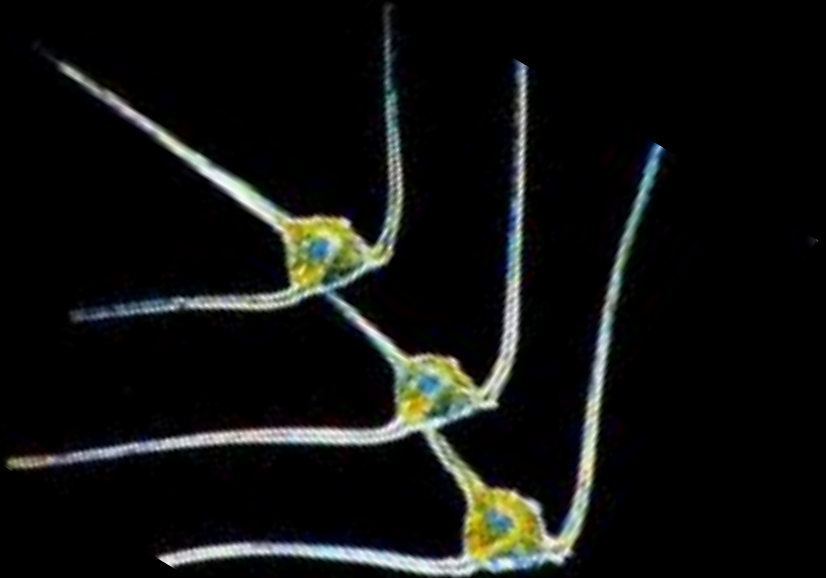
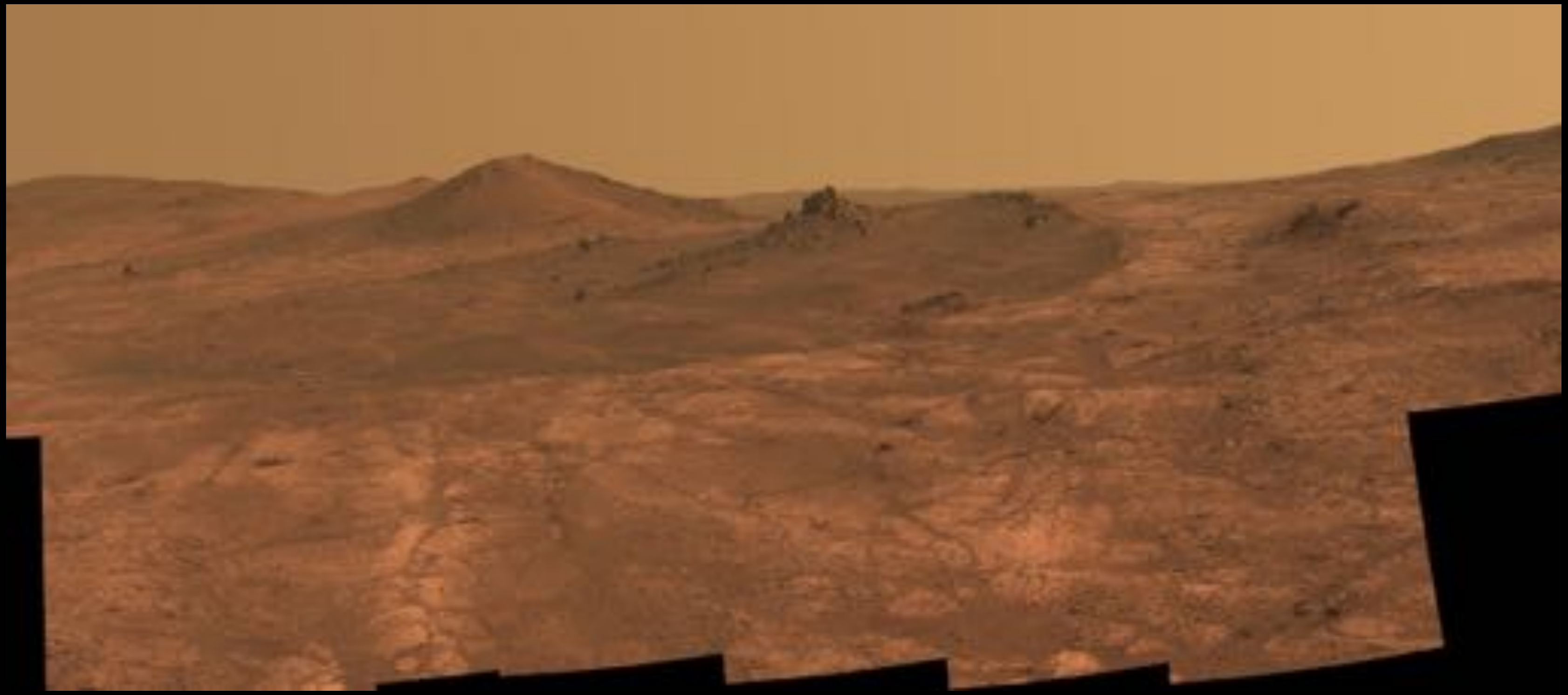
Marine

Primary Production



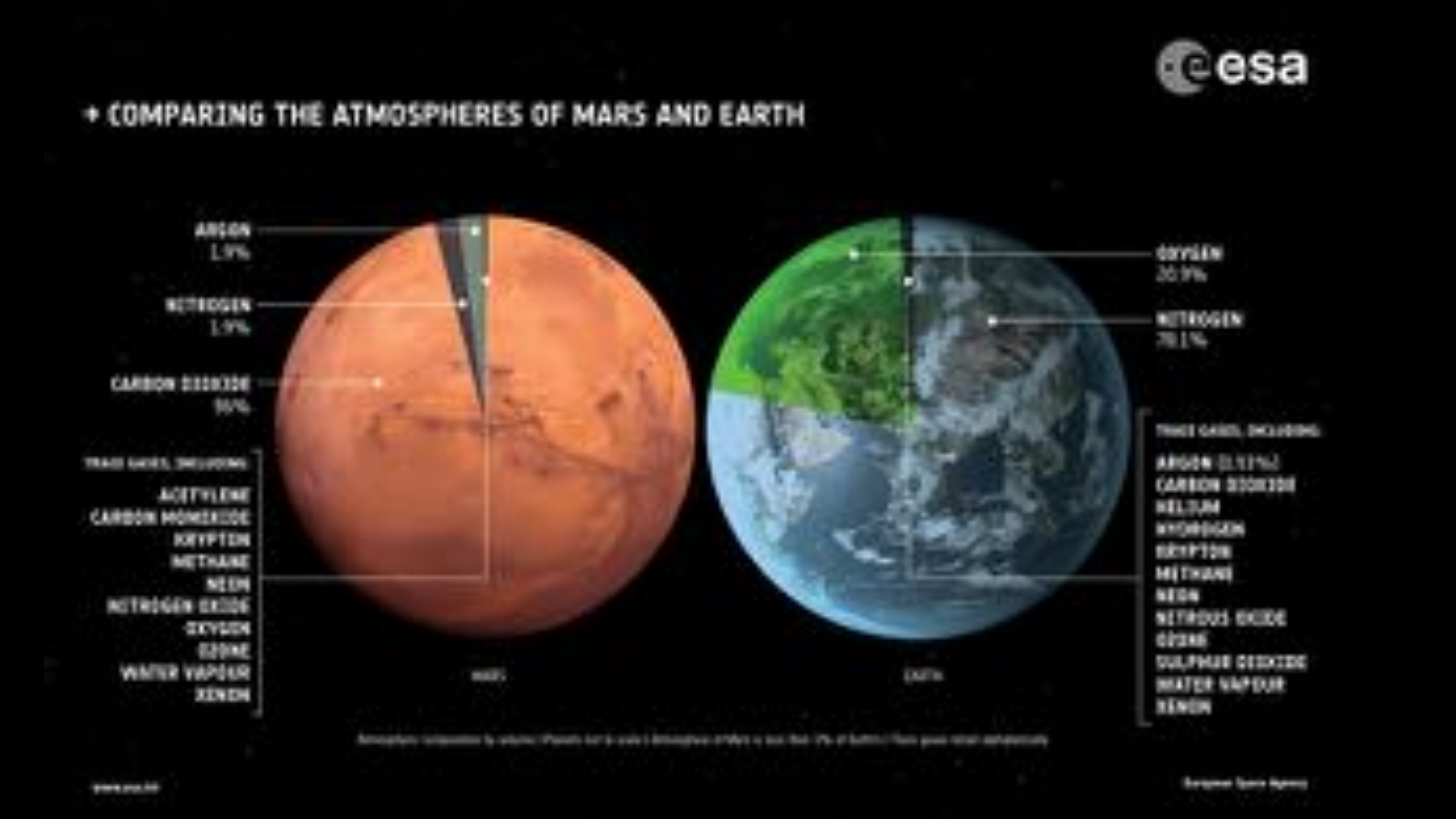


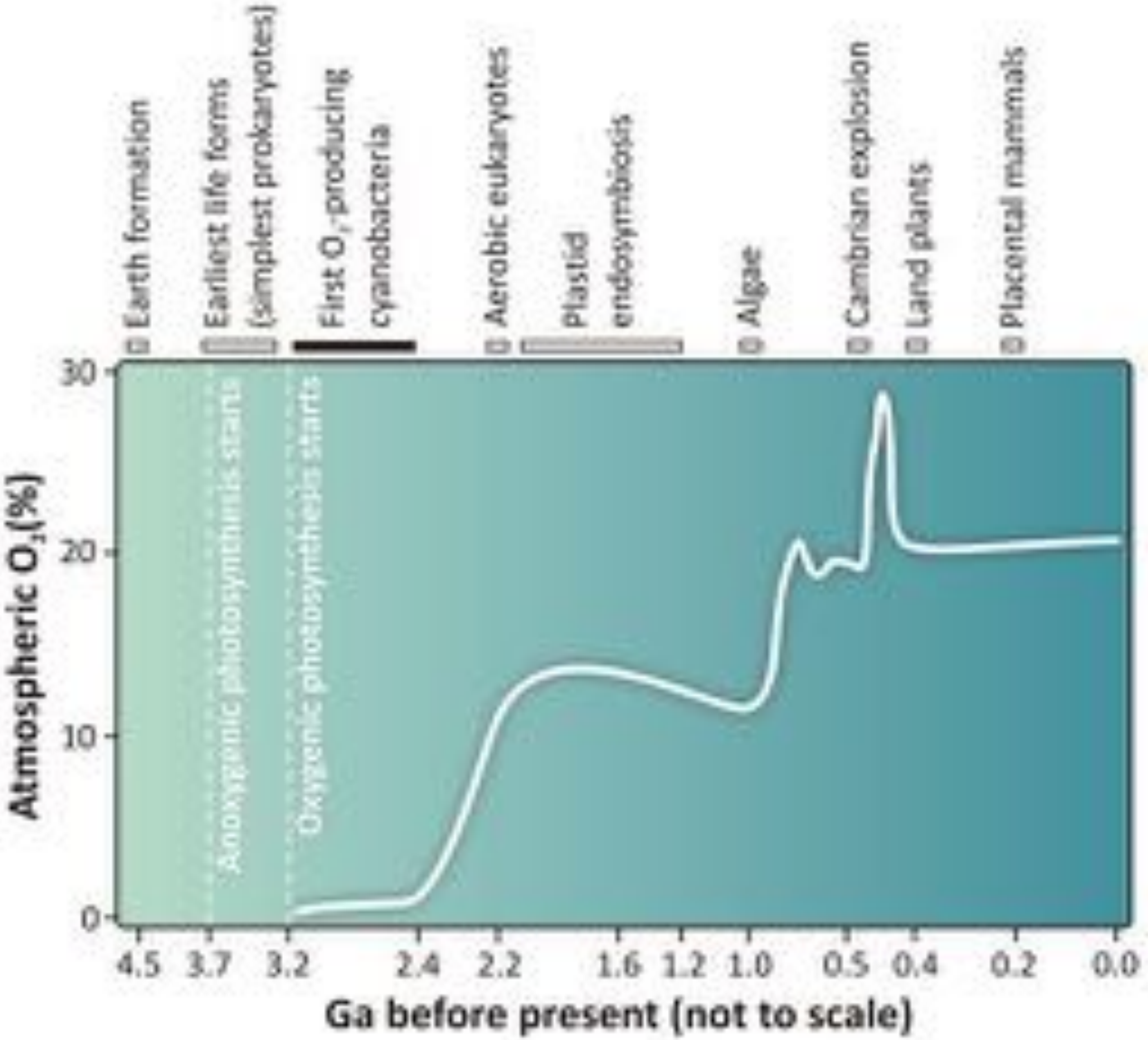
Mars: the red planet

Mars Exploration:
A motivation since the 1960s: Is there life on Mars?

James Lovelock:

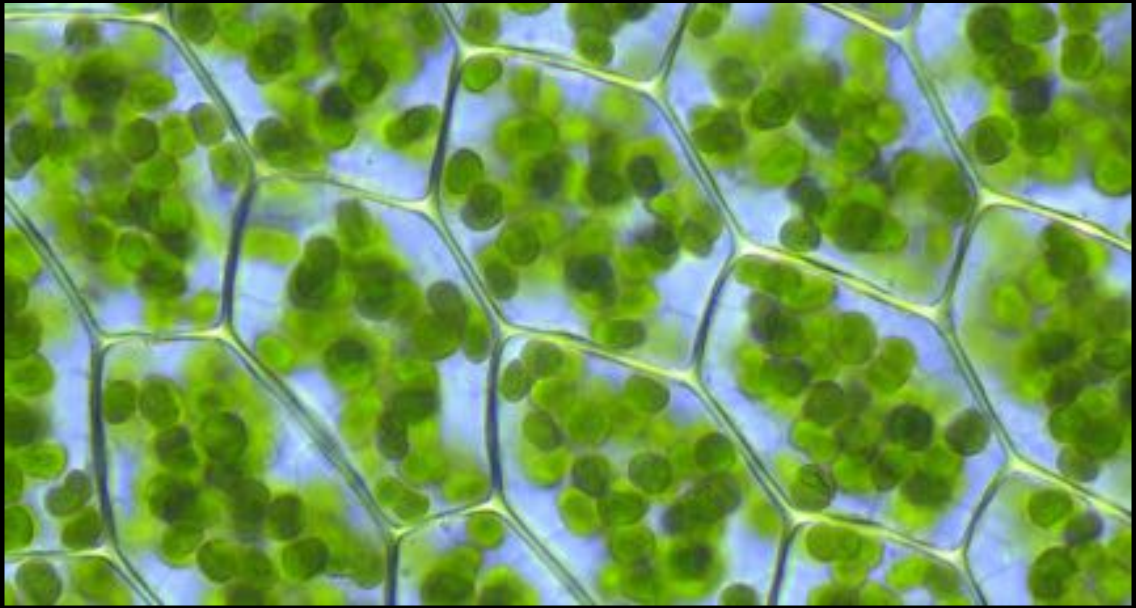
- Is the composition of the Mars atmosphere thermodynamic equilibrium?
- His 1965 paper on “A physical basis on life detection experiments” in *Nature*

