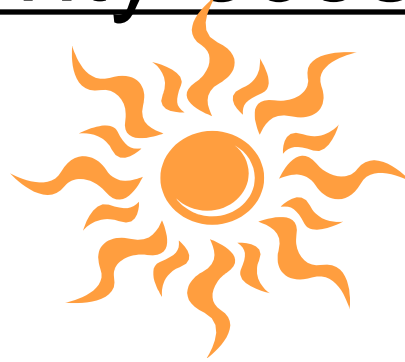




# An inverted food web in low productivity ecosystems?



Primary producers

Primary consumers (Bacteria)

Secondary consumers (microzooplankton)

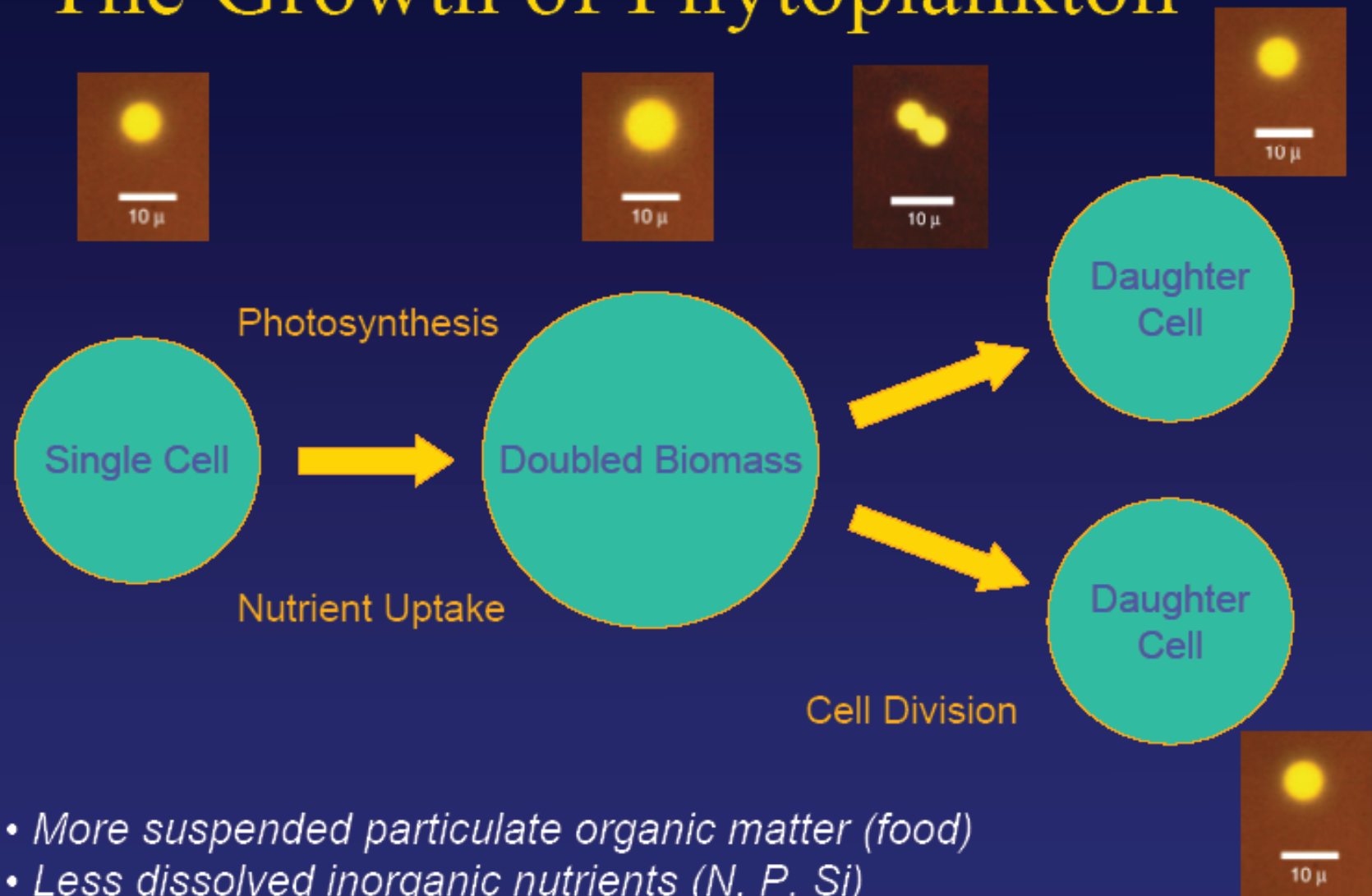
Tertiary consumers (mesozooplankton)

**How is this biomass pyramid sustained?  
Rapid turnover of phytoplankton biomass.**

# What is it we want to know?

- **Biomass** (biogenic carbon, trophic linkages)
- **Carbon fluxes** (production, respiration, DOC utilization rates)
- **Rates of growth** (cell physiology, nutritional status)

# The Growth of Phytoplankton



## Result:

- More suspended particulate organic matter (food)
- Less dissolved inorganic nutrients (N, P, Si)
- Less dissolved inorganic carbon ( $\text{CO}_2$ ) —(Oxygen is produced)

# Biomass Production

- Production is defined as the change in biomass over time.
- Production is mathematically related to biomass and growth as:

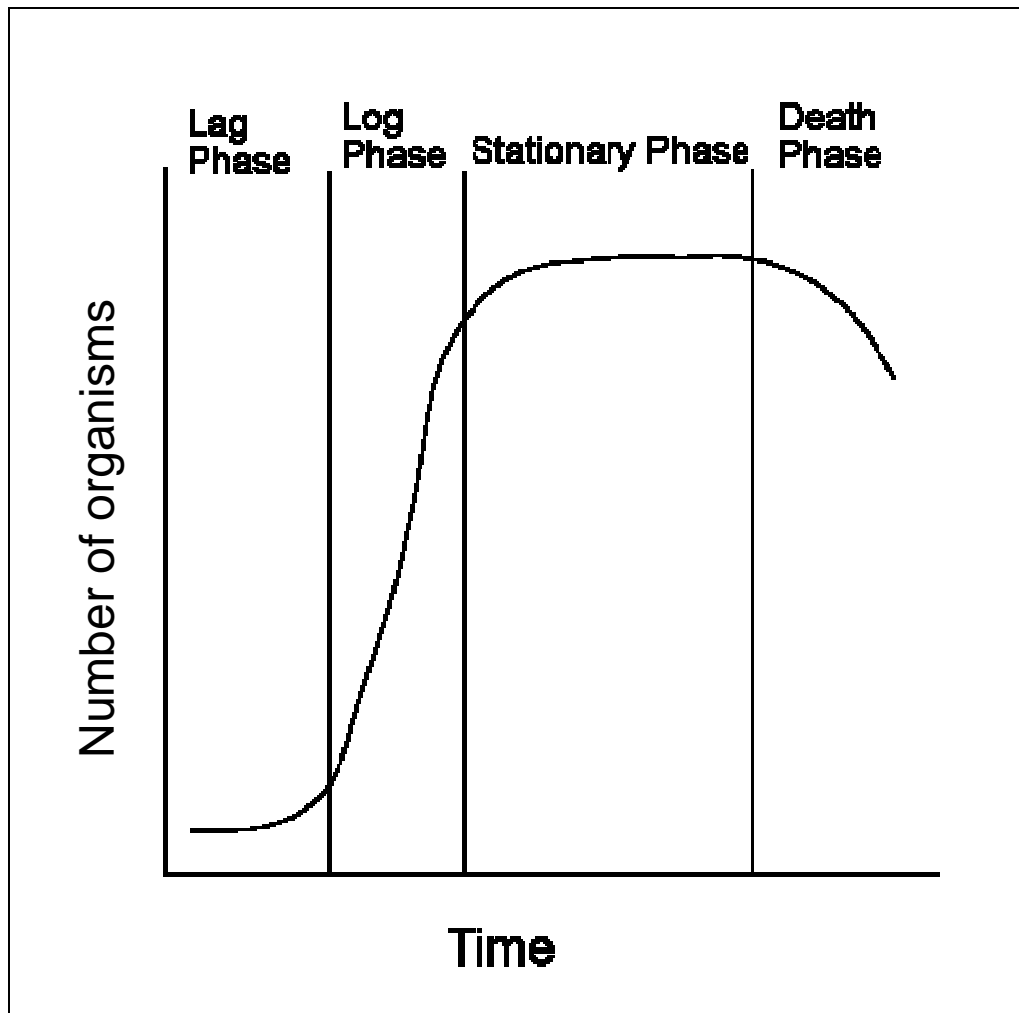
$$P = \mu B$$

$\mu$  = specific growth rate (time<sup>-1</sup>)

$B$  = biomass (mg C L<sup>-1</sup>)

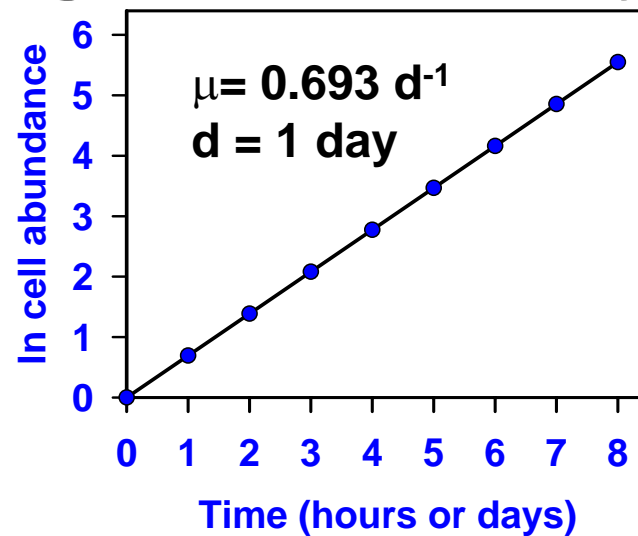
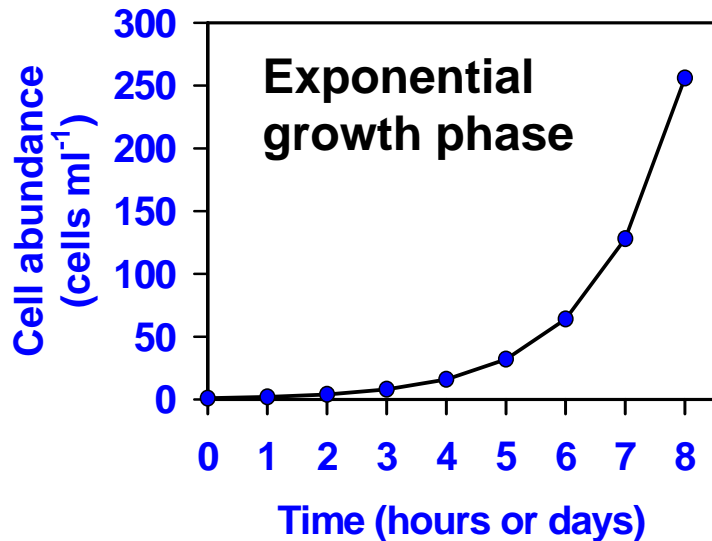
- \*\*Note that  $\mu = P/B$
- Thus,  $P$  has units of mg C L<sup>-1</sup> d<sup>-1</sup>

# Growth in a closed system



**Closed system; variable growth rate – cells are inoculated into media and grow until resources are depleted.**

# Calculating growth rates from a population dividing exponentially



T (hours or days)	N <sub>t</sub> (cells or biomass)
0	1
1	2
2	4
3	8
4	16
5	32
6	64
7	128
8	256

