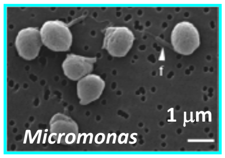
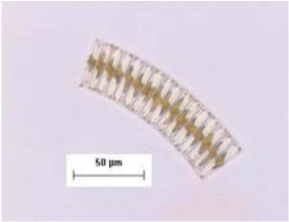
Major divisions and classes of photosynthetic plankton in the ocean

- **Prokaryotes**
  - **Cyanobacteria**

- **Eukaryotes:**
  - **Chlorophyta (green algae); include the following classes:**
    - **Chlorophyceae**
    - **Prasinophceae**
    - **Euglenophyceae**



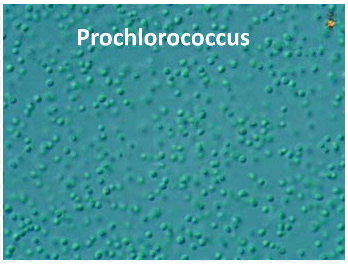
  - **Chromophyta (brown algae); include the following classes:**
    - **Chrysophyceae**
    - **Pelagophyceae**
    - **Prymnesiophyceae**
    - **Bacillariophyceae (diatoms)**
    - **Dinophyceae (dinoflagellates)**
    - **Cryptophyceae (crytophytes)**
    - **Phaeophyceae (phaeophytes)**

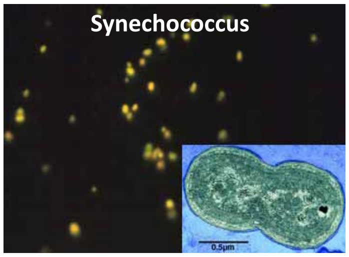


  - **Rhodophyta (red algae)-mostly macrophytes**

Marine cyanobacteria

- **Cyanobacteria:** major groups of cyanobacteria in the oceans include: *Prochlorococcus*, *Synechococcus*, *Trichodesmium*, *Crocosphaera*, *Richelia*
  - Wide range of morphologies: unicellular, filamentous, colonial
  - Some species fix N_2
  - Hugely abundant in the open sea – often dominate photosynthetic biomass and production

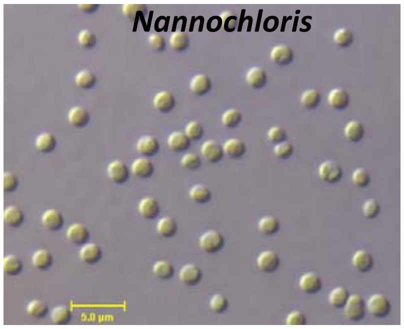




Many images from: http://www.sb-roscoff.fr/Phyto/gallery/main.php?g2_itemId=19

Chlorophyta (green algae)

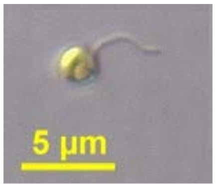
- Chlorophytes
  - Contain Chl *b*
  - Uncommon in open ocean; mostly freshwater.
  - Very diverse (more than 7000 species described)
  - Can be single cells or colonies, coccoid or flagellated
  - *Chlorella, Chlamydomonas, Dunaliella*
- Prasinophytes
  - Contain Chl *b*
  - Predominately unicellular
  - Relatively common, but not abundant in ocean
  - Can be single cells or colonies, coccoid, biflagellated, or quadri-flagellated


Nannochloris


Prasinophyceae

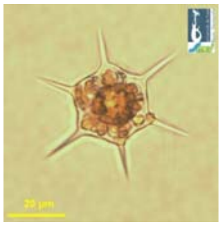
Chromophyta (brown algae)

- **Pelagophytes**
  - **Contain Chl *c***
  - **Very common in open ocean.**
  - **Coccoid or monoflagellated**



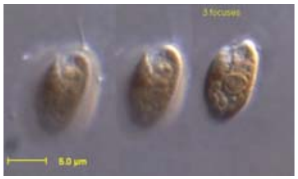
Pelagomonas

- **Chrysophytes**
  - **Contain Chl *c***
  - **Relatively rare in open ocean**
  - **Mostly bi-flagellated (flagella of unequal length)**



Dictyocha

- **Cryptophytes**
  - **Contain Chl *c***
  - **Contain carotenoid alloxanthin**
  - **Contain phycoerythrin or phycocyanin**
  - **Flagellated unicells**

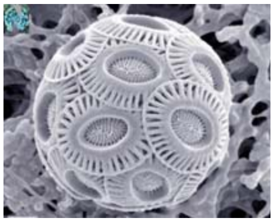


Rhodomonas salina

Images from: http://planktonnet.sb-roscoff.fr/index.php#search

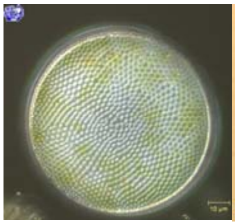
Chromophyta (brown algae)-Cont.