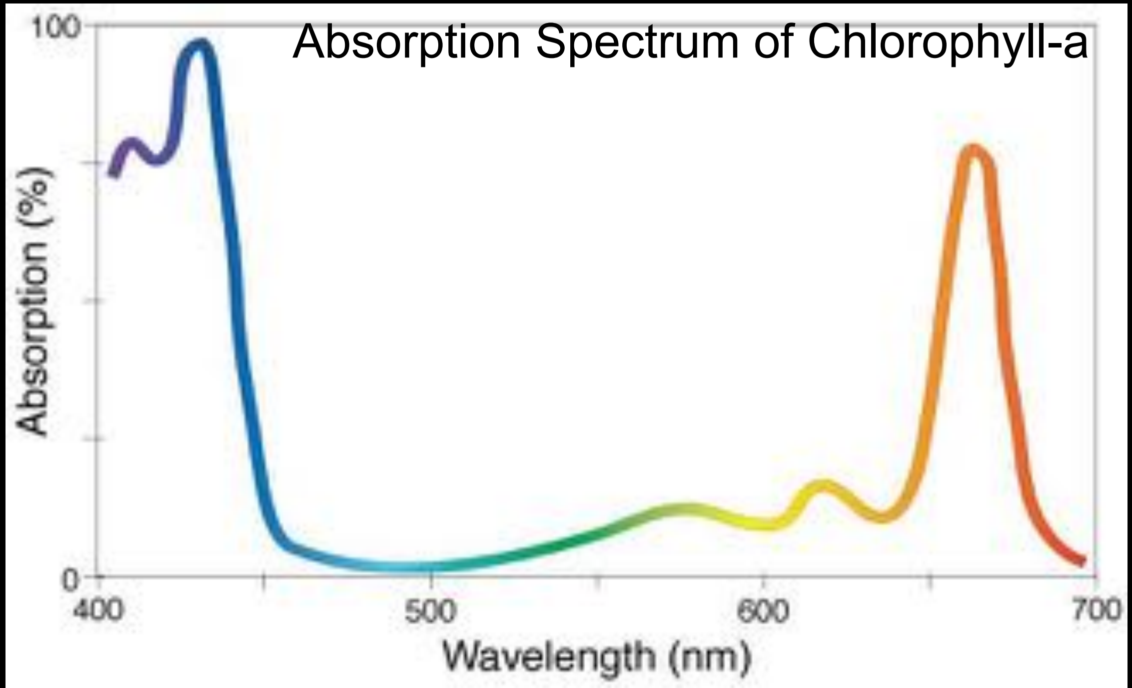

esa
COMPARING THE ATMOSPHERES OF MARS AND EARTH
ARGON
1.9%
NITROGEN
1.9%
CARBON DIOXIDE
96%
TRACE GASES, INCLUDING
ACETYLENE
CARBON MONOXIDE
KRYPTON
METHANE
NEON
NITROGEN OXIDE
OXYGEN
OZONE
WATER VAPOUR
XENON
MARS
EARTH
OXYGEN
20.9%
NITROGEN
78.1%
TRACE GASES, INCLUDING
ARGON
CARBON DIOXIDE
HELIUM
HYDROGEN
KRYPTON
METHANE
NEON
NITROUS OXIDE
OZONE
SULPHUR DIOXIDE
WATER VAPOUR
XENON



Earth formation
Earliest life forms (simplest prokaryotes)
First O2-producing cyanobacteria
Aerobic eukaryotes
Plastid endosymbiosis
Algae
Cambrian explosion
Land plants
Placental mammals
Anoxygenic photosynthesis starts
Oxygenic photosynthesis starts
Atmospheric O2 (%)
30
20
10
0
4.5
3.7
3.2
2.4
2.2
1.6
1.2
1.0
0.5
0.4
0.2
0.0
Ga before present (not to scale)

Chlorophyll: the Magic Molecule





The Photosynthesis Equation

Available Energy

↓

$H_2O + CO_2 +$ Absorbed Energy → $CH_2O + O_2 +$ Dissipated Energy

↑ Chl-a   ↓ Stored Energy

Our preoccupation is related to the ocean forests

Forests on Land

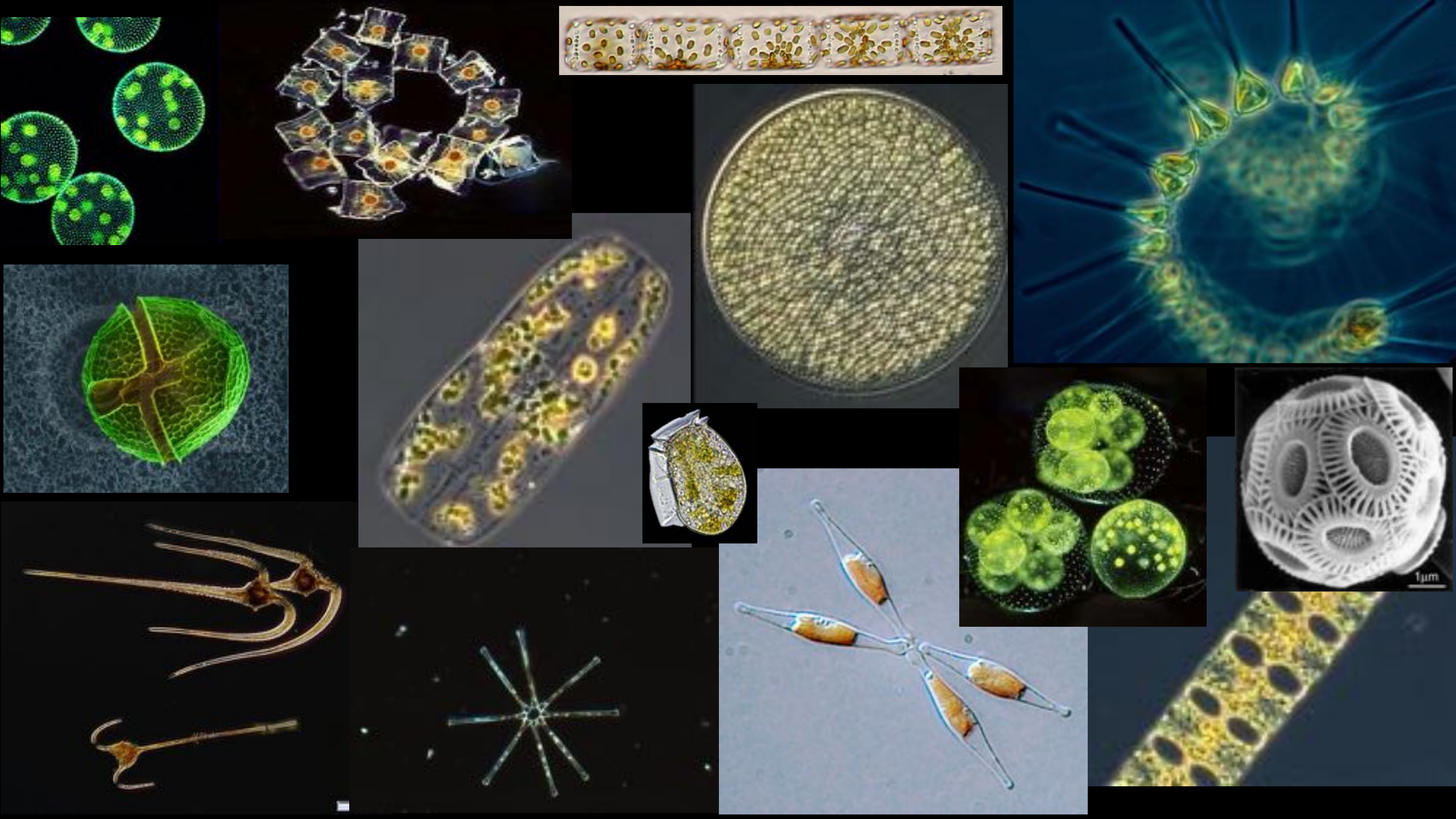
National Geographic

Coastal Forests

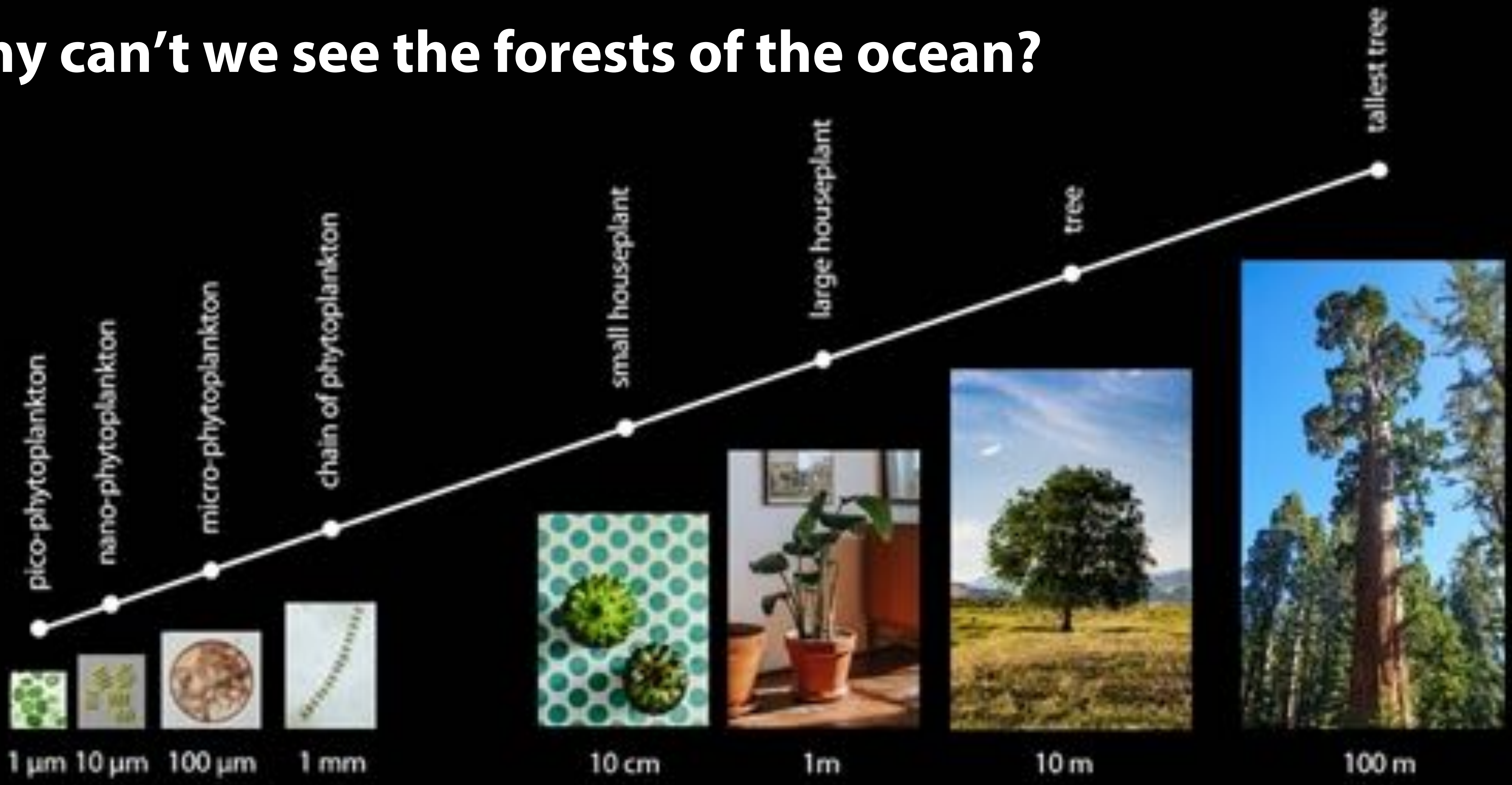
Wikipedia

Forests in Open Ocean?

Woods Hole Oceanographic Institute


1µm

Why can't we see the forests of the ocean?



The size of the smallest and largest phytoplankton cells compared to plants and trees on land.
The smallest phytoplankton cell is about one hundred million times smaller than the tallest tree.

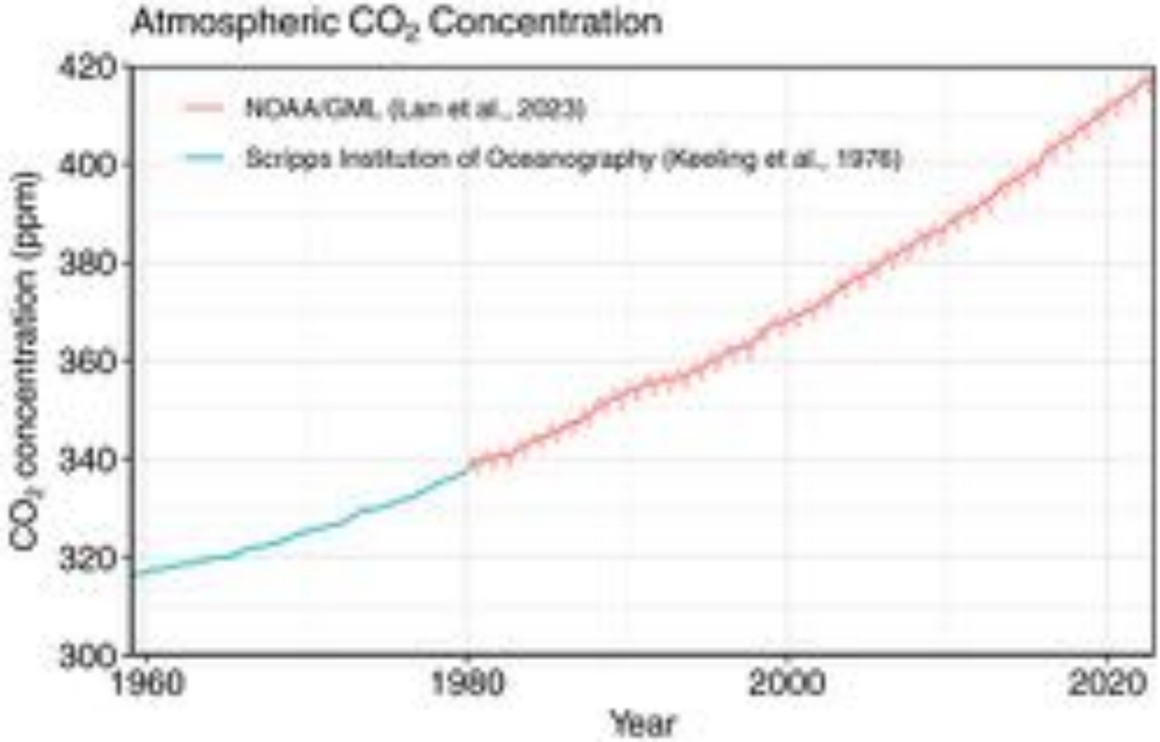
Gemma Kulk

The Big Picture

- Globally, some 50 Tg C fixed by marine phytoplankton per annum
- Approximately one third of this (~16 Tg C) exported from the surface layer by sinking and other processes

