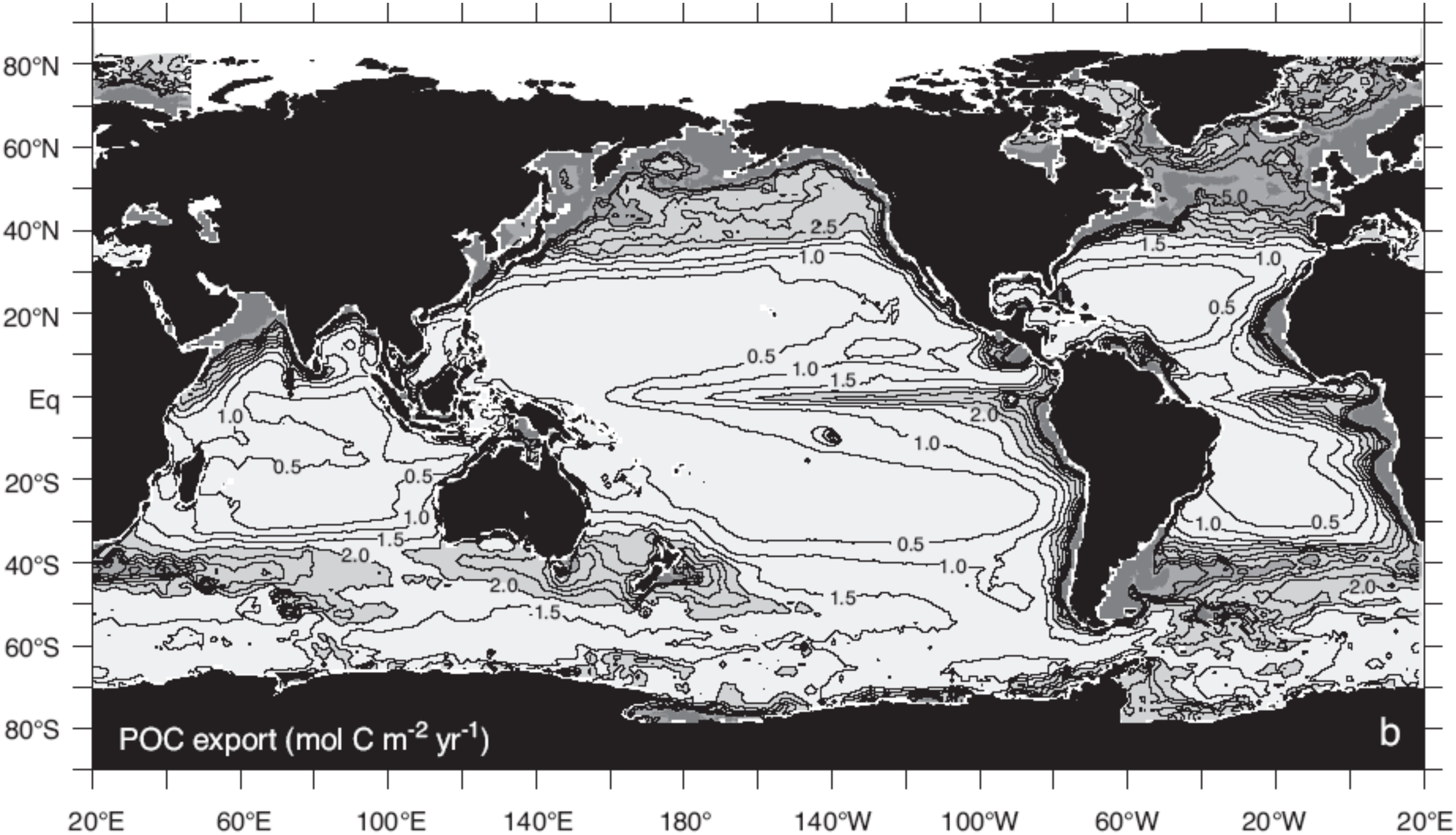
Iron (Fe) is delivered to the ocean largely as dust.
Its supply is very low in the Southern Ocean, and the Equatorial Pacific, both “High Nutrient - Low Chlorophyl” (i.e., low NPP) zones.