- From an exponentially growing population the specific growth rate ( $\mu$ ) can be derived from:  

$$dN/dt = \mu N$$

$$N_t = N_o e^{\mu t}$$
 or alternatively:  

$$\mu = (\ln N_t - \ln N_o) / t$$

$$\mu \text{ has units of time}^{-1}$$

**Doubling time (d)** is the time required for the population to increase by 100%; it is related to  $\mu$  by:

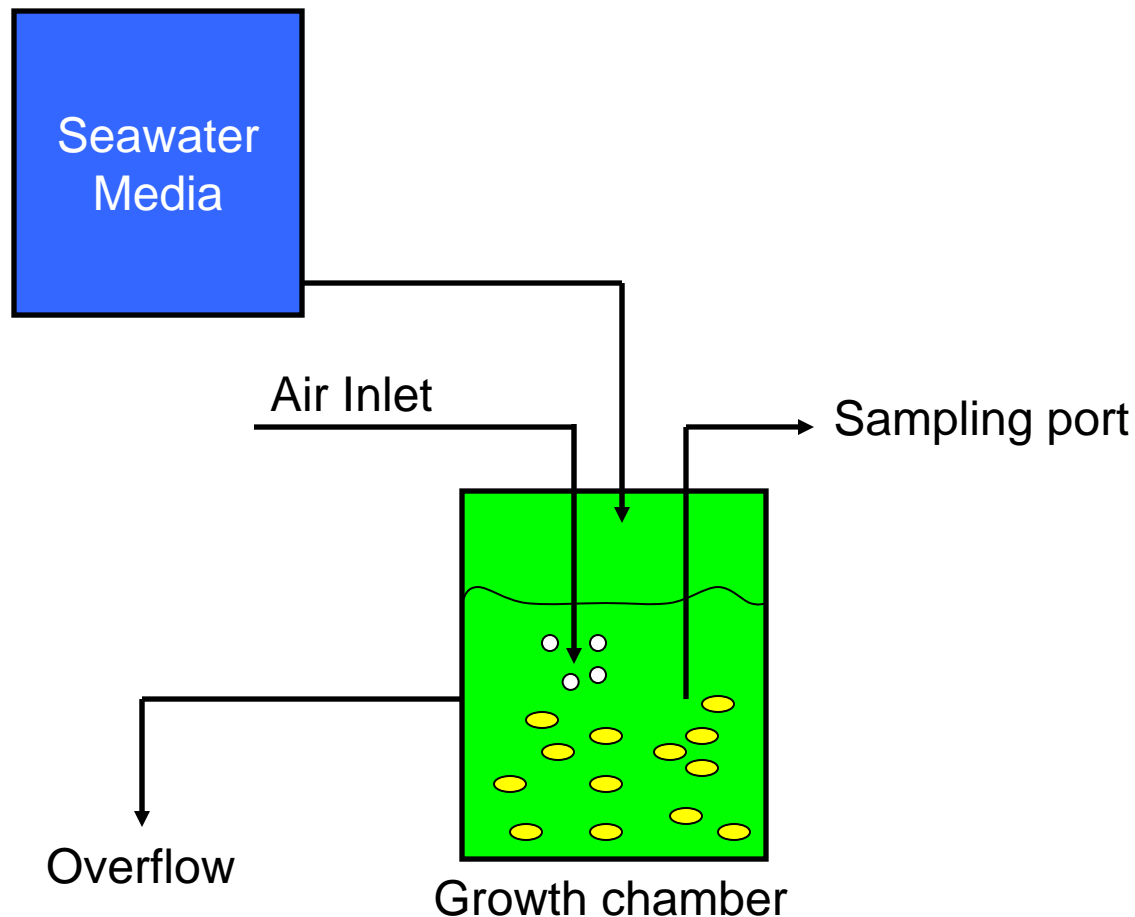
$$N_t = N_o e^{\mu d}$$

$$N_t / N_o = e^{\mu d} = 2$$

$$d = \ln 2 / \mu$$

$d$  has units of days or hours.

# Growth in a chemostat



**Open system: constant supply of limiting nutrients; growth rate is determined by the rate that a limiting nutrient is added or removed from the system. Typically use an exponential model to describe growth dynamics.**

**Is the ocean more like a batch culture or a chemostat?**

# **Measuring the rate of growth by natural assemblages of plankton is complicated...**

- Most direct method would be to measure changes in biomass over time.**

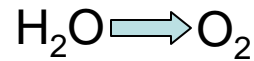
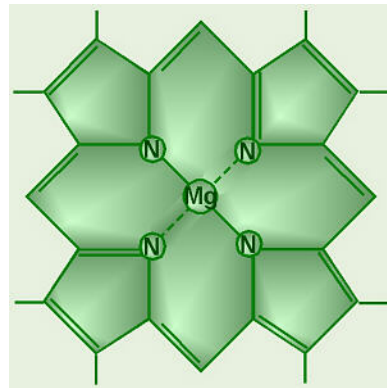
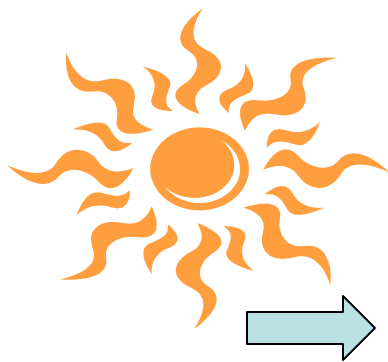
**Why is that difficult for naturally occurring plankton?**

**In natural seawater sample....**

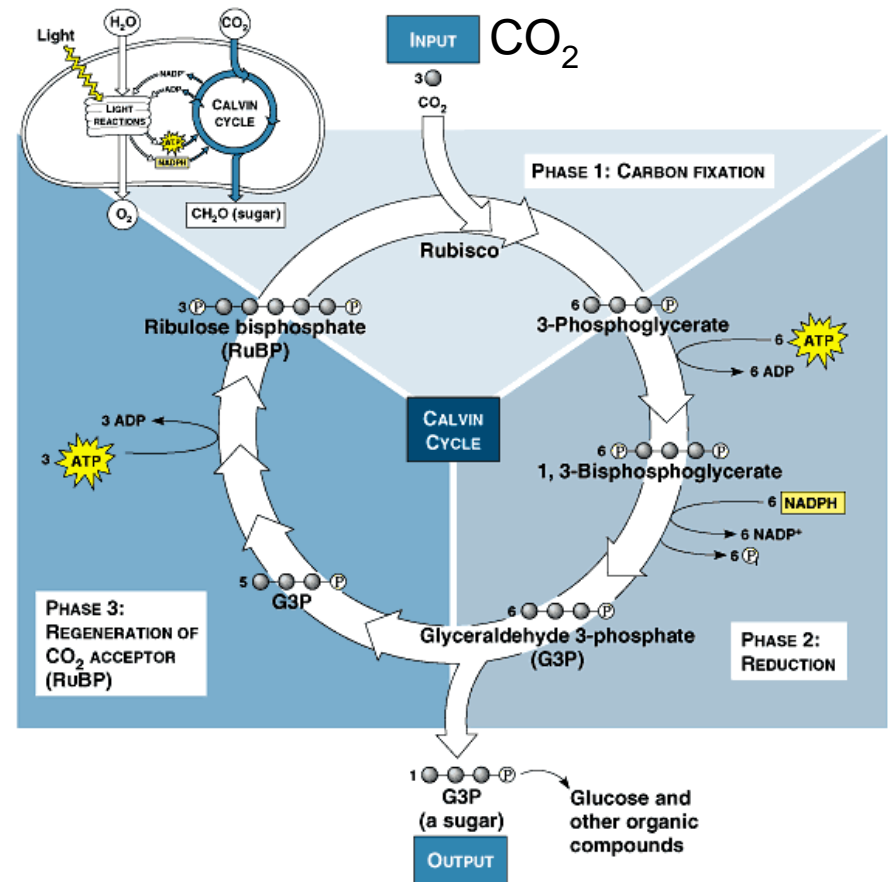
- Mixed assemblage of organisms with variable growth rates.**
- Growth is often balanced by loss (predation or disease), this no net change in biomass with time.**

- **Two main forms of biomass production:**
  - **Primary production: is the rate of biomass synthesis via reduction of CO<sub>2</sub>; in the ocean this is mostly controlled by the growth and biomass of photosynthetic organisms.**
  - **Secondary production: formation of biomass via assimilation of organic matter; controlled by growth and biomass of chemoheterotrophs (heterotrophic bacteria, zooplankton, etc.)**

# Photosynthesis



ATP,  
NADPH



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3 mol ATP and 2 mol NADPH are consumed for every 1 mol CO<sub>2</sub> fixed.

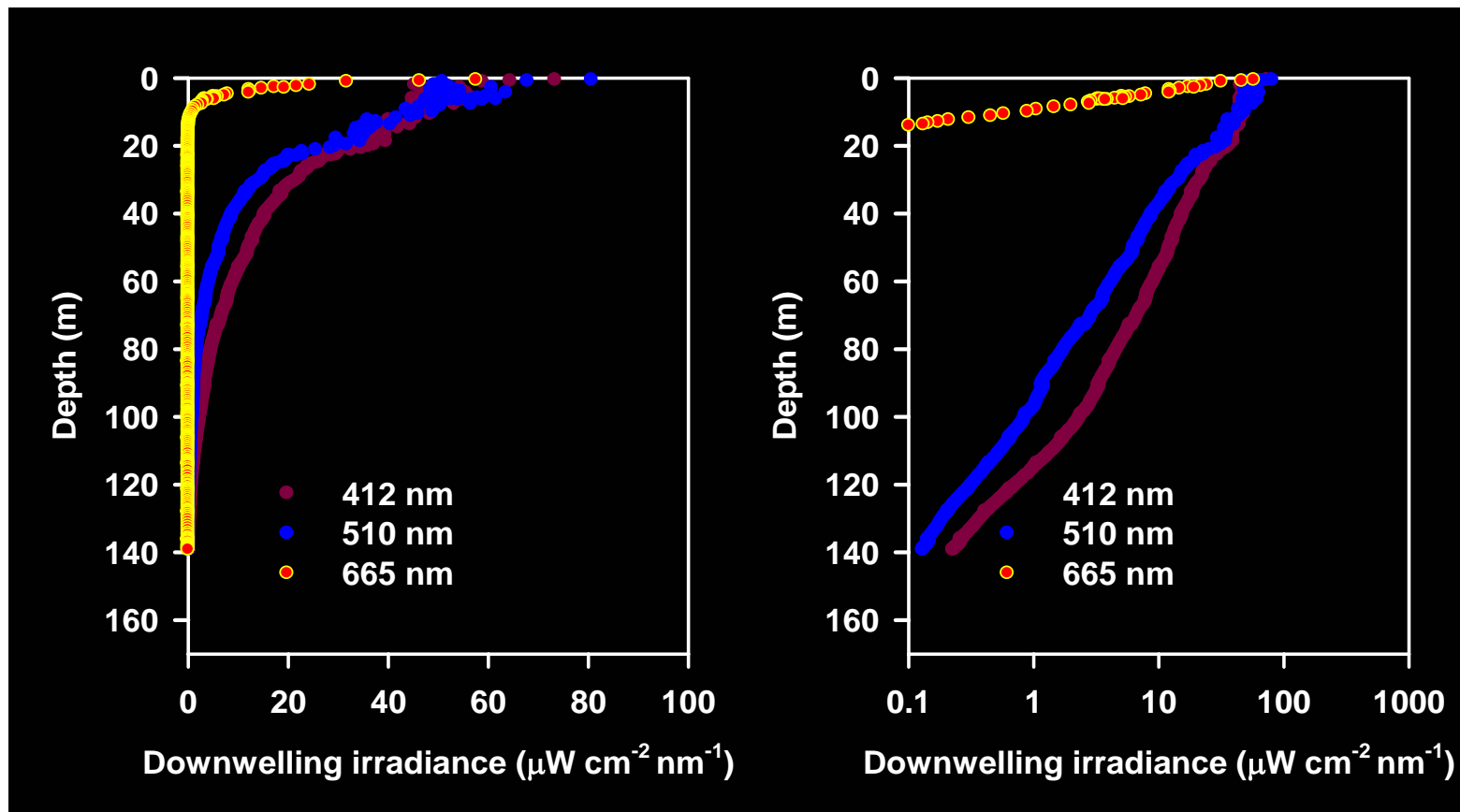
## The exponential decay of light with depth:

$$I_z = I_0 e^{-kZ}$$

$I_z$  = light at depth  $Z$  (units of mol quanta  $\text{m}^{-2} \text{s}^{-1}$ )