Biological Pump

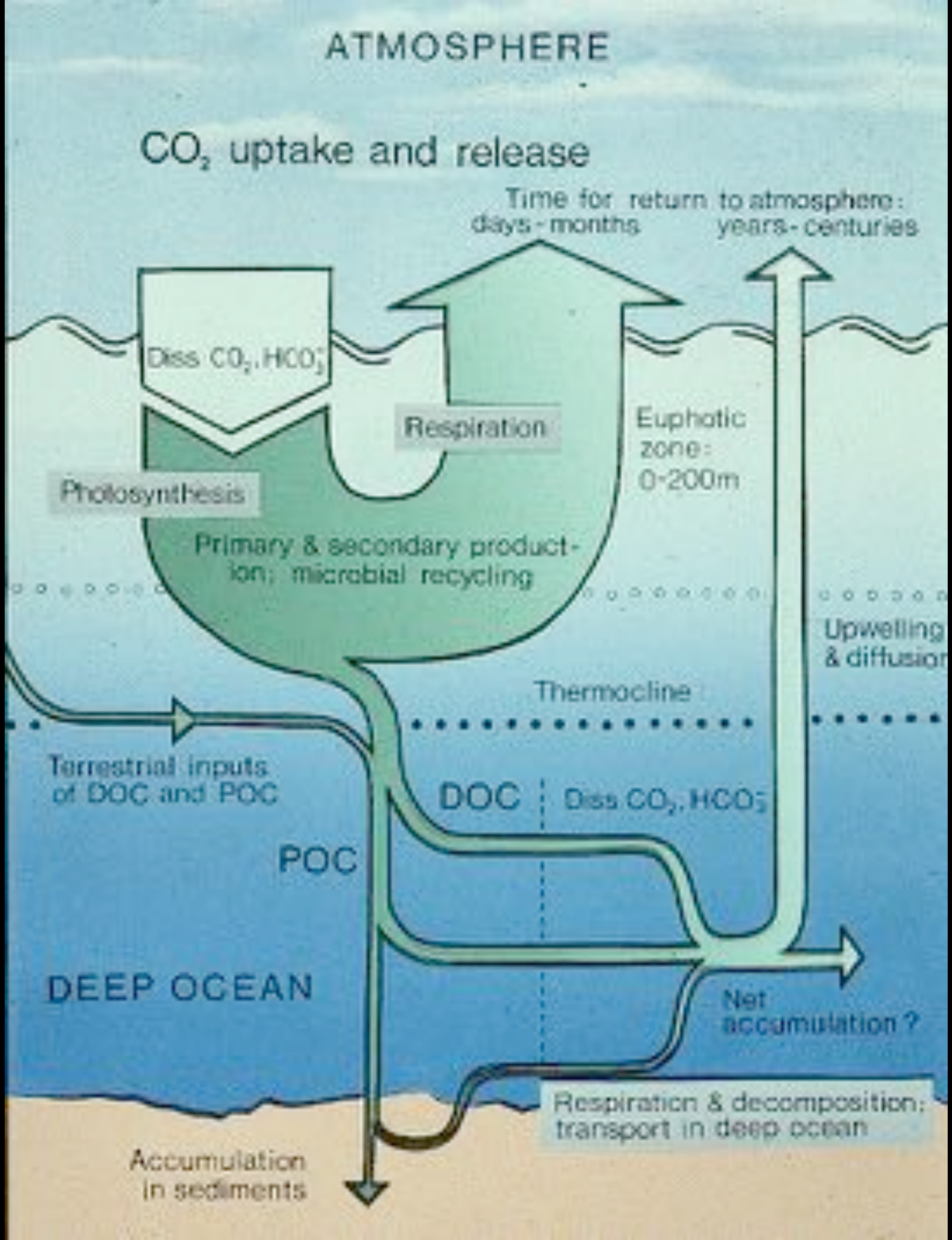
- Scale for comparison: fossil fuel emissions: 10 Tg C per annum



Fossil fuel emissions excluding cement carbonation

1960 = 2 GtC Yr^{-1}
2022 = 10 GtC Yr^{-1}

Friedlingstein et al. (2023)



JGOFS, Phil Williamson

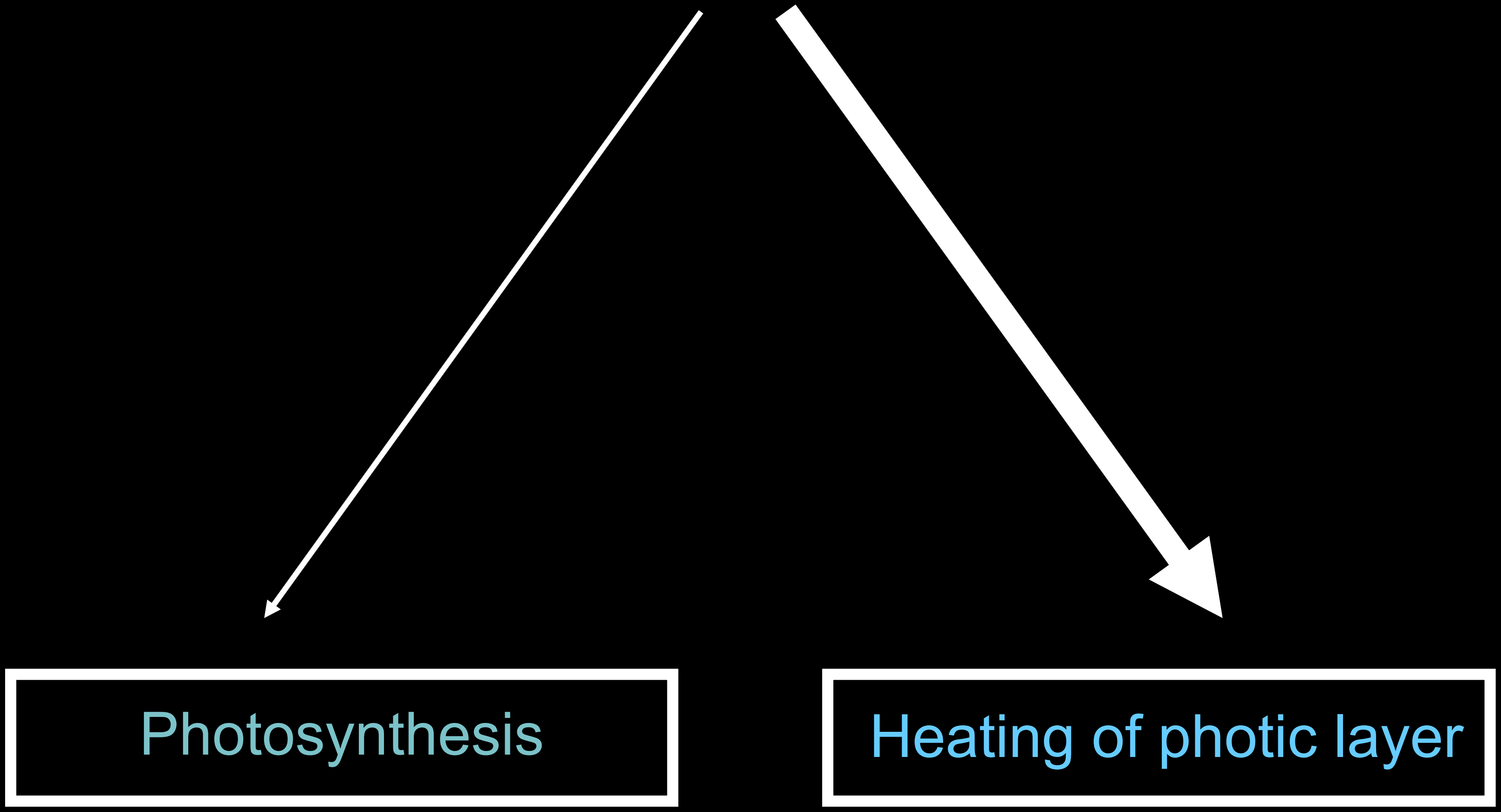
Ocean Ecosystem as Thermodynamic System

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.

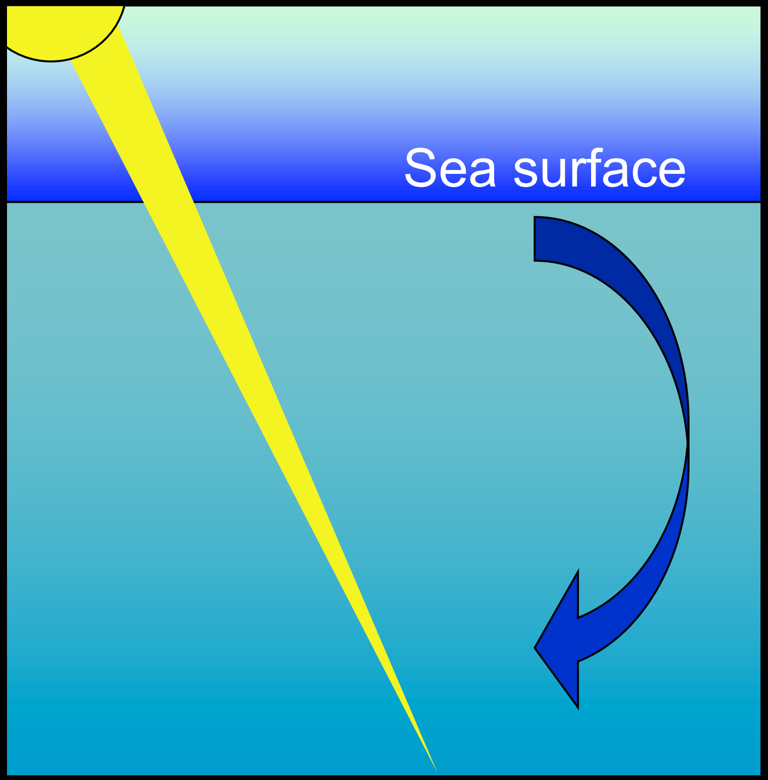
Emil Nolde

Dual Role for Light Absorbed by Phytoplankton



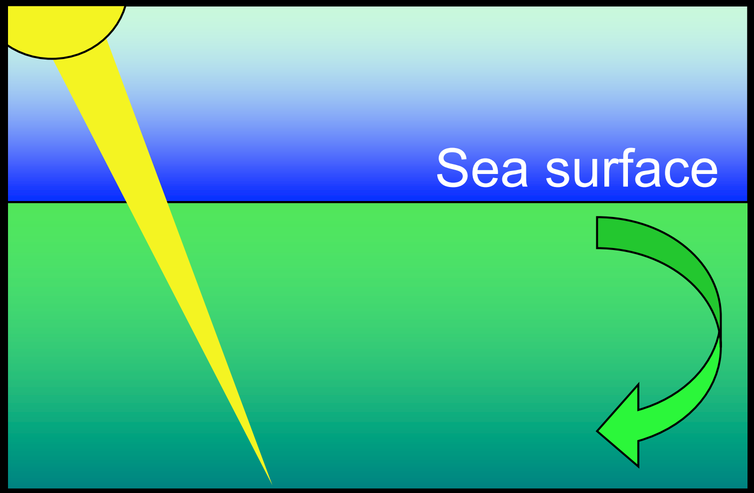
Diffuse attenuation coefficient *K* and mixed-layer depth

Low *K*

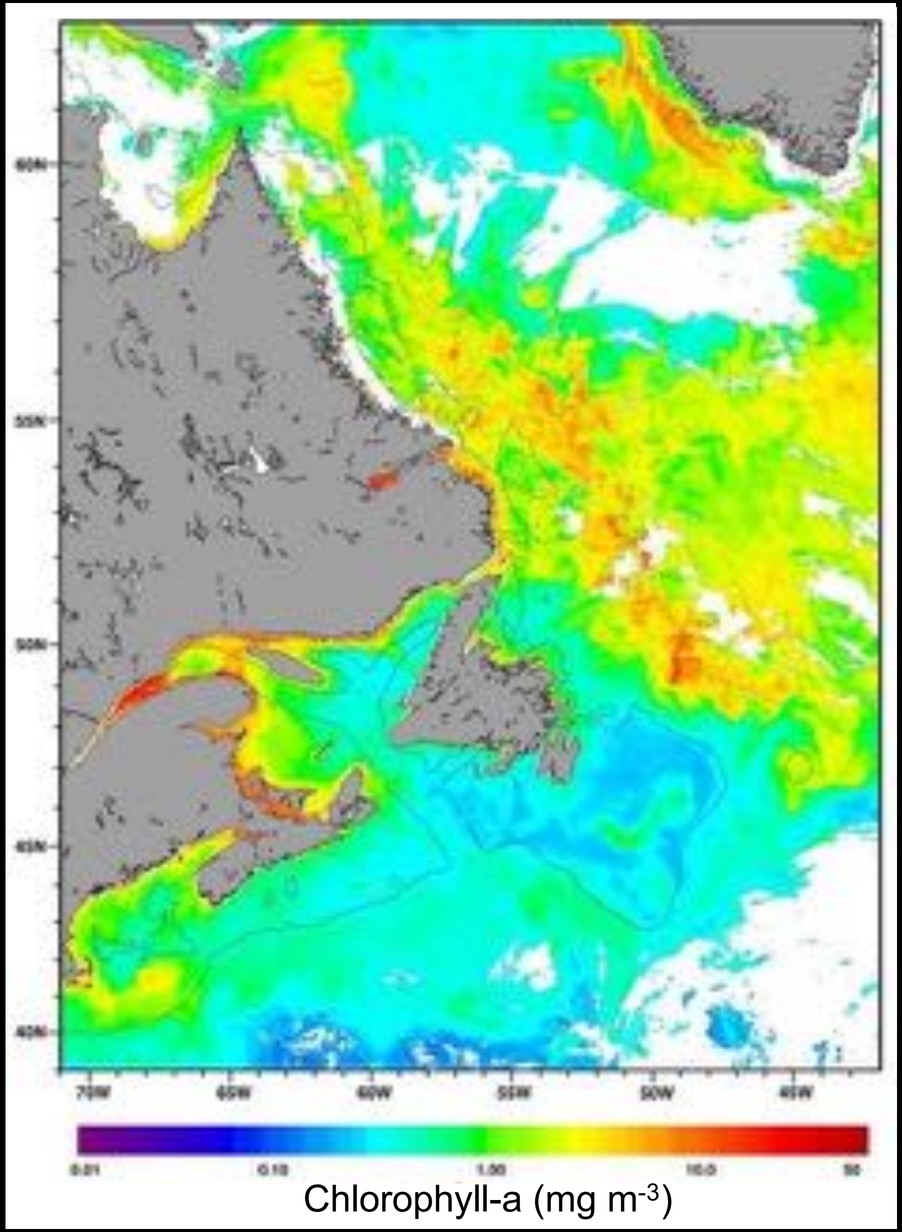


Deep photic layer
Favours deep mixed layer

High *K*



Shallow photic layer
Favours shallow mixed layer



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.

Measurement of Concentration

Dimensions

It has dimensions of mass per unit volume.

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.

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.

The Photosynthesis Equation

Available Energy

↓

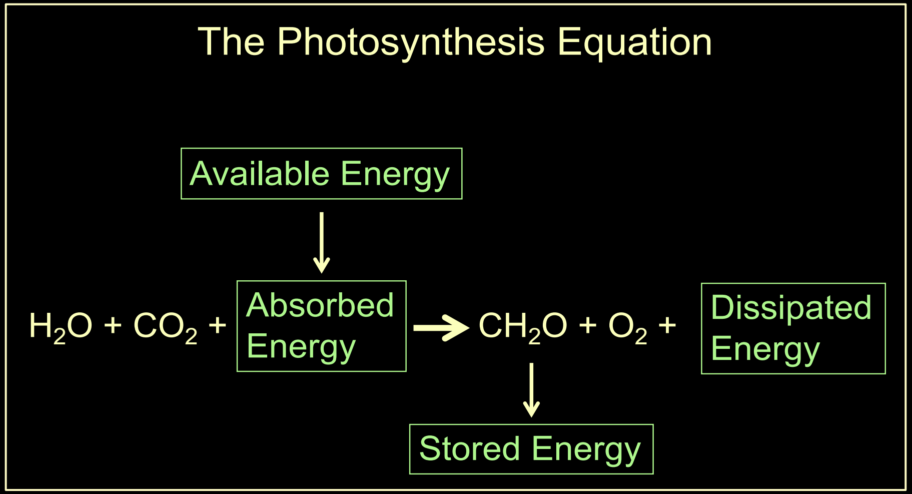
$H_2O + CO_2 +$ Utilised Energy → $CH_2O + O_2 +$ Dissipated Energy

↓

Stored Energy

What is primary production?

