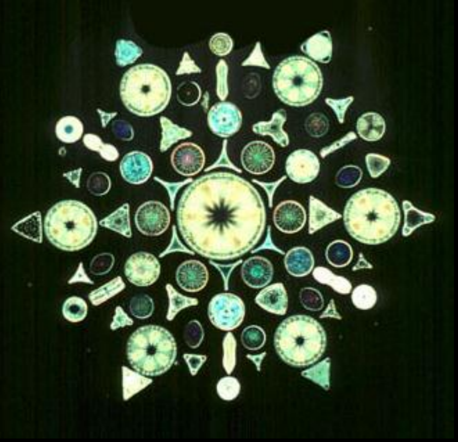


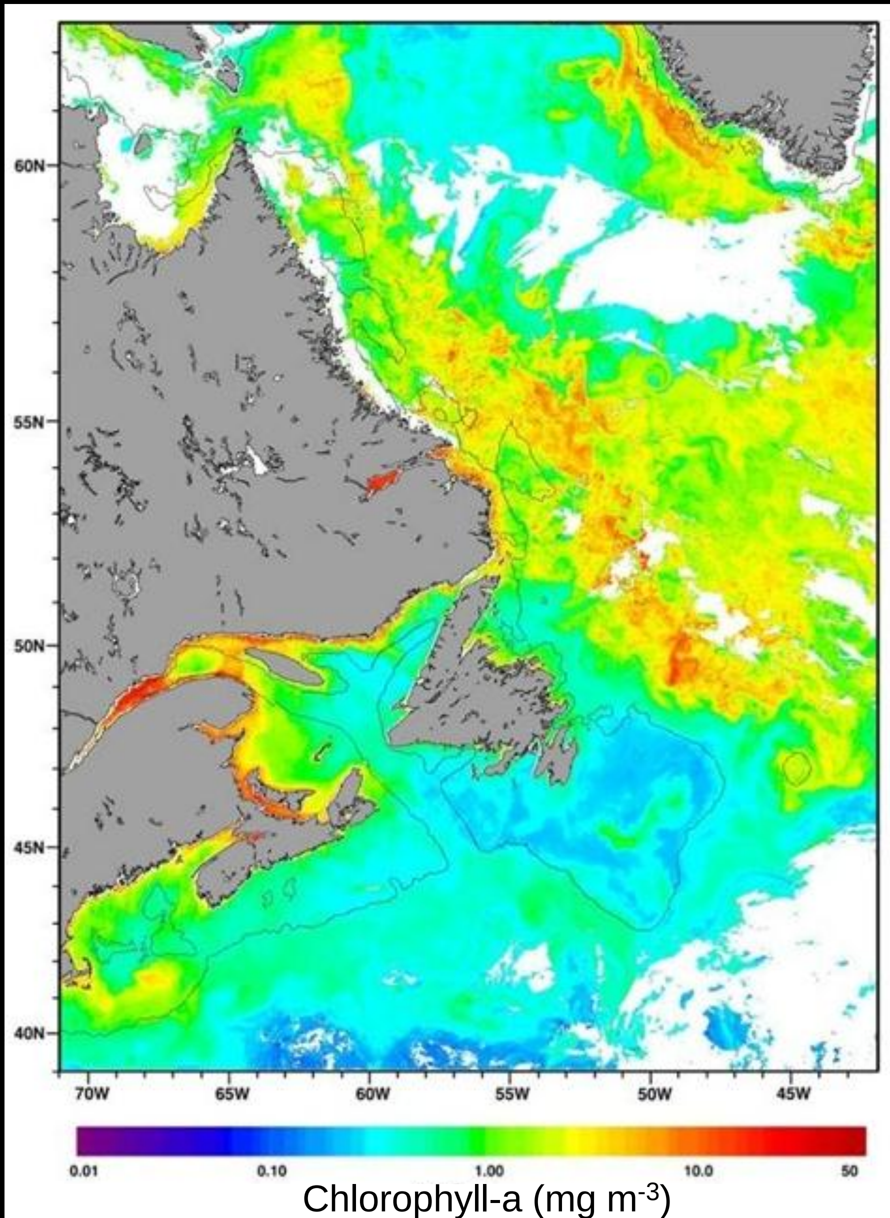
Computation of Primary Production

Ocean Ecosystem as Thermodynamic System

The pelagic ecosystem is an open, dissipative system sustained by regular energy supply from sun, to which it is coupled through the pigment molecules contained in phytoplankton. The light penetrating into the ocean allows biogeochemistry, where otherwise only geochemistry would be possible.

Furthermore, the light that escapes from the ocean (the basis of the ocean-colour signal), carries coded information on ocean biology and biogeochemistry.

Emil Nolde



SeaWiFS composite image
1-15 June 1998

A major product of ocean-colour remote sensing is distribution of chlorophyll concentration, the most fundamental property of the ocean ecosystem. It has been designated an Essential Climate Variable (UNFCCC).

The maps are strikingly beautiful. Furthermore, they are based on strict radiative transfer theory, and contain a wealth of information, with many applications.

The technique exploits the absorption of light by the pigment. What happens to the absorbed light? One pathway for the absorbed light is photosynthesis (primary production).

What is Plankton Biomass?

Biomass of plankton is its local abundance. The equivalent term in fisheries is the stock size. For phytoplankton the index is concentration of chlorophyll.

What is Primary Production?

Primary production is the rate of production of phytoplankton. The equivalent term in fisheries is reproduction and growth. If biomass like money in the bank, primary production is like the interest earned by the capital.

The Photosynthesis Equation

Available Energy

$H_2O + CO_2 +$ Absorbed Energy $\rightarrow CH_2O + O_2 +$ Dissipated Energy

Stored Energy

Chlorophyll-a is at the heart of the photosynthetic reaction.

Growth Requirements of Phytoplankton

The growth requirements of phytoplankton are similar to those of any green plant:

- Water
- Carbon dioxide
- Visible light
- Chemical nutrients (nitrogen, phosphorus, … often in short supply)

What makes primary production change?

Primary production varies with region and season, because of changes in those factors essential for phytoplankton growth. These include

- the phytoplankton biomass;
- the intensity and duration of sunshine;
- the intensity of turbulence in the water;
- the concentration of certain chemicals (nutrients) in the water;
- the temperature;
- the kinds of phytoplankton present.

What is the fate of primary production?

Phytoplankton may be lost (erosion of capital) by a number of mechanisms

- They may sink to the bottom;
- They may be swept away by currents;
- They might die from disease;
- They may be eaten.

Oceanic CO_2 Pools and Fluxes (Global)

- Surface biota ~ 3 GT C
- Globally, some 50 GT of carbon fixed by marine phytoplankton per annum
- About one third (~16 GT of carbon) is exported from surface layer by sinking

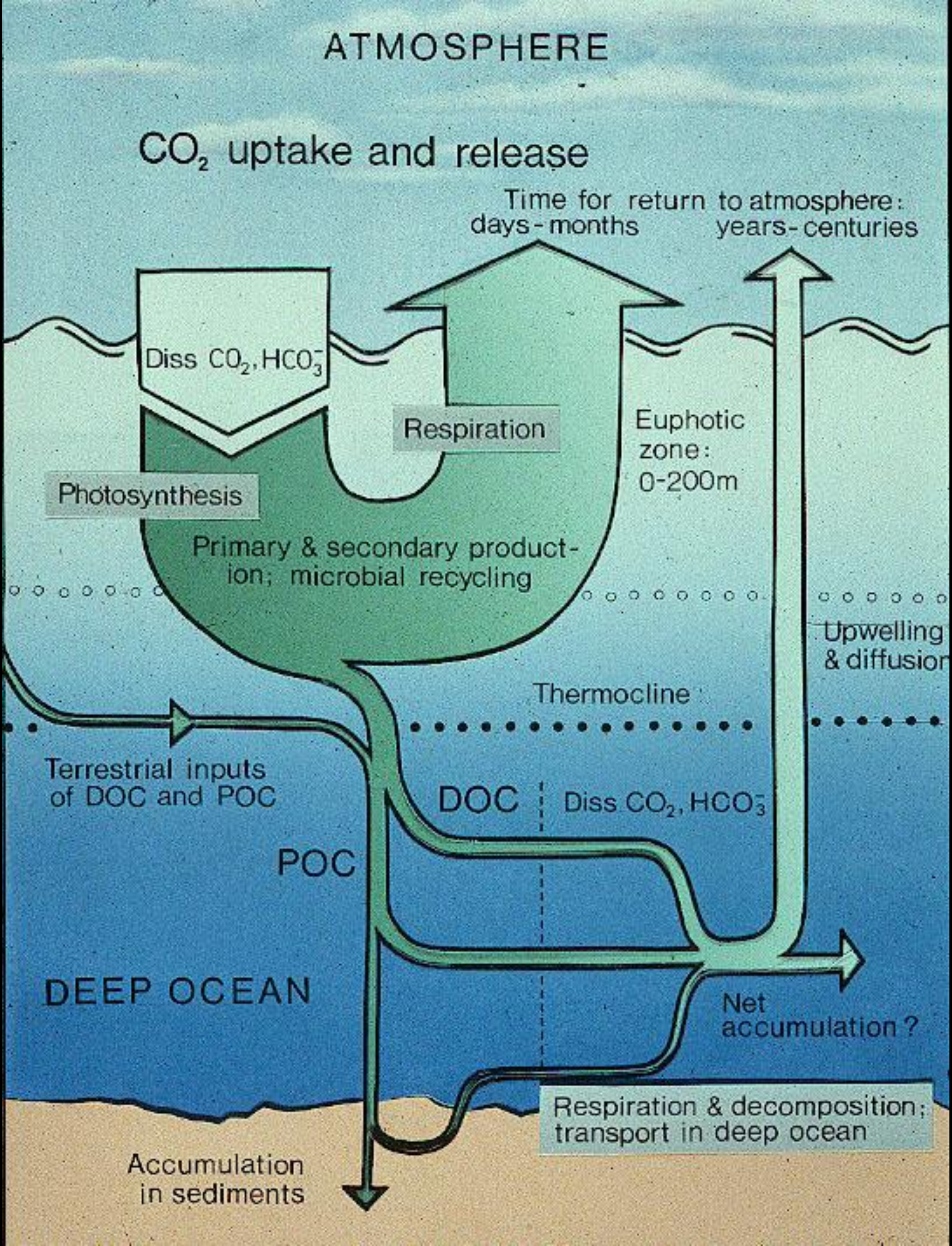
⇩

Biological Pump

- Scales of comparison:

  Fossil fuel emissions are ~10 GT of carbon per annum

  Net primary production by terrestrial plants is considered to be roughly the same as marine primary production


ATMOSPHERE
CO2 uptake and release
Time for return to atmosphere:
days - months
years - centuries
Diss CO2, HCO3-
Respiration
Euphotic zone: 0-200m
Photosynthesis
Primary & secondary production; microbial recycling
Upwelling & diffusion
Thermocline
Terrestrial inputs of DOC and POC
DOC
Diss CO2, HCO3-
POC
DEEP OCEAN
Net accumulation ?
Respiration & decomposition; transport in deep ocean
Accumulation in sediments

Determinants of Primary Production

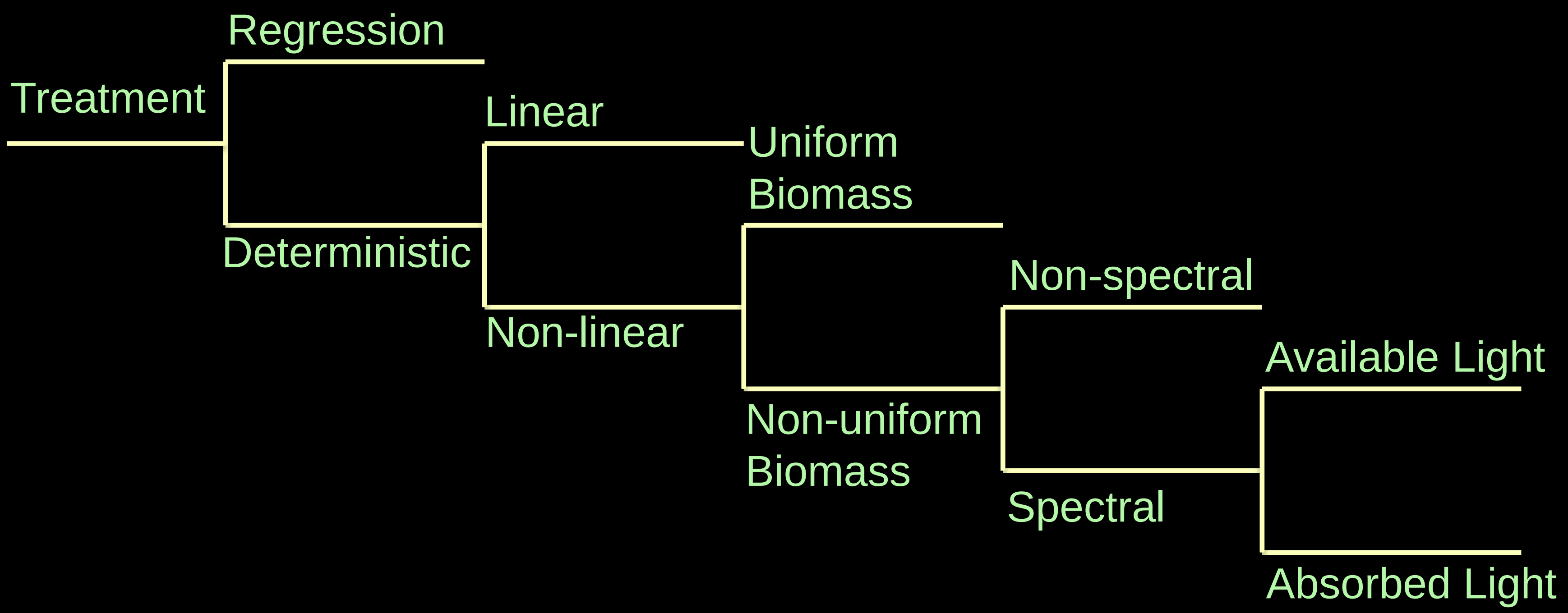
First-order:

- Light
- Pigment Concentration

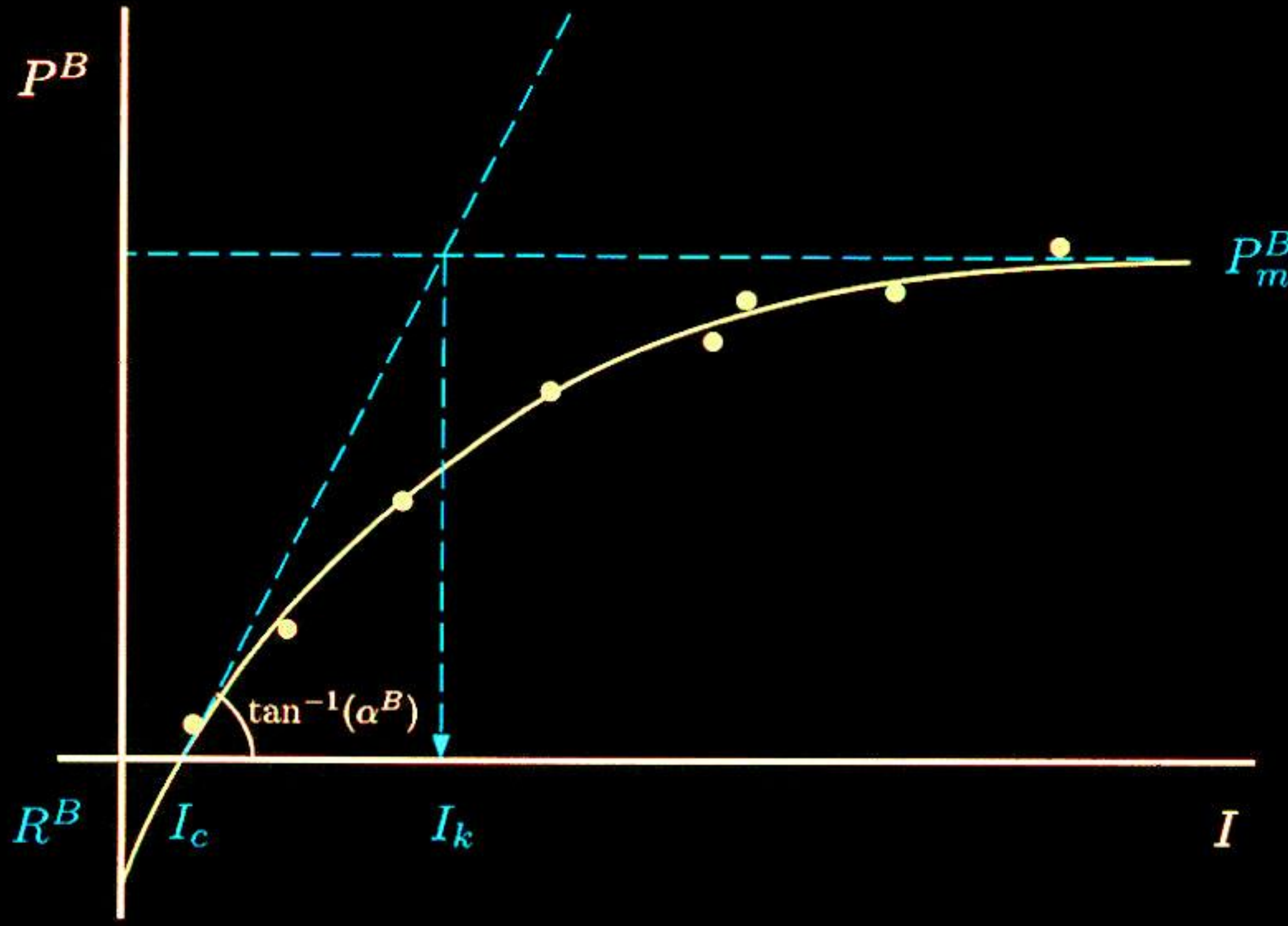
Second-order:

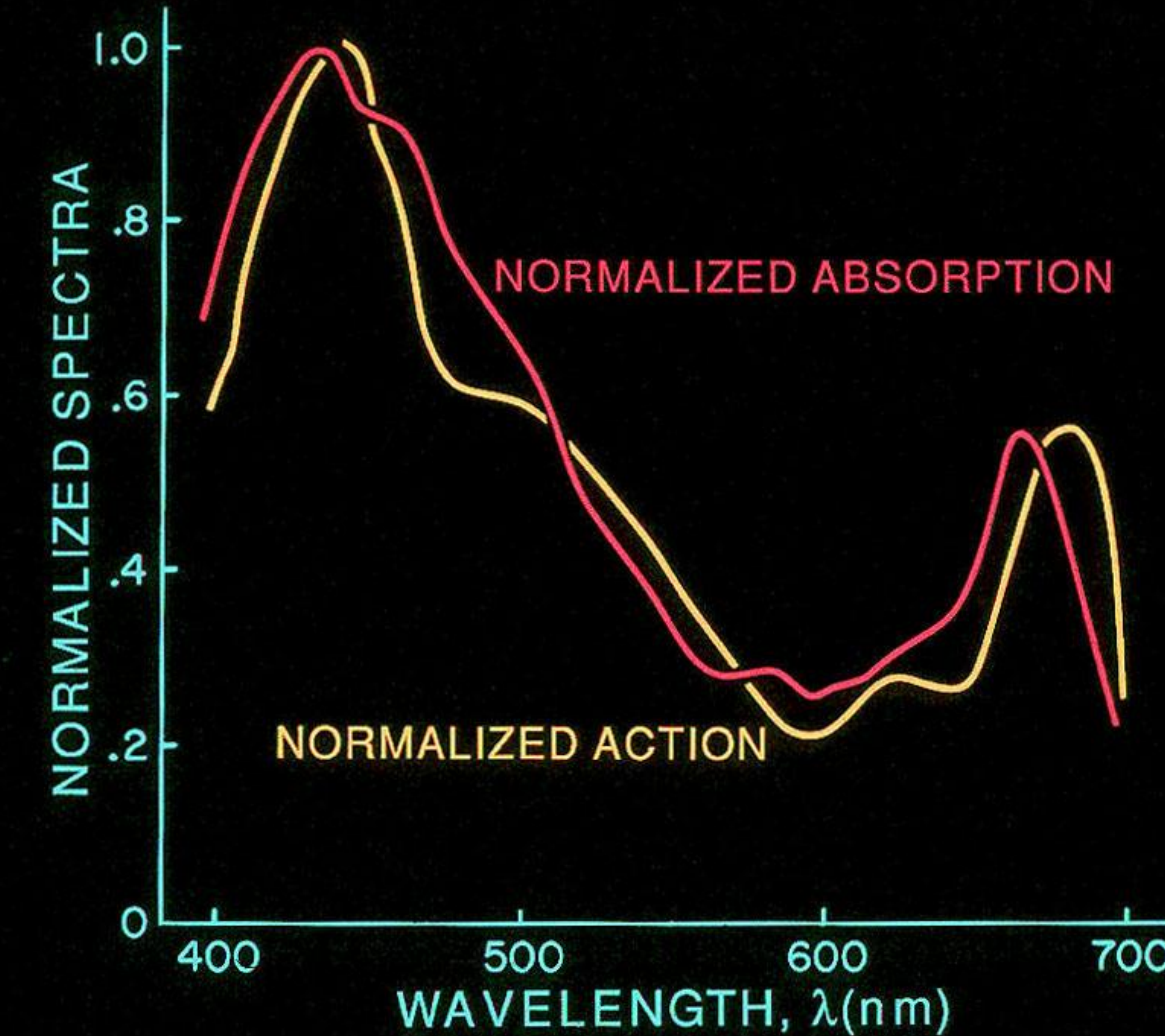
- Nutrients
- Temperature
- Community structure (cell size, taxa);
- Growth history (light; temperature)
- Stratification/ Vertical mixing

