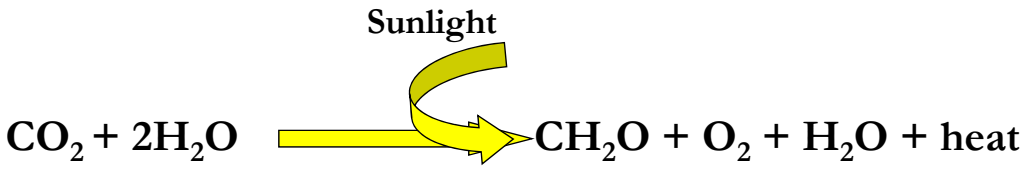


Photosynthesis

Gross Primary Production (GPP): The rate of organic carbon production via the reduction of CO_2 inclusive of all respiratory losses.

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

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

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

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

****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?

- ΔO_2
- ΔCO_2
- ΔOrganic matter
- Isotopic tracers of C and/or O_2

What methods are most suitable for measuring aquatic primary production?

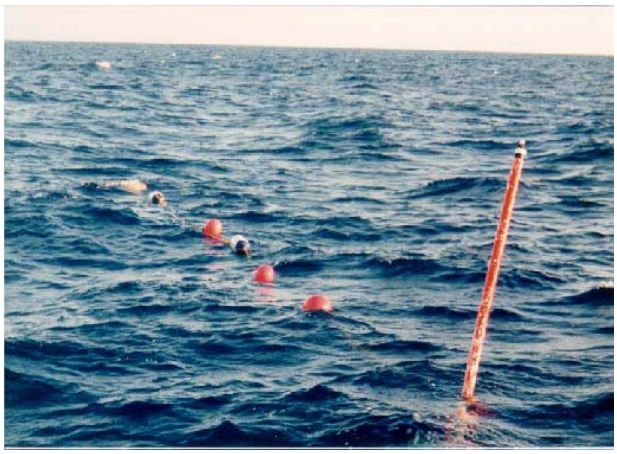
- Typical rates of photosynthesis in the ocean range between
  - 0.2-2 μmol C L^{-1} d^{-1} or
  - 0.3-3 μmol O_2 L^{-1} d^{-1}
- Concentrations of DIC ~2000 μmol C $L^{-1,}$ O_2 ~220 μmol $L^{-1,}$ and TOC ~80-100 μmol L^{-1}
- Analytical sensitivity of carbon and oxygen determinations:
  - CO_2 by coulometry = 1 μmol C L^{-1}
  - O_2 by Winkler titration = 0.4 to 2 μmol O_2 L^{-1}
  - TOC by HTC = 2-4 μmol C L^{-1}

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

Commonly used methods for measuring aquatic photosynthesis

- **Changes in O_2 concentrations – incubations (Gaarder and Gran 1927) and *in situ* dynamics.**
- **CO_2 assimilation: stable or radioisotopes of carbon (^{13}C or ^{14}C) – technique first applied by Steeman-Nielsen 1951.**
- **Oxygen isotope disequilibria (^{18}O, ^{17}O, ^{16}O)**
- **Satellite remote sensing**

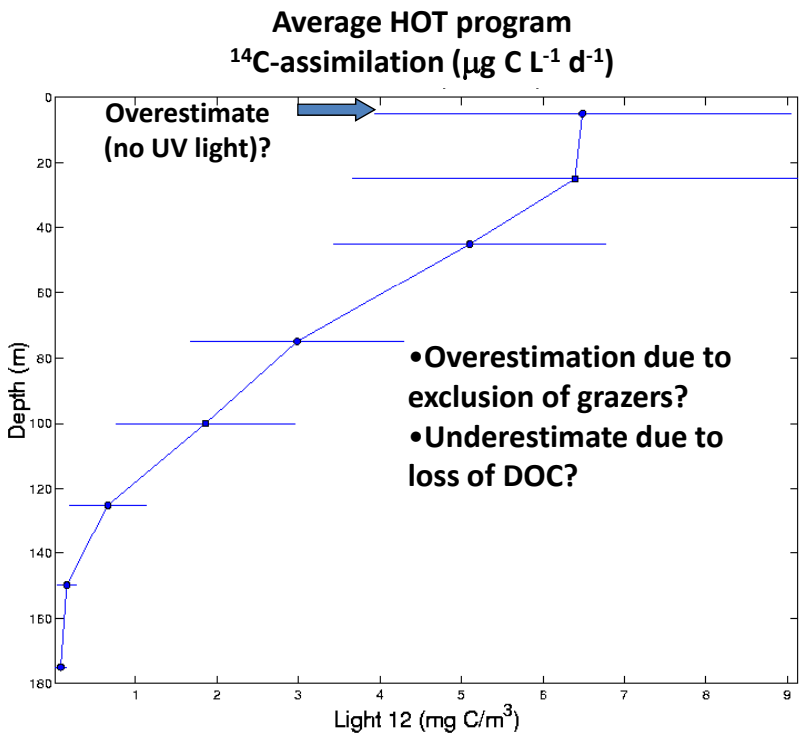
Primary production approach 1: ^{14}C-bicarbonate assimilation