- Rate of fixation of carbon dioxide in the presence of sunlight, into organic matter, through photosynthesis.
- It is a rate, with dimension:
  $[M(C)]\ [L]^{-3}[T]^{-1}$ (Mass of Carbon per unit volume and unit time), or
  $[M(C)][M]^{-2}[T]^{-1}$ (Mass of Carbon per unit surface area, and per unit time).
- Chlorophyll-a (a measure of phytoplankton biomass, dimension $[M^{-3}]$)
- Chlorophyll-a is the transducer that acts to connect the supply of energy from the sun to the ecosystems on our planet.
- Any map of chlorophyll concentration shows how the strength of this energy–ecosystem coupling varies across the global ocean: the higher the chlorophyll concentration, the stronger the coupling.



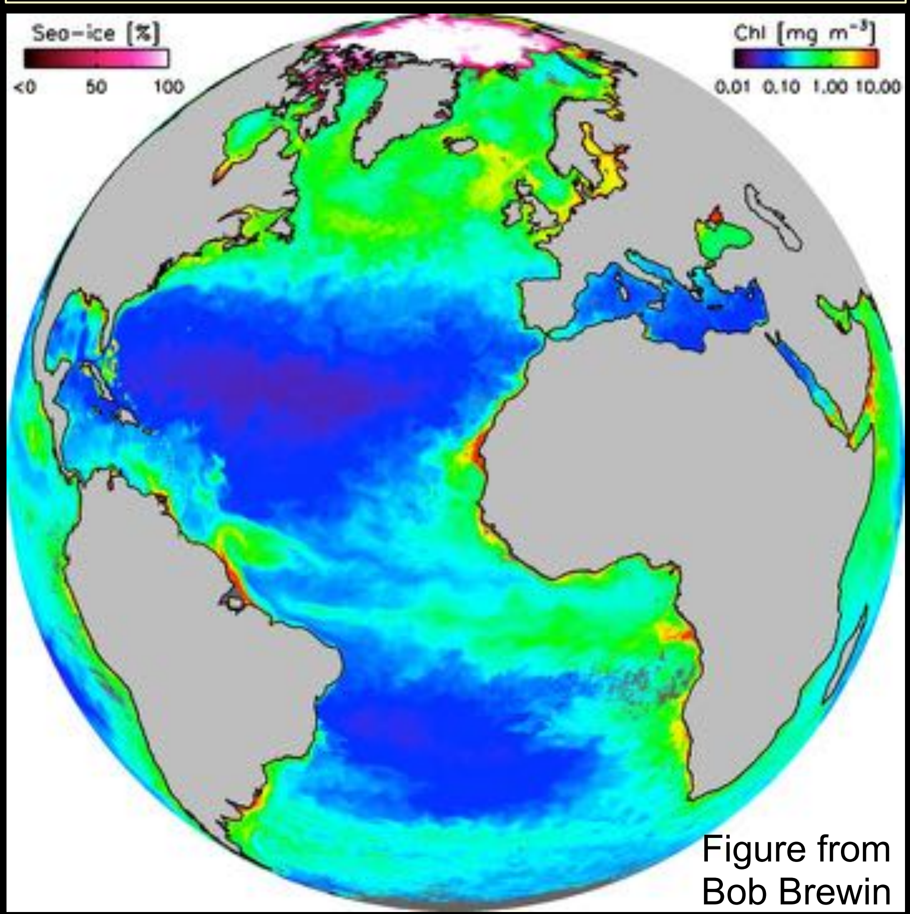


Figure from Bob Brewin

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.

Determinants of Primary Production

First-order:

- Light
- Pigment Biomass

Second-order:

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

Goal:

To estimate daily primary production of the ocean water column

$$P = P(I)$$

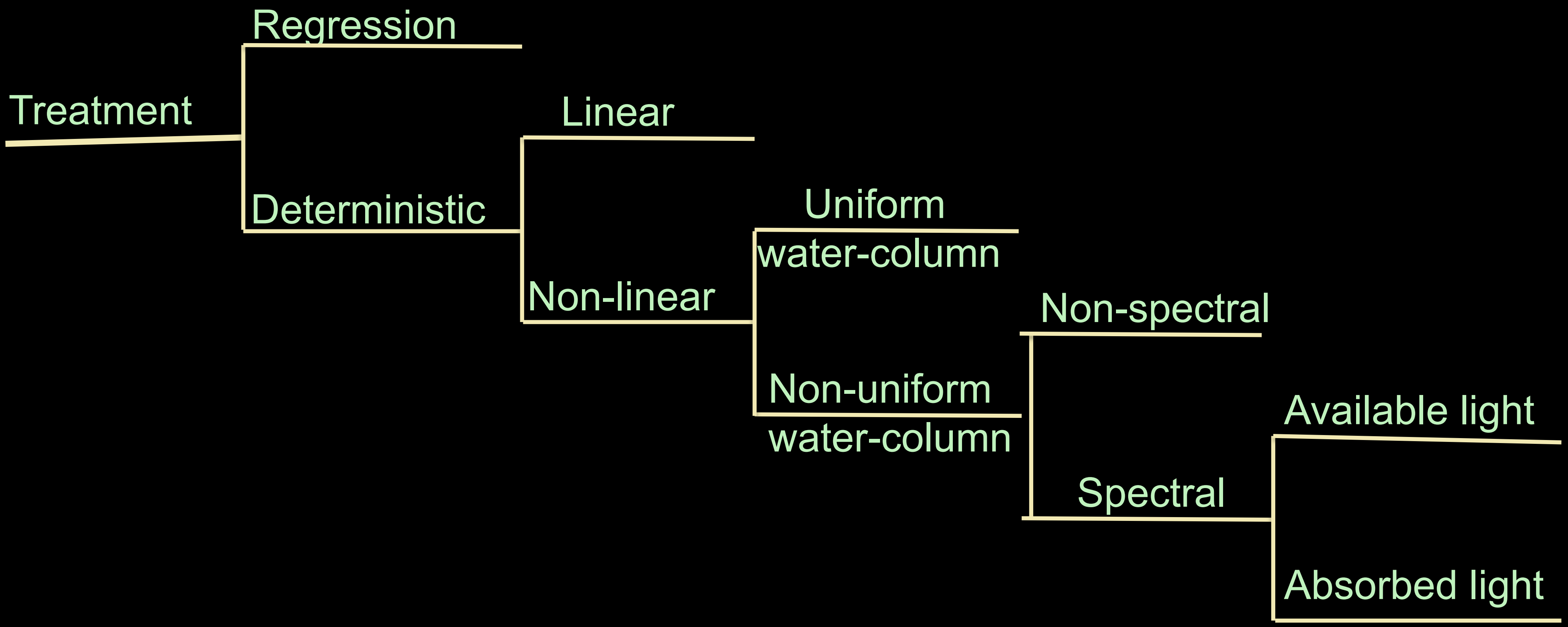
$$I = I(z) = I(0)e^{-Kz}$$

$$I(0) = I(0,t)$$

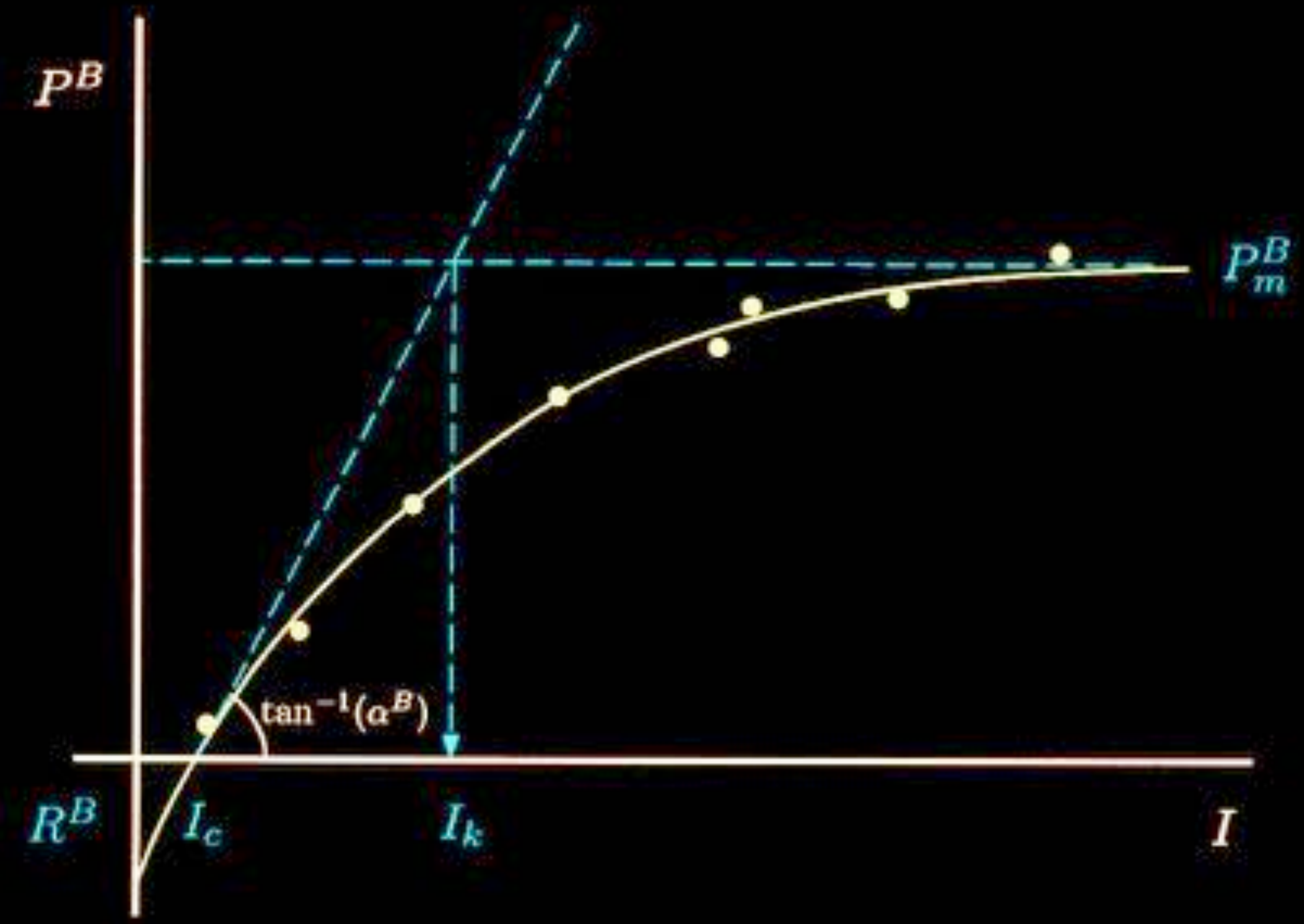
$$P(I(z,t))$$

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

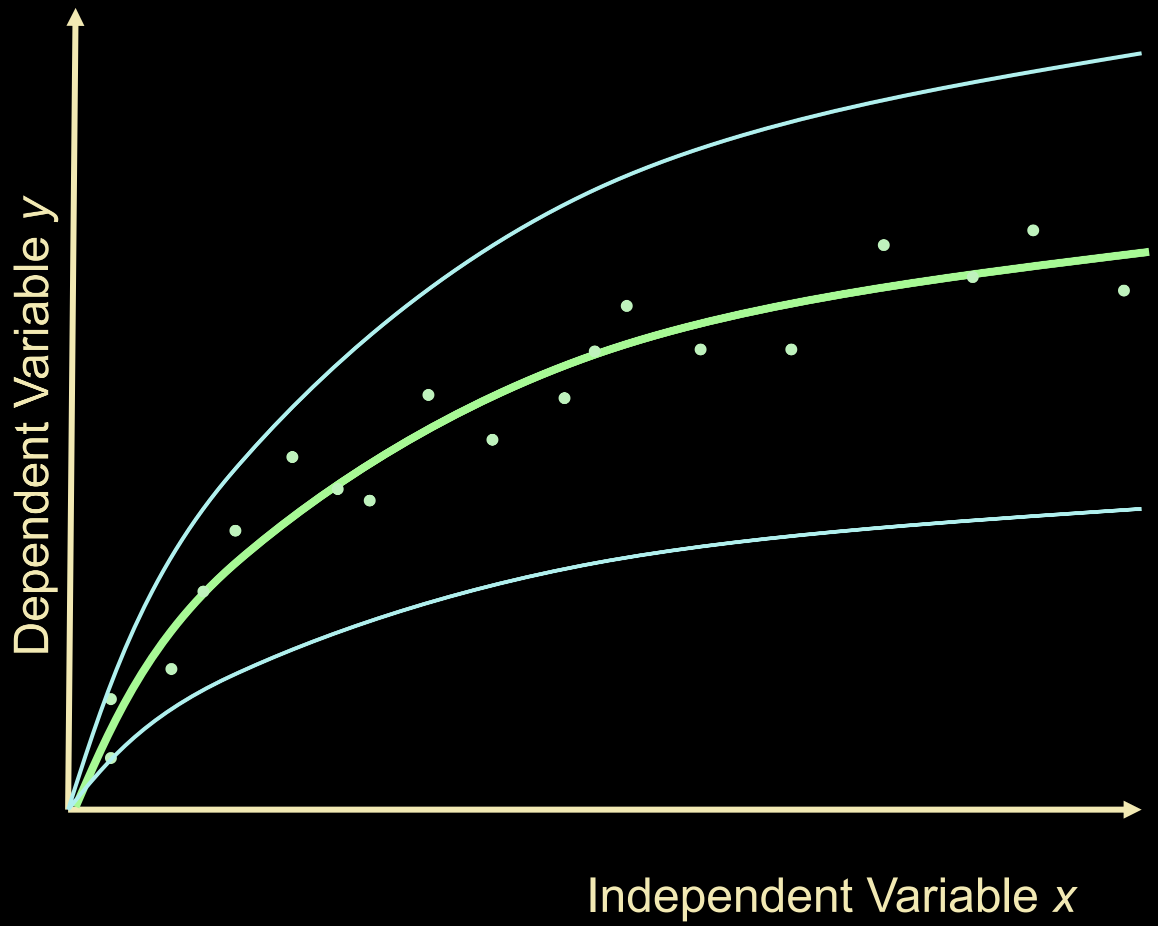
Hierarchy of Primary Production Models



Photosynthesis-Irradiance curve



Variables and Parameters



Consider a dependent variable *y* which is a nonlinear function of an independent variable *x.*

Non-linear functions need a minimum of 2 parameters to describe the curve that determines the functional dependence of *y* on *x*.

The parameters let you choose a particular curve to describe the relationship between x and y, from a family of all possible curves with the same functional form.

Parameters let you describe multiple observations in a parsimonious way.

Getting your parameters wrong can impact the predictability of your model.

It is always good practice in modelling to ask if model performance is affected by choice of model or choice of parameters.