Hierarch of Primary Production Models

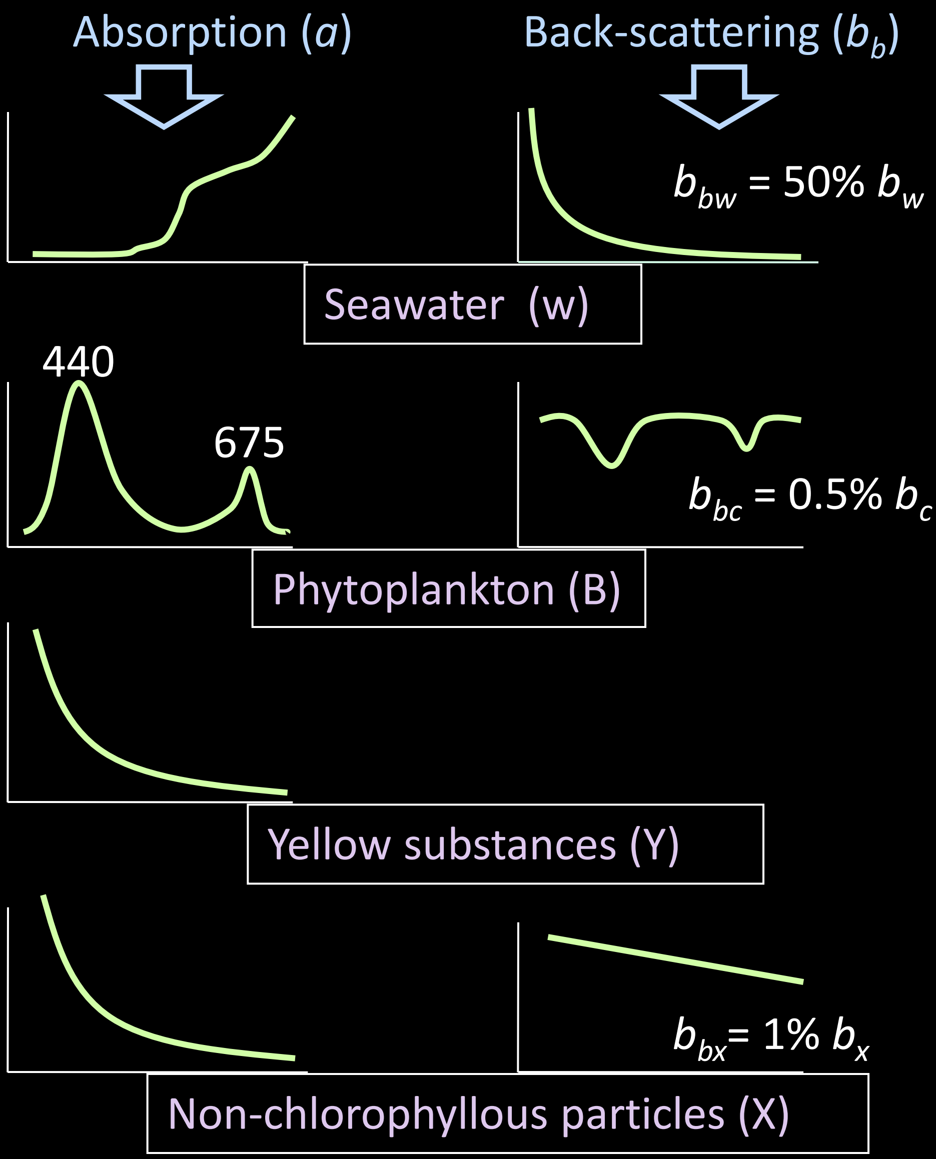


Photosynthesis-Irradiance Curve




NORMALIZED SPECTRA
1.0
.8
.6
.4
.2
0
400
500
600
700
WAVELENGTH, λ(nm)
NORMALIZED ABSORPTION
NORMALIZED ACTION

Inherent spectral optical properties of seawater and its contents



Light penetration underwater is influenced by the inherent optical properties and by the angular distribution of light underwater:

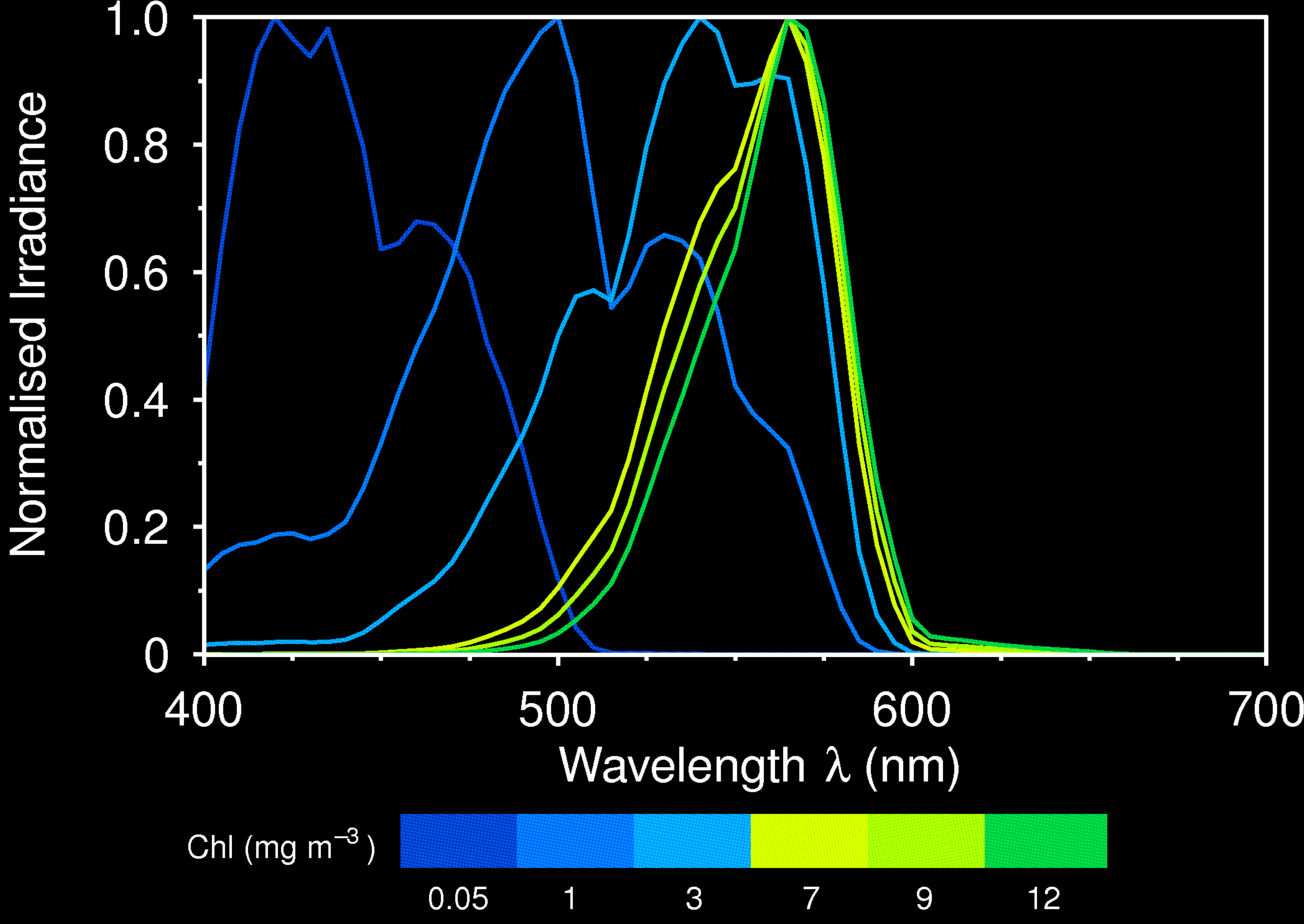
$$K = f\,(a, b_{b,}\, \mu_d)$$

where K is the diffuse attenuation coefficient for downwelling light.