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

- Examine assimilation of ^{14}C (as bicarbonate) by plankton.
- Add ^{14}C labeled 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}C-label assimilated into particles relative to the total DIC pool

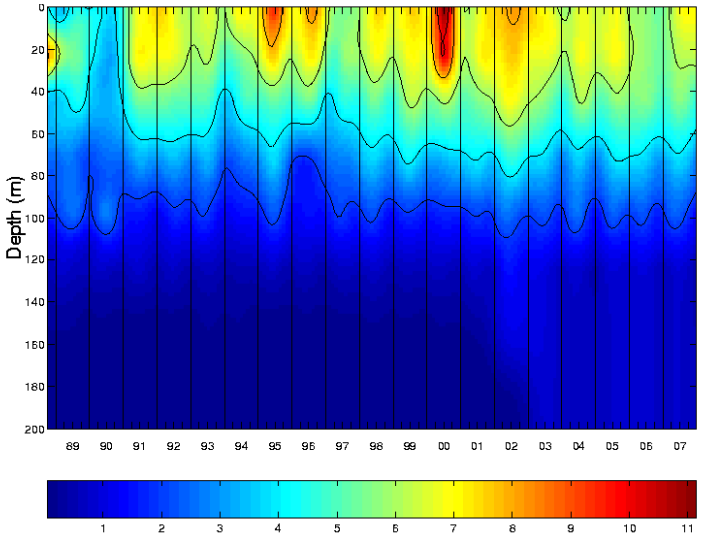
What does the method measure?



- **Gross primary production?**
- **Net primary production?**
- **Net community production?**

^{14}C-based determinations of aquatic primary production abound…

HOT program ^{14}C-assimilation (μg C L^{-1} d^{-1})



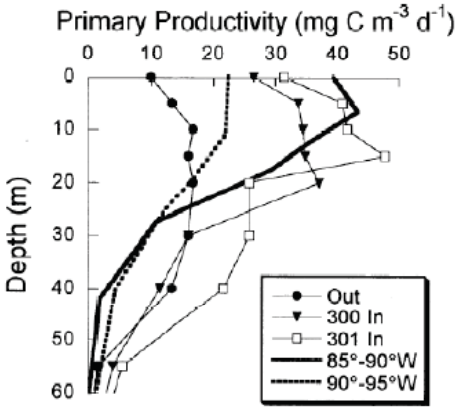


Fig. 1. Primary productivity at and near the site of the open-ocean enrichment experiment (near 5°S, 90°W). Profiles from out of the patch and in the patch 2 d (calendar day 300) and 3d (calendar day 301) after enrichment are from Martin et al. (1994). Profiles of historical averages east (4–6°S, 85–90°W; 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}C-bicarbonate

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

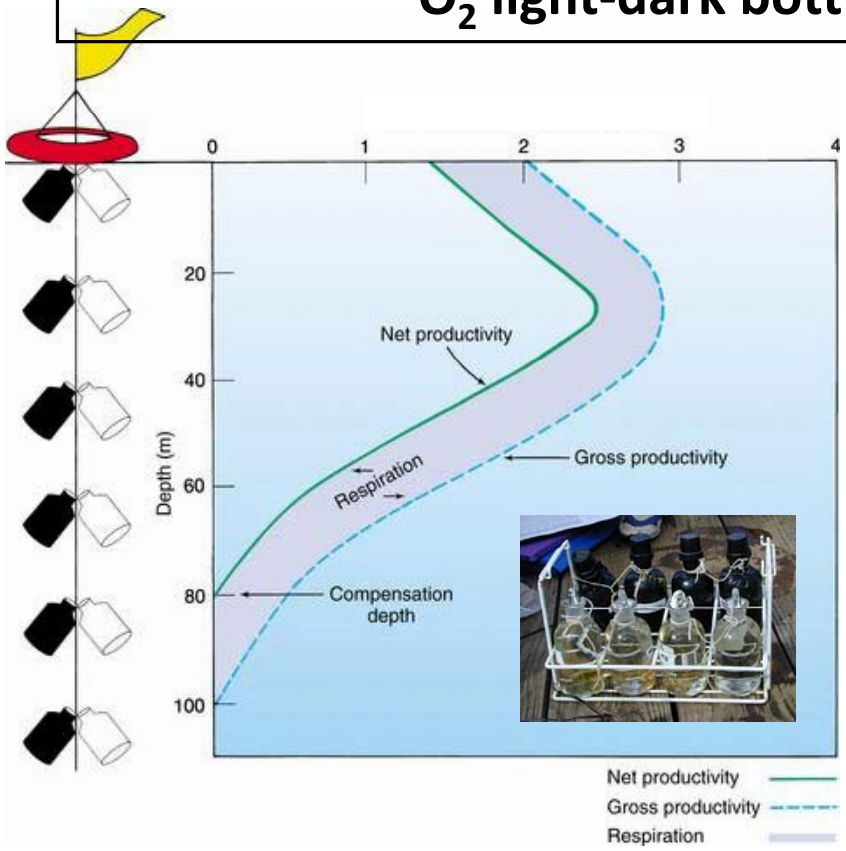
Several caveats:

- 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

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

- ΔO_2
- ΔCO_2
- ΔOrganic matter
- Isotopic tracers of C and/or O_2

Primary production approach 2: O_2 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

GPP = ΔO_2 (light) - ΔO_2(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.

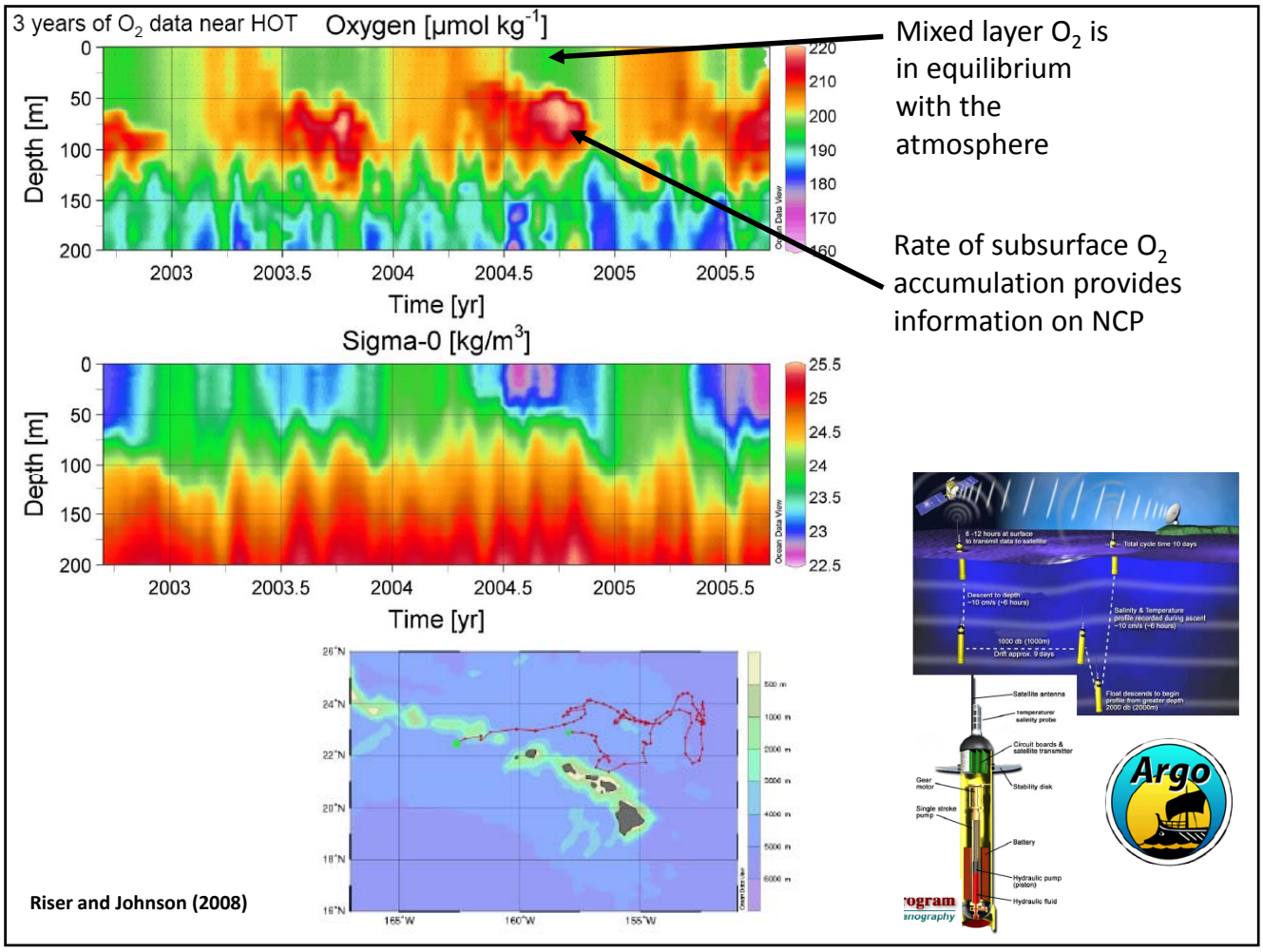
  2) requires incubation and confinement of samples.
- 3) requires conversion of O_2 to carbon (photosynthetic quotient, PQ). O_2/C PQ values can vary between 1.1 to 1.4 depending on nitrogen sources and end products of photosynthesis.