- **Prymnesiophytes**
  - Mainly biflagellates
  - Very common in open ocean
  - 2-5 μm
  - Some species form $CaCO_3$ plates (coccoliths)

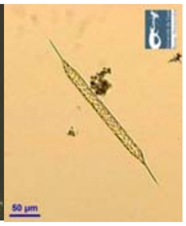


Emiliana huxleyi

- **Bacillariophytes**
  - Ubiquitous
  - All contain Chl *c* and carotenoid fucoxanthin
  - Rigid silica-impregnated cell wall
  - Many form colonies
  - 2 prominent cell morphologies: centric and pennate

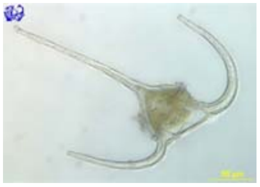


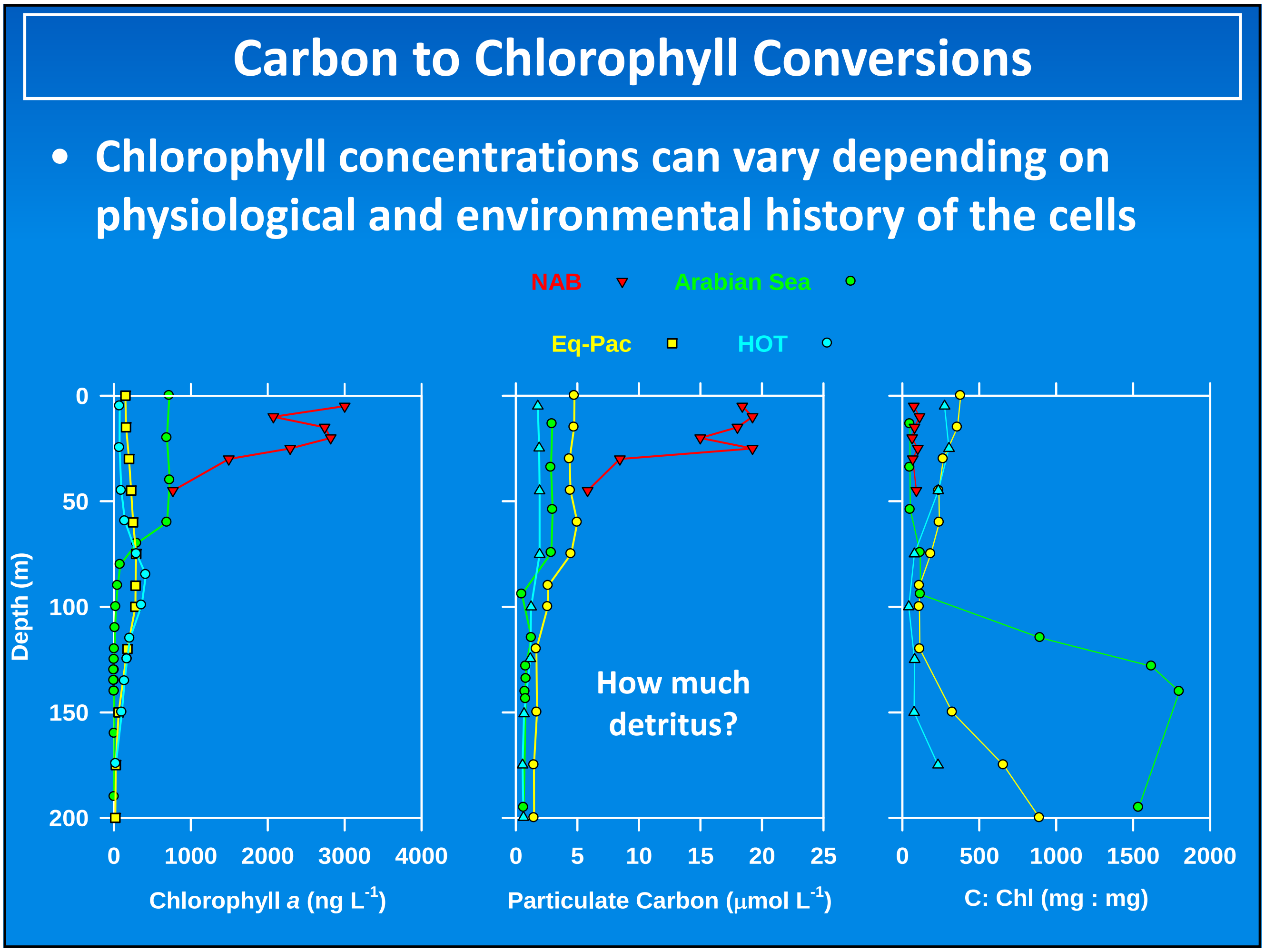
Coscinodiscus



Rhizosolenia

- **Dinophytes**
  - Possess the carotenoid peridinin
  - Widely distributed (estuaries, open ocean)
  - Mostly unicellular and autotrophic, but colorless heterotrophs can also be abundant
  - 2 flagella
  - Many are bioluminescent and some case toxic red tides blooms