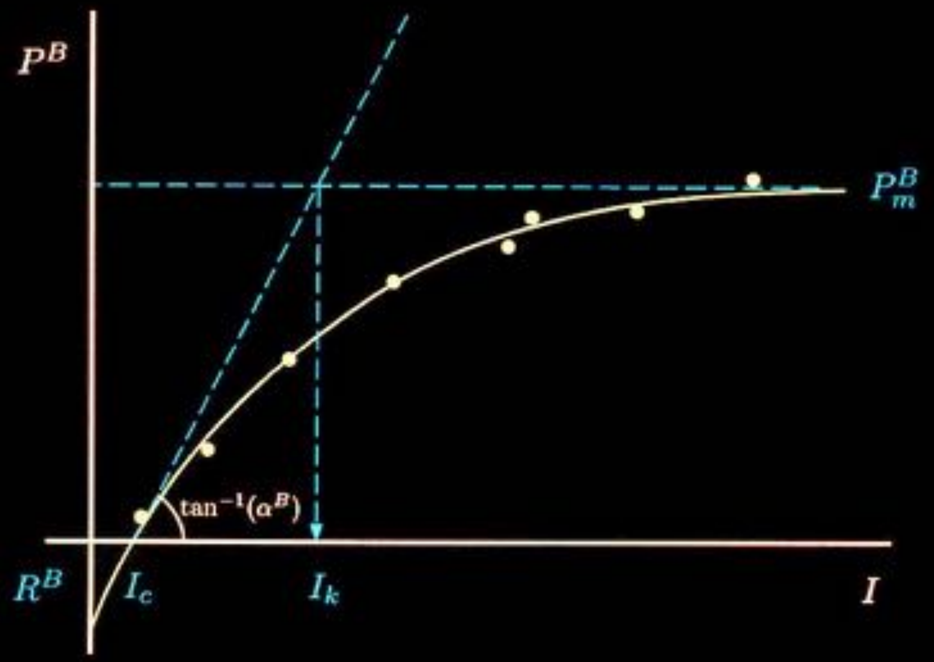
Basic Set of Parameters Needed in Primary Production Models

- 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.

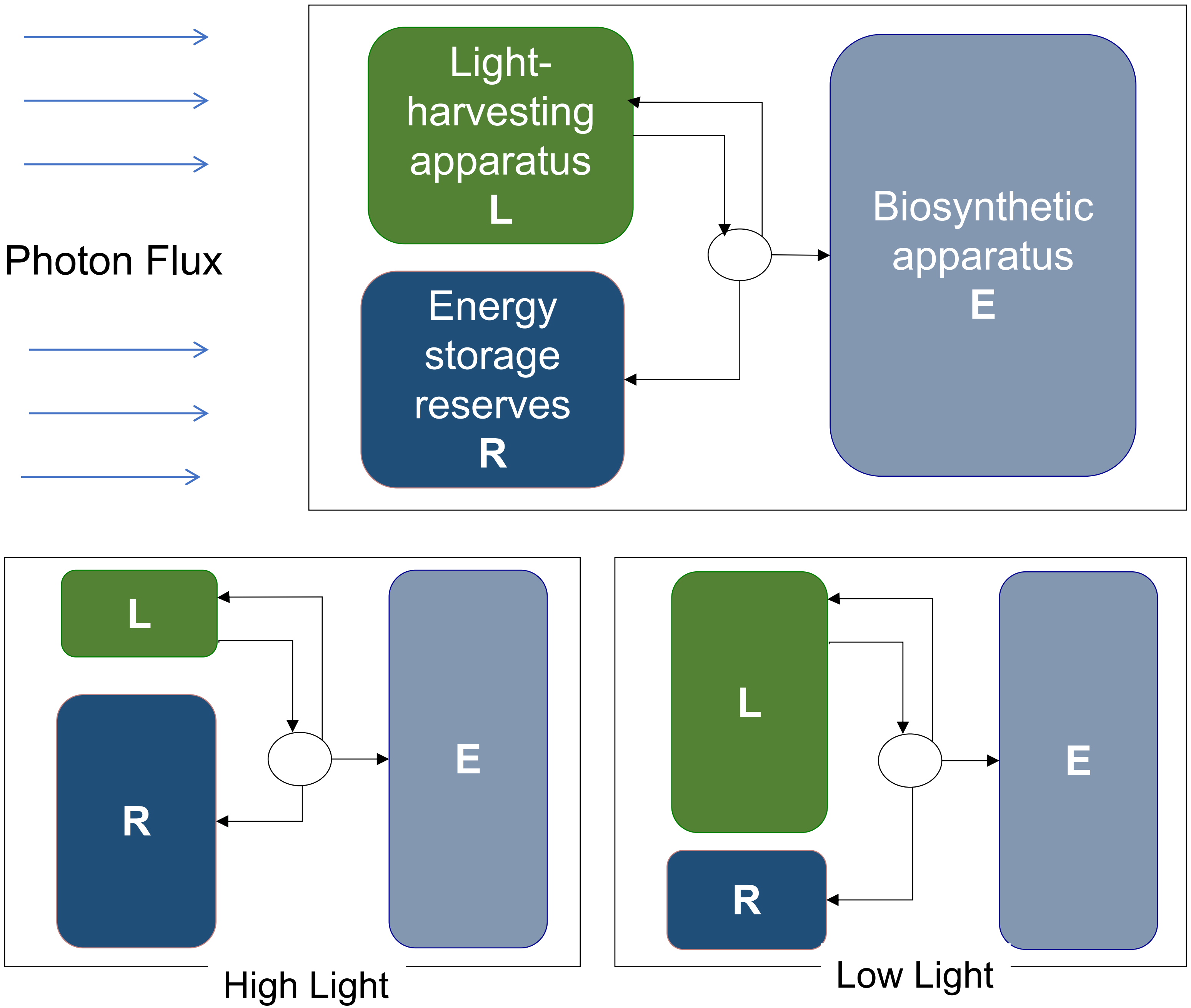
Carbon-to-chlorophyll ratio is invoked when fields of phytoplankton carbon computed in biogeochemical models are converted to fields of chlorophyll-a, for comparison with satellite data.

Photosynthesis-Irradiance Curve



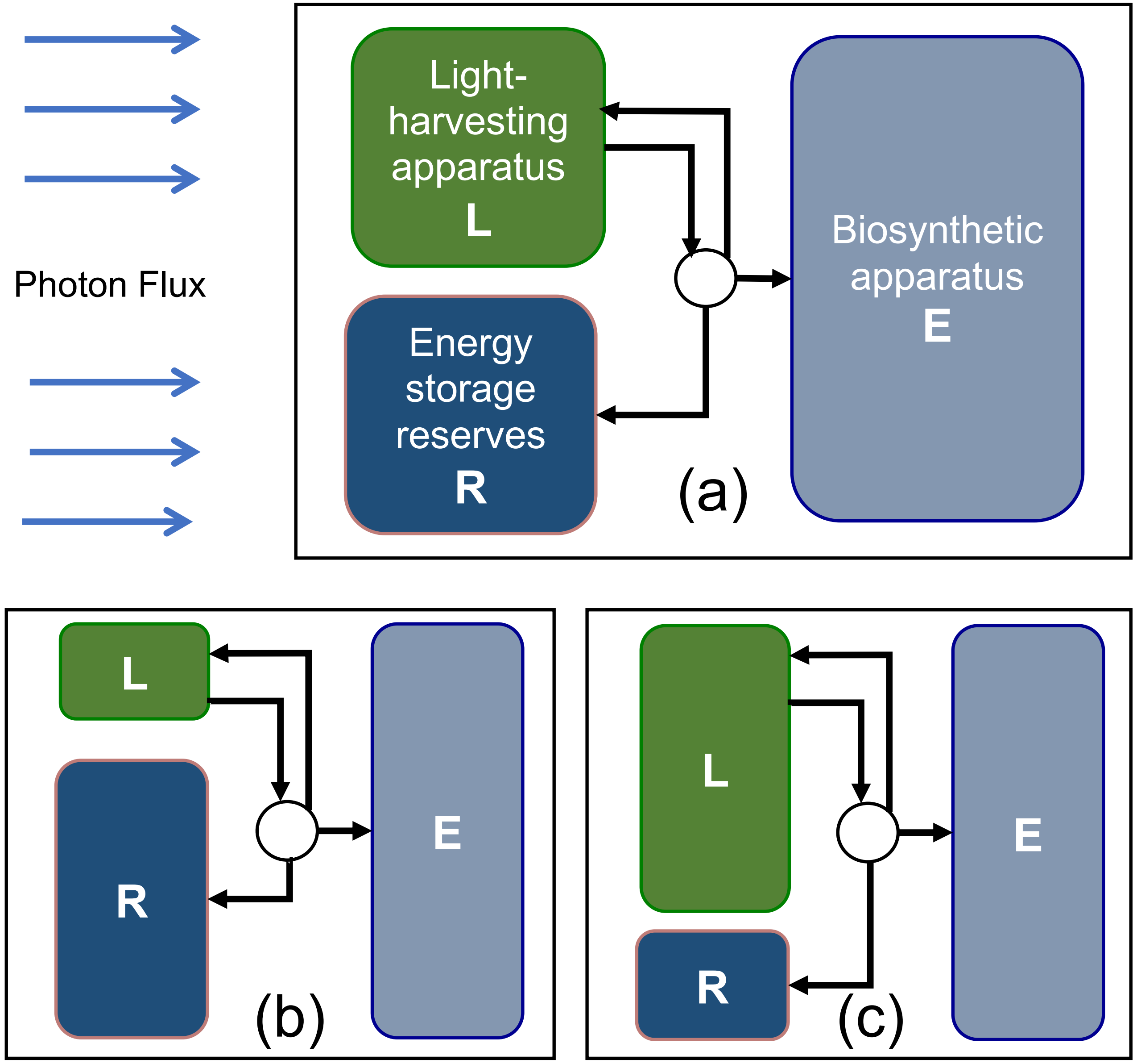
Platt and Sathyendranath (1993)
Sathyendranath and Platt (2001)
Sathyendranath *et al.* (2009)
Sathyendranath *et al.* (2020)

Coupling Photosynthesis and Photo-acclimation

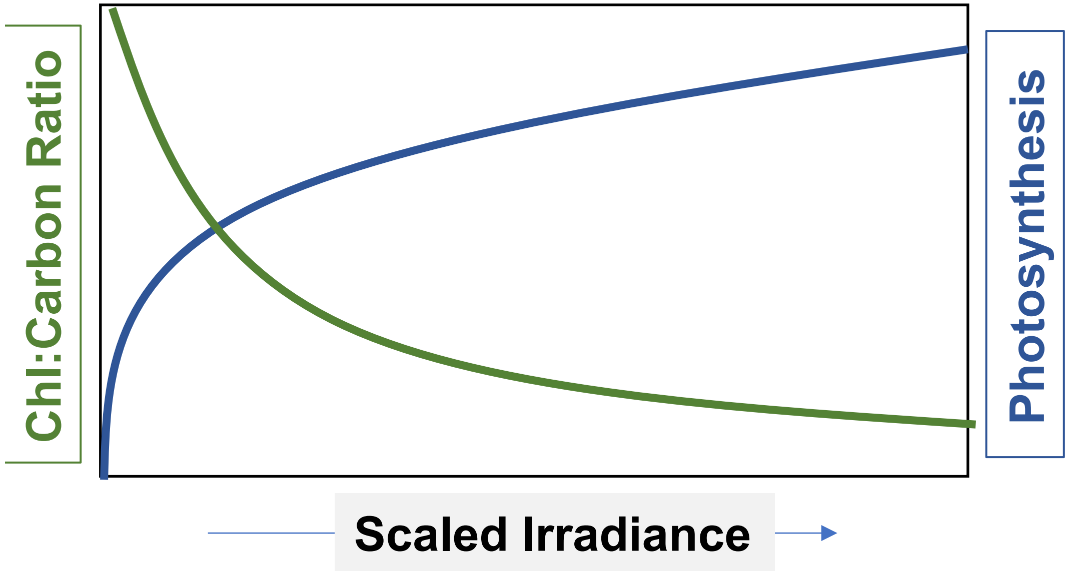


Geider *et al.* (1997)

Photosynthesis and Photo-acclimation as a Coupled System

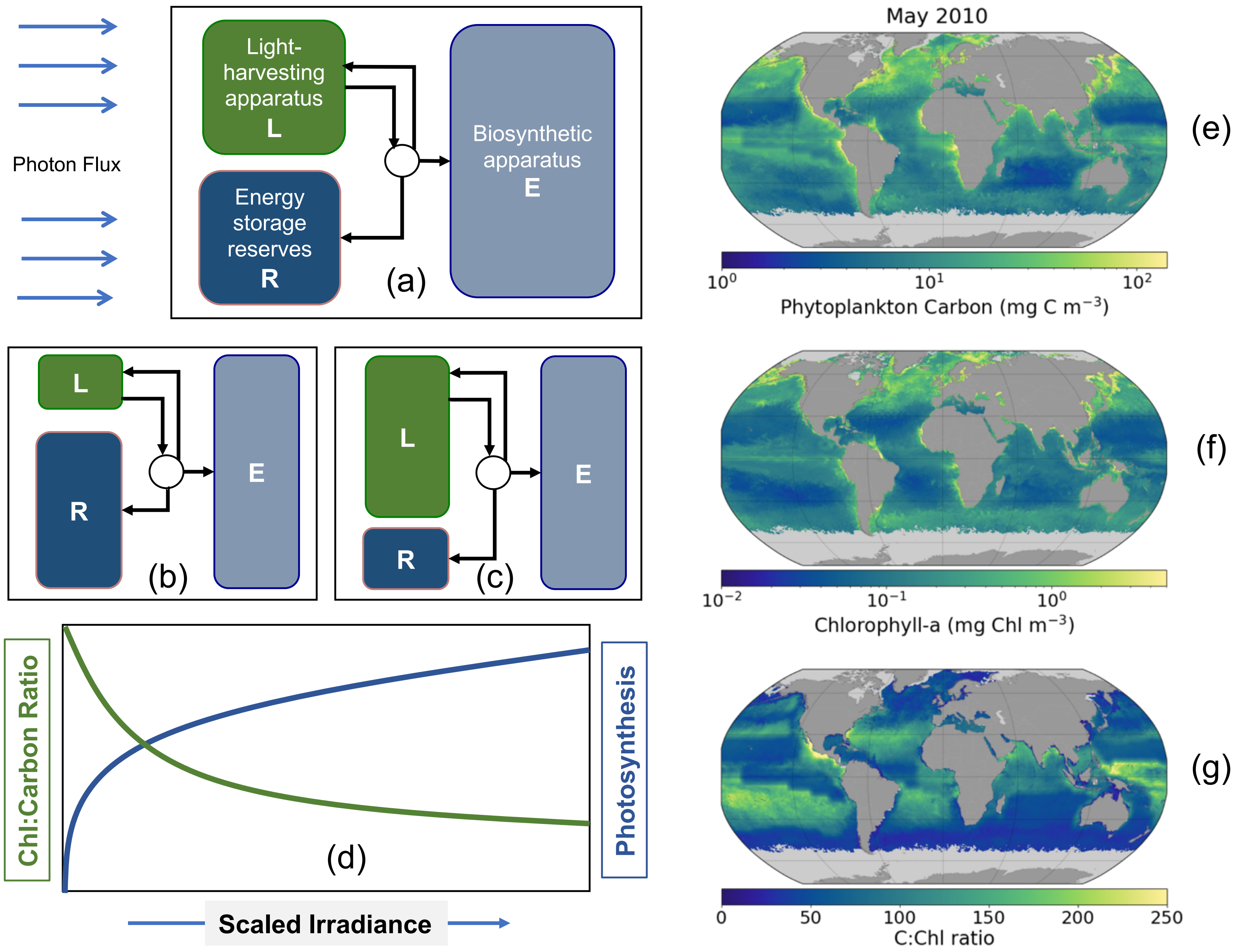


Geider *et al.* (1997)



Sathyendranath *et al.* (2020)