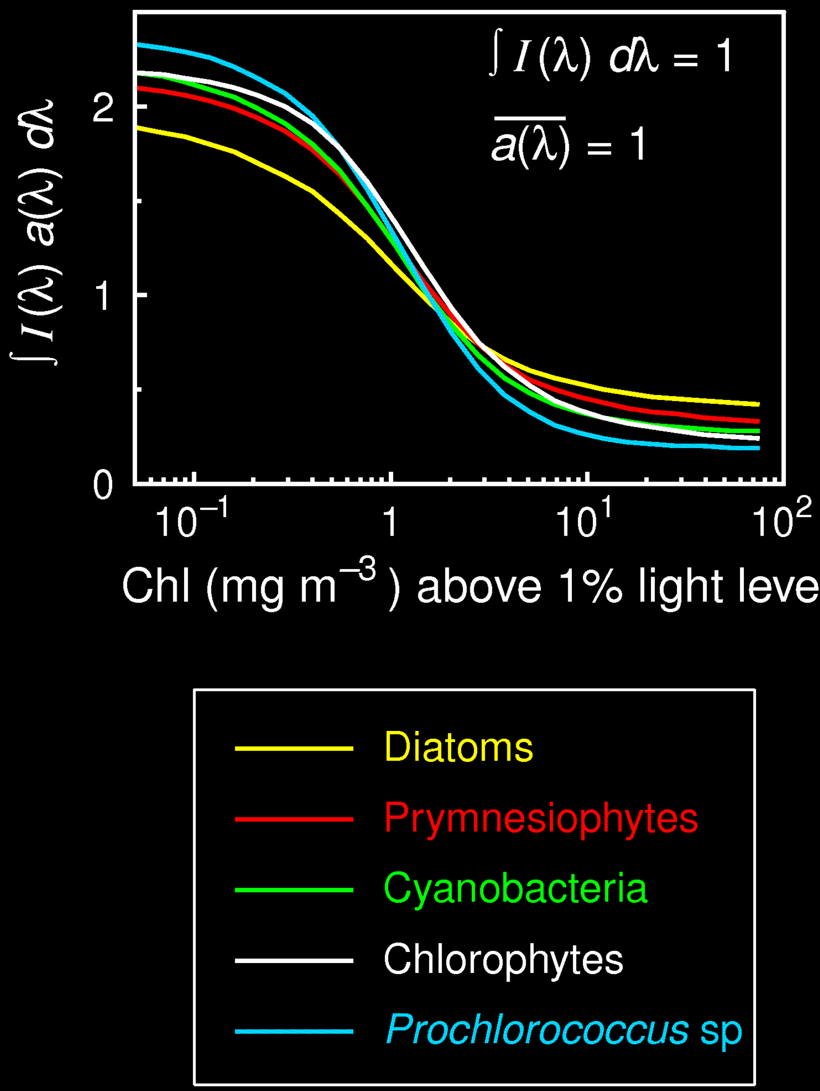
Both absorption and back-scattering can be expressed as sum of contributions from individual constituents.

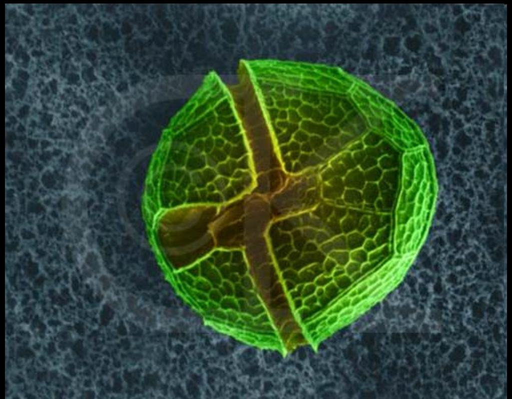
Both absorption and back-scattering vary spectrally in a characteristic manner.

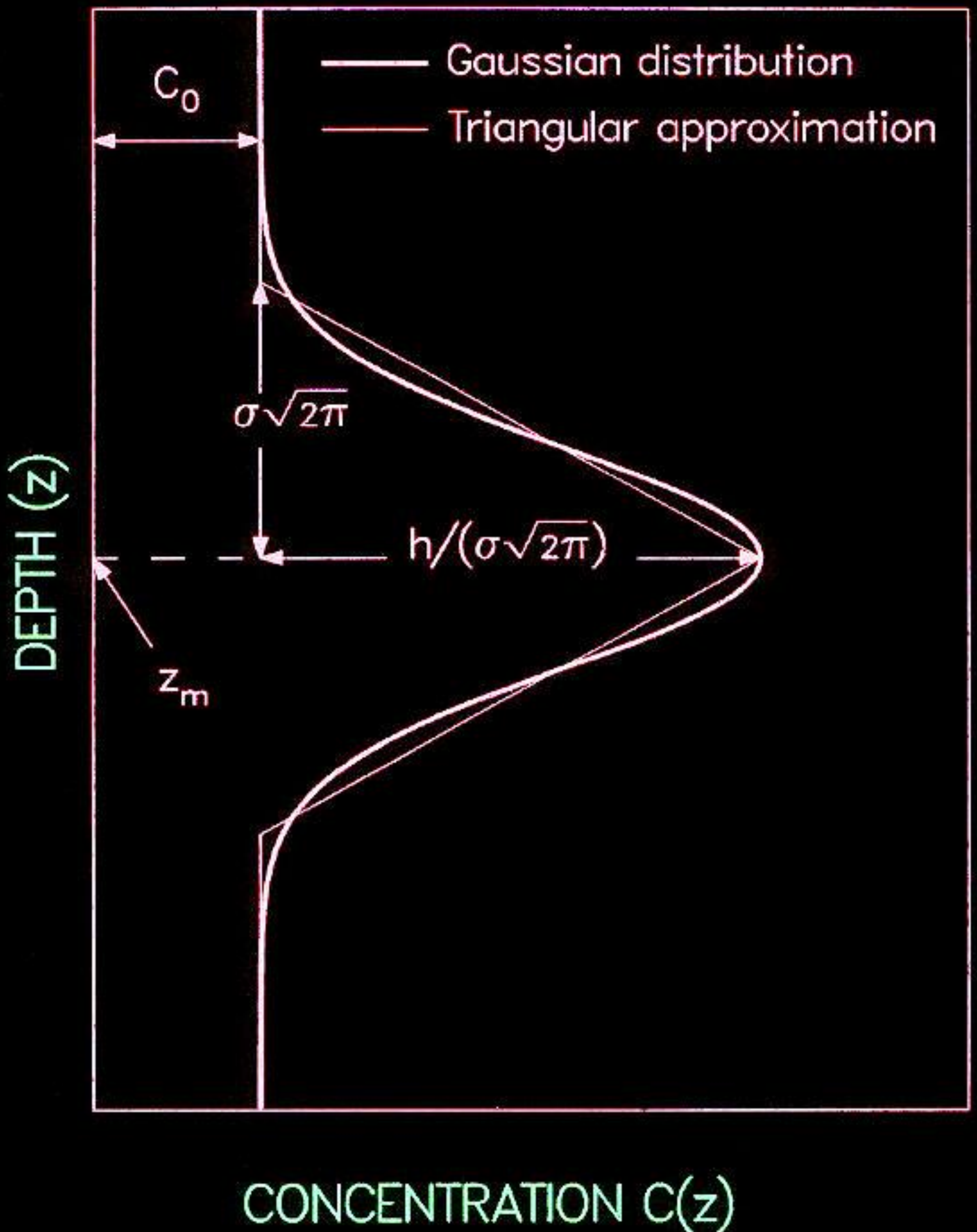
Spectral Quality of Irradiance at 1% Light Level



Light Absorbed by Phytoplankton at 1% Light Level



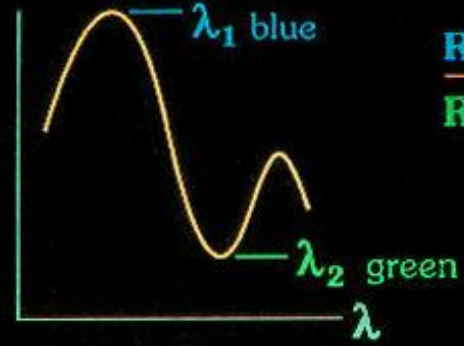




Vertical Structure in Chlorophyll Concentration

It is also necessary to account for the vertical structure in chlorophyll concentration.

The simplest representation of chlorophyll peaks (for application in primary production studies) is as a Gaussian peak superimposed on a constant background.