Primary production approach 3: $^{18}O_2$ gross production

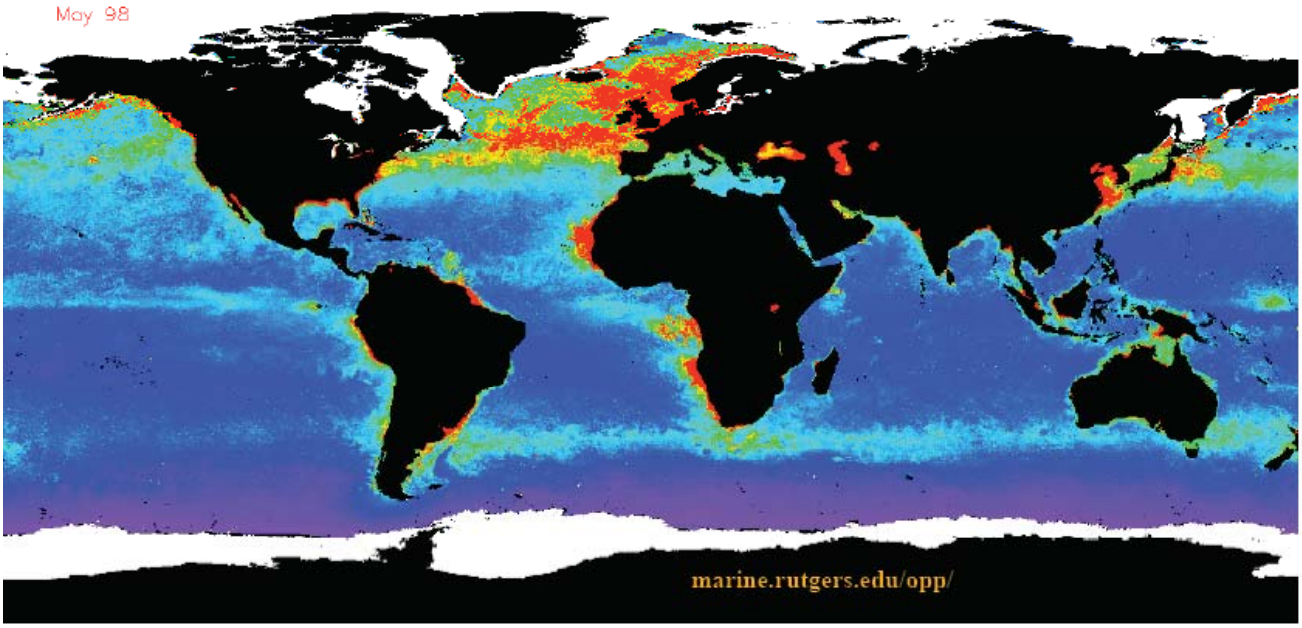
- Addition of $H_2{}^{18}O$: light bottle/dark bottle incubation approach. Photosynthetic splitting of H_2O yields $^{18}O_2$.
- $^{18}O_2$ produced during photosynthesis measured by mass spectrometry.
- Only measures GPP; no measurement of R or NCP by this method.

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

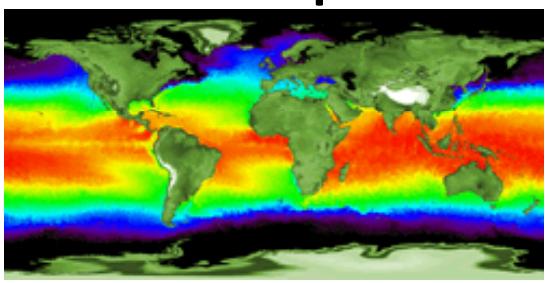
- Examine annual or seasonal scale changes in O_2, NO_3^-, CO_2, Chl *a* concentrations in the upper ocean.
- As long as exchange, diffusive losses, and grazing (for Chl *a*) can be accounted for this approach should provide an estimate of NCP.