Particle Export Ratio



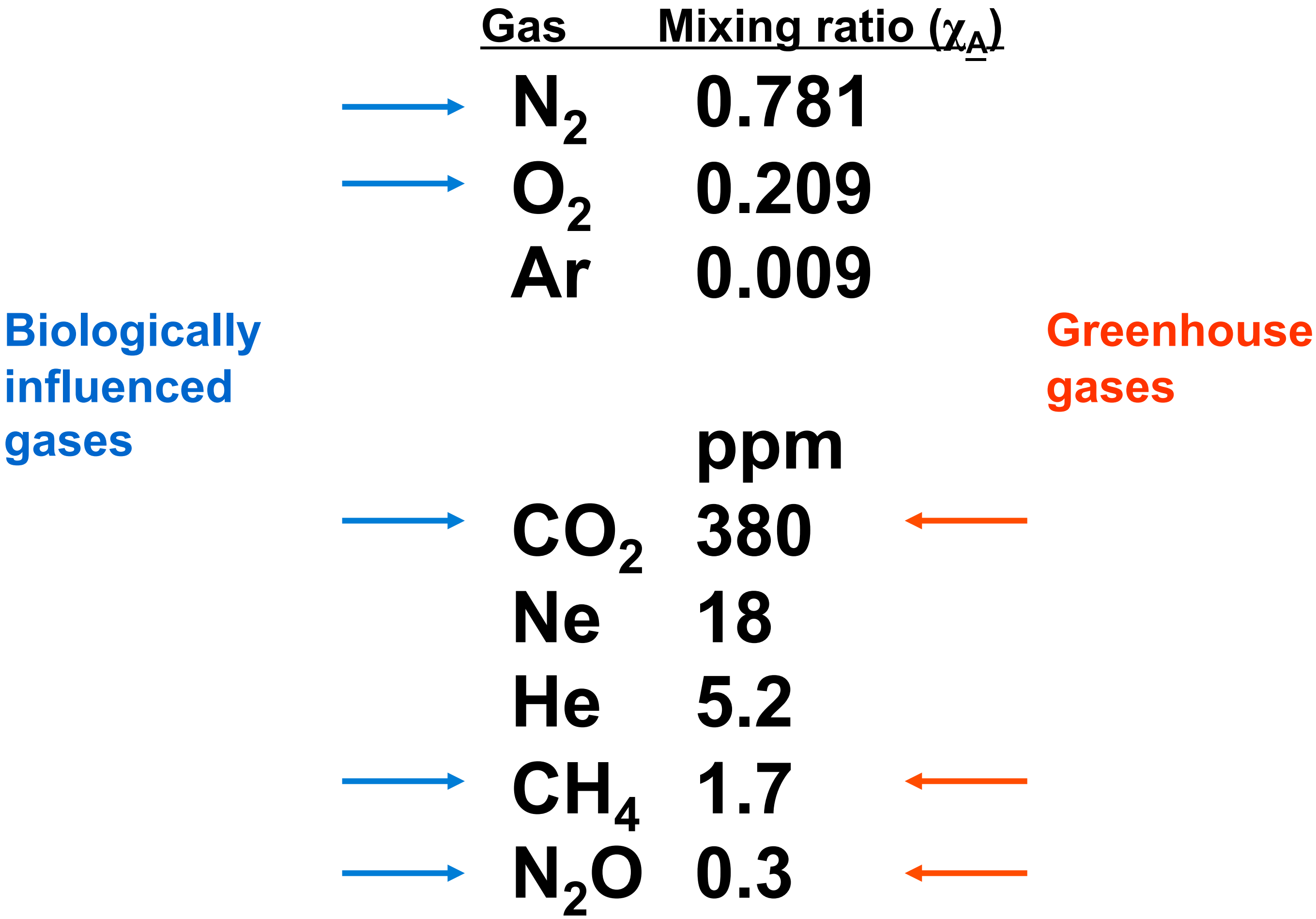
f-ratio: **R**egions with low productivity are good at recycling nutrients, whereas high productivity areas let a larger fraction of organic matter to escape to the deep ocean. (A metaphor for human societies here? --- rich ones are wasteful and poor ones resourceful.)

Export Production



Export production = NPP * f-ratio, where maps of both NPP and f-ratio are on earlier slides. There are large uncertainties in this estimate, which have not been well quantified. The uncertainty in EP is amplified relative to NPP's by the f-ratio's.

Air-Sea Gas Exchange:
Atmospheric concentrations



Biologically influenced gases

Greenhouse gases

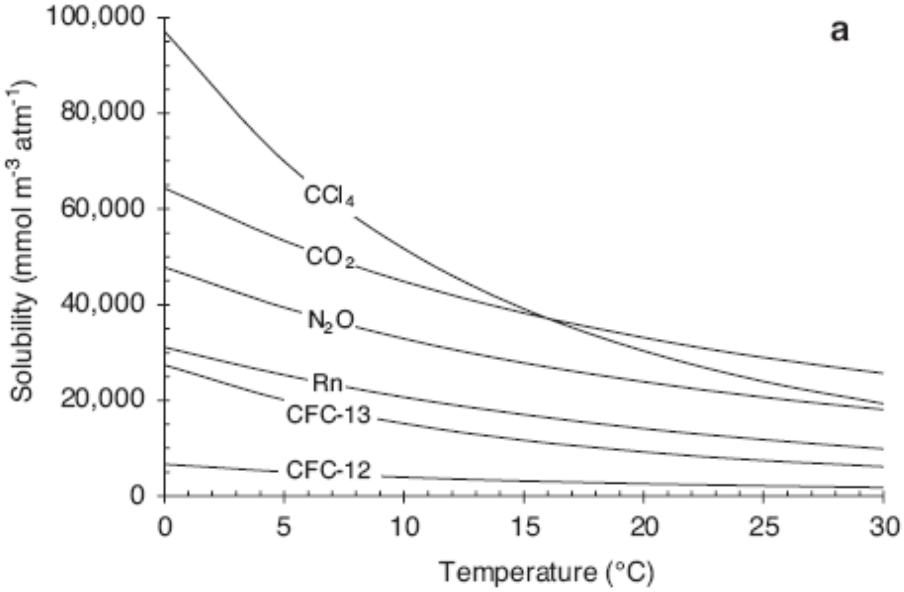
Gas	Mixing ratio (χ_A)
N_2	**0.781**
O_2	**0.209**
Ar	**0.009**
	ppm
CO_2	**380**
Ne	**18**
He	**5.2**
CH_4	**1.7**
N_2O	**0.3**

Henry's Law: $C_A = S_A * p_A$; S_A is solubility of gas A.