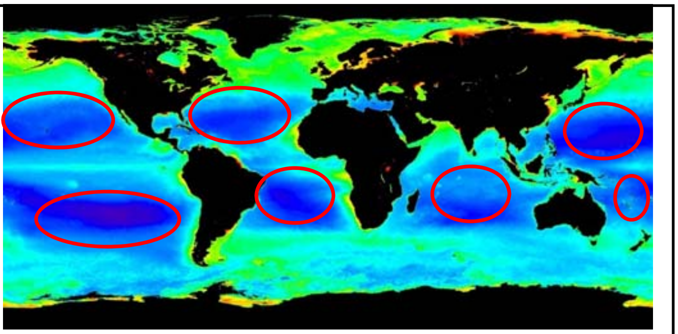


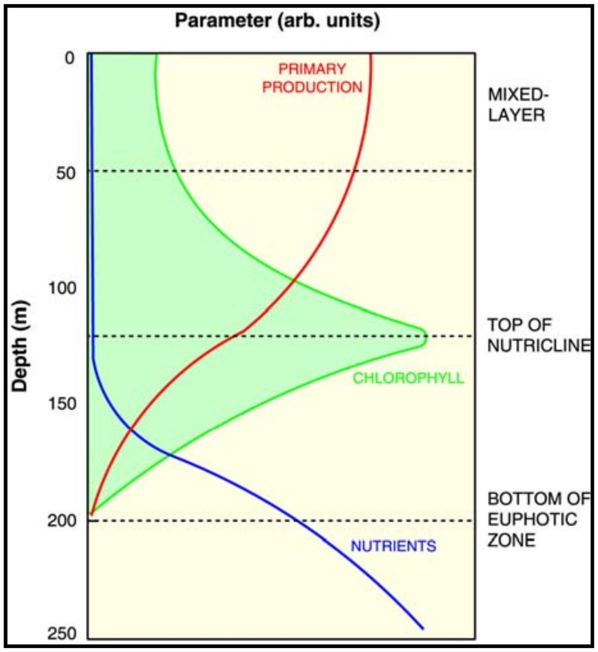


Carbon to Chlorophyll Conversions

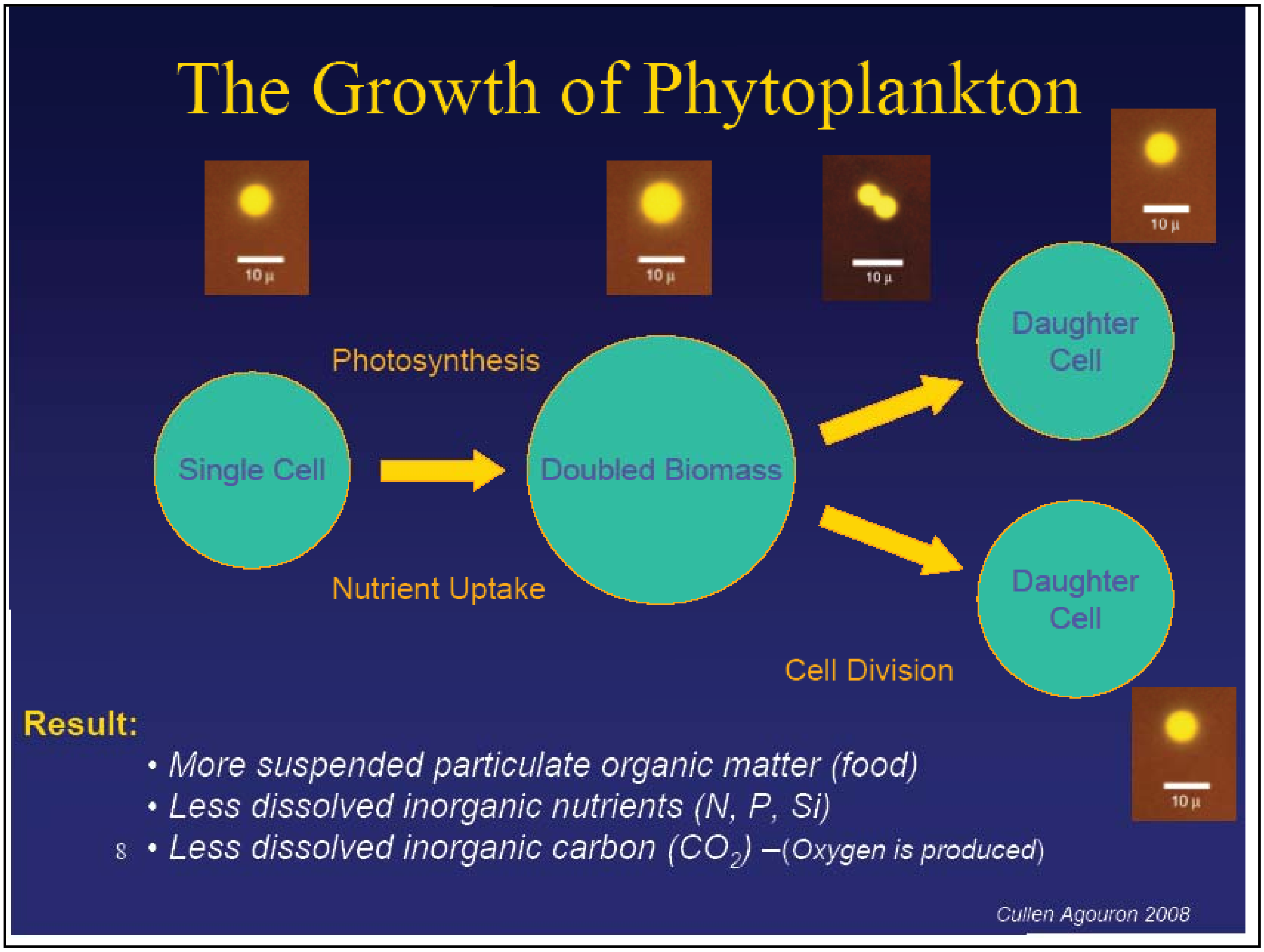
- Chlorophyll concentrations can vary depending on physiological and environmental history of the cells

How much detritus?





In the ocean gyres, chlorophyll concentrations are low in the surface water, greater at depth (80-150 m). In contrast, most of the production (=synthesis of biomass) occurs in the well-lit upper ocean.