3 years of O_2 data near HOT
Oxygen [µmol kg^{-1}]
Depth [m]
Time [yr]
Sigma-0 [kg/m^3]
Mixed layer O_2 is in equilibrium with the atmosphere
Rate of subsurface O_2 accumulation provides information on NCP
Argo
Riser and Johnson (2008)

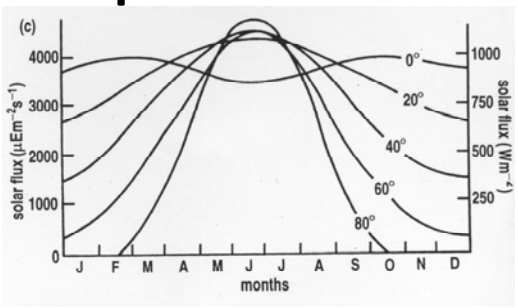
Direct Measurements will Never Provide Synoptic Estimates of Productivity



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

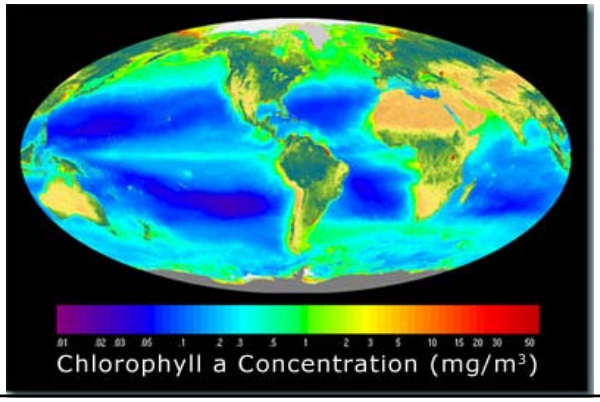


Temperature



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 photosyntheron can be used to quantify photosynthesis as a function of irradiance.

•^{14}C-bicarbonate is added to whole seawater samples, samples are placed in temperature and light controlled incubation.

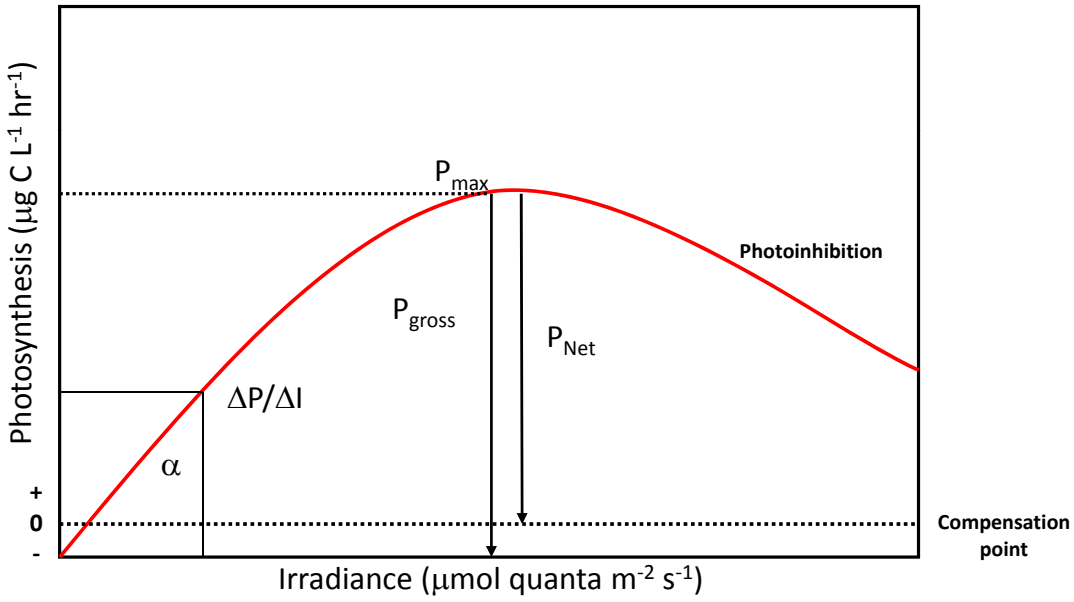
•After short incubations (<2 hrs) rates of photosynthesis are derived.