$I_0$  = light at surface of ocean (incident irradiance; units of mol quanta  $\text{m}^{-2} \text{s}^{-1}$ )

$k$  = attenuation coefficient (units of  $\text{m}^{-1}$ )



**The euphotic zone is typically defined by the depth to which 1% (sometimes 0.1%) of the surface irradiance penetrates**

$$\begin{aligned}I_z &= I_0 e^{(-kZ)} \\0.01 &= I_z/I_0 = e^{(-KZ)} \\ \ln(0.01) &= -KZ \\ &= -((\ln 0.01)/K) = Z\end{aligned}$$

**The larger K, the shallower the euphotic zone depth.**

**K for pure water = 0.038 m<sup>-1</sup>**

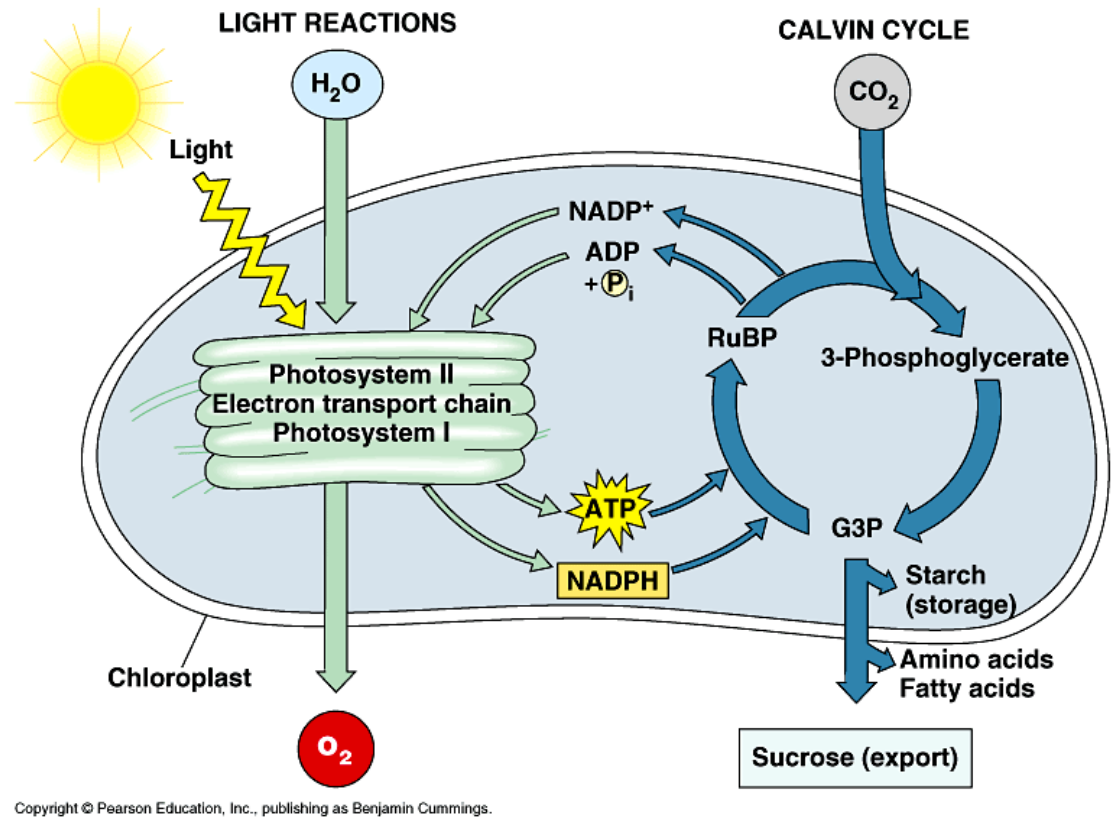
**K for turbid water = 0.4 m<sup>-1</sup>**

**K for the open ocean = 0.05 m<sup>-1</sup>**

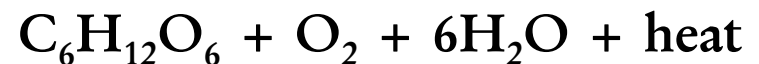
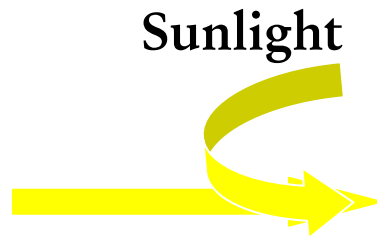
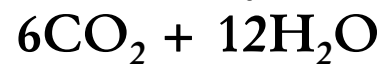
**K is influenced by light scattering and light absorption.**

**Primary controls on light attenuation in the ocean are particles that scatter or absorb light and dissolved constituents that scatter or absorb light.**

- Absorption of light energy by pigments or photoproteins (light antenna) excites  $e^-$  in these molecules; these molecules then pass  $e^-$  to protein complexes (reaction centers) via an electron transport chain.
- The transfer of electrons through the transport chain creates reducing power (NADPH) and chemical energy (ATP).
- Energy and reducing power gained from light harvesting are used to reduce  $\text{CO}_2$  to organic matter (dark reactions).

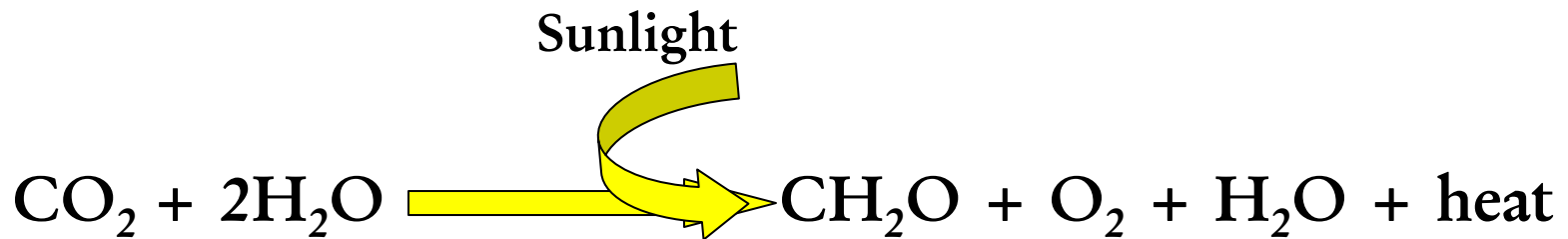


**Photosynthesis:**



## 2 Key enzymes for phytoplankton photosynthesis

- **RUBISCO** (1,5-bisphosphate carboxylase/oxygenase)-key enzyme in the Calvin-Benson cycle, incorporates  $\text{CO}_2$  into 3-phosphoglycerate. Most abundant protein on Earth.
- **Carbonic anhydrase**: converts bicarbonate to  $\text{CO}_2$ , and vice versa. Most marine phytoplankton transport bicarbonate and carbonic anhydrase dehydrates to  $\text{CO}_2$  intracellularly near RUBISCO.



## Photosynthesis

**Gross Primary Production (GPP):** The rate of organic carbon production via the reduction of  $\text{CO}_2$  inclusive of all respiratory losses.

**Net Primary Production (NPP):** Gross primary production less photosynthetic respiration ( $R_A$ ):

$$\text{NPP} = P_N - R_A$$

**Net Community Production (NCP):** Gross primary production less all autotrophic and heterotrophic losses due to respiration ( $R_{A+H}$ ).

$$\text{NCP} = P_G - R_{A+H}$$

**\*\*If we are interested in carbon available for export or consumption by higher trophic levels, NCP is the key term. If we want to know how much total energy was captured by photosynthesis, we need to know GPP.**

# What methods would you use to measure primary production in the sea?

- $\Delta\text{O}_2$
- $\Delta\text{CO}_2$
- $\Delta\text{Organic matter}$
- Isotopic tracers of C and/or  $\text{O}_2$

## What methods are most suitable for measuring aquatic primary production?

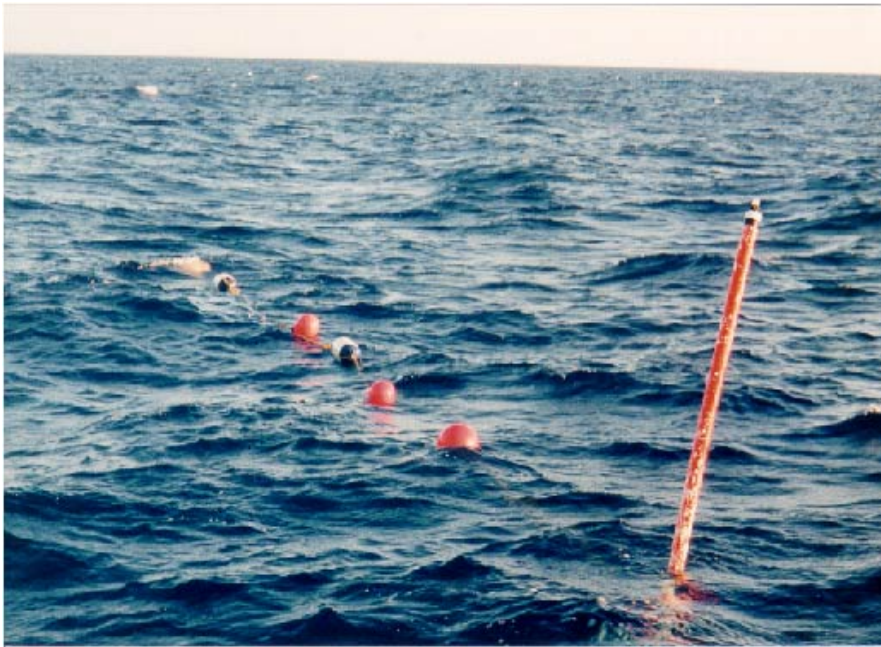
- Typical rates of photosynthesis in the ocean range between  
0.2-2  $\mu\text{mol C L}^{-1} \text{ d}^{-1}$  or  
0.3-3  $\mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$
- Concentrations of DIC  $\sim 2000 \mu\text{mol C L}^{-1}$ ,  $\text{O}_2 \sim 220 \mu\text{mol L}^{-1}$ , and TOC  $\sim 80\text{-}100 \mu\text{mol L}^{-1}$
- Analytical sensitivity of carbon and oxygen determinations:
  - $\text{CO}_2$  by coulometry =  $1 \mu\text{mol C L}^{-1}$
  - $\text{O}_2$  by Winkler titration =  $0.4 \text{ to } 2 \mu\text{mol O}_2 \text{ L}^{-1}$
  - TOC by HTC =  $2\text{-}4 \mu\text{mol C L}^{-1}$