The Growth of Phytoplankton

Single Cell

Photosynthesis

Nutrient Uptake

Doubled Biomass

Daughter Cell

Daughter Cell

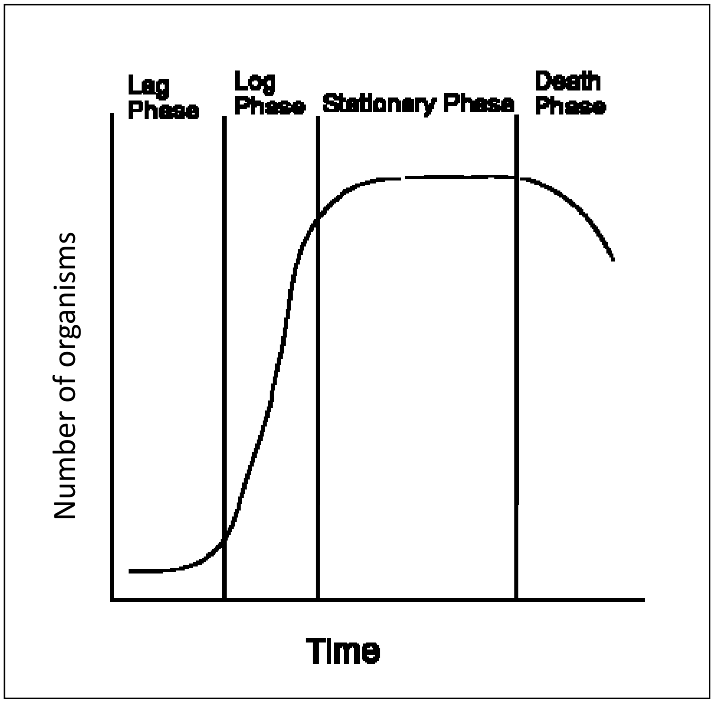
Cell Division

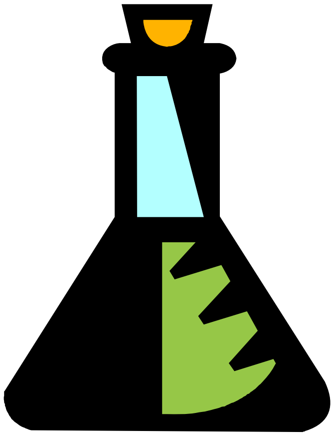
Result:

- *More suspended particulate organic matter (food)*
- *Less dissolved inorganic nutrients (N, P, Si)*
- *Less dissolved inorganic carbon (CO_2) –(Oxygen is produced)*

Cullen Agouron 2008

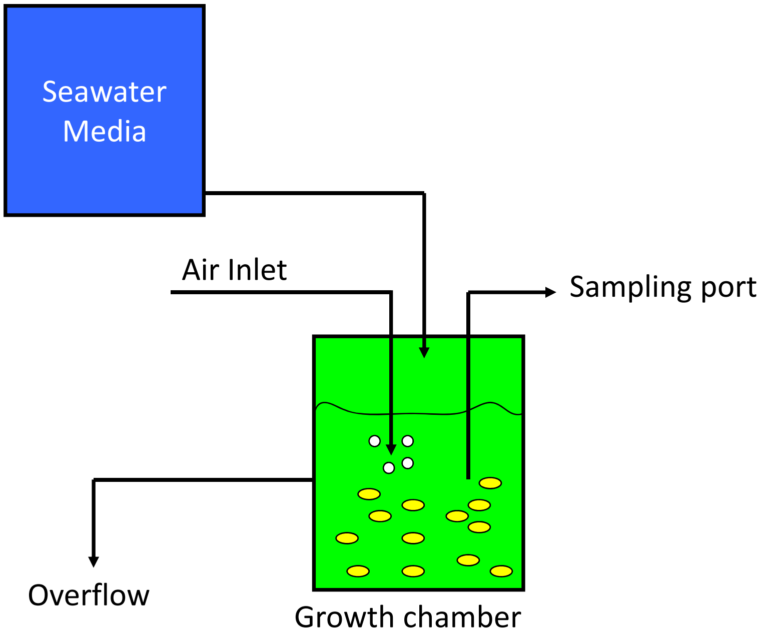
Growth in a closed system





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

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…

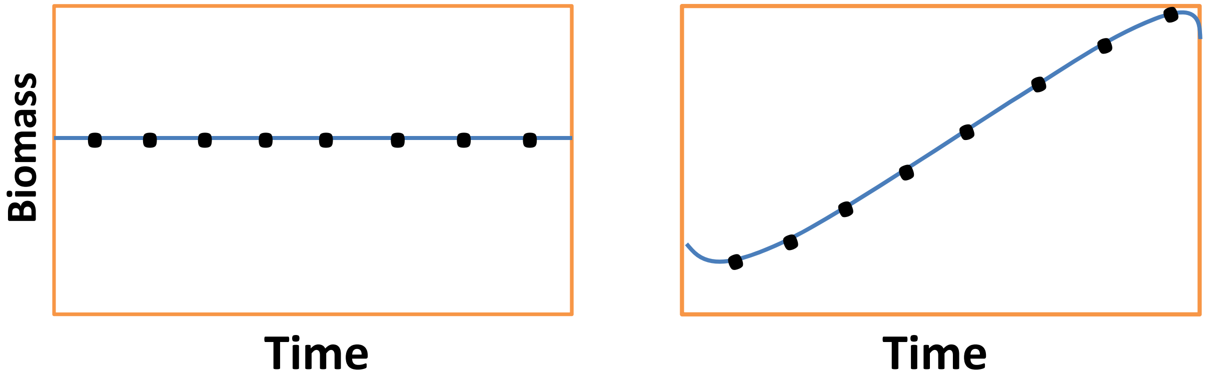
- Most direct method would be to measure changes in biomass over time.

Why is that difficult for naturally occurring plankton?

In natural seawater sample….

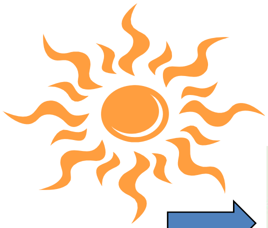
- Mixed assemblage of organisms with variable growth rates.
- Growth is often balanced by loss (predation or disease), thus no net change in biomass with time.