From Photo-acclimation to Phytoplankton Carbon



Spectral and Non-spectral Models

Light dependence of photosynthesis:

$$P^B(z,t) = p\,(\Pi(z,t), P_m^B$$

Non-spectral models:

$$\Pi(z,t) = I(z,t)\alpha^B(z,t)$$

Spectral models:

$$\Pi(z,t) = \int_{\lambda 1}^{\lambda 2} I(\lambda,z,t)\alpha^B(\lambda,z,t)\mathrm{d}\lambda$$

Or,

$$\Pi(z,t) = \phi_m \int_{\lambda 1}^{\lambda 2} I(\lambda,z,t)a^B(\lambda,z,t)\mathrm{d}\lambda$$

where ϕ_m is the maximum realized quantum yield,
and we make use of the identity: $\phi_m = \frac{\alpha}{a}$

Model Parameters

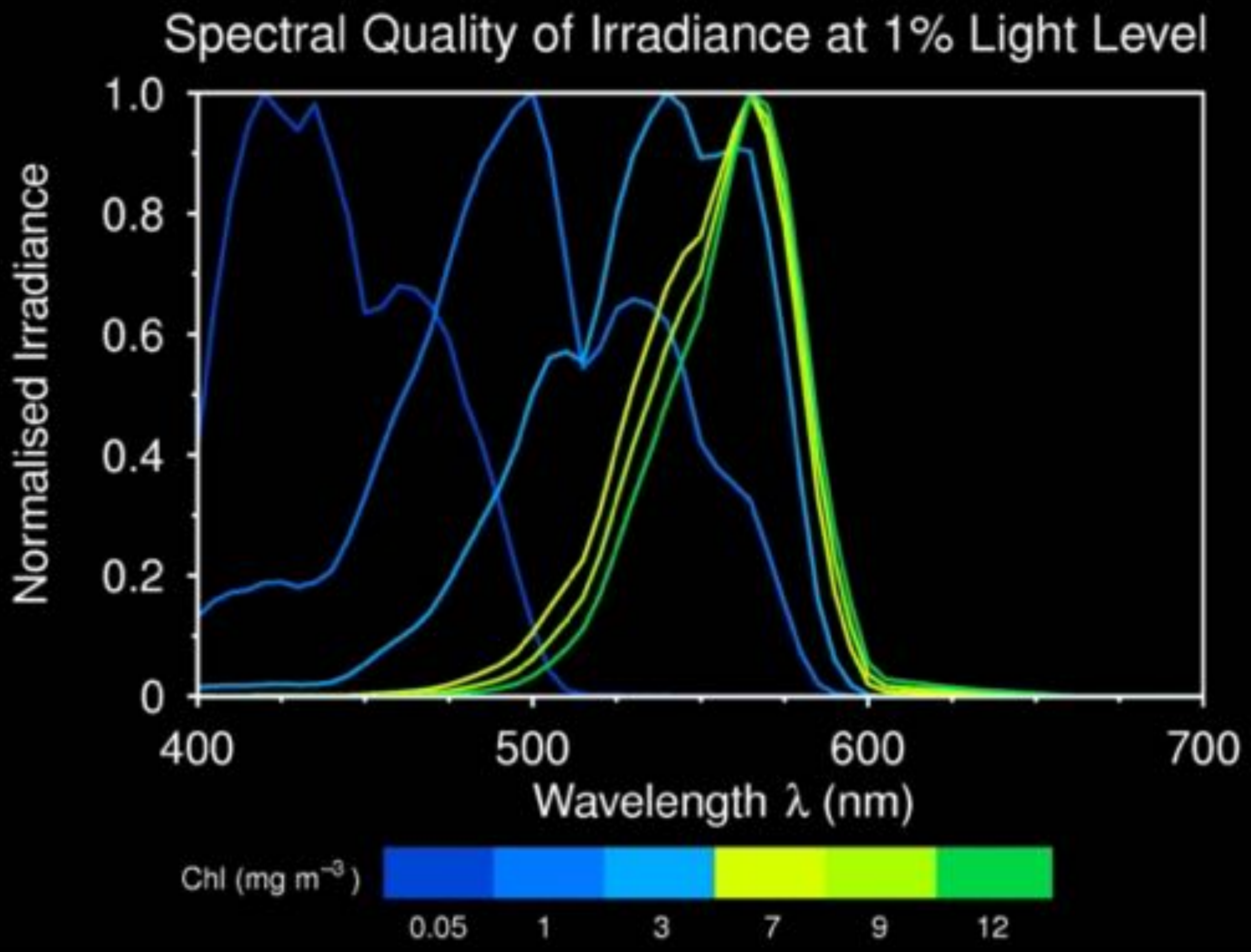
P_m^B : Light saturation parameter
α^B: Initial slope of photosynthesis-irradiance curve
ϕ_m: maximum realized quantum yield

Forcing variable

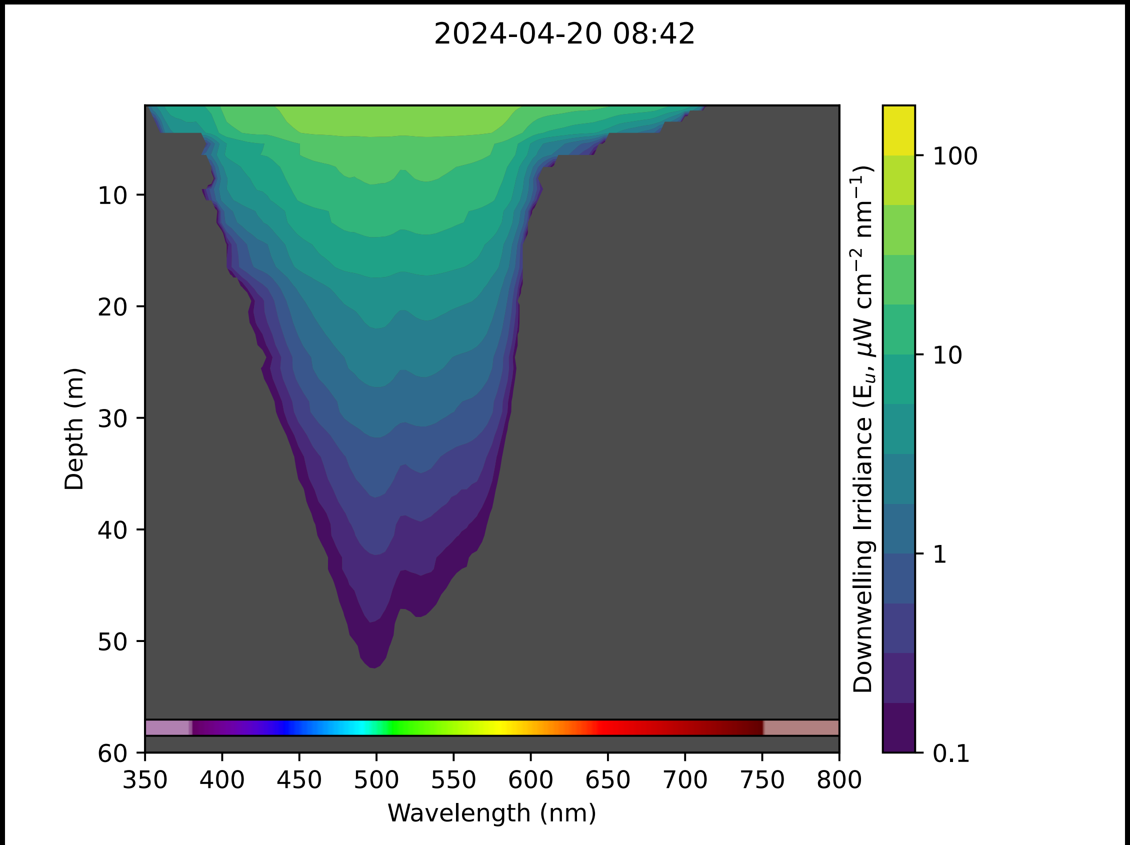
E: irradiance

Arguments

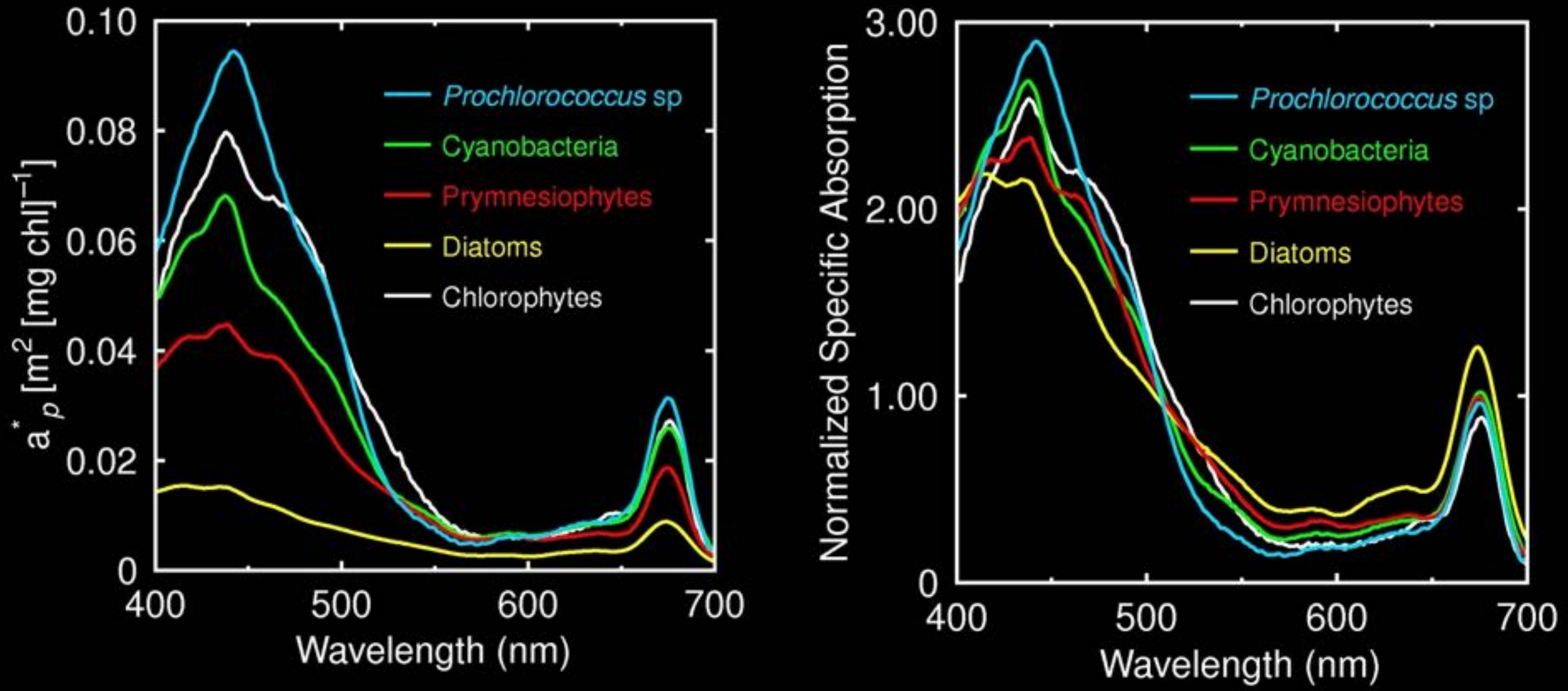
λ: wavelength
z: depth
t: time



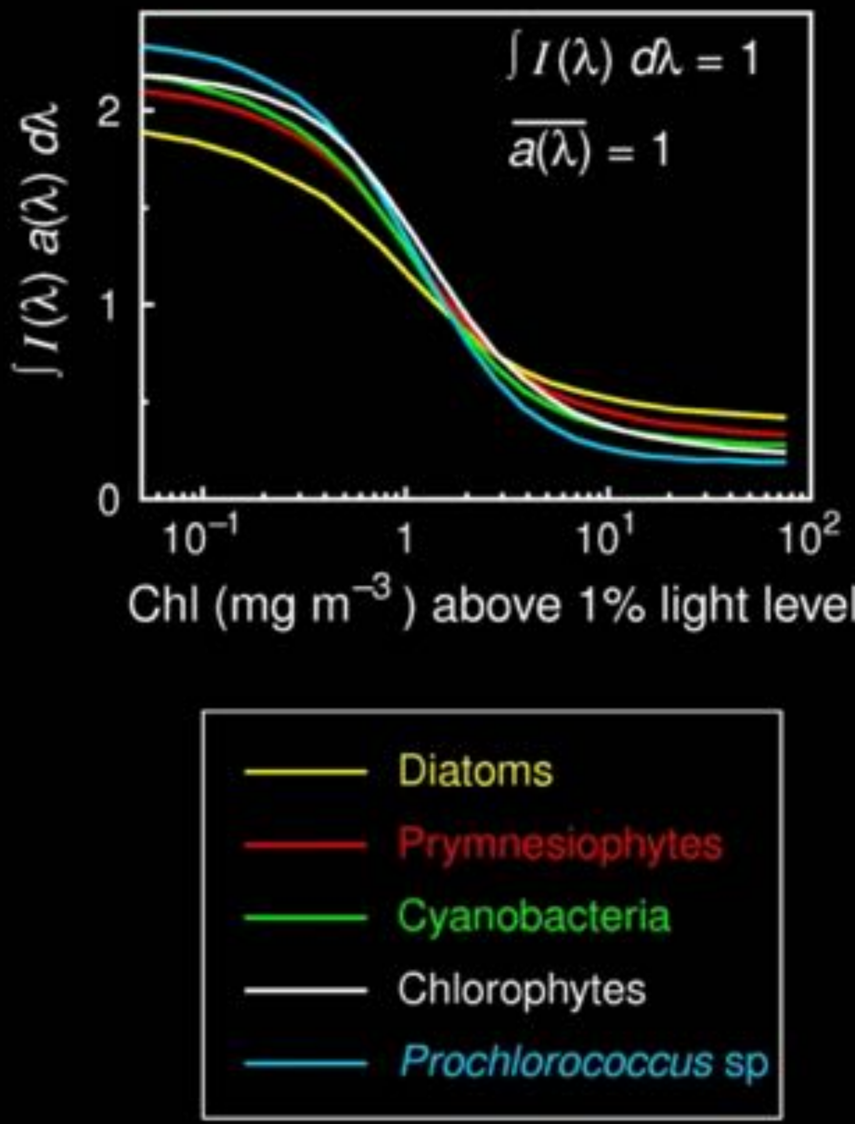
Model output (Sathyendranth and Platt(1988)