**\*\*Measuring very small signals against large background pools\*\***

# Commonly used methods for measuring aquatic photosynthesis

- Changes in O<sub>2</sub> concentrations – incubations (Gaarder and Gran 1927) and *in situ* dynamics.
- CO<sub>2</sub> assimilation: stable or radioisotopes of carbon (<sup>13</sup>C or <sup>14</sup>C) – technique first applied by Steeman-Nielsen 1951.
- Oxygen isotope disequilibria (<sup>18</sup>O, <sup>17</sup>O, <sup>16</sup>O)
- Satellite remote sensing

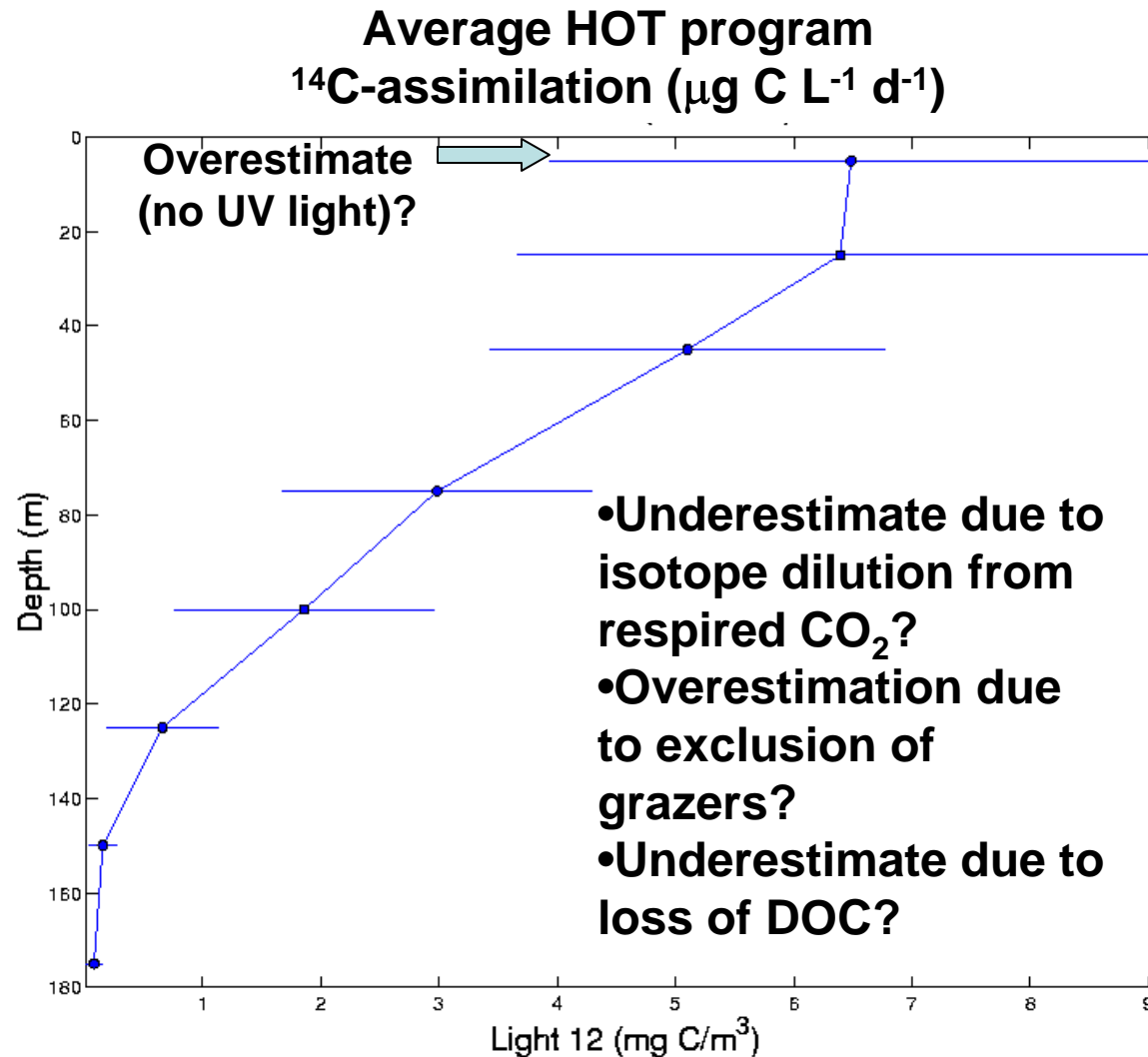
# Primary production approach 1: $^{14}\text{C}$ -bicarbonate assimilation



Typically PAR (400-700 nm) transparent polycarbonate bottles are used for these experiments...but UV is excluded.

- Examine assimilation of  $^{14}\text{C}$  (as bicarbonate) by plankton.
- Add  $^{14}\text{C}$  labeled  $\text{HCO}_3^-$  to bottles containing seawater; incubate in the light.
- Harvest plankton by filtration, acidify the filter, and count radioactivity (using liquid scintillation counter) assimilated into plankton biomass during incubation period.
- Rate of primary production is determined by the amount of  $^{14}\text{C}$ -label assimilated into particles relative to the total DIC pool

# What does the method measure?



•Gross  
primary  
production?

•Net primary  
production?

•Net  
community  
production?

# $^{14}\text{C}$ -based determinations of aquatic primary production abound...

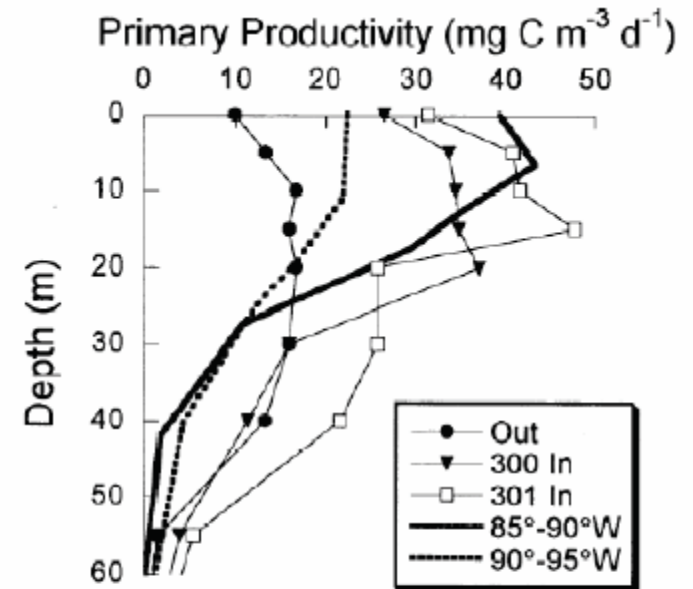
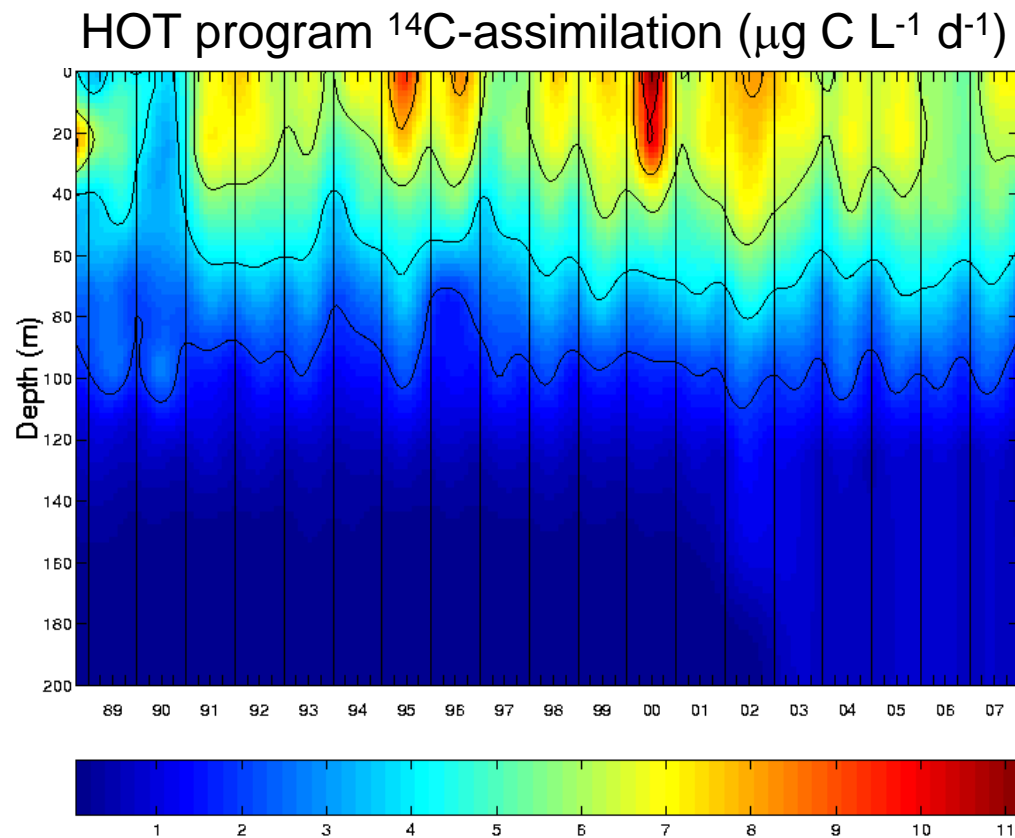


Fig. 1. Primary productivity at and near the site of the open-ocean enrichment experiment (near 5°S, 90°W). Profiles from out of the patch and in the patch 2 d (calendar day 300) and 3d (calendar day 301) after enrichment are from Martin et al. (1994). Profiles of historical averages east (4–6°S, 85–90°W;  $n = 10$ ) and west of the site (4–6°S, 90–95°W;  $n = 11$ ) are from R. Barber and F. Chavez as presented by Martin and Chisholm (1992). Error bars for the measurements during IronEx were presented by Martin et al. (1994) but not defined. For the average profiles, errors (presumed to be SE) were 16–22% ( $\bar{x} = 18\%$ ) of the mean for 85–90°W and 7–22% ( $\bar{x} = 13\%$ ) for 90–95°W.