Photosynthetic responses to irradiance

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

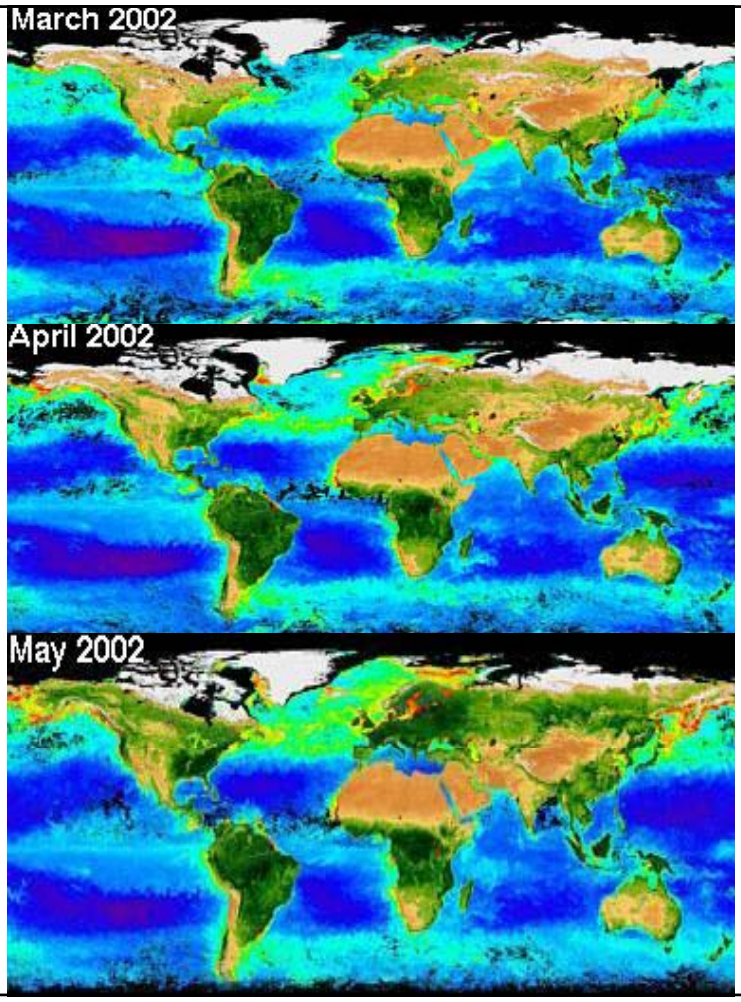
α varies based on physiological changes to the cellular photosynthetic machinery

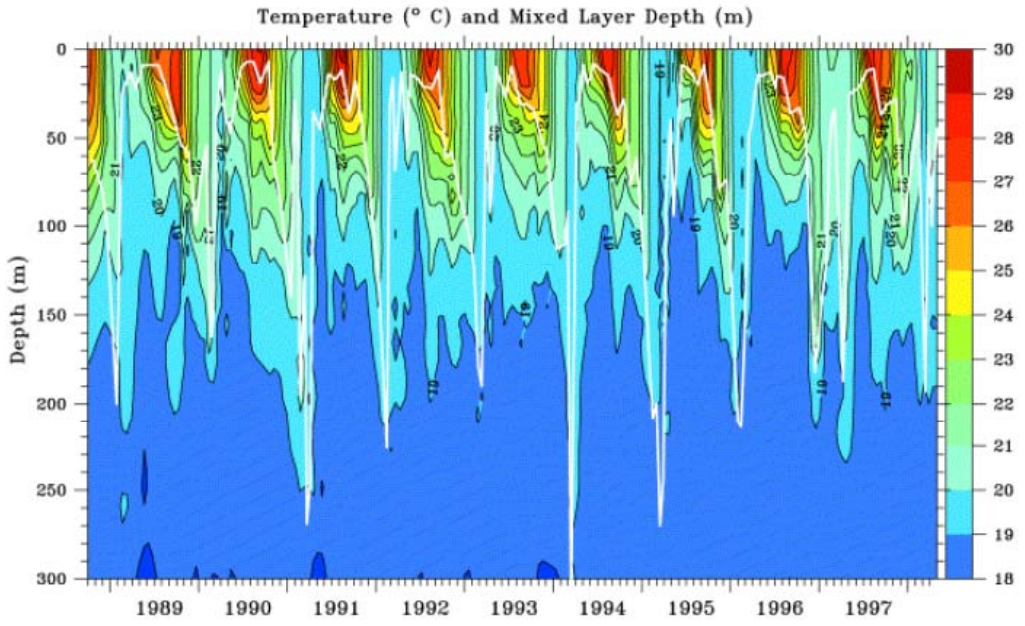
P_{max} varies depending on environmental conditions such as nutrients and temperature



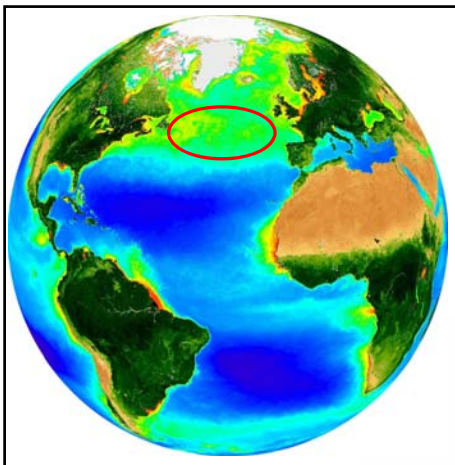
Satellites "measure" chlorophyll, temperature, and light