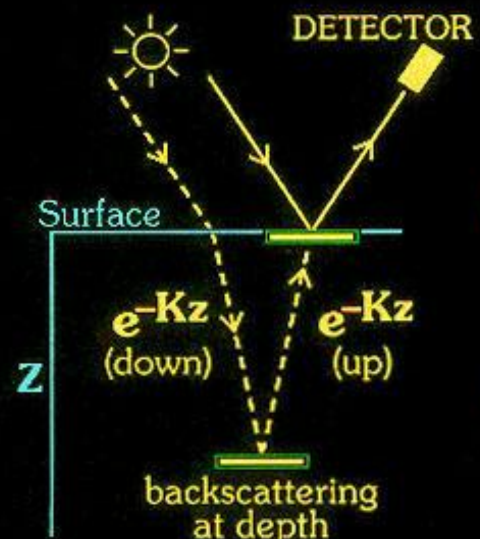
ABSORPTION SPECTRUM FOR PHYTOPLANKTON

$$\frac{R(\lambda_1)}{R(\lambda_2)} = f\,(\text{chlorophyll})$$

REMOTE SENSING ALGORITHM

WEIGHTING FUNCTION

$$f(z) = e^{-2\int_0^z K(z')\,dz'}$$

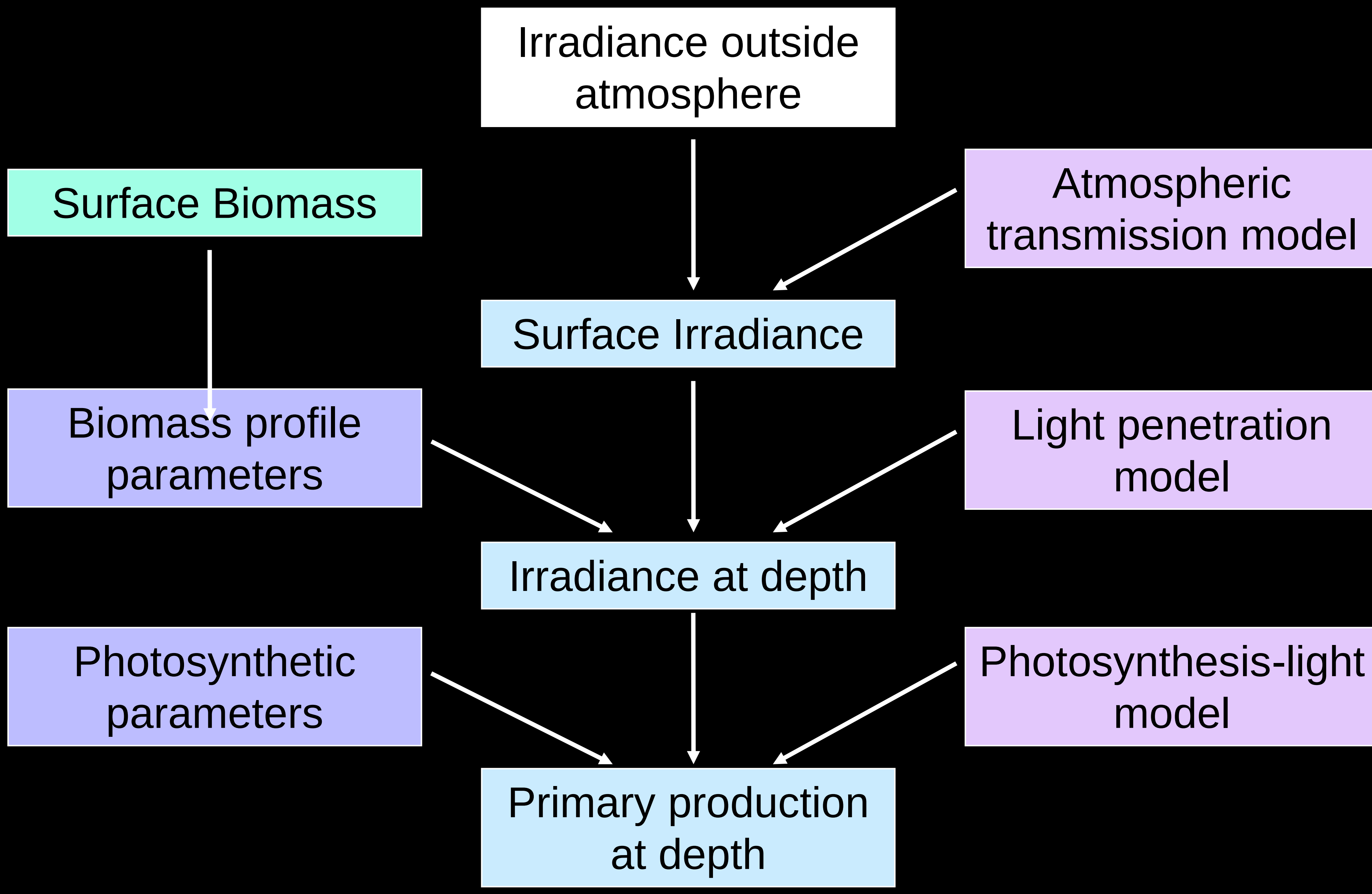


EFFECTIVE BIOMASS CONCENTRATION

$$B(s) = \frac{\int_0^{1/K} B(z)\,f(z)\,dz}{\int_0^{1/K} f(z)\,dz}$$

Effective biomass ("satellite chlorophyll") is a weighted function of actual biomass.

Computation of primary production



Sathyendranath and Platt (1989)

Goal: To estimate the daily primary production of the ocean water column

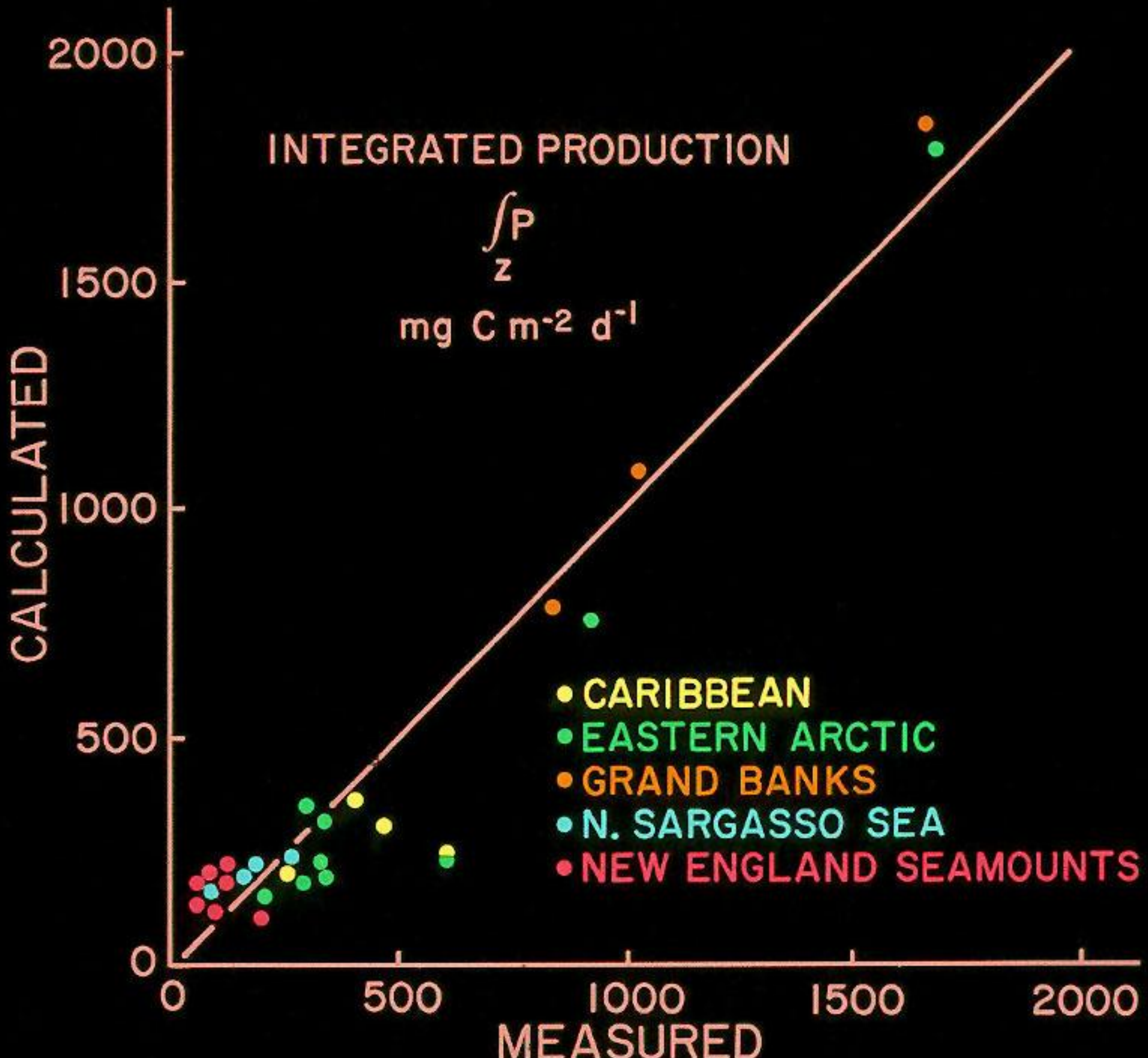
$$P = P(I)$$

$$I = I(z) = I_0 e^{-Kz}$$

$$I_0 = I_0(t)$$

$$P\left(I(z,t)\right)$$

$$P_{Z,T} = \int_0^D \int_0^\infty P(z,t)\, dz\, dt$$


INTEGRATED PRODUCTION
$\int_z P$
mg C m^{-2} d^{-1}
CALCULATED
MEASURED
2000
1500
1000
500
0
0
500
1000
1500
2000
CARIBBEAN
EASTERN ARCTIC
GRAND BANKS
N. SARGASSO SEA
NEW ENGLAND SEAMOUNTS

Basic Methodology for Computation of Primary Production

1. Compute light just below the sea surface
2. Estimate biomass at the surface
3. Define the biomass profile
4. Estimate parameters of the photosynthesis-light model
5. Compute parameters of light transmission underwater
6. Compute water-column primary production

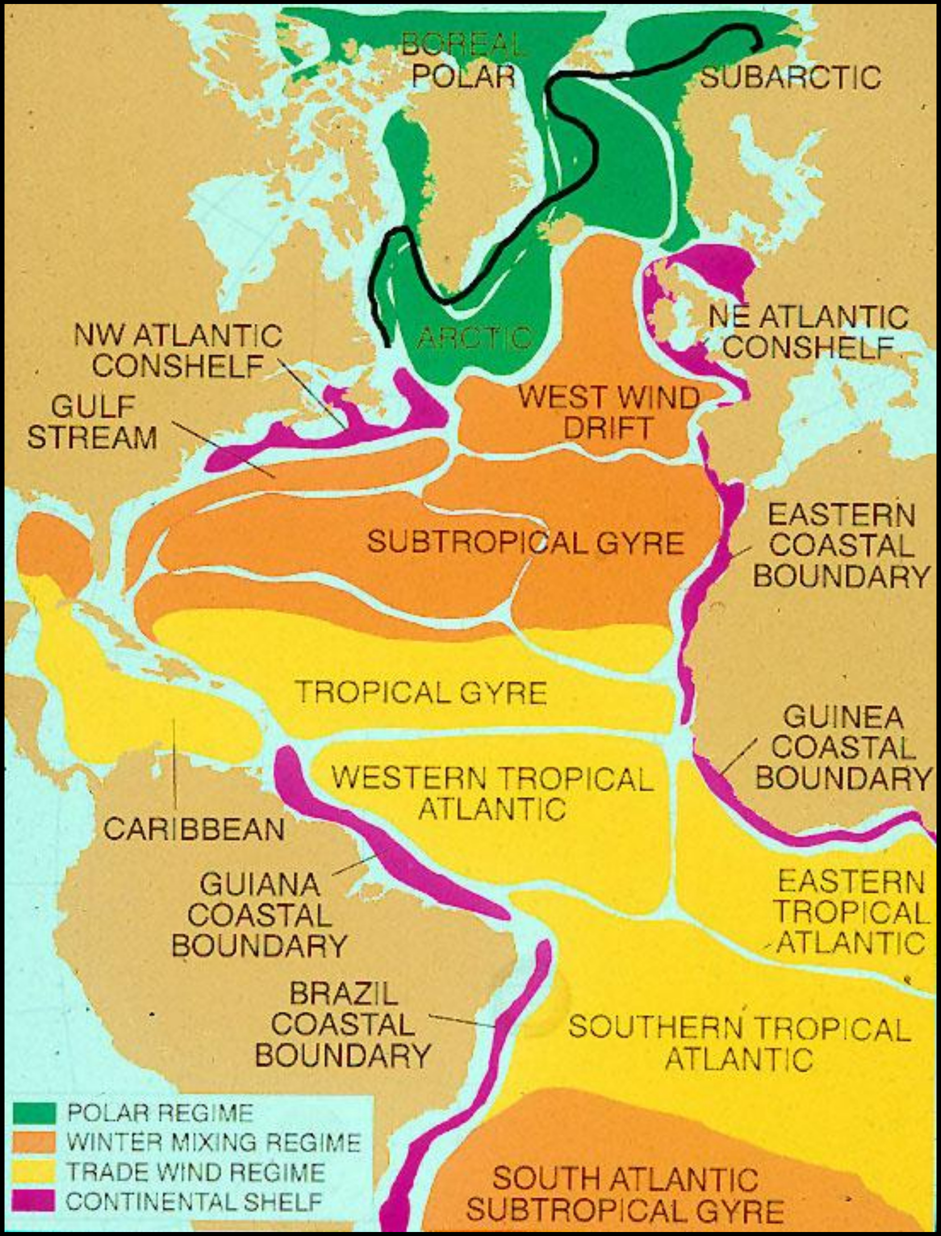
Primary Production at Regional Scale

Computation of primary production at regional scale has two components:

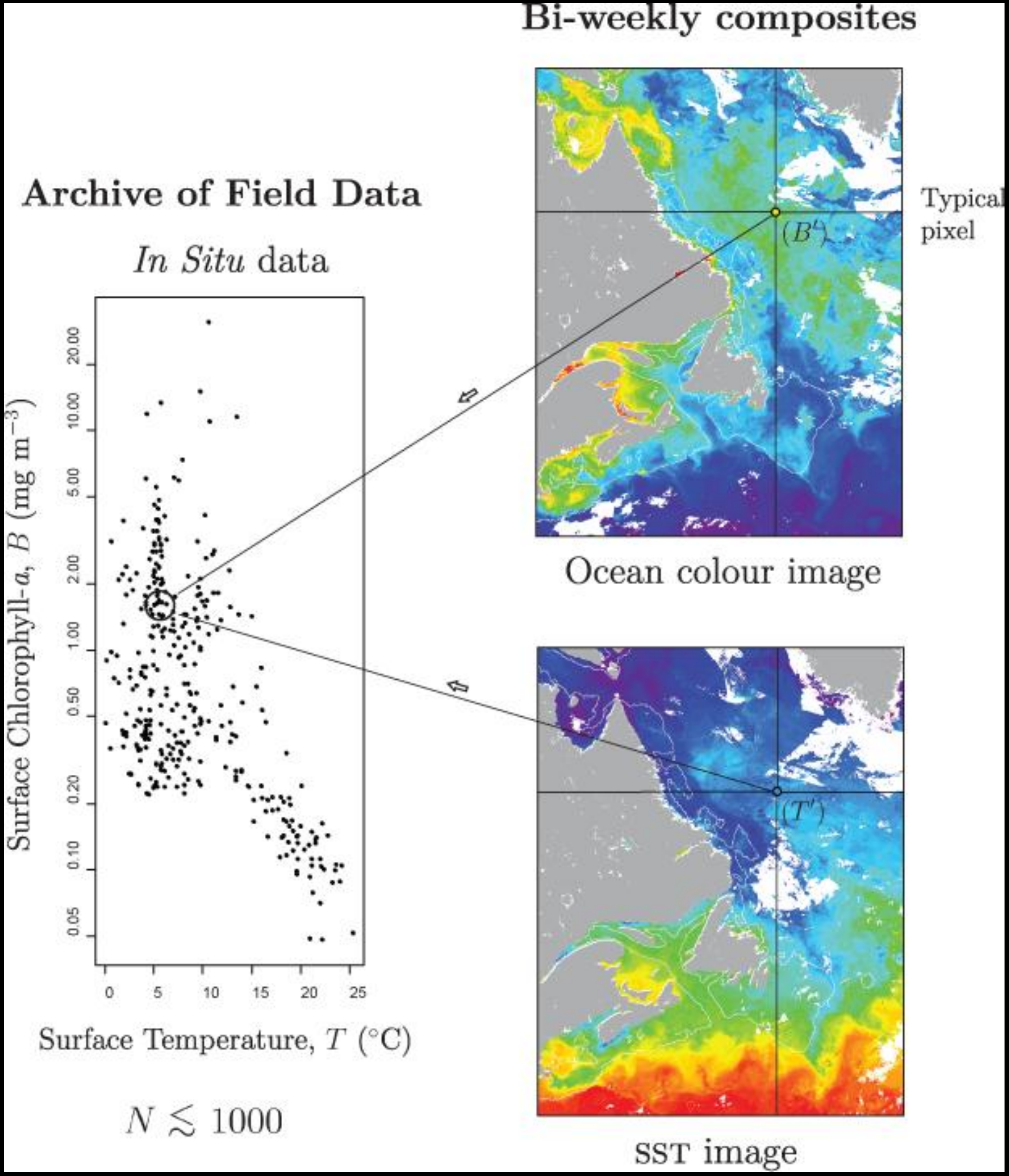
1. Construct local algorithm, assuming all necessary information will be available.

2. Establish protocol for extrapolation of local algorithm to larger scale.

Ecological Provinces of the Ocean according to Longhurst



Assignment of Parameters for Computation of Primary Production



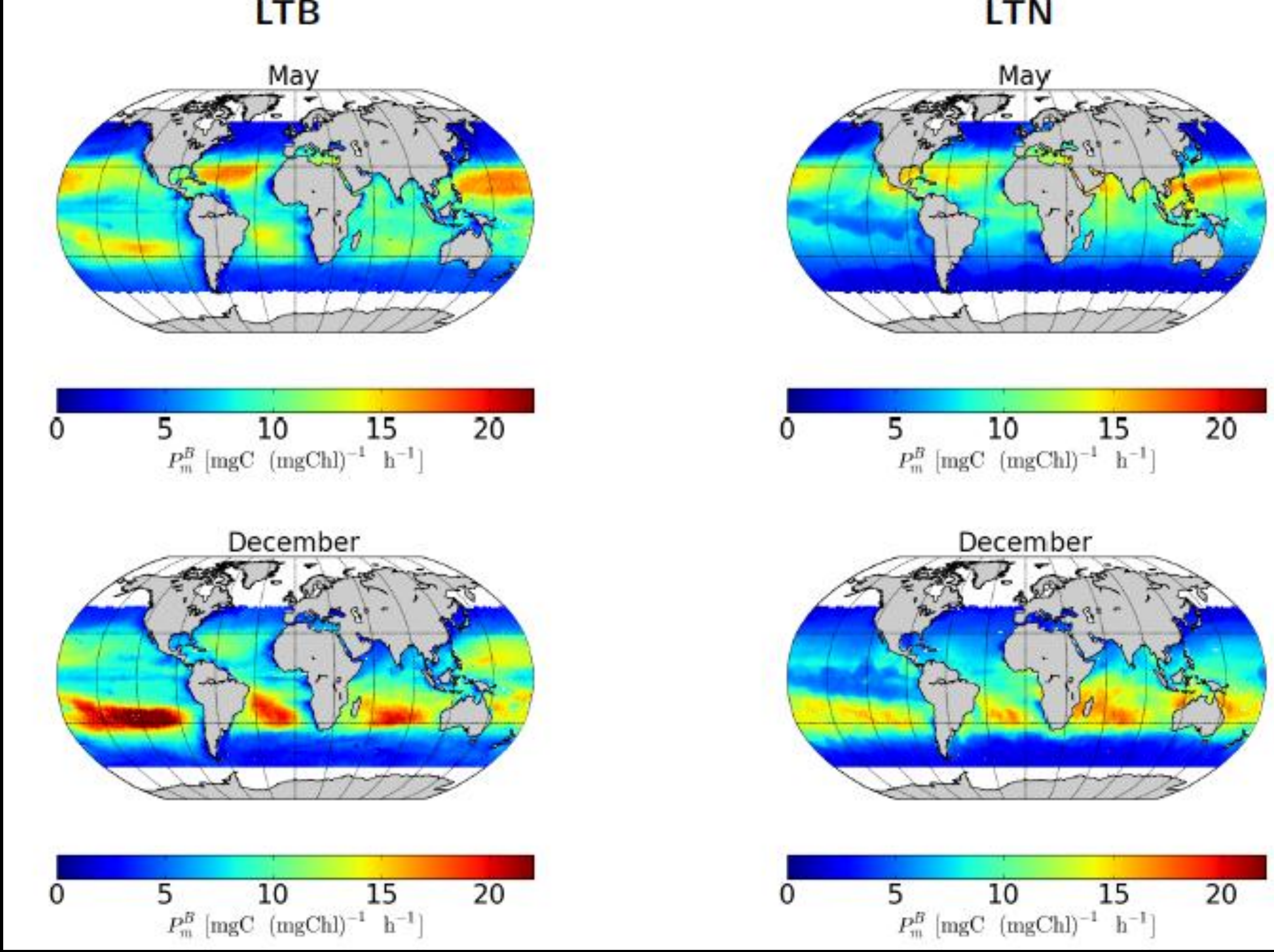
The model is robust, but needs a protocol for assignment of parameters relating to

(1) photosynthetic response; and

(2) vertical structure.