Equatorial Pacific iron  
addition experiment

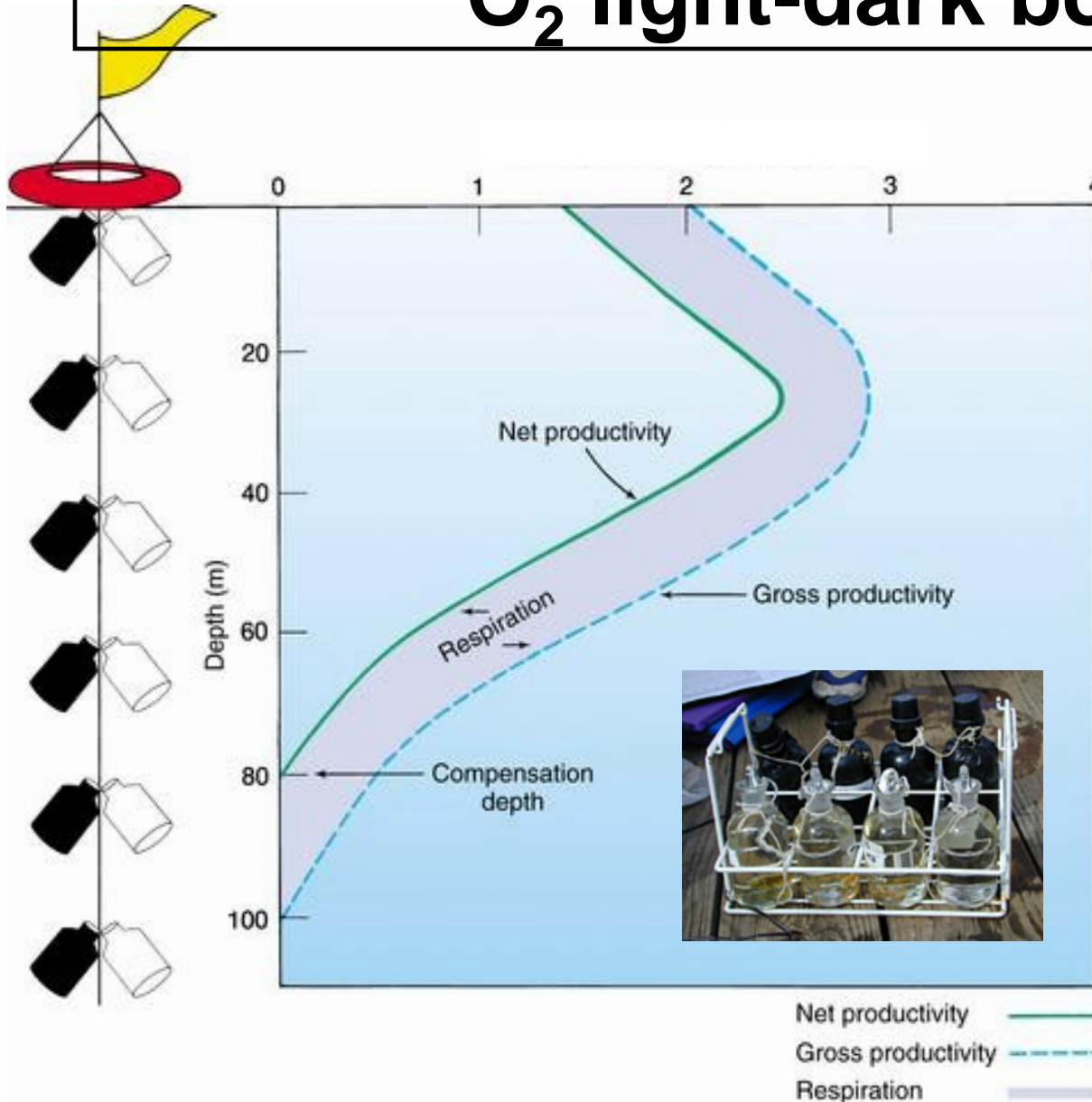
# Assimilation of $^{14}\text{C}$ -bicarbonate

- 1000's of ocean measurements
- Relatively “easy” to measure
- Estimates carbon fixation directly

Several caveats:

- 1) Always returns a positive result.
- 2) Does not discriminate light and dark respiration.
- 3) Typically measures something between NPP and gross production.
- 4) Generally ignores organic carbon produced and excreted or lost during incubation.
- 5) Requires incubation and confinement of samples

# Primary production approach 2: O<sub>2</sub> light-dark bottle



- Measures changes in oxygen concentrations in light and dark bottles following incubation
- Light bottle = net community production (photosynthesis and community respiration).
- Dark bottle: community respiration.
- Light + Dark = Gross primary production

$$\text{GPP} = \Delta\text{O}_2 (\text{light}) - \Delta\text{O}_2 (\text{dark})$$

# The light bottle/dark bottle $O_2$ technique

- Measures gross and net primary production
- Relatively “easy” to measure

Several caveats:

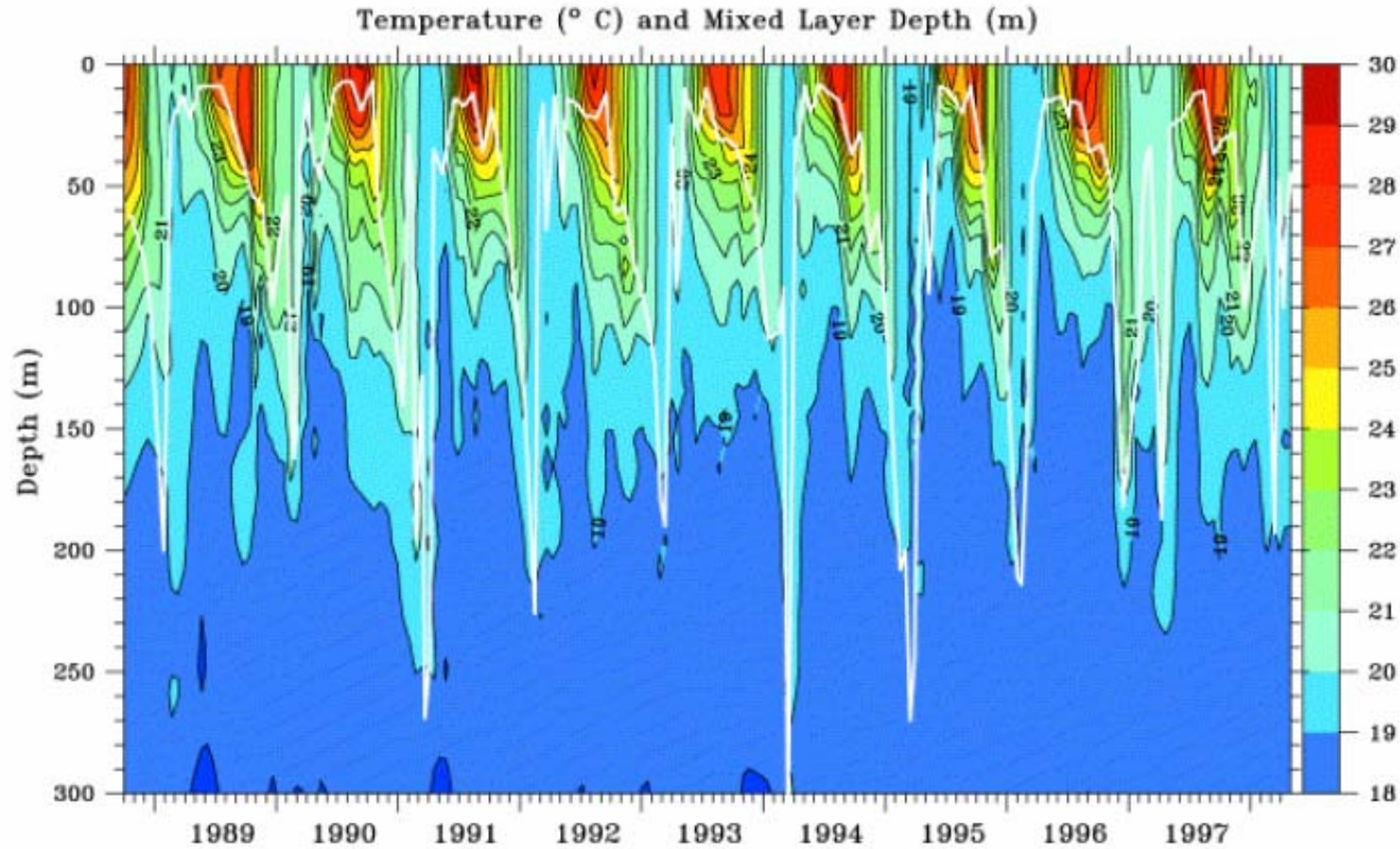
- 1) assumes rate of respiration in dark = light.
- 2) requires incubation and confinement of samples.
- 3) requires conversion of  $O_2$  to carbon (photosynthetic quotient, PQ).  $O_2/C$  PQ values can vary between 1.1 to 1.4 depending on nitrogen sources and end products of photosynthesis.

## **Primary production approach 3: $^{18}\text{O}_2$ gross production**

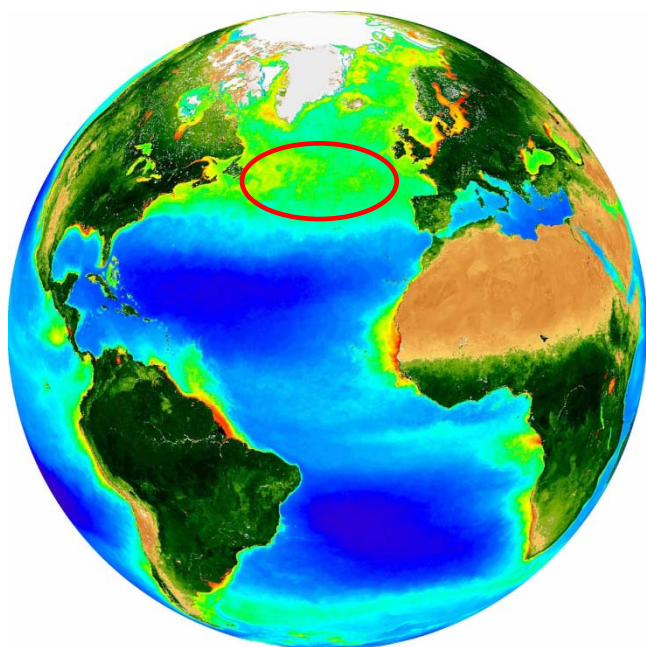
- Addition of  $\text{H}_2^{18}\text{O}$ : light bottle/dark bottle incubation approach. Photosynthetic splitting of  $\text{H}_2\text{O}$  yields  $^{18}\text{O}_2$ .
- $^{18}\text{O}_2$  produced during photosynthesis measured by mass spectrometry.
- Only measures GPP; no measurement of R or NCP by this method.

Primary production approach 5: Estimate Net community production based on *in situ* variations in oxygen, nutrients, carbon, or biomass (often chlorophyll)