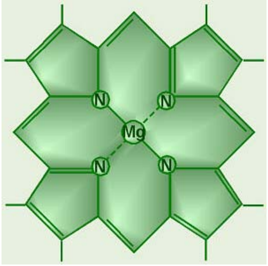
In which system is growth greater? Which system has a greater rate of production?



- **Two main forms of biomass production:**
  - **Primary production: is the rate of biomass synthesis via reduction of CO_2; 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.)**

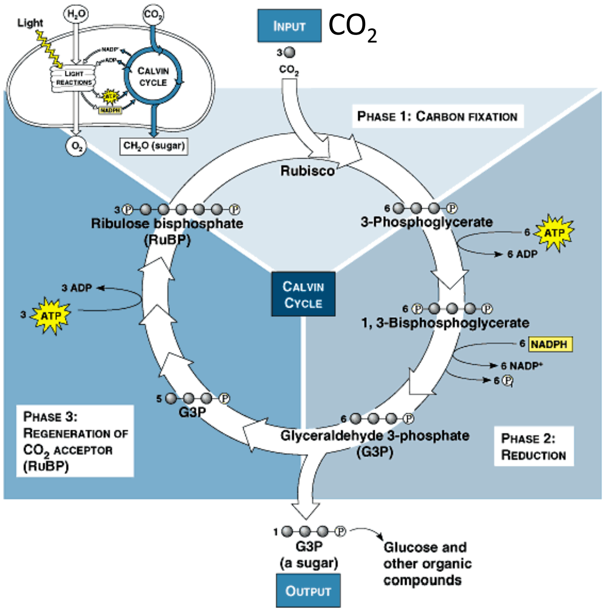
Photosynthesis





ATP,
NADPH

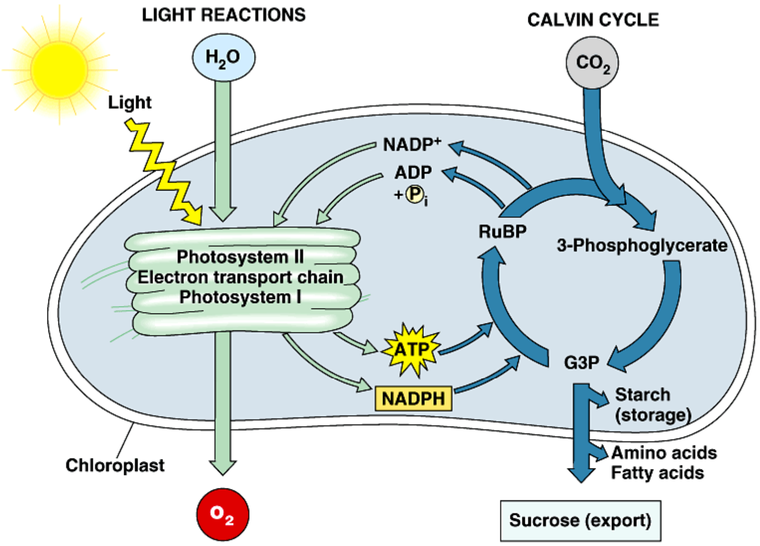
$H_2O \rightarrow O_2$



$$CO_2 + 2H_2O \xrightarrow{\text{Sunlight}} CH_2O + O_2 + H_2O + \text{heat}$$

3 mol ATP and 2 mol NADPH are consumed for every 1 mol CO_2 fixed.

- 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 CO_2 to organic matter (dark reactions).



Photosynthesis:

$$6CO_2 + 12H_2O \xrightarrow{\text{Sunlight}} C_6H_{12}O_6 + O_2 + 6H_2O + \text{heat}$$

2 Key enzymes for phytoplankton photosynthesis

- **RUBISCO** (1,5-bisphosphate carboxylase/oxygenase)- key enzyme in the Calvin-Benson cycle, incorporates CO_2 into 3-phosphoglycerate. Most abundant protein on Earth.
- **Carbonic anhydrase**: converts bicarbonate to CO_2, and vice versa. Most marine phytoplankton transport bicarbonate and carbonic anhydrase dehydrates to CO_2 intracellularly near RUBISCO.

$$CO_2 + 2H_2O \xrightarrow{\text{Sunlight}} CH_2O + O_2 + H_2O + \text{heat}$$

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}

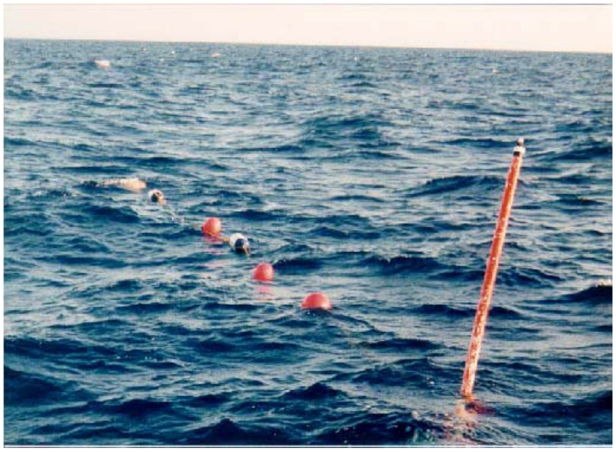
- Analytical sensitivity of carbon and oxygen determinations:
  - CO_2 by coulometry = 1 μmol C L^{-1}
  - O_2 by Winkler titration = 0.4 to 2 μmol O_2 L^{-1}
  - TOC by HTC = 2-4 μmol C L^{-1}