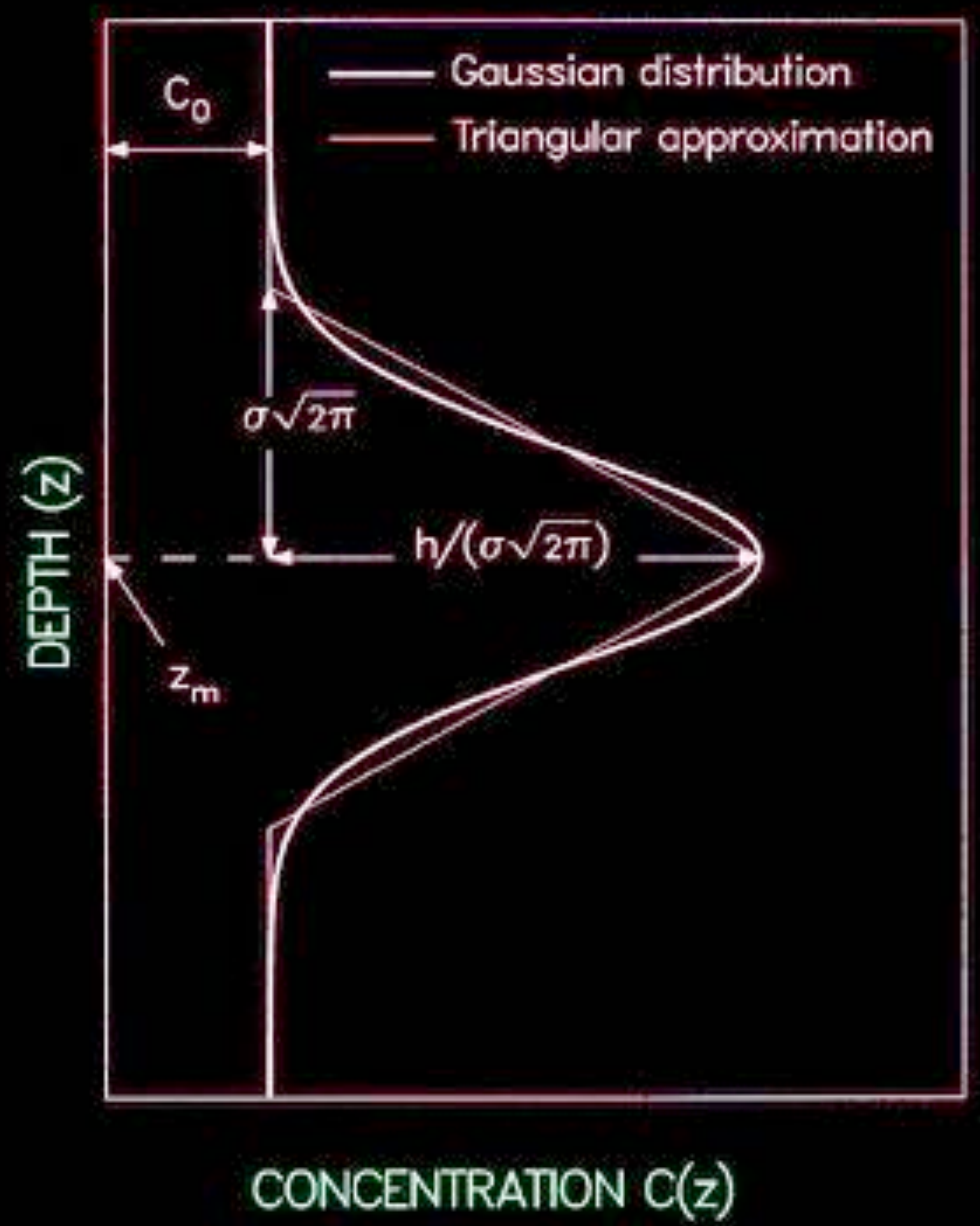


Data and figure from Bror Jönsson


0.10
0.08
0.06
0.04
0.02
0
a^*_p [m^2 [mg chl]$^{-1}$]
400
500
600
700
Wavelength (nm)
Prochlorococcus sp
Cyanobacteria
Prymnesiophytes
Diatoms
Chlorophytes
3.00
2.00
1.00
0
Normalized Specific Absorption
400
500
600
700
Wavelength (nm)
Prochlorococcus sp
Cyanobacteria
Prymnesiophytes
Diatoms
Chlorophytes

Light Absorbed by Phytoplankton at 1% Light Level



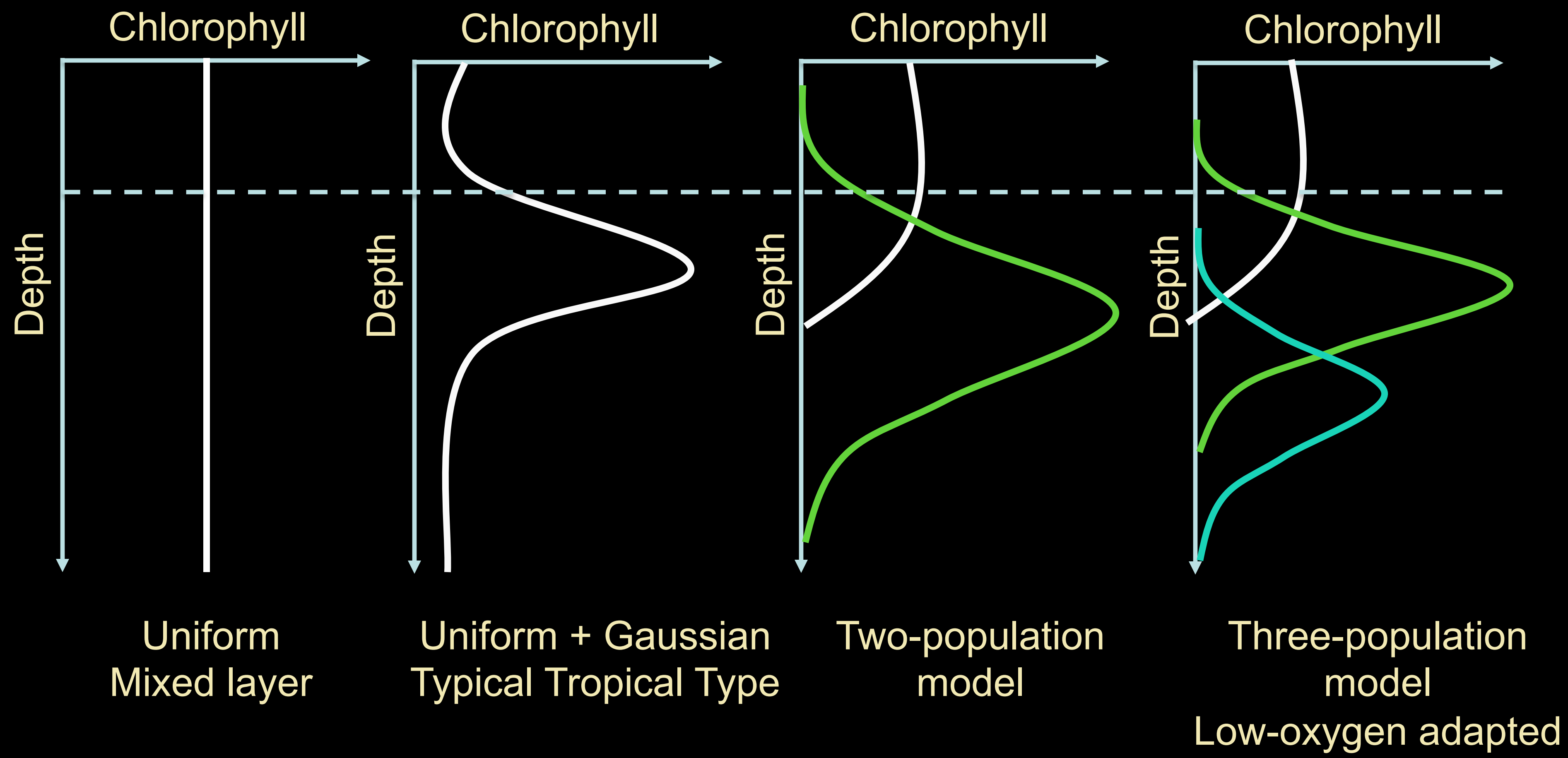


Vertical Structure in Chlorophyll Concentration

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.

Cryptic Biology: Vertical Structure in phytoplankton



Vertical Structure impacts:

- Magnitude of production
- Source of systematic error
- Partition of production into new and recycled parts
- Are we losing production in oxygen minimum zones?
- Tied to mixed-layer dynamics

- Can we improve what we do in remote sensing?

Platt & Sathyendranath (1988)
Morel & Berthon (1989)
Carranza et al. (2018)
Brewin et al. (2022)
Cox et al. (2023)

Estimation of Primary Production at Large Scales

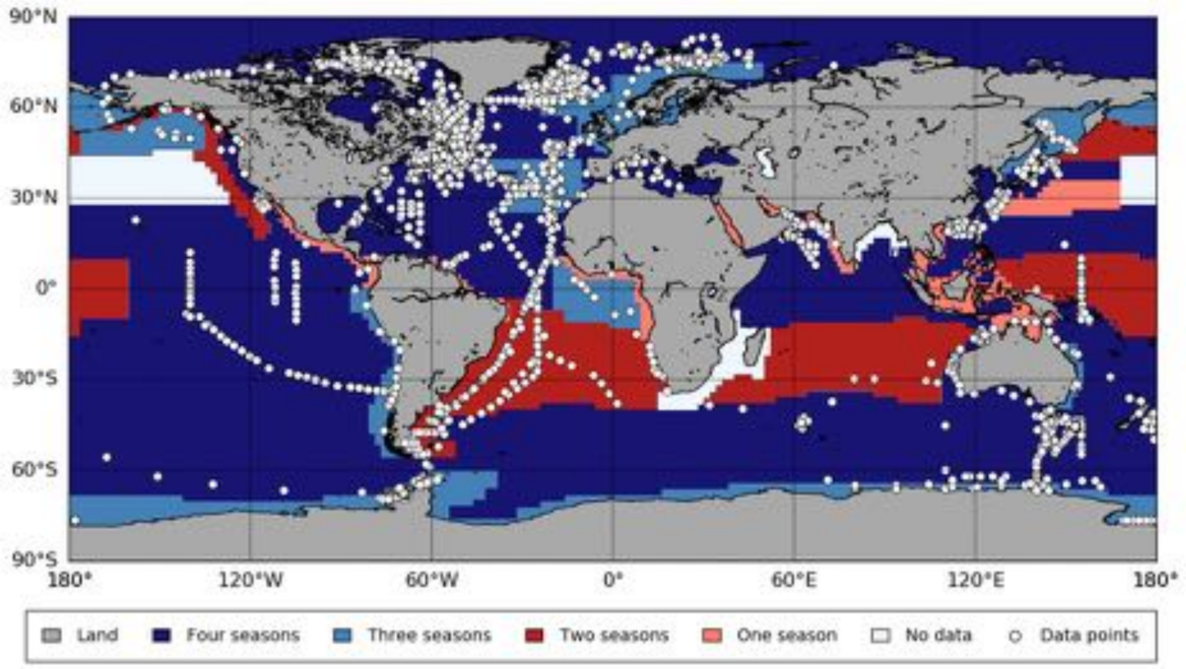
1. Establish a local algorithm
2. Extrapolate to large scales

Extrapolation Methods

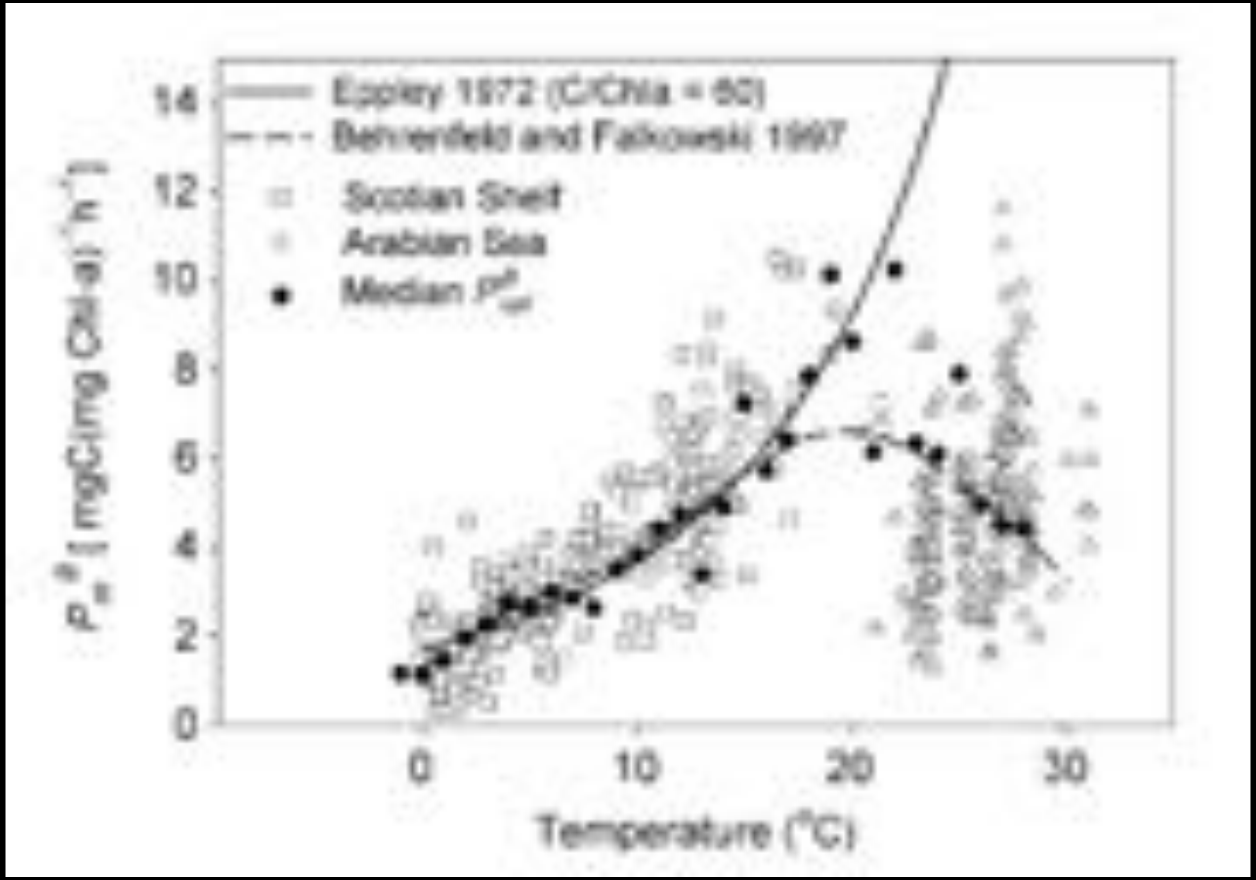
Biogeochemical Provinces (Sathyendranath and Platt 1988; Longhurst et al. 1995; Longhurst 2007; Kulk et al. 2020)

Temperature-Dependent Functions (Antoine and Morel 1996; Behrenfeld at al. 1997)

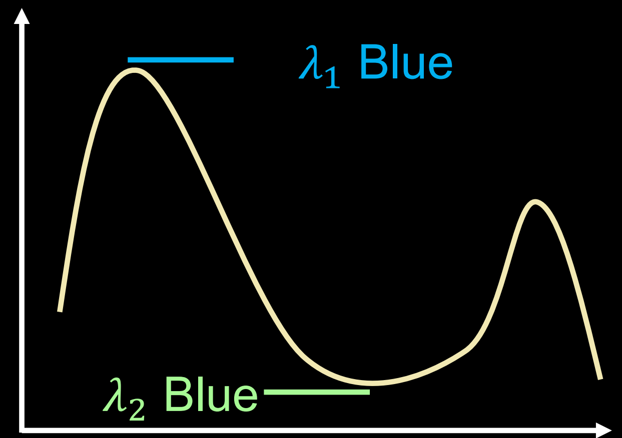
Field Observations of P_m^B and α^B



Bouman et al. (2018); Kulk et al. 2020)