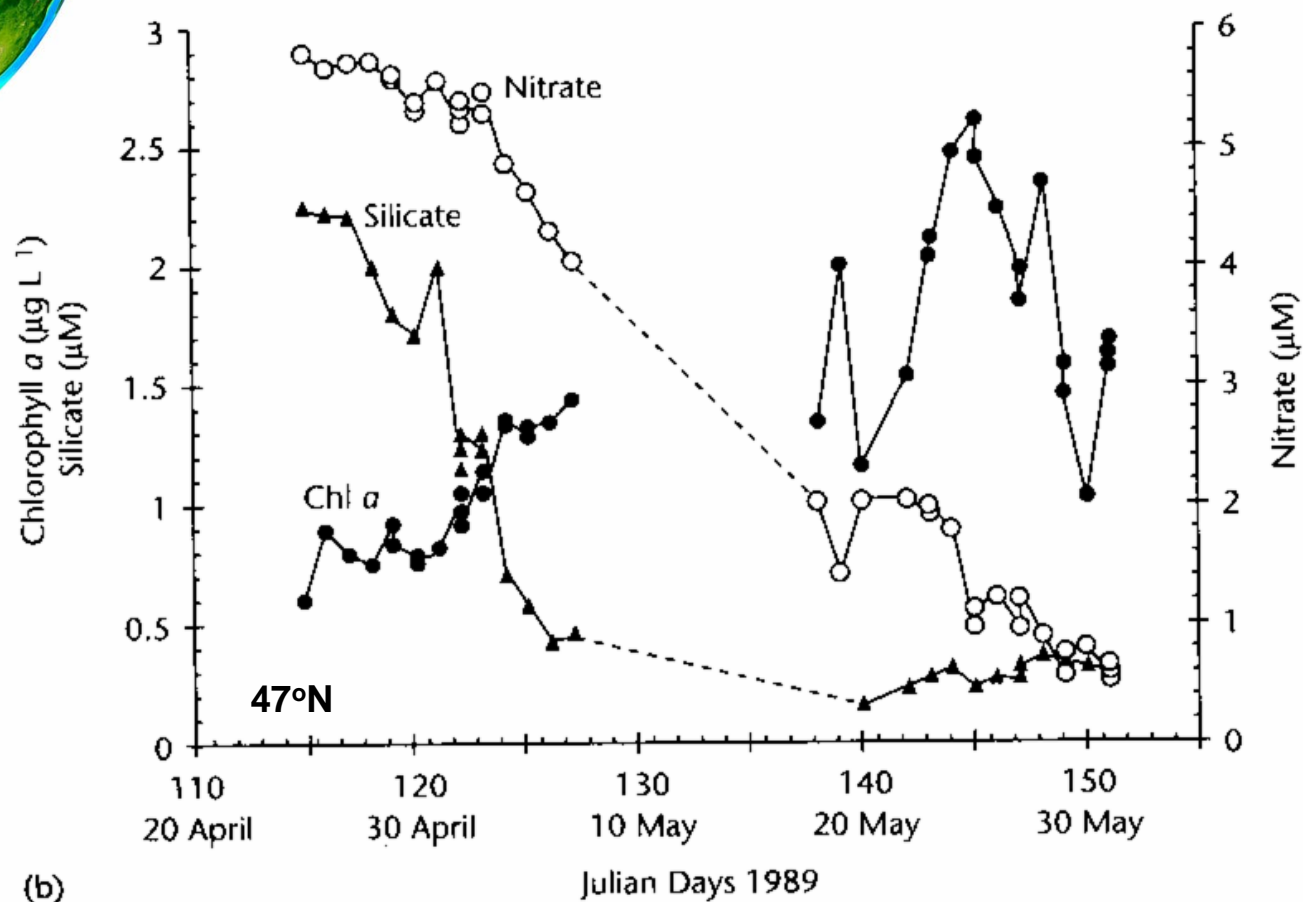
- Examine annual or seasonal scale changes in  $O_2$ ,  $NO_3^-$ ,  $CO_2$ , Chl *a* concentrations in the upper ocean.
- As long as exchange and diffusive loss can be accounted for this approach should provide an estimate of NCP.



**Seasonal variations in mixing and temperature in the Sargasso Sea-note winter time deepening of the mixed layer coincides with seasonal cooling.**

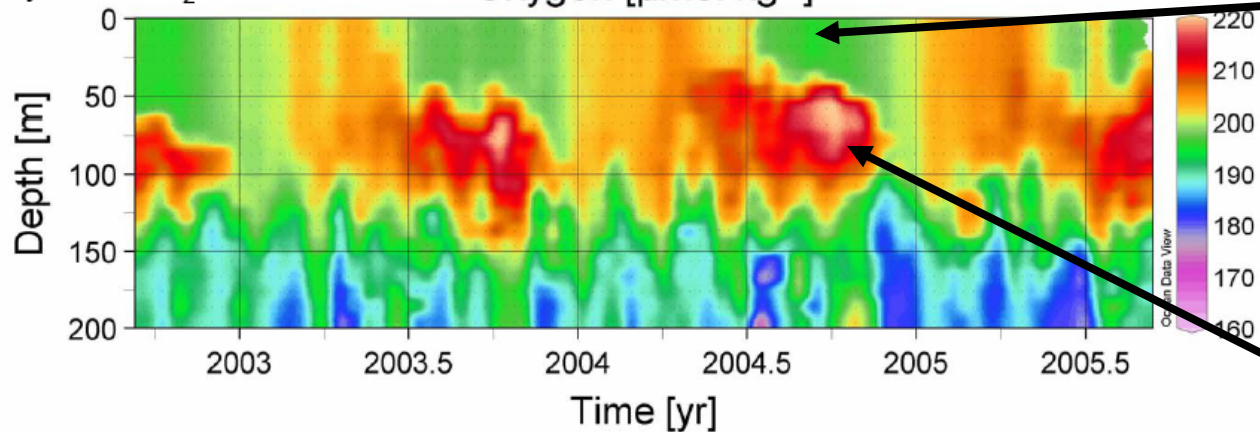


## North Atlantic Spring Bloom



(b)

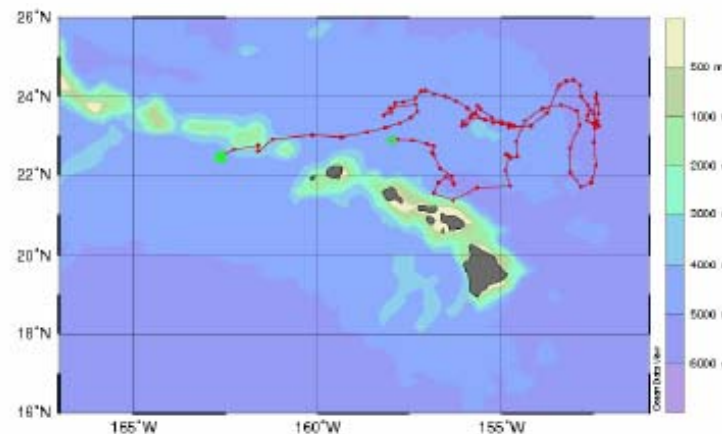
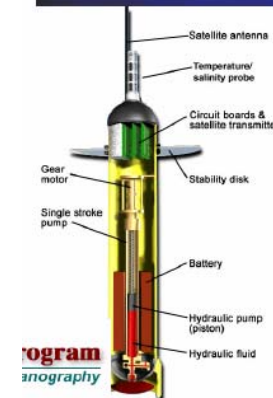
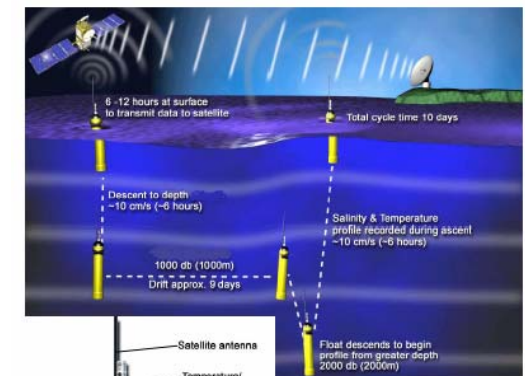
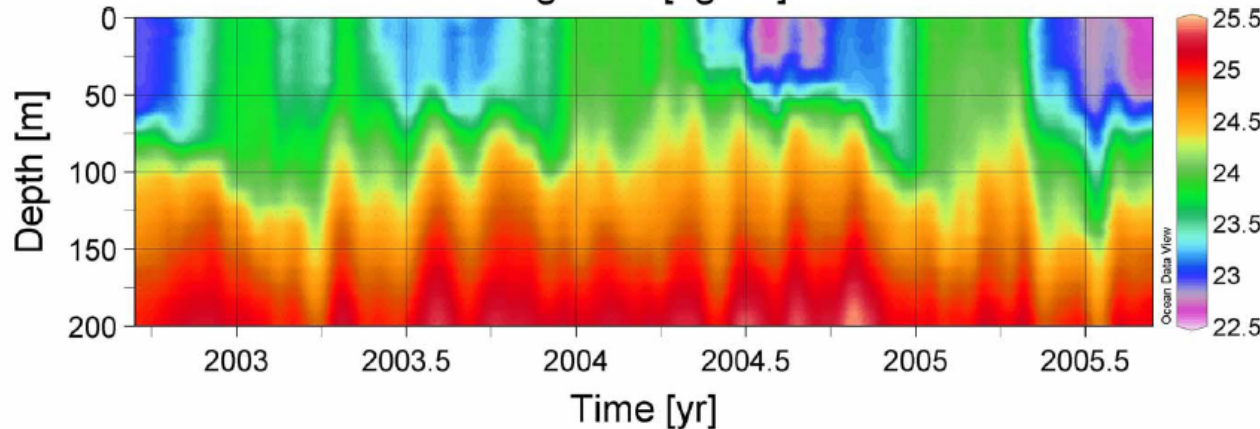
3 years of O<sub>2</sub> data near HOT Oxygen [ $\mu\text{mol kg}^{-1}$ ]



Mixed layer O<sub>2</sub> is in equilibrium with the atmosphere

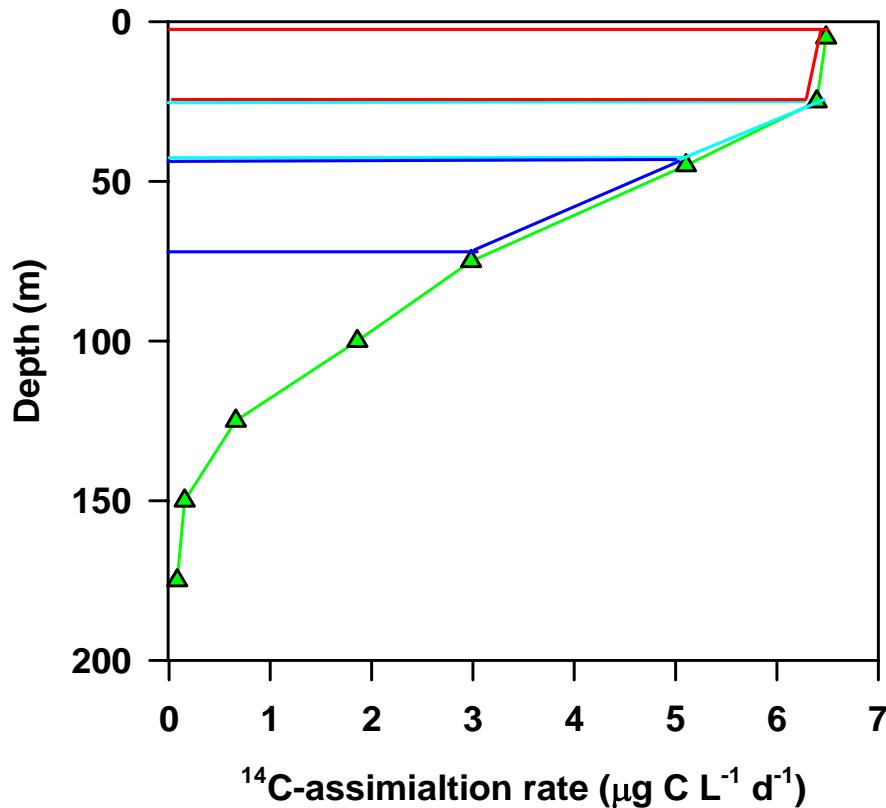
Rate of subsurface O<sub>2</sub> accumulation provides information on NCP

Sigma-0 [ $\text{kg/m}^3$ ]



Riser and Johnson (2008)

# Trapezoidal integration



Depth (m)	Production ( $\mu\text{g C L}^{-1} \text{d}^{-1}$ )
5	6.5
25	6.4
45	5.0
75	3.0
5-75 m Int.	363 $\text{mg C m}^{-2} \text{d}^{-1}$

**Area of trapezoid = Height \* avg. base**

$$[(25 \text{ m} - 5 \text{ m}) * ((6.5 \text{ mg C m}^{-3} \text{d}^{-1} + 6.4 \text{ mg C m}^{-3} \text{d}^{-1})/2)] = 129 \text{ mg C m}^{-2} \text{d}^{-1}$$