****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

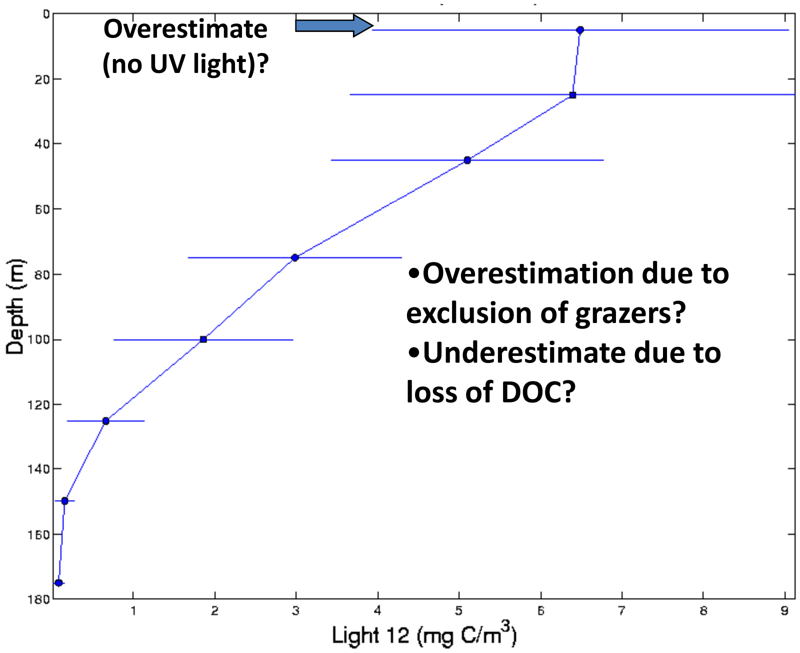


Typically PAR (400-700 nm) transparent polycarbonate bottles are used for these experiments...but UV is excluded.

- 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?

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



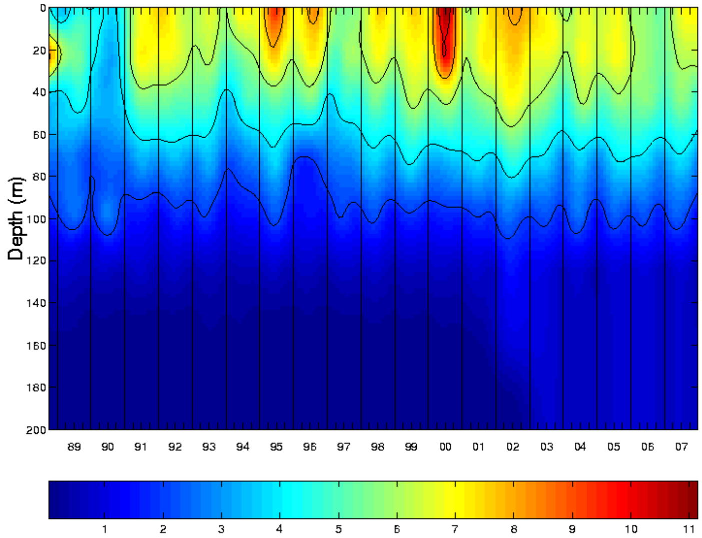
Overestimate (no UV light)?

- Overestimation due to exclusion of grazers?
- Underestimate due to loss of DOC?

- 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})



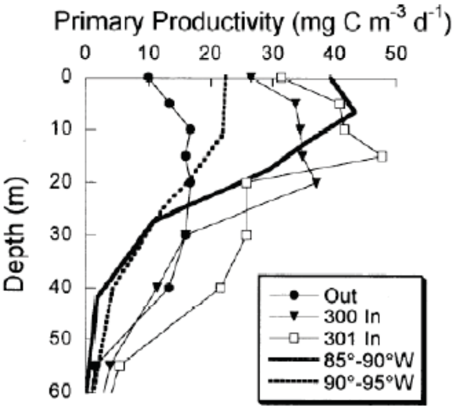


Fig. 1. Primary productivity at and near the site of the open-ocean enrichment experiment (near 5°S, 90°W). Profiles from out of the patch and in the patch 2 d (calendar day 300) and 3d (calendar day 301) after enrichment are from Martin et al. (1994). Profiles of historical averages east (4–6°S, 85–90°W;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

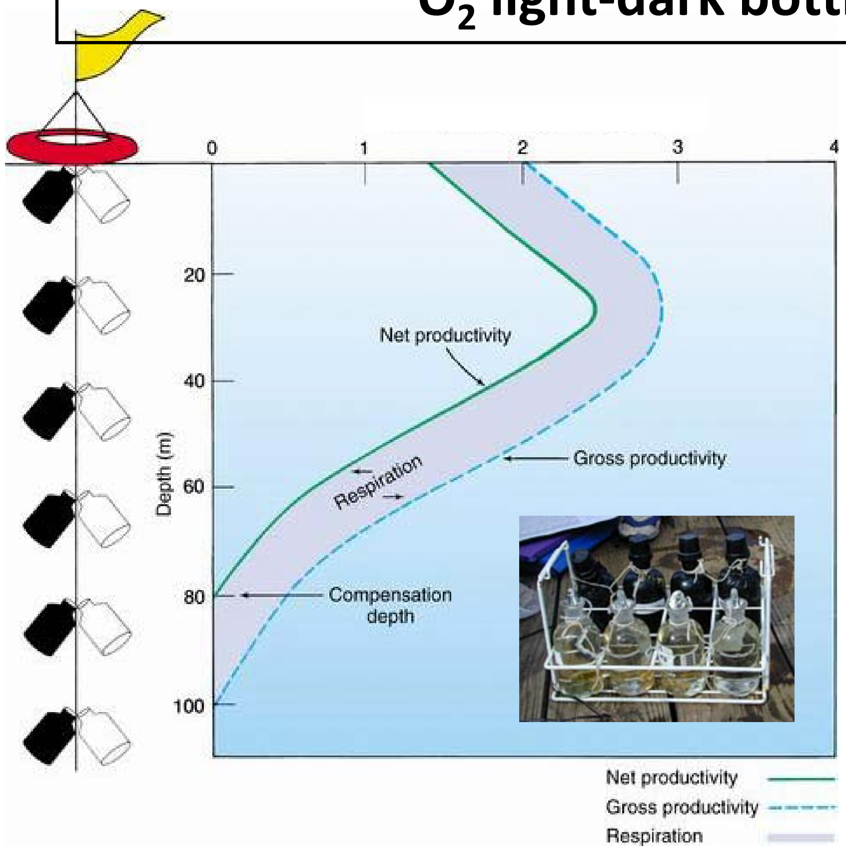
Several caveats:

- 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.