- **~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.**

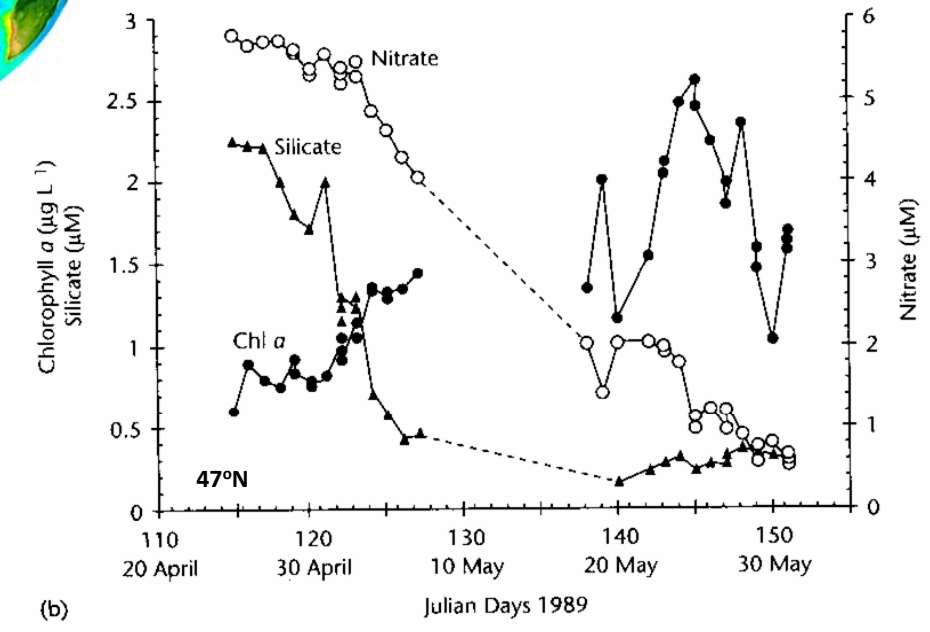

March 2002
April 2002
May 2002



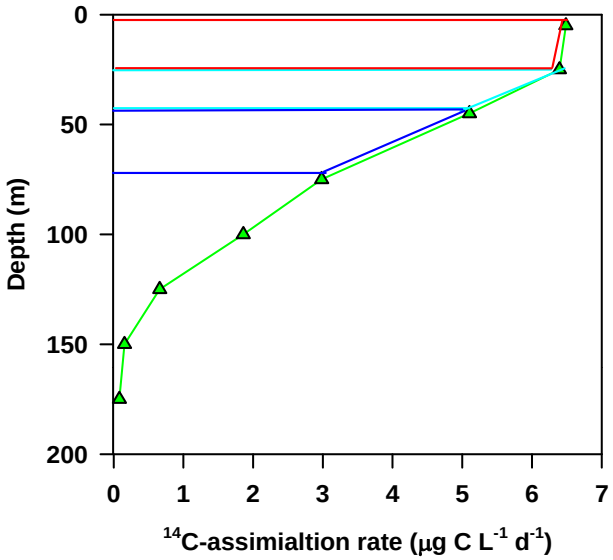
Seasonal variations in mixing and temperature in the Sargasso Sea-note winter time deepening of the mixed layer coincides with seasonal cooling.