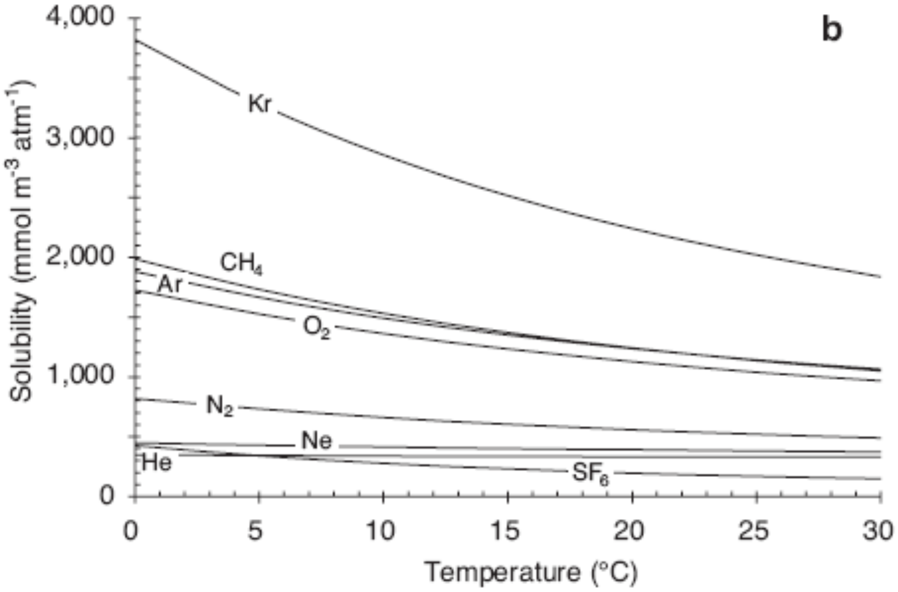
Dalton's Law: $p_A = \chi_A * P$; p_A is partial pressure.

Gas Solubility

High solubility gases



Low solubility gases



For all gases, solubility decreases with increasing temperature.
Solubility increases with molecular weight, but is also increased for gases with a dipole moment (e.g. CO_2 and N_2O) that can attract that of H_2O.

Gas Disequilibrium

Temperature Eqn.

$$\frac{DT}{Dt} + D(T) = \frac{H}{\rho c_p z_{bl}}$$

Tracer (gas) Eqn.