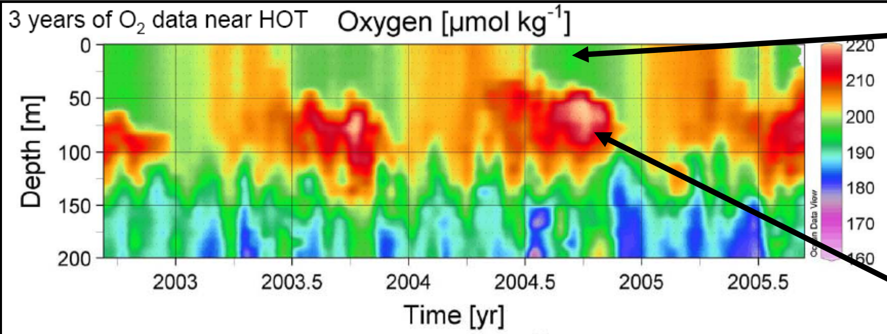
  2) requires incubation and confinement of samples.
- 3) requires conversion of O_2 to carbon (photosynthetic quotient, PQ). O_2/C PQ values can vary between 1.1 to 1.4 depending on nitrogen sources and end products of photosynthesis.

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)

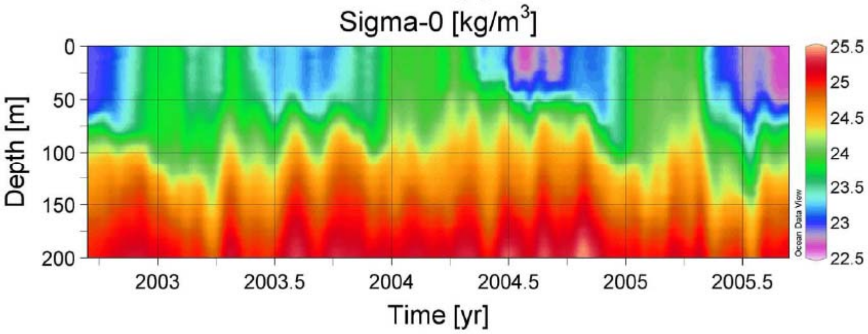
- Examine annual or seasonal scale changes in O_2, NO_3^-, CO_2, Chl *a* concentrations in the upper ocean.
- As long as exchange, diffusive losses, and grazing (for Chl *a*) can be accounted for this approach should provide an estimate of NCP.