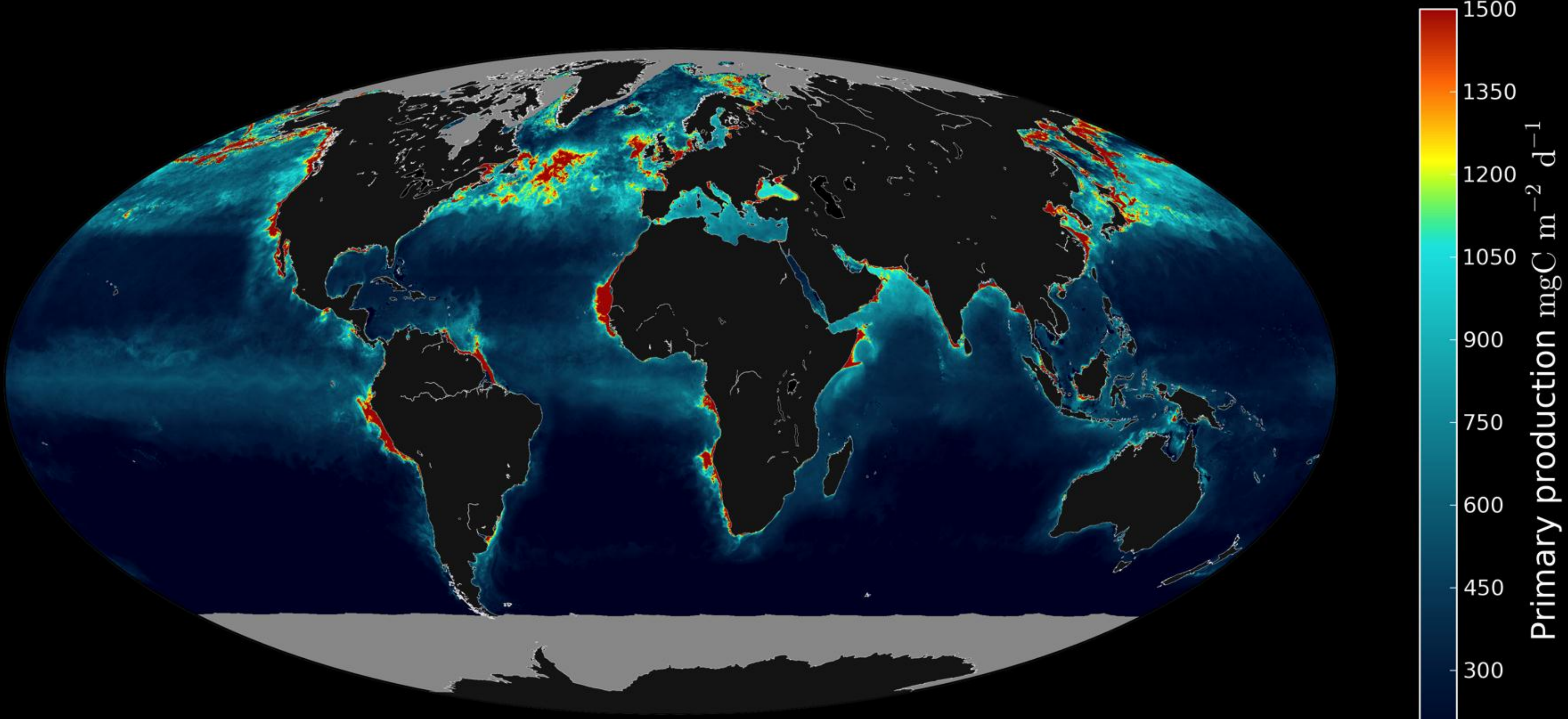
The protocol uses remotely-sensed data as input

Platt *et al.* (2008)



Saux-Picart et al. 2013, RSE

Computed Global Primary Production



May 2004, using OC-CCI data

Utility of Remote Sensing
For Estimation of Oceanic Primary Production

Primary production P can be written as the product of production per unit chlorophyll concentration P^B and the chlorophyll concentration B.

$$P = P^B \times B$$

- Effect of environmental conditions (light, temperature, nutrients …) on primary production is contained explicitly (light) or implicitly (through model parameters) in the chlorophyll-normalised term.

- Chlorophyll concentration has a dynamic range of more then four decades.

- Remote sensing method is an extrapolation tool, which:
  - Uses all available ship data to define model parameters
  - Uses the satellite data to input the state variable (chlorophyll) and the forcing field (light)
  - Sees the ship and satellite as complementary tools
  - It is the method of choice

Measurement of Instantaneous Rates

Dimensions

The dimensions of a rate quantity include time in the denominator

Applicability

The intrinsic time scale for the method, or the time scale on which the results can be expected to apply, is related to the duration of measurement

METHODS FOR MEASURING PRIMARY PRODUCTION

Method	Nominal component of production	Nominal time-scale
In vitro		
^{14}C assimilation	P_T ($\equiv P_n$)	Hours to 1 d
O_2 evolution	P_T	Hours to 1 d
$^{15}NO_3$ assimilation	P_{new}	Hours to 1 d
$^{15}NH_4$ assimilation	P_r	Hours to 1 d
$^{18}O_2$ evolution	P_{new} ($\equiv P_c$)	Hours to 1 d
Bulk property		
NO_3 flux to photic zone	P_{new}	Hours to days
O_2 utilization rate OUR below photic zone	P_{new}	Seasonal to annual
Net O_2 accumulation in photic zone	P_{new}	Seasonal to annual
$^{238}U/^{234}Th$	P_{new}	1d to 300d
$^{3}H/^{3}He$	P_{new}	Seasonal and longer
Optical		
Double-flash fluorescence	P_T	$< 1s$
Passive fluorescence	P_T	$< 1s$
Remote Sensing	P_T, P_{new}	Days to annual
Upper and lower limits		
Sedimentation rate below photic zone	P_{new} ($\equiv P_c$): (lower limit)	Days to months
Optimal conversion of photons absorbed	P_T (upper limit)	Any
Depletion of winter accumulation of NO_3	P_{new} (lower limit)	Seasonal

Problems with Validation

1. No independent method available for comparison. Remote-sensing approach uses all available data, from ship as well as from satellite.

2. Comparison with bulk-property, or indirect, methods compromised by incompatibility of time scales. Further, bulk-property methods and in vitro incubation methods (used to derive photosynthesis parameters) address different components of primary production.

3. Validation by prediction of biomass at some future time requires information on loss terms and on flow field: these are usually unavailable.

ERRORS IN COMPUTATION OF PRIMARY PRODUCTION

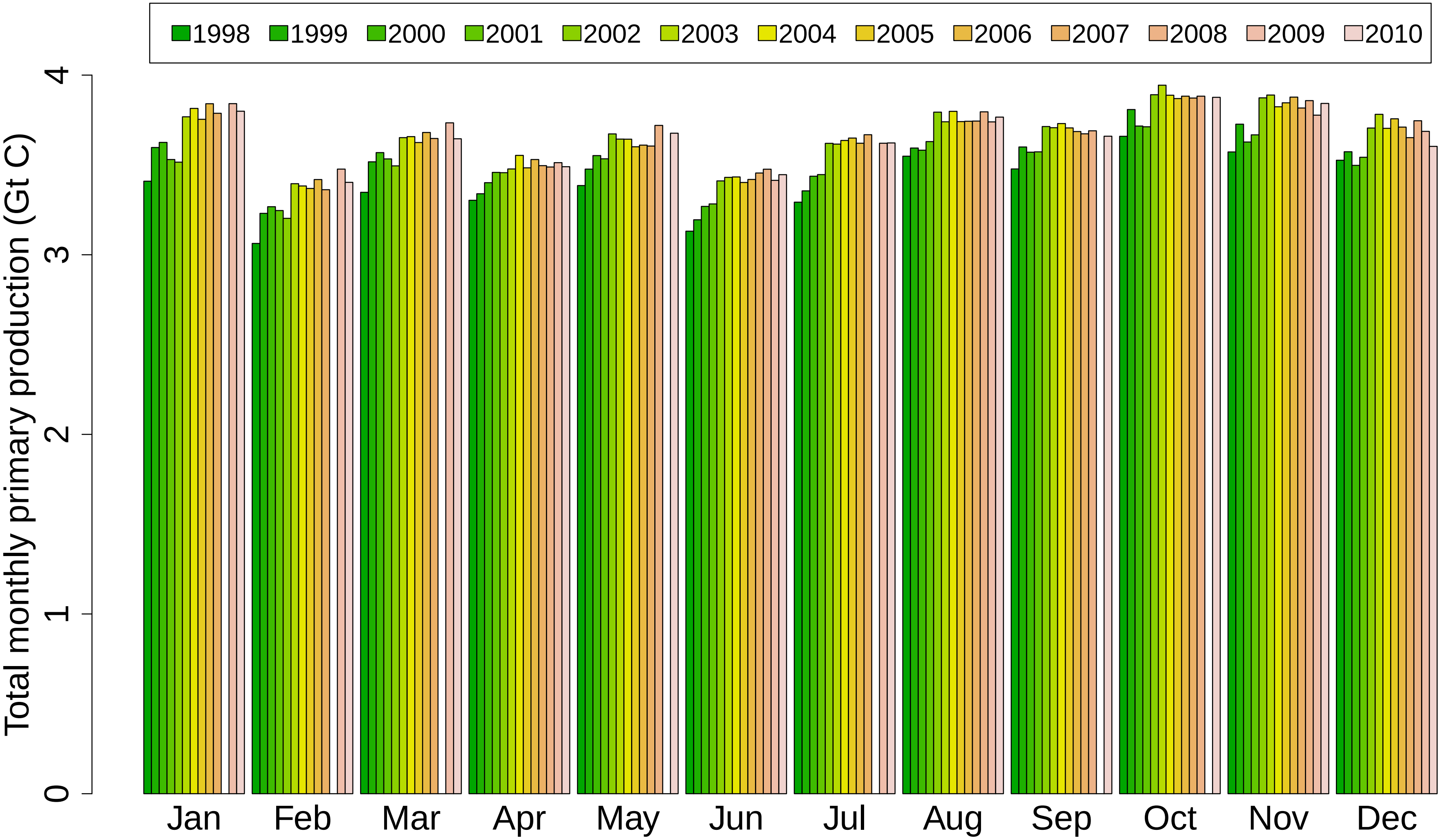
Examine precision of each element of the calculation separately:

1. Surface irradiance $\sim 10\%$
2. Satellite-derived biomass $\sim 35\%$
3. Photosynthesis parameters
   a. Measurement error $\sim 5\%$ for P_m^B and $\sim 20\%$ for α^B
   b. Error arising from aggregation within domains $\sim 7\%$
4. Vertical profile shape $\leq 10\%$ at the basin scale

The local algorithm for the vertically-uniform, nonspectral model has an estimated precision of $\sim 42\%$ (compounding of errors 1, 2, and 3a).