$$\frac{DC}{Dt} + D(C) = Source(C) + \frac{F}{z_{bl}}$$

Solubility

$$C_{sat} \approx a_0 + a_1 T + a_2 T^2$$

Disequilibrium

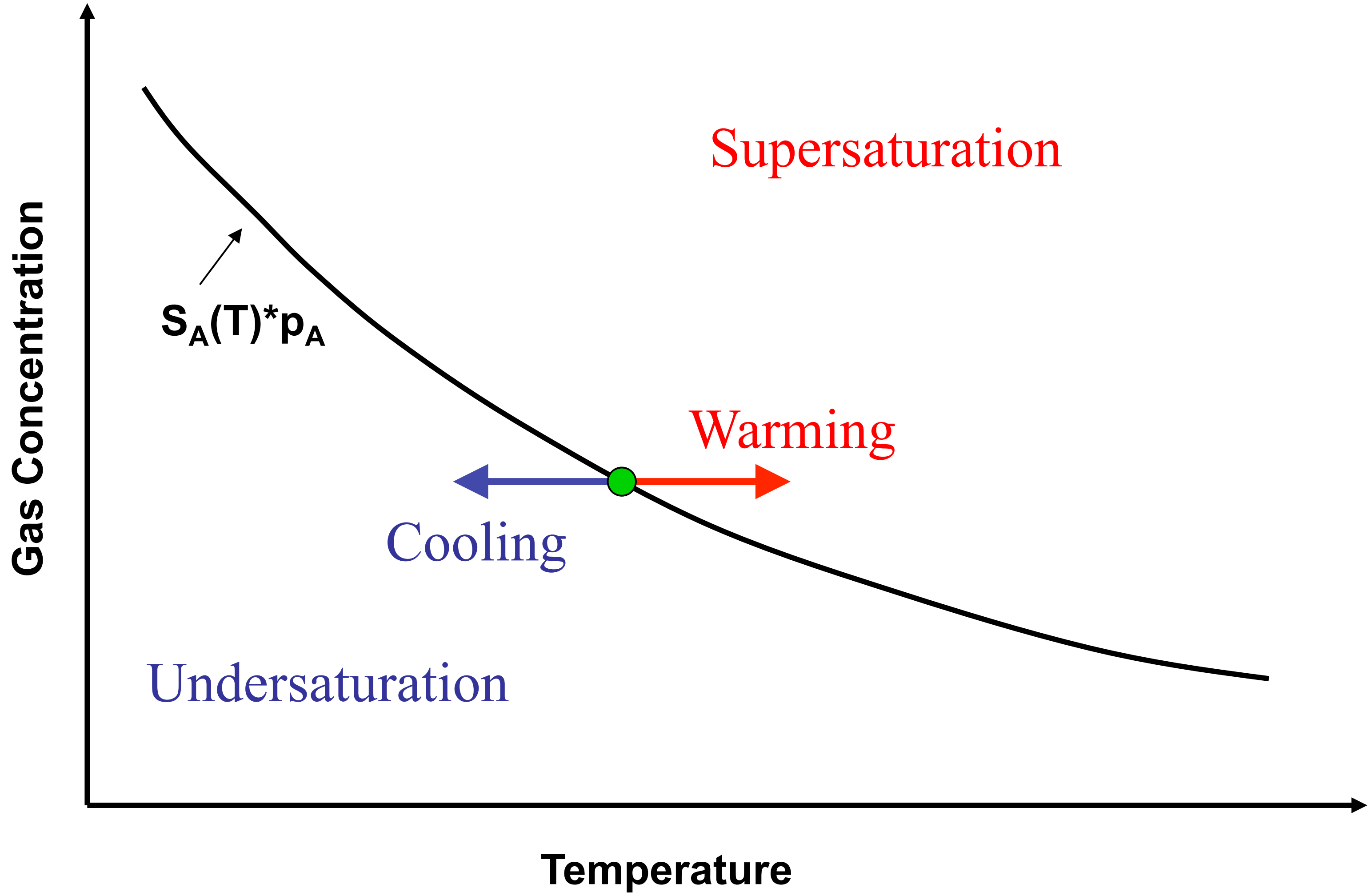
$$\delta C = C - C_{sat}$$

Disequilibrium Equation

$$\frac{D(\delta C)}{Dt} \underbrace{+ D(\delta C)}_{\text{Transport/Mixing}} = \underbrace{a_2 \kappa \left(\nabla T\right)^2}_{\text{Mixing Supersat.}} - \underbrace{a_1 \frac{H}{\rho c_p z_{bl}}}_{\text{Heating/cooling}} + \underbrace{S(C)}_{\text{Bio/Chem Source}} + \underbrace{\frac{F}{z_{bl}}}_{\text{Air-Sea Exchange}}$$

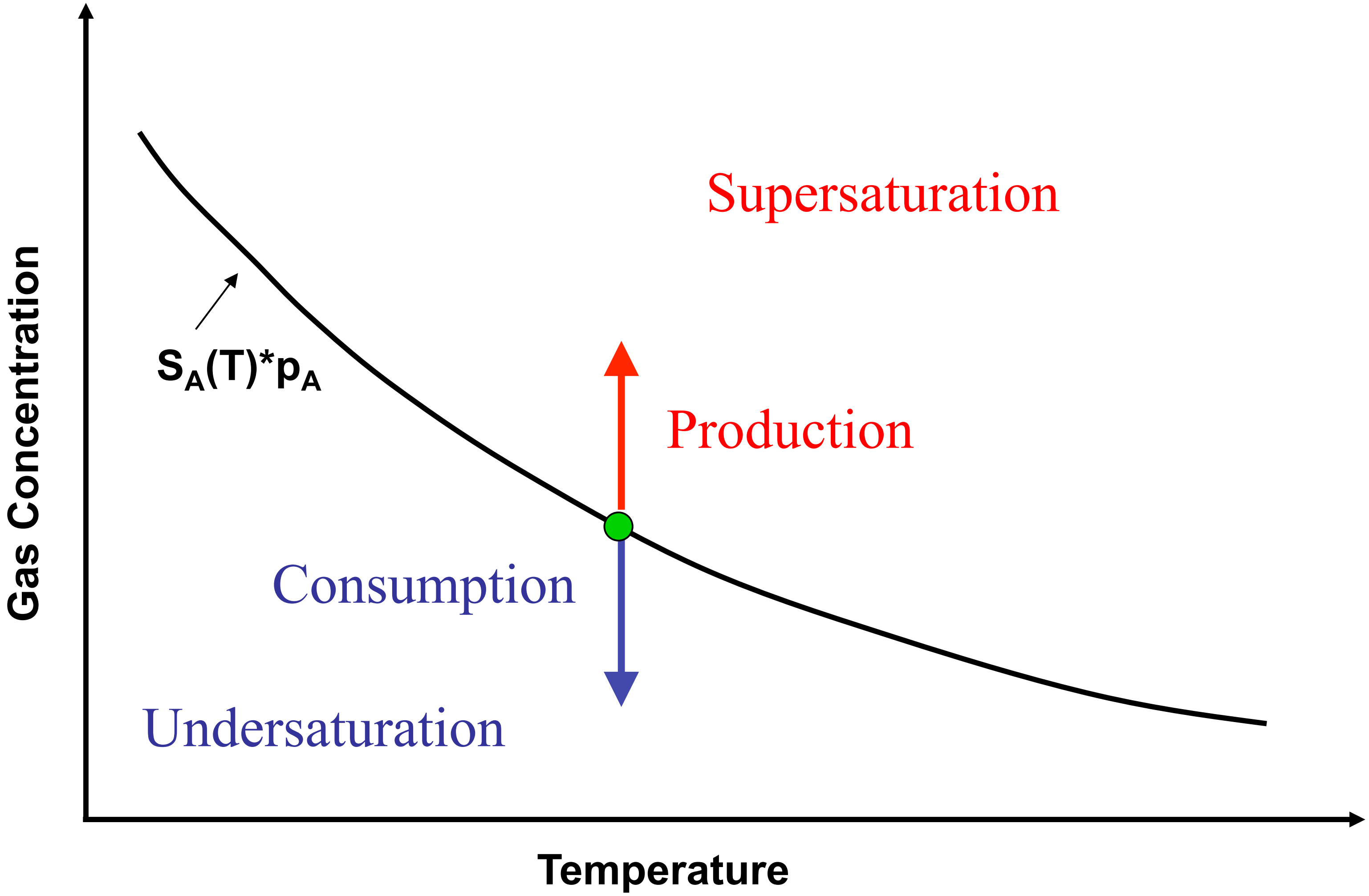
Sources of Disequilibrium:

1) Heating and Cooling



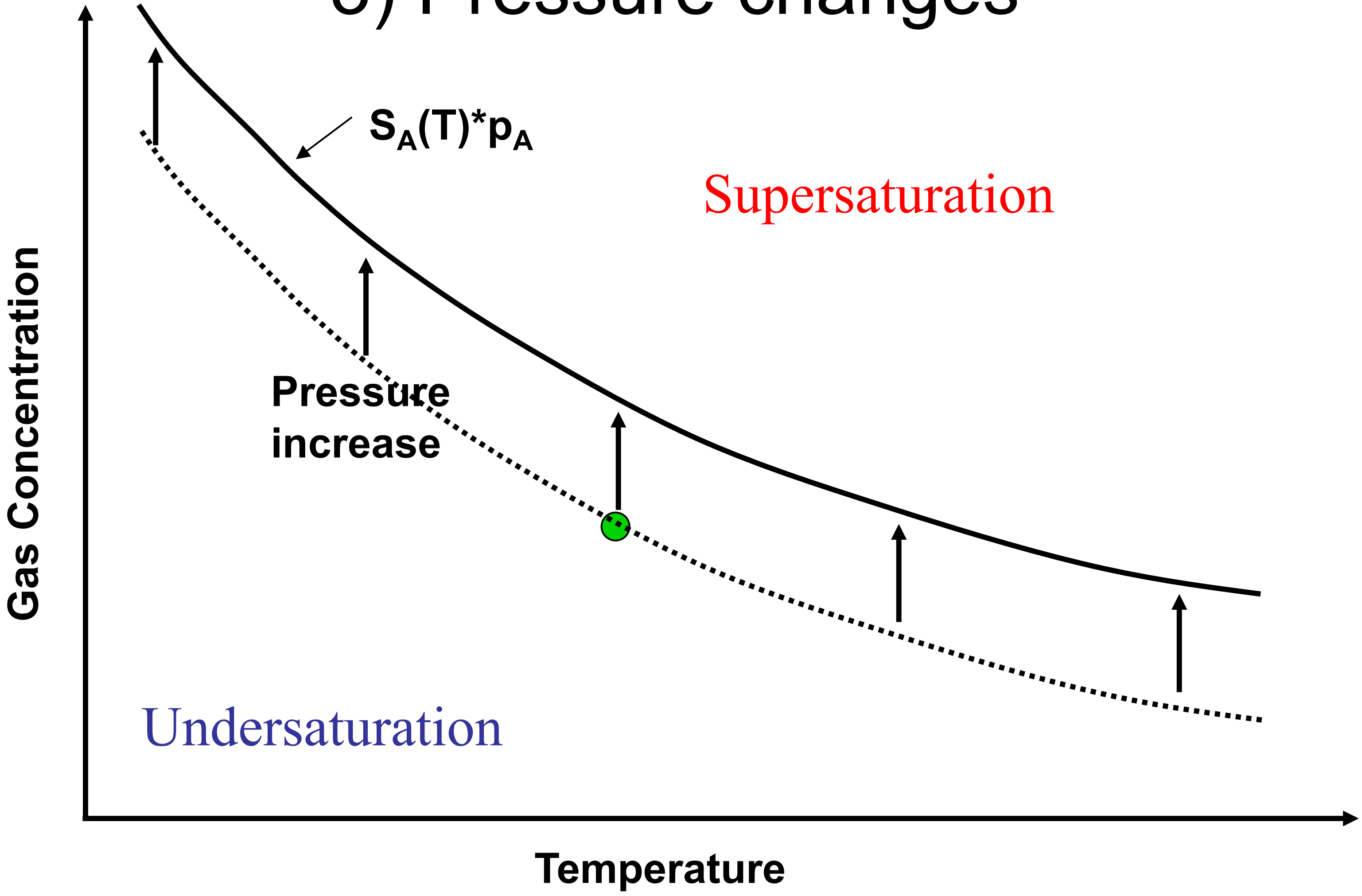
Sources of Disequilibrium:

2) Production and Consumption



Sources of Disequilibrium:

3) Pressure changes

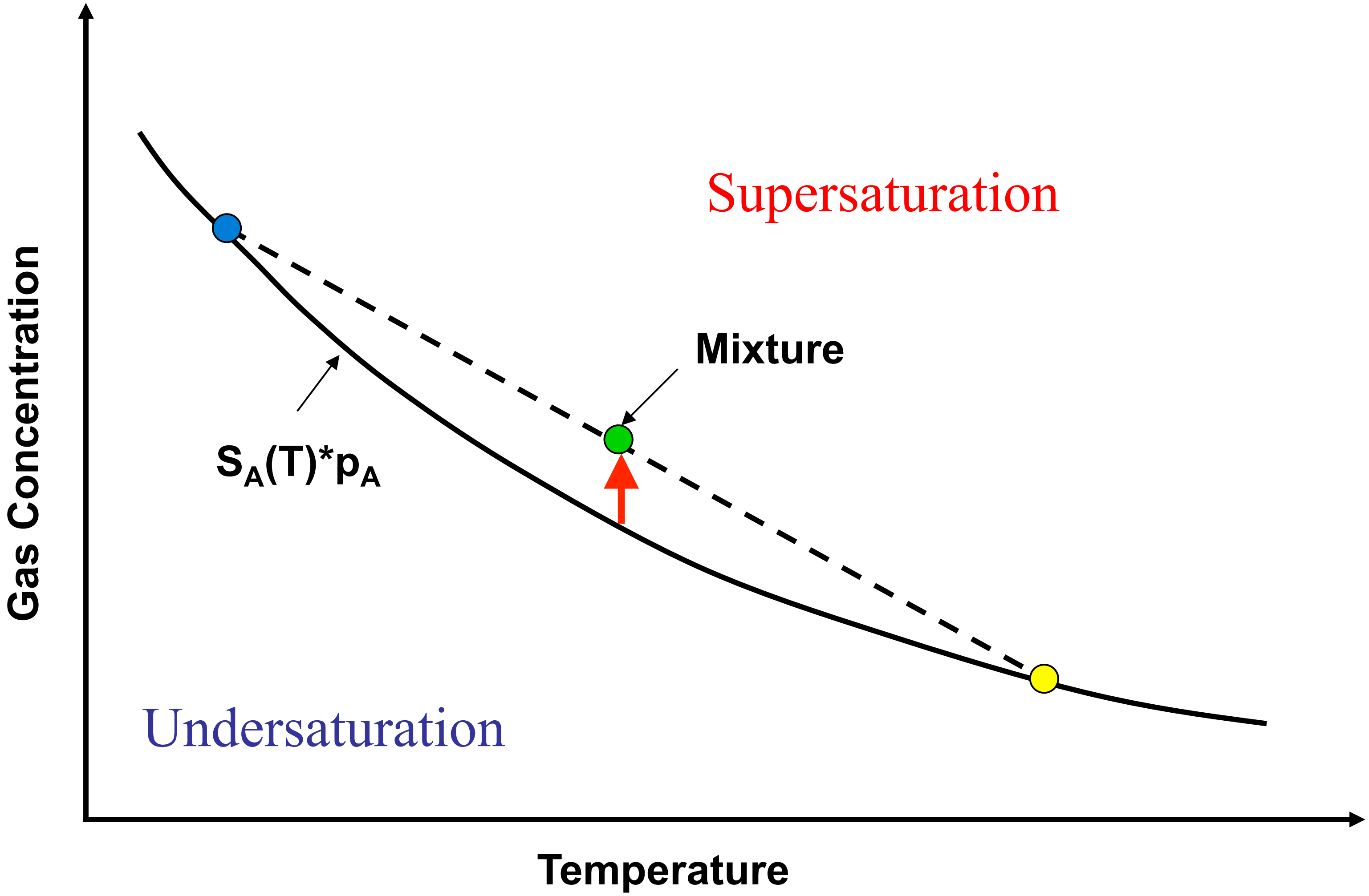


Causes:

1) Changes in air pressure (e.g. bubbles, storm systems)
2) Changes in gas mixing ratio (e.g. fossil fuel CO_2, pollutants)

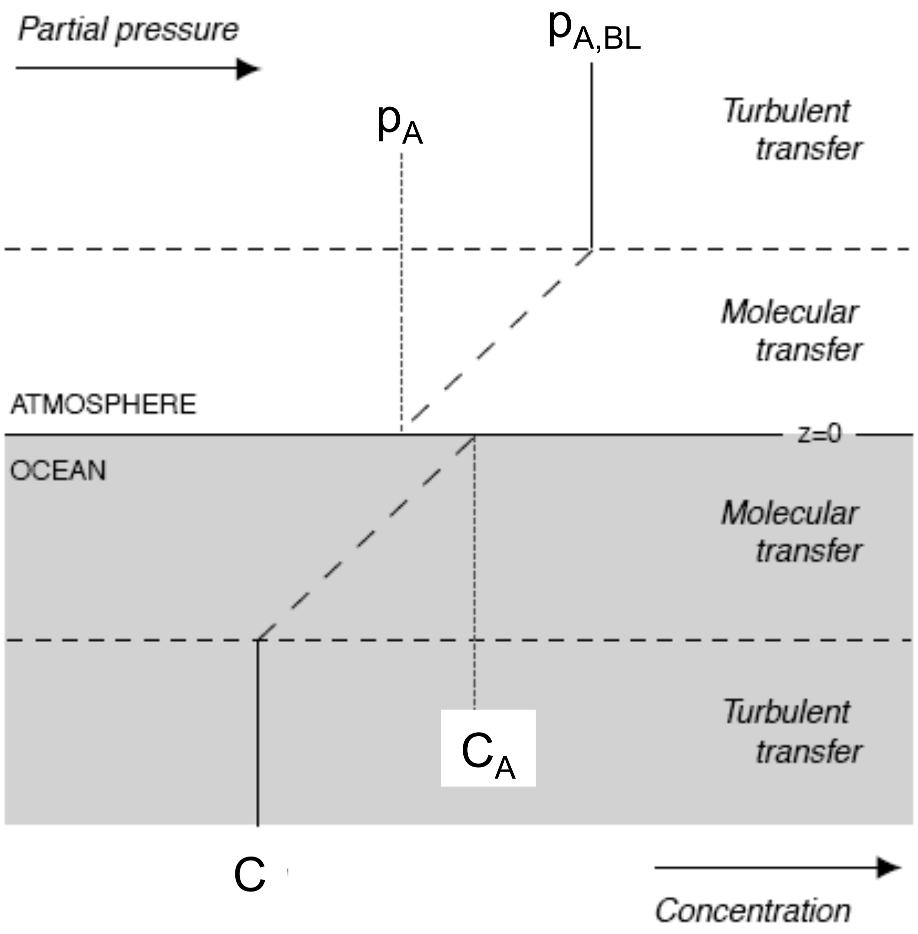
Sources of Disequilibrium:

4) Water mixing



Diathermal mixing leads saturated parcels to supersaturation by a few percent.