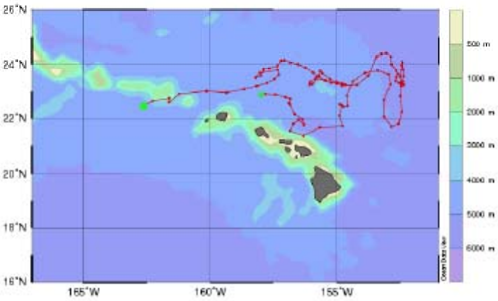


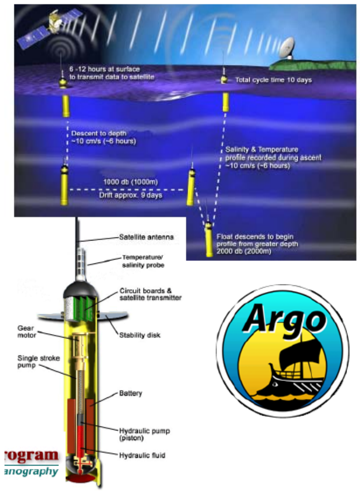
3 years of O_2 data near HOT

Mixed layer O_2 is in equilibrium with the atmosphere

Rate of subsurface O_2 accumulation provides information on NCP

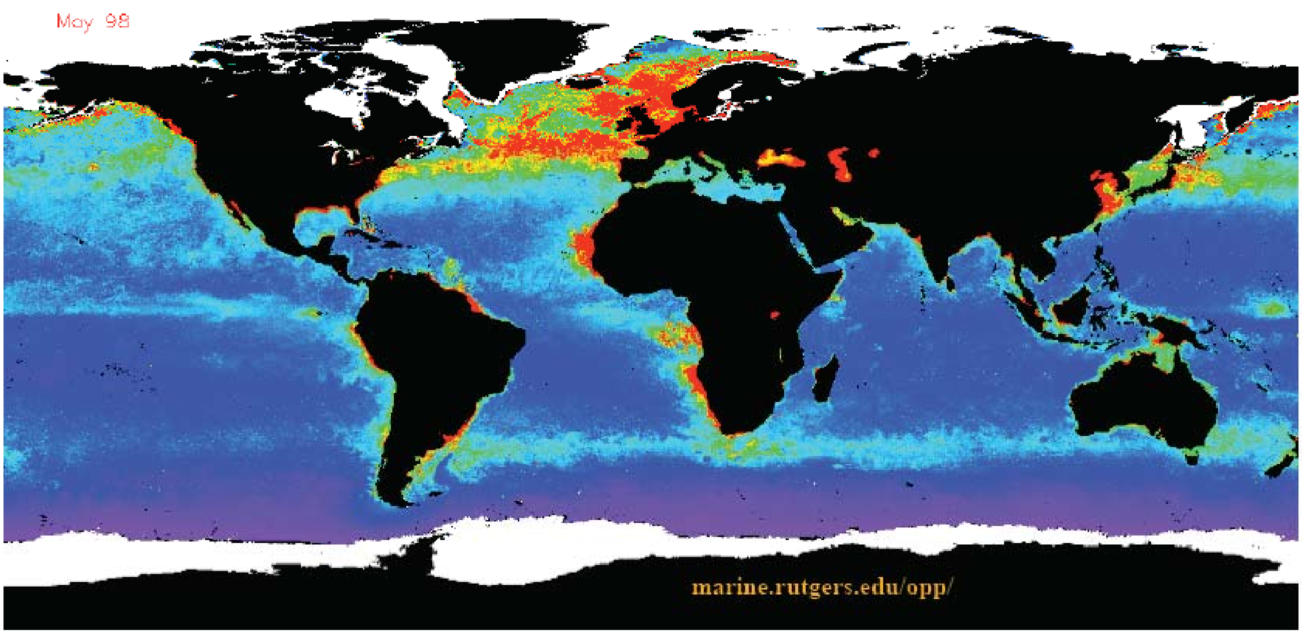






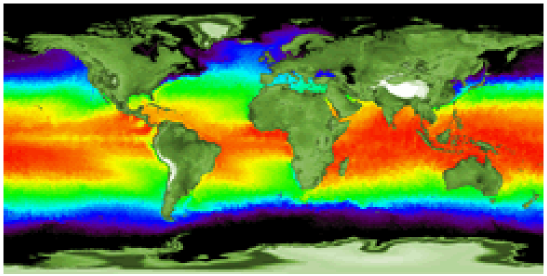
Riser and Johnson (2008)

Direct Measurements will Never Provide Synoptic Estimates of Productivity

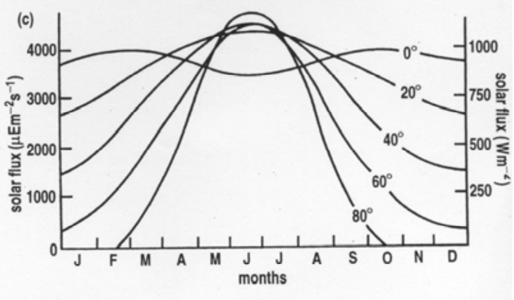


marine.rutgers.edu/opp/

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

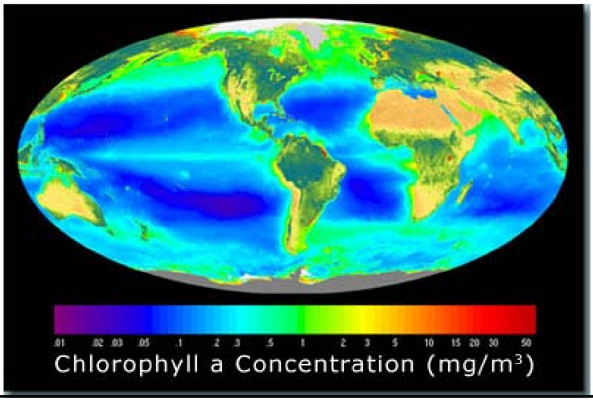


Temperature



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.

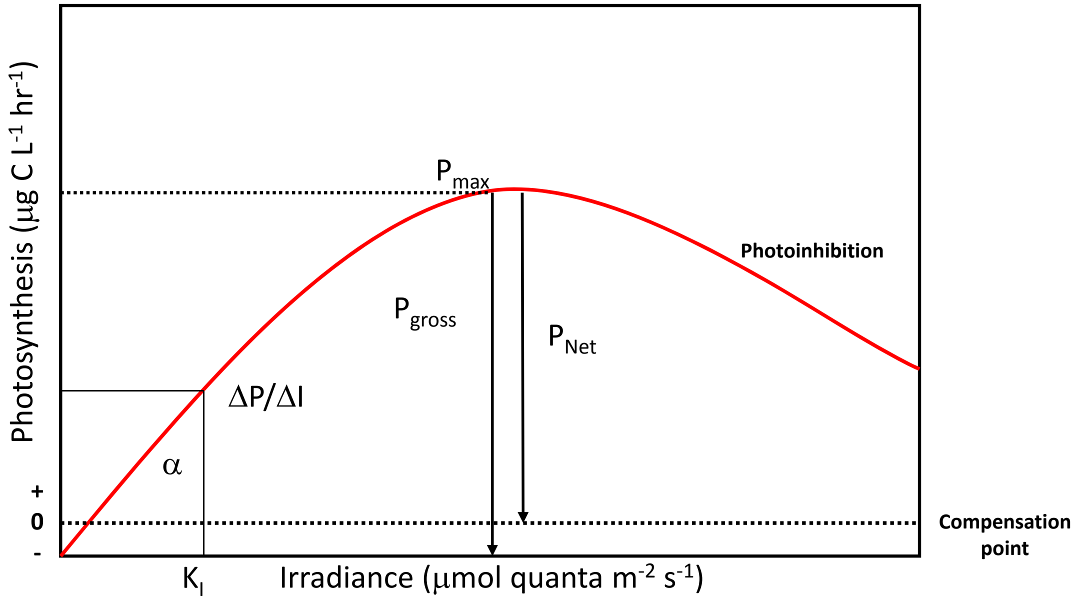
- After short incubations (<2 hrs) rates of photosynthesis are derived.

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.