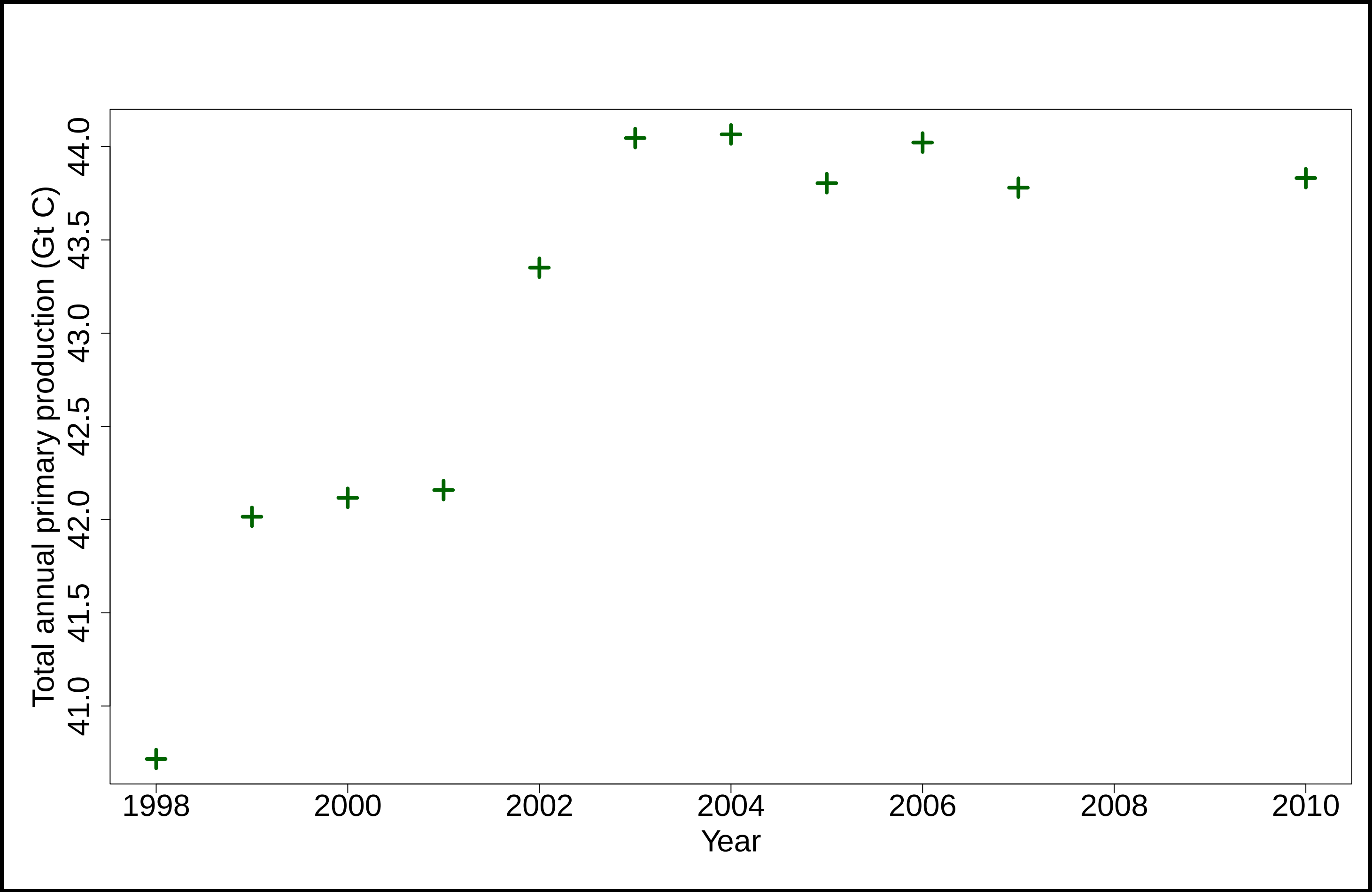
Combining with the aggregation error (3b) gives a best-case estimate of $\sim 50\%$ for the precision of a primary-production estimate in a spatially-extrapolated calculation.

Monthly time Series of Primary production



(using OC-CCI chlorophyll data and NASA data on surface light)

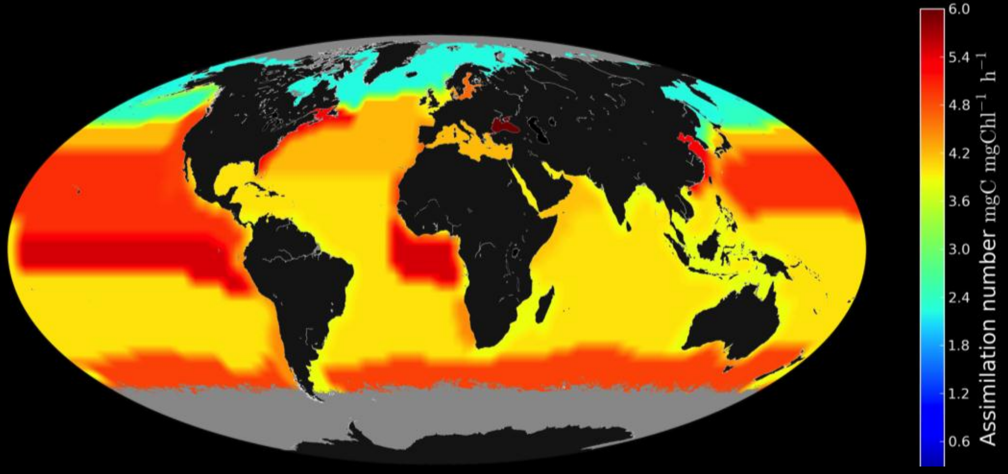
Time Series of Annual Primary Production



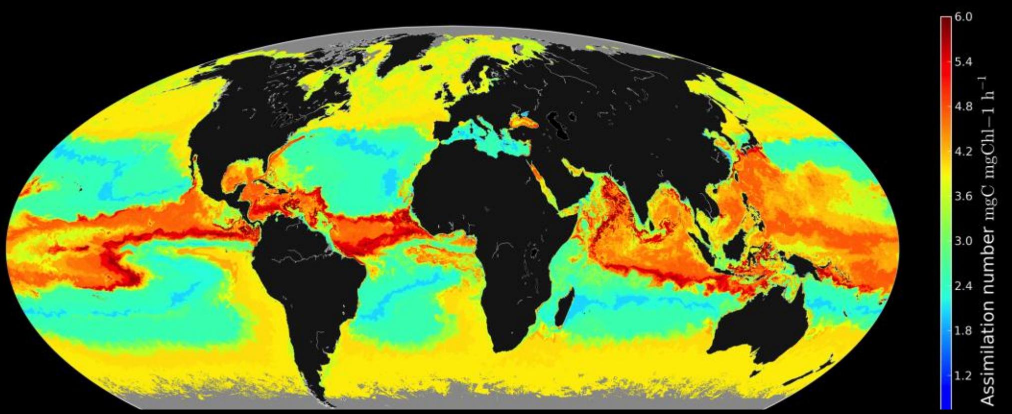
- Do we have “representational” error here when looking at “trends”? Satellite coverage improved in 2002.

- What about effect of inter-annual environmental variability on photosynthesis parameters? (Not accounted in this calculation)

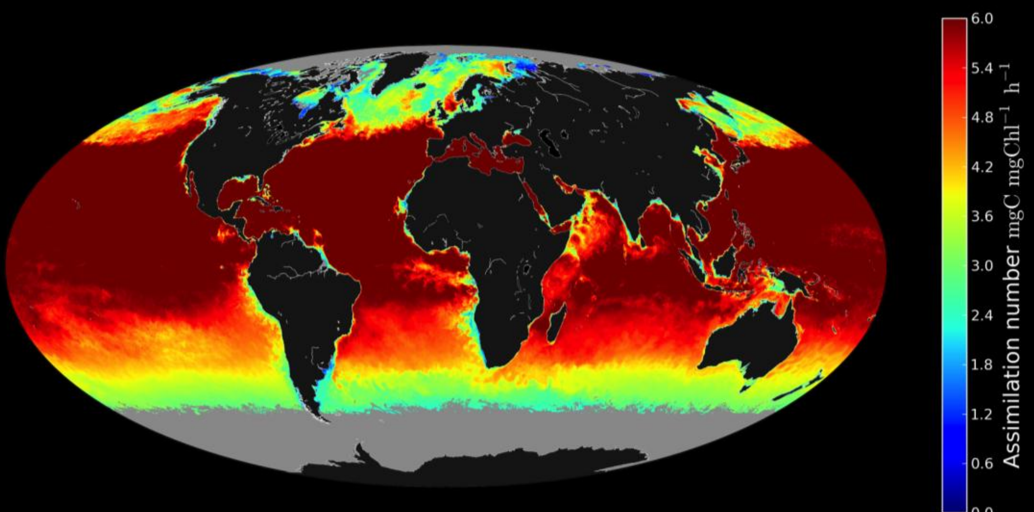
Three different methods for assigning Assimilation Number



Province-based (no interannual variation)



Nearest Neighbour Method (Platt et al. 2008) based on temperature and chlorophyll



Dynamic assignment based on chlorophyll, temperature and light (Saux-Picart et al. 2013)

This is a challenging area of research where progress has to be made

In Conclusion

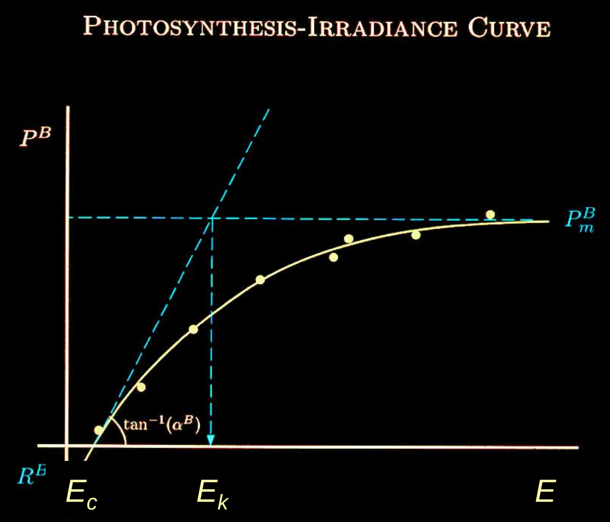
1. Remote sensing provides much of the information essential for computing primary production at large scales.

2. Potential exists for assigning parameters of the photosynthesis-irradiance curve using satellite data. This should be a priority for research.

3. Important to maintain a long time series of consistent ocean-colour data to study responses of marine primary production to climate variability and change.

Basic Set of Parameters Needed in Primary Production Models

- Initial slope of photosynthesis-irradiance curve
- Assimilation number of photosynthesis-irradiance curve
- Specific absorption coefficient of phytoplankton
- Carbon-to-chlorophyll ratio of phytoplankton



Of these, the carbon-to-chlorophyll ratio is the property we know the least about.

Carbon-to-chlorophyll ratio is invoked when fields of phytoplankton carbon computed in biogeochemical models are converted to fields of chlorophyll-a, for comparison with satellite data.

Sathyendranath *et al.* 2009