Stagnant Film Model



This is a physical conception of gas diffusion through an undisturbed interface. Its relevance to the actual air-sea gas flux is limited because waves, bubbles, and droplets expose a much larger exchange surface and because turbulent motions do penetrate all the way to the interface and even rupture it.

Gas Exchange:
The Response to Disequilibrium

$$F = k_w * (C_A - C)$$

Air-sea flux of C

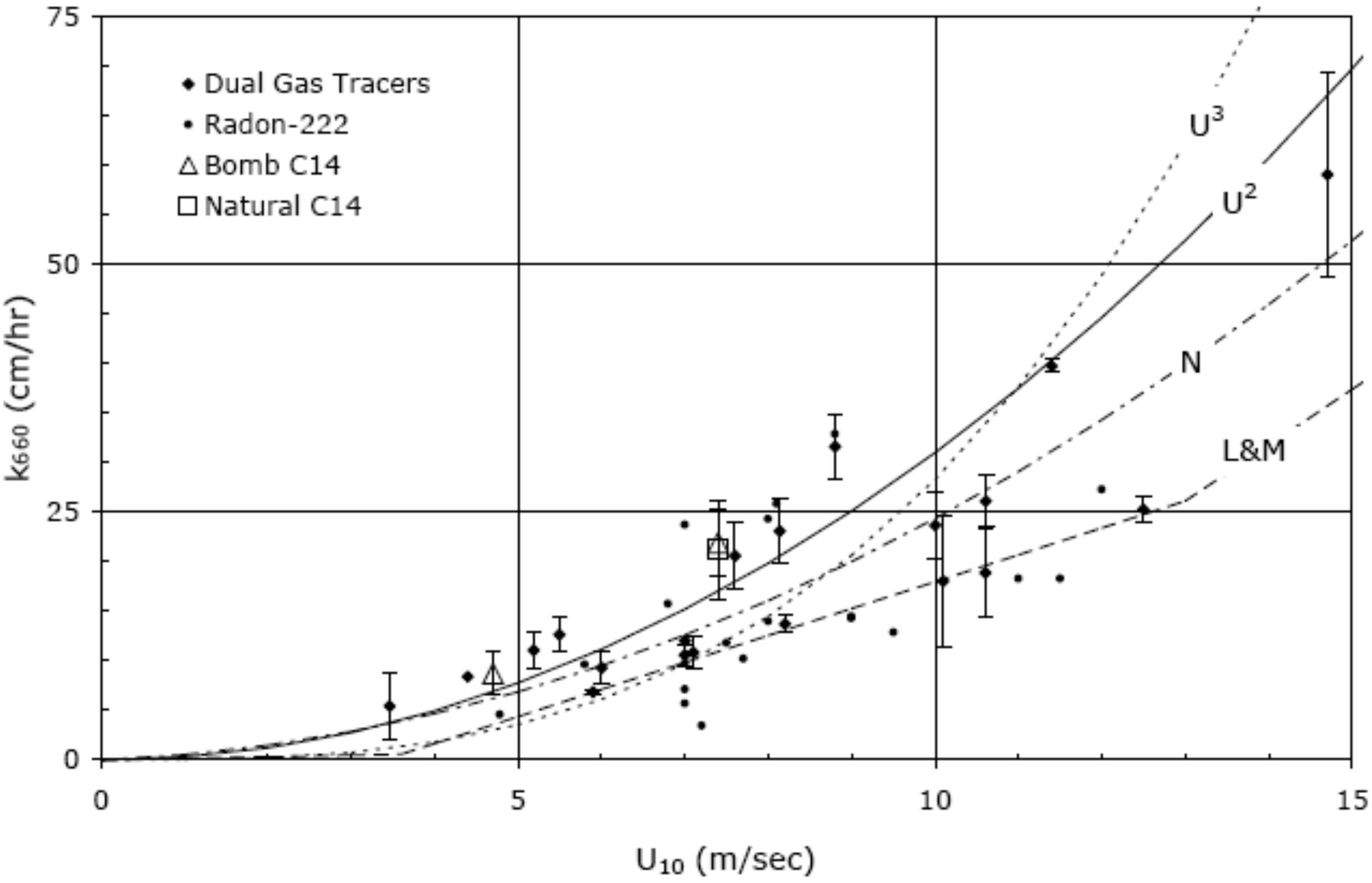
Piston Velocity
[m/s]

Disequilibrium between gas concentration (C) and its saturation (C_A)

Dissolved gases reach new equilibrium with air by

1) **outgassing when supersaturated ($C > C_A$)**
2) **ingassing when undersaturated ($C < C_A$)**