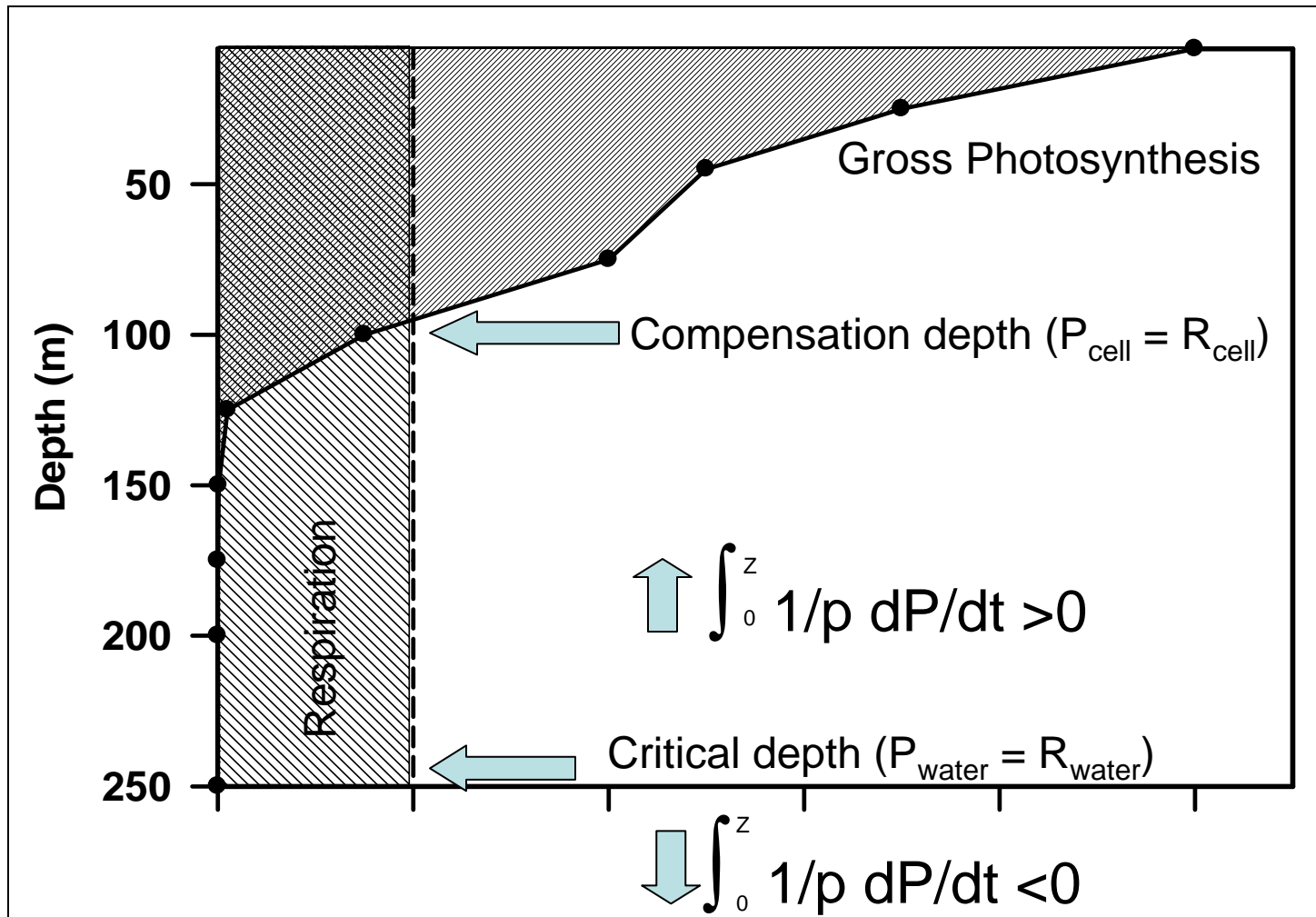
$$[(45 \text{ m} - 25 \text{ m}) * (6.4 \text{ mg C m}^{-3} \text{d}^{-1} + 5.0 \text{ mg C m}^{-3} \text{d}^{-1})/2] = 114 \text{ mg C m}^{-2} \text{d}^{-1}$$

$$[(75 \text{ m} - 45 \text{ m}) * ((5.0 \text{ mg C m}^{-3} \text{d}^{-1} + 3.0 \text{ mg C m}^{-3} \text{d}^{-1})/2)] = 120 \text{ mg C m}^{-2} \text{d}^{-1}$$

$$\text{Sum 5-75 m} = 363 \text{ mg C m}^{-2} \text{d}^{-1}$$

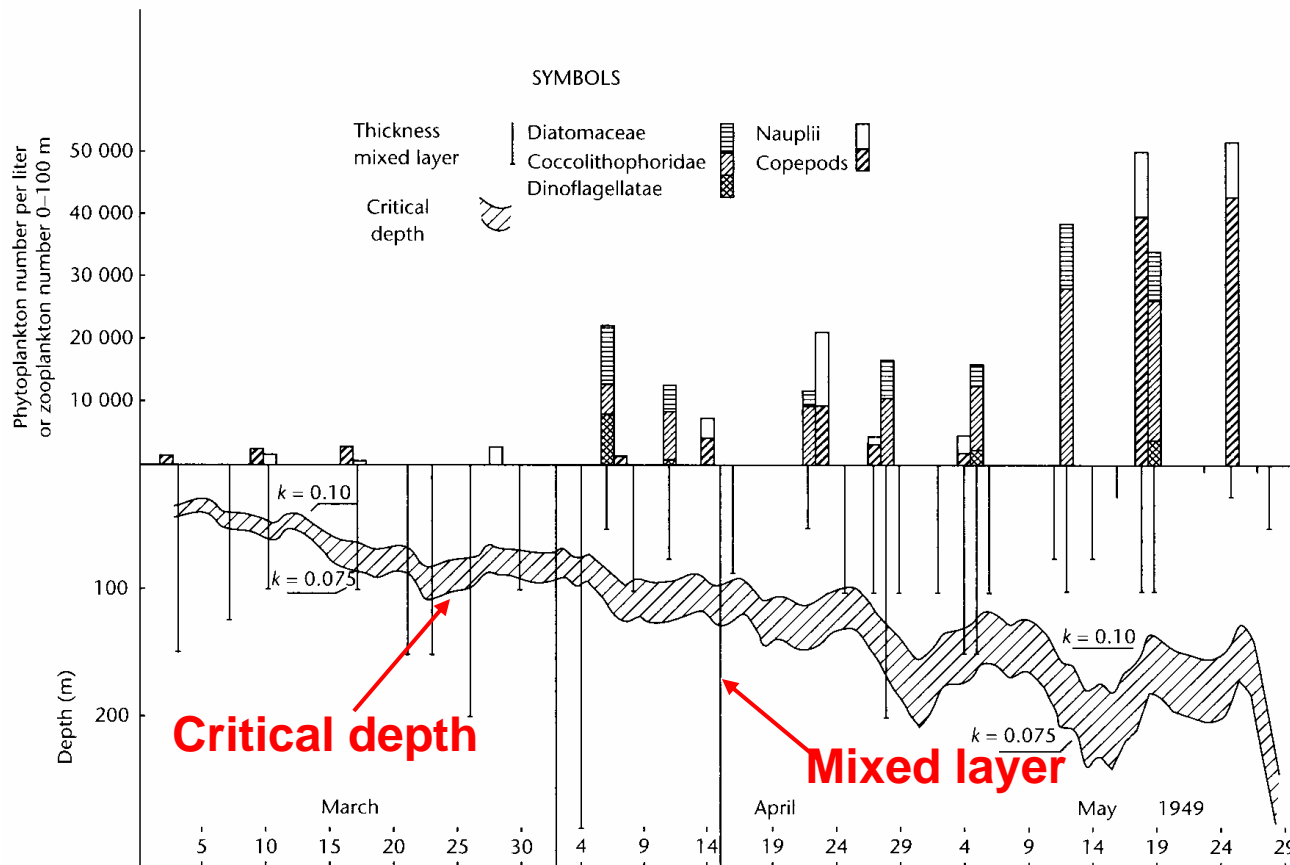
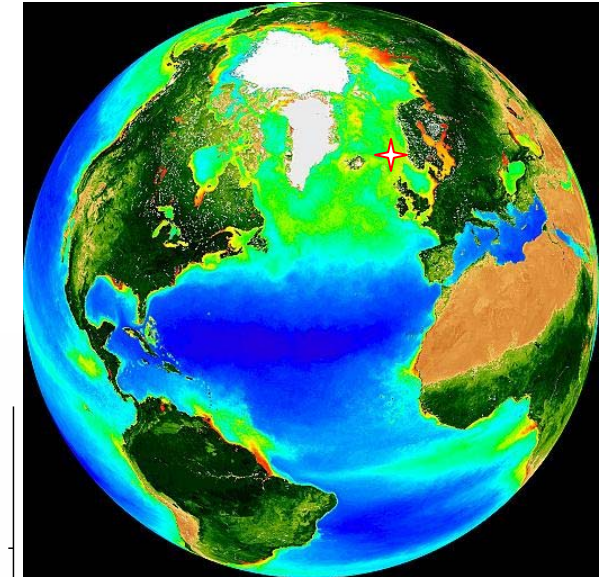


# Conditions for net primary productivity



# The Spring Bloom

Sverdrup (1953)

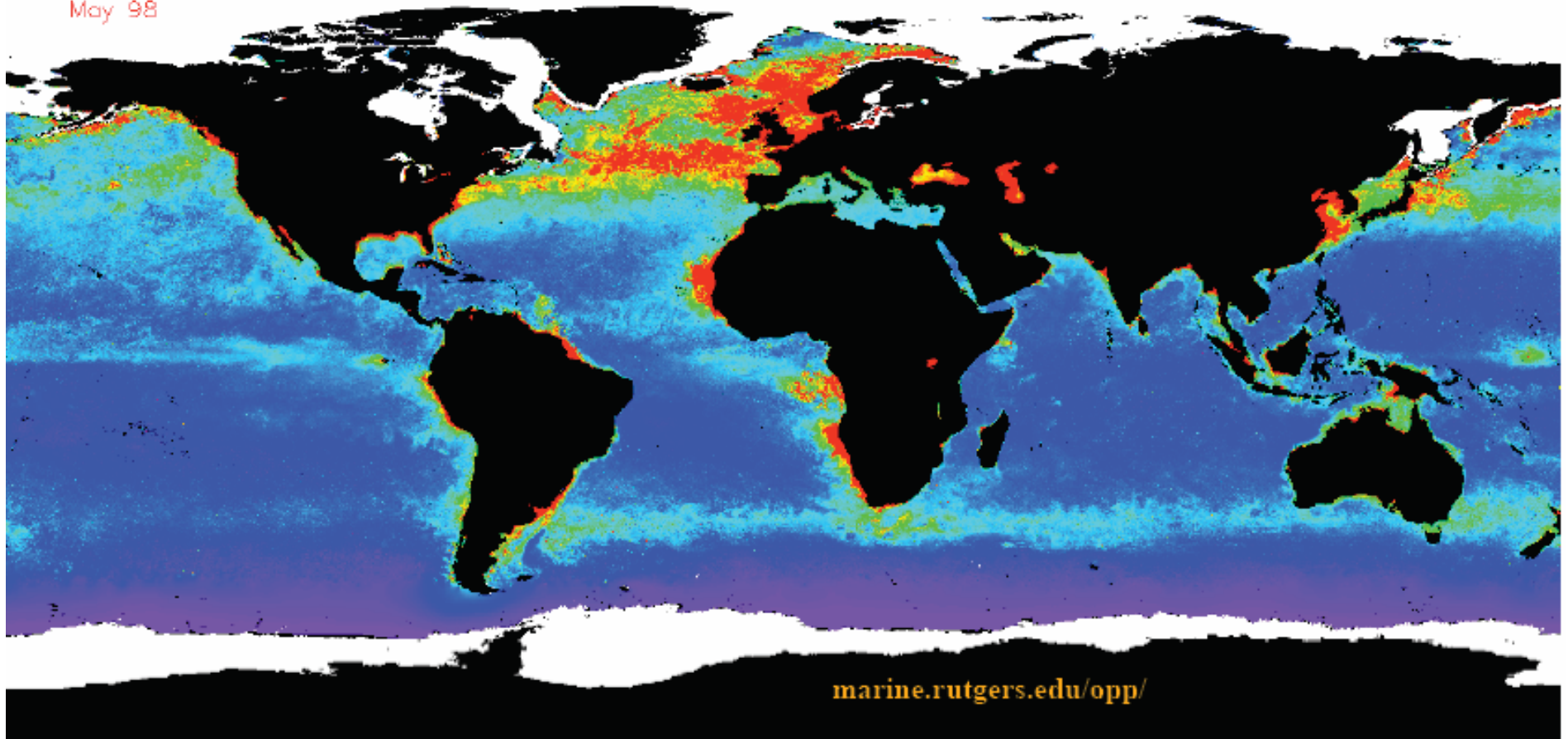


**Winter mixing introduces nutrients to the upper ocean; seasonal increases in irradiance results in deepening of the critical depth and shoaling of the mixed layer. The result: net accumulation of biomass.**