North Atlantic Spring Bloom



Trapezoidal integration



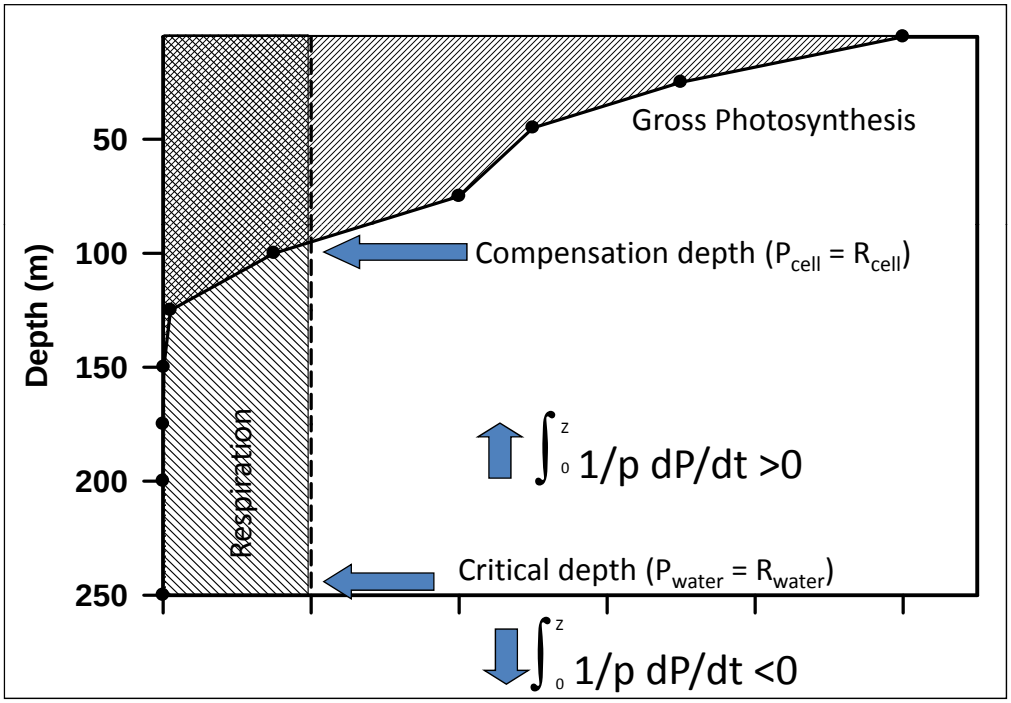
Depth (m)	Production (µg C L^{-1} d^{-1})
5	6.5
25	6.4
45	5.0
75	3.0
5-75 m Int.	363 mg C m^{-2} d^{-1}

Area of trapezoid = Height * avg. base

[(25 m -5 m) * ((6.5 mg C m^{-3} d^{-1} + 6.4 mg C m^{-3} d^{-1})/2)] = 129 mg C m^{-2} d^{-1}
[(45 m -25 m) * (6.4 mg C m^{-3} d^{-1} + 5.0 mg C m^{-3} d^{-1})/2] = 114 mg C m^{-2} d^{-1}
[(75 m -45 m) * ((5.0 mg C m^{-3} d^{-1} + 3.0 mg C m^{-3} d^{-1})/2)] = 120 mg C m^{-2} d^{-1}

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

Conditions for net primary productivity



The Spring Bloom

Sverdrup (1953)

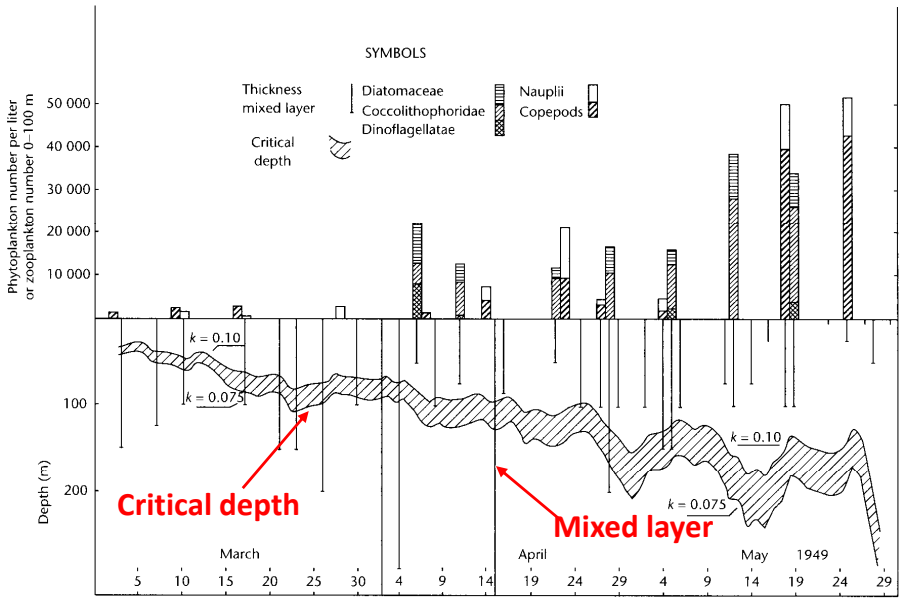
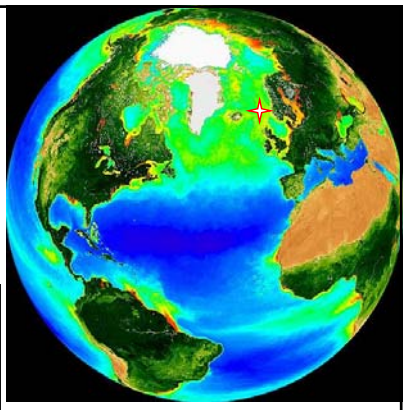


Fig. 1.4 Data for 1949 from Weathership "M" (66°N, 2°E) showing the relationship between the approximate critical depth (shading between approximate k values of 0.075 and 0.10) and mixing depth. Phytoplankton counts increased in April–May, when critical depth exceeded the mixing depth. While these data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



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.