Piston (or “Transfer”) Velocity



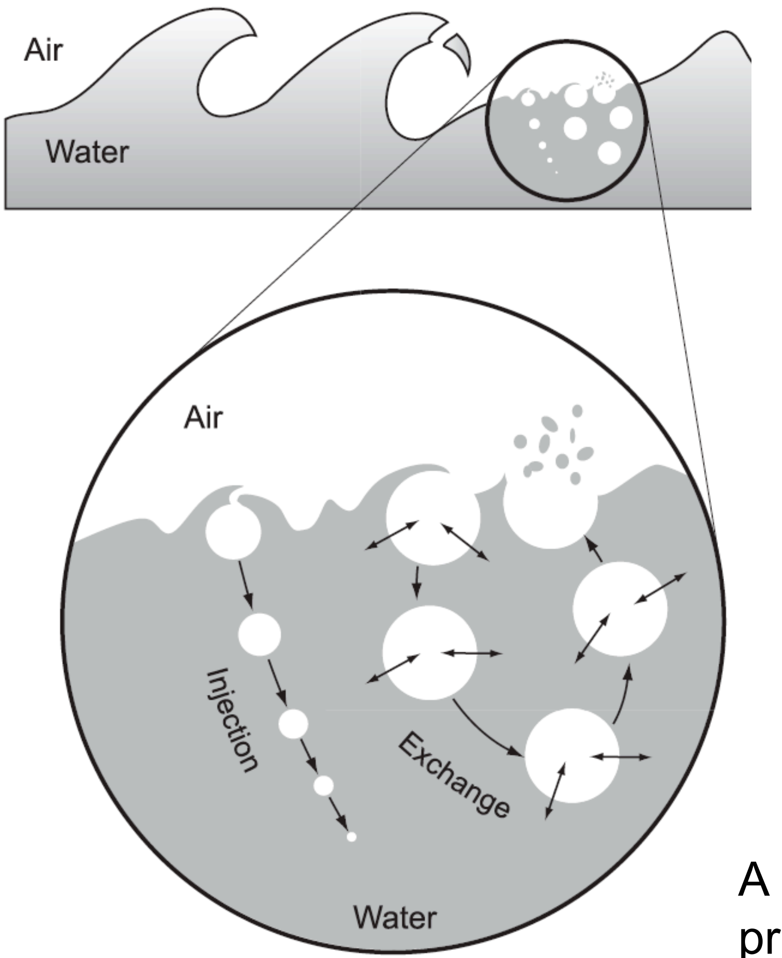
Piston velocity (k_w) depends strongly on windspeed (more than C_D):

Strong winds → high k_w → rapid equilibration

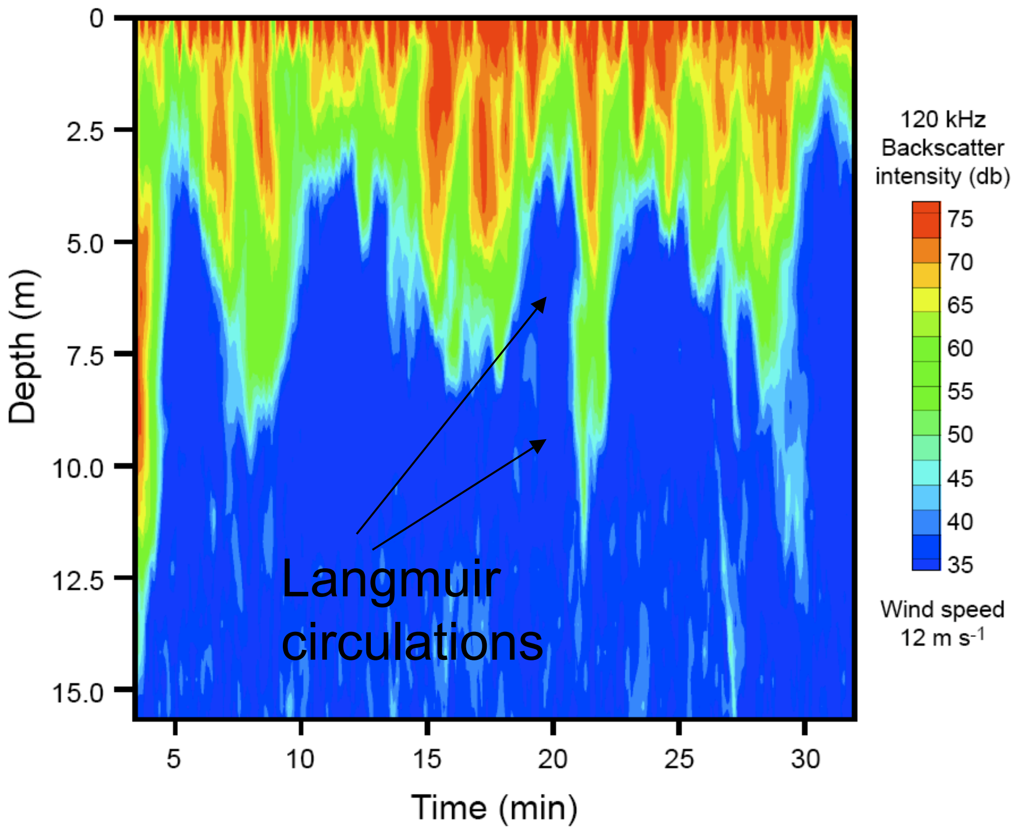
Weak winds → low k_w → slow equilibration

Values are poorly constrained at high U_{atm}, where wave breaking and evolution of injected bubbles are the controlling processes.

Bubble-induced Gas Exchange



Emerson [2008]



A bubble population model: injection, transport, pressure-induced size change, buoyant rise, dissolution into seawater (coupling to BGC model).