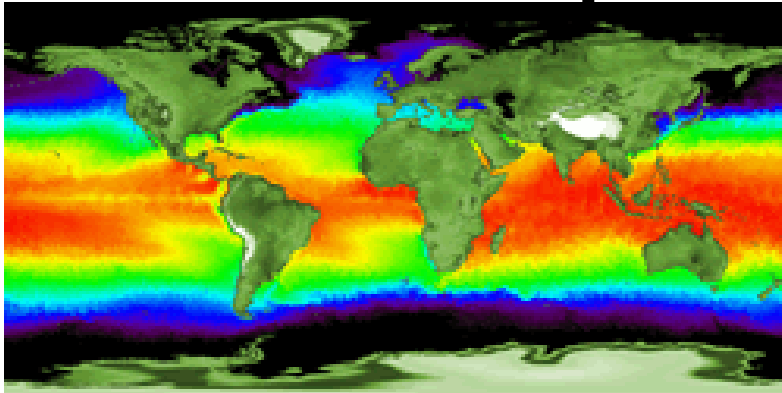
**Fig. 1.4** Data for 1949 from Weather ship "M" (66°N, 2°E) showing the relationship between the approximate critical depth (shading between approximate  $k$  values of 0.075 and 0.10) and mixing depth. Phytoplankton counts increased in April-May, when critical depth exceeded the mixing depth. While these data are crude, the observation set has never been duplicated. (After Sverdrup 1953.)

# Direct Measurements will Never Provide Synoptic Estimates of Productivity

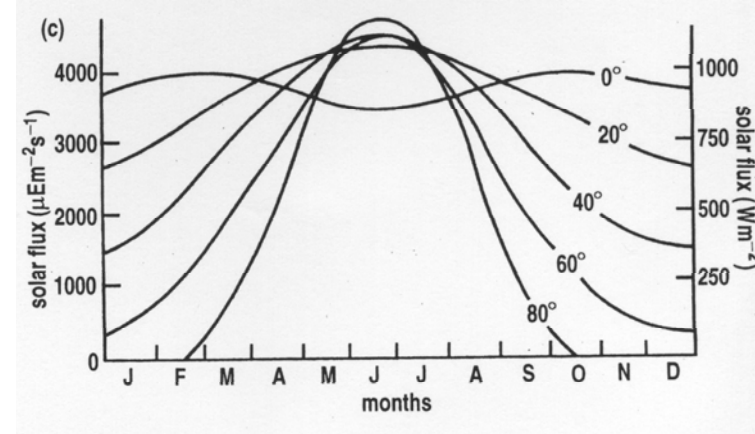
May 98



# Satellites to the rescue...but we don't measure production from space

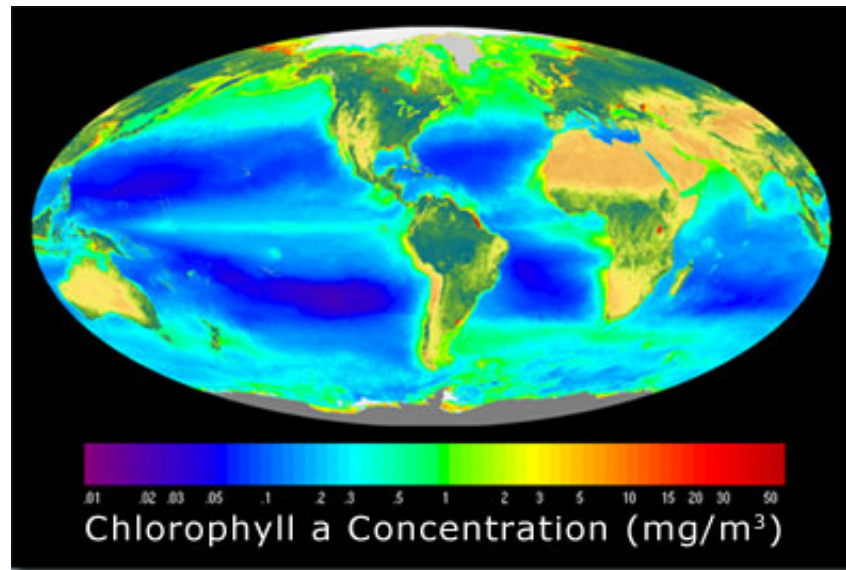


Temperature



PAR

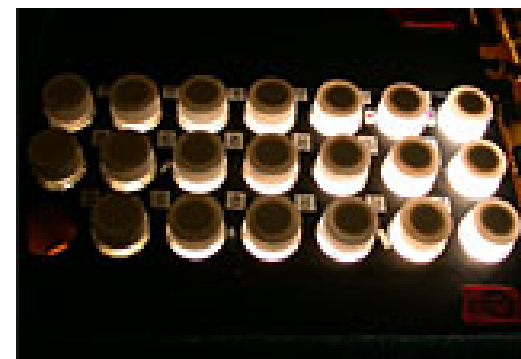
Satellites can provide measurements of temperature, sea surface irradiance, and chlorophyll. Need models that relate these to primary production.



Chlorophyll

# Deriving Photosynthesis-Irradiance Relationships

- A photosynthron can be used to quantify photosynthesis as a function of irradiance.
- $^{14}\text{C}$ -bicarbonate is added to whole seawater samples, samples are placed in temperature and light controlled incubation.
- After short incubations (<2 hrs) rates of photosynthesis are derived.

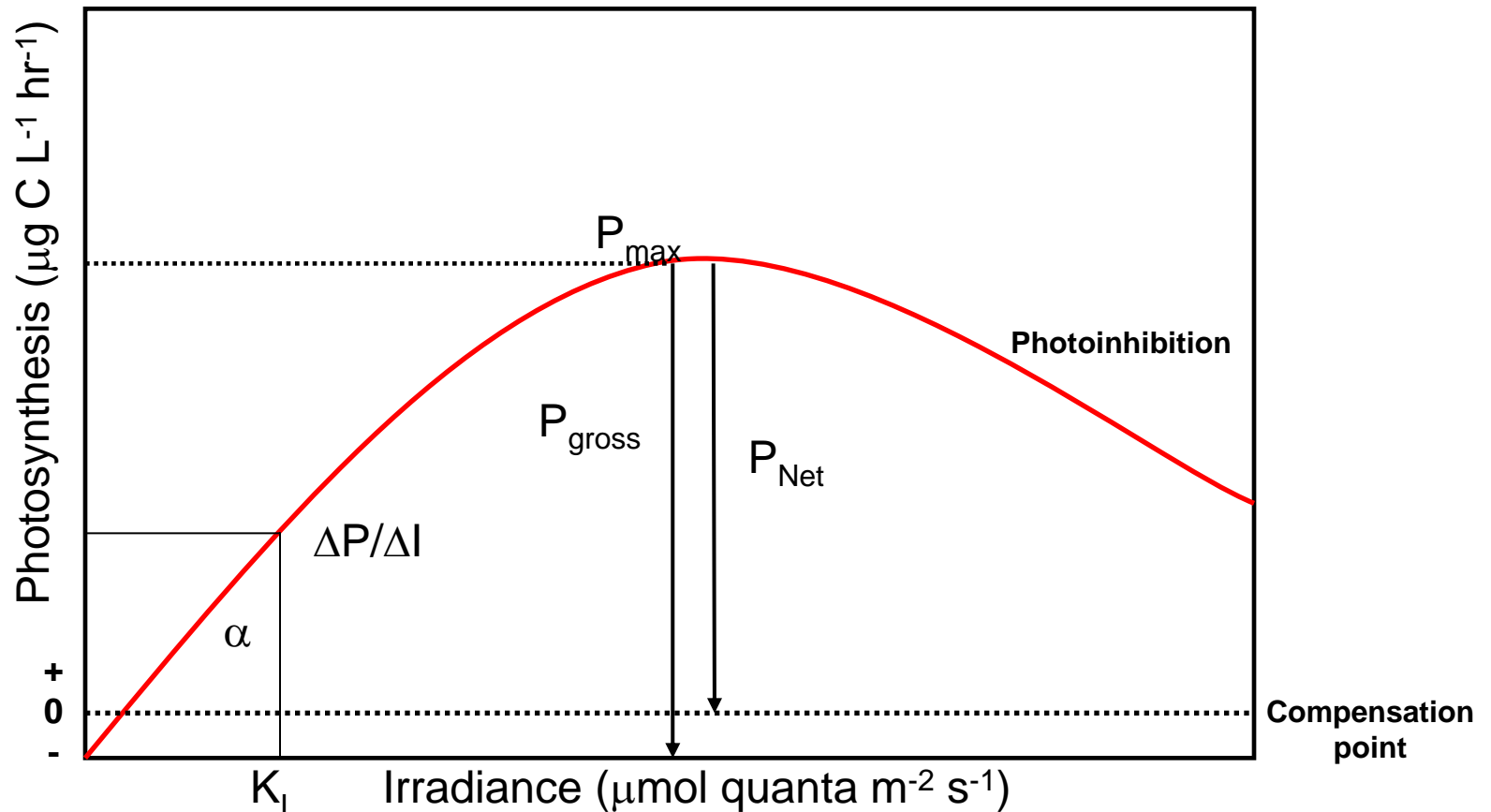


# Photosynthetic responses to irradiance

$\alpha = \Delta P / \Delta I$  = initial slope of the P vs. I relationship

$\alpha$  varies based on physiological changes to the cellular photosynthetic machinery

$P_{\max}$  varies depending on environmental conditions such as nutrients and temperature



# **Satellites “measure” chlorophyll, temperature, and light**

- **~1 km resolution**
- **Need models that relate photosynthesis to these remotely sensed variables.**
- **Nontrivial challenges with remote sensing: stability and accuracy of sensors, correction for atmospheric interferences, and conversion from ocean color to chlorophyll.**
- **Depth-dependent descriptions of phytoplankton productivity generally include the following terms: vertical light attenuation, biomass normalized productivity, photoperiod length, and incident light flux.**