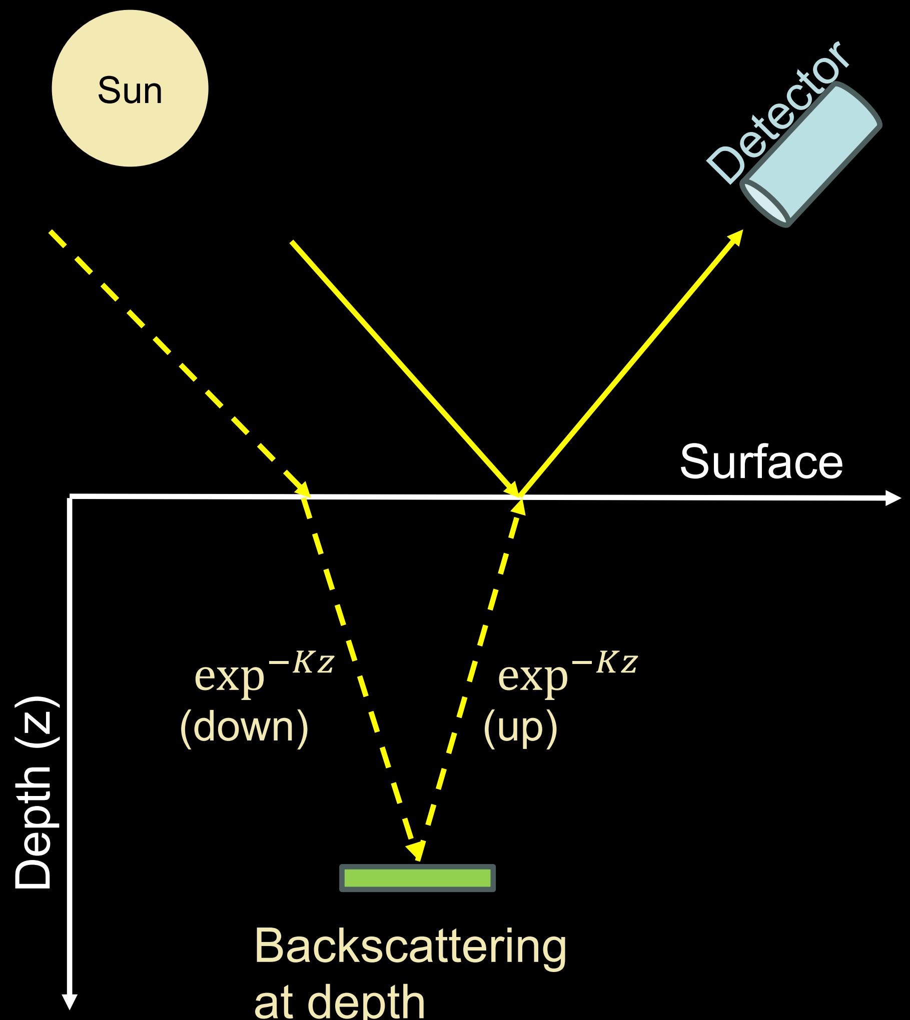
Bouman et al. (2005)



Absorption Spectrum of phytoplankton

$$\frac{R_{rs}(\lambda_1)}{R_{rs}(\lambda_2)} = f\ (\text{chlorophyll})$$

Remote sensing algorithm



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

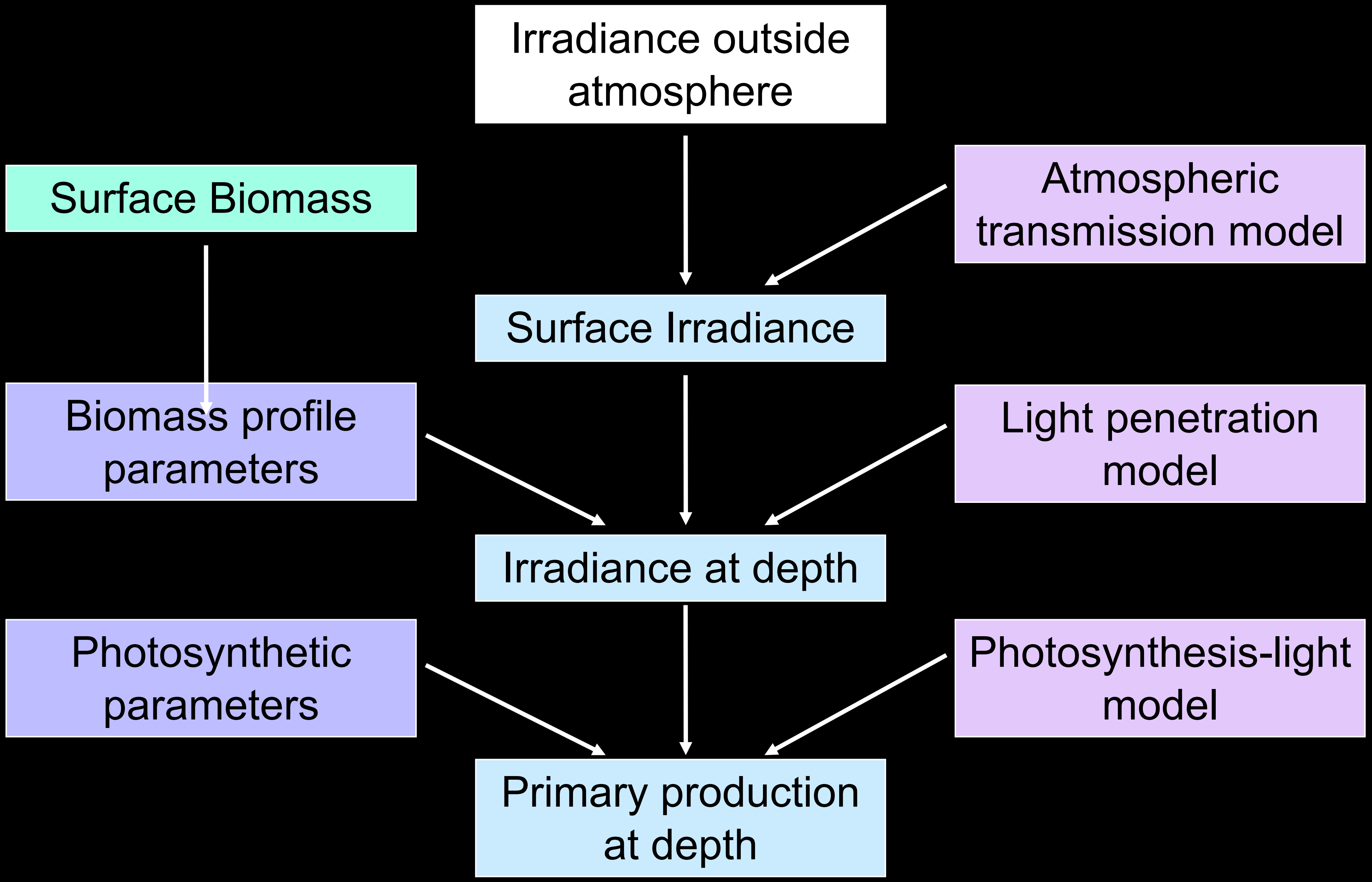
Weighting function:

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

Effective chlorophyll concentration

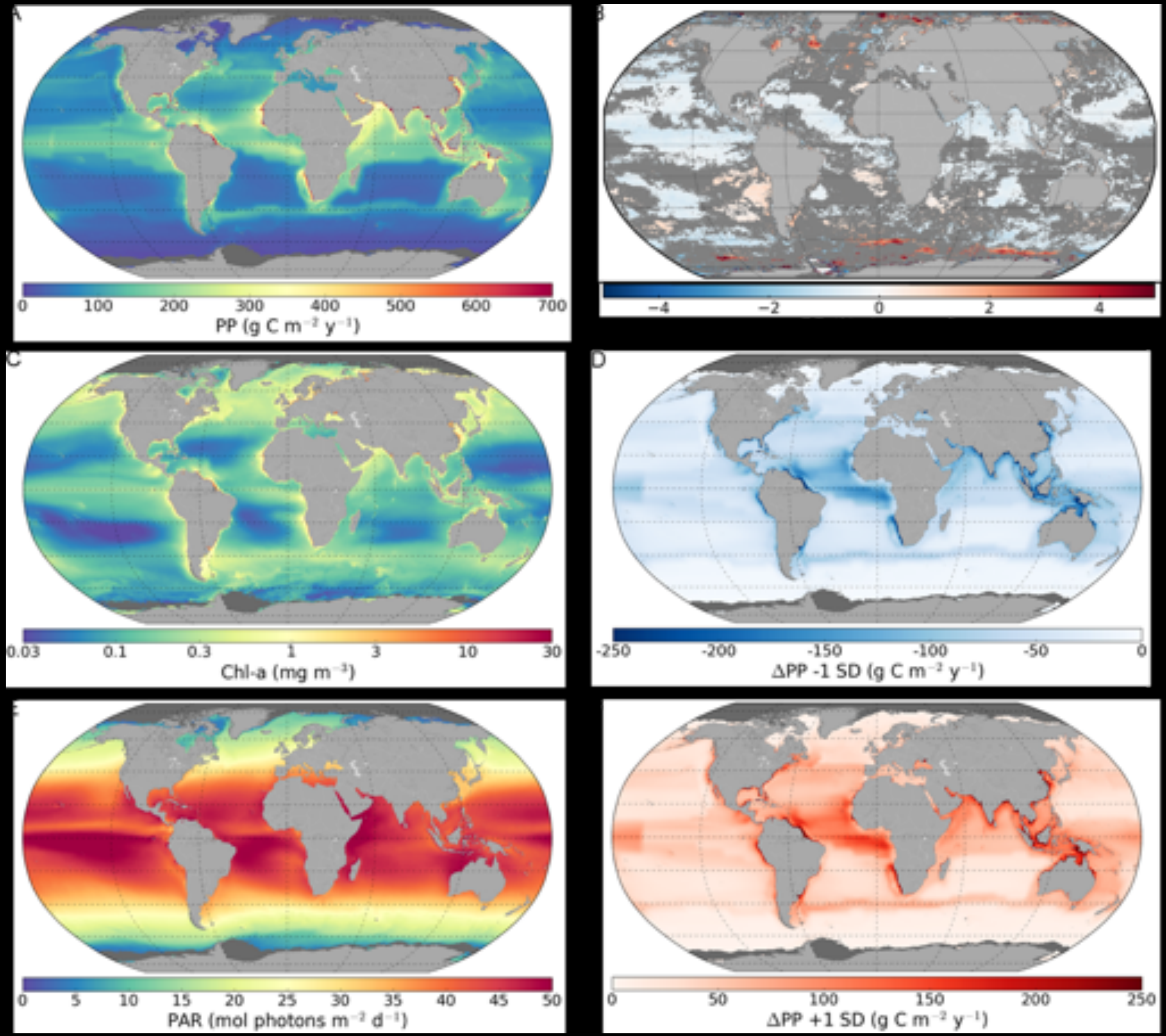
$$B(s) = \frac{\int_0^{1/K} B(z)f(z)dz}{\int_0^{1/K} f dz}$$

Computation of primary production



Sathyendranath and Platt (1989)

Computed Global Primary Production



Kulk *et al*. (2020)

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.

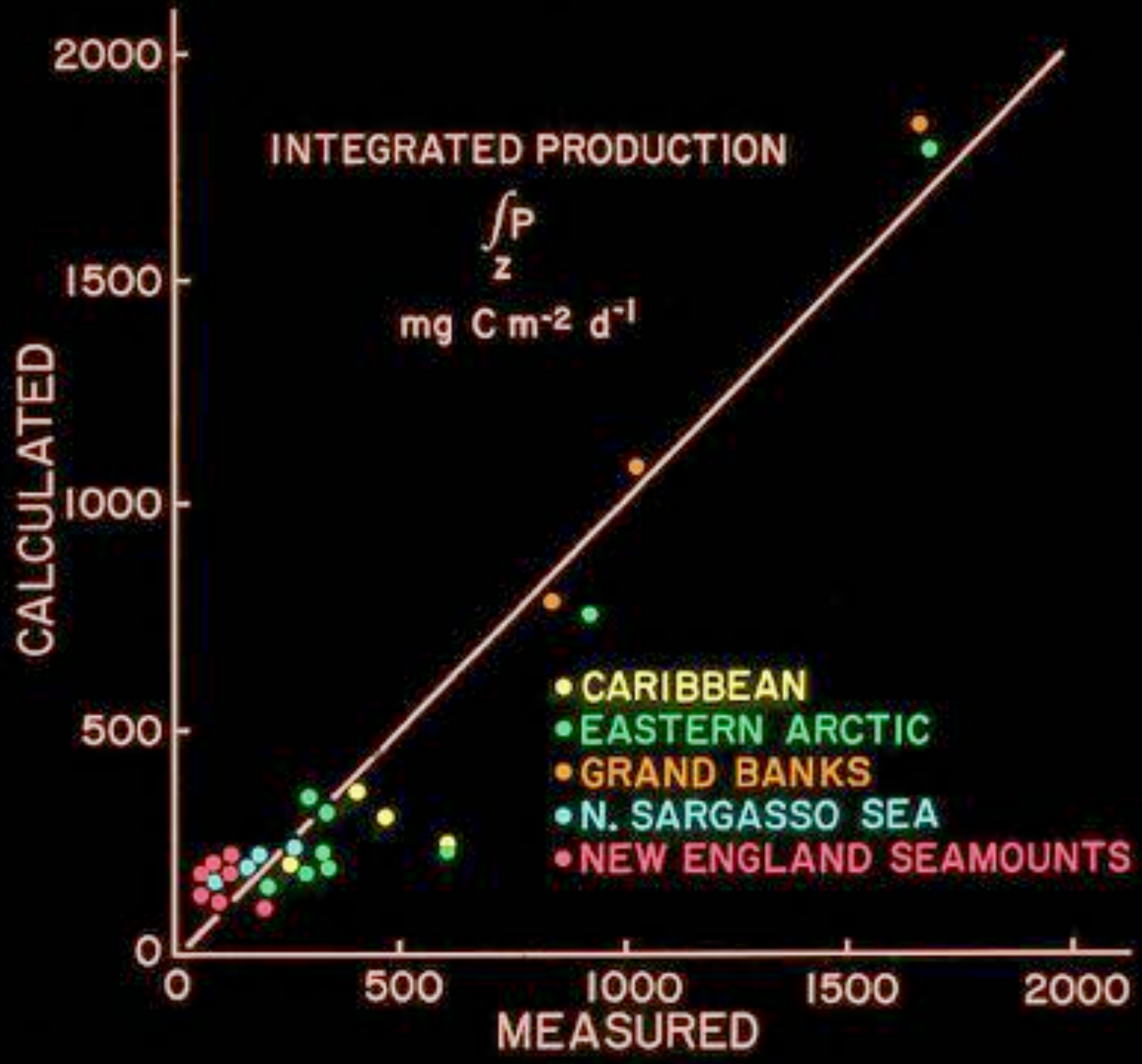
$$P = P^B \times B$$

- 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

Validation



Platt and Sathyendranath (1988)

Problems with Validation and Uncertainty Estimation

1. Sometimes, there is no independent method available for comparison. Remote-sensing approach uses all available data, from *in situ* as well as from satellites. Sensitivity analyses could be a solution to establishing uncertainty.

2. Quality of in situ data available could be a problem.

3. Incompatibility of scales could make comparisons inconclusive at best. For point *in vitro* observations, relevant spatial scale is ~1m^{-2}, and it would be ~1-100 km^{-2} for satellites.

4. 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.

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

6. Formal error propagation or Monte Carlo methods can be explored. But in both these methods, we need estimates of uncertainties in each of the steps.

Errors in computation of primary production

Examine precision of element of the calculation separately:

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

The local algorithm for the vertically-uniform, non-spectral model has an estimated precision of ~42% (compounding of errors 1, 2, and 3a).
Combining with the aggregation error (3b) gives a best-case estimate of ~50% for the precision of a primary-production estimate in a spatially-extrapolated calculation.

Note: this calculation does not include the decrease in standard error in the mean (as inverse of N^2 where N is number of observations). Remote sensing, with high number of observations, helps to reduce this error substantially. But covariance of observations need to be assessed.

Platt *et al.* (1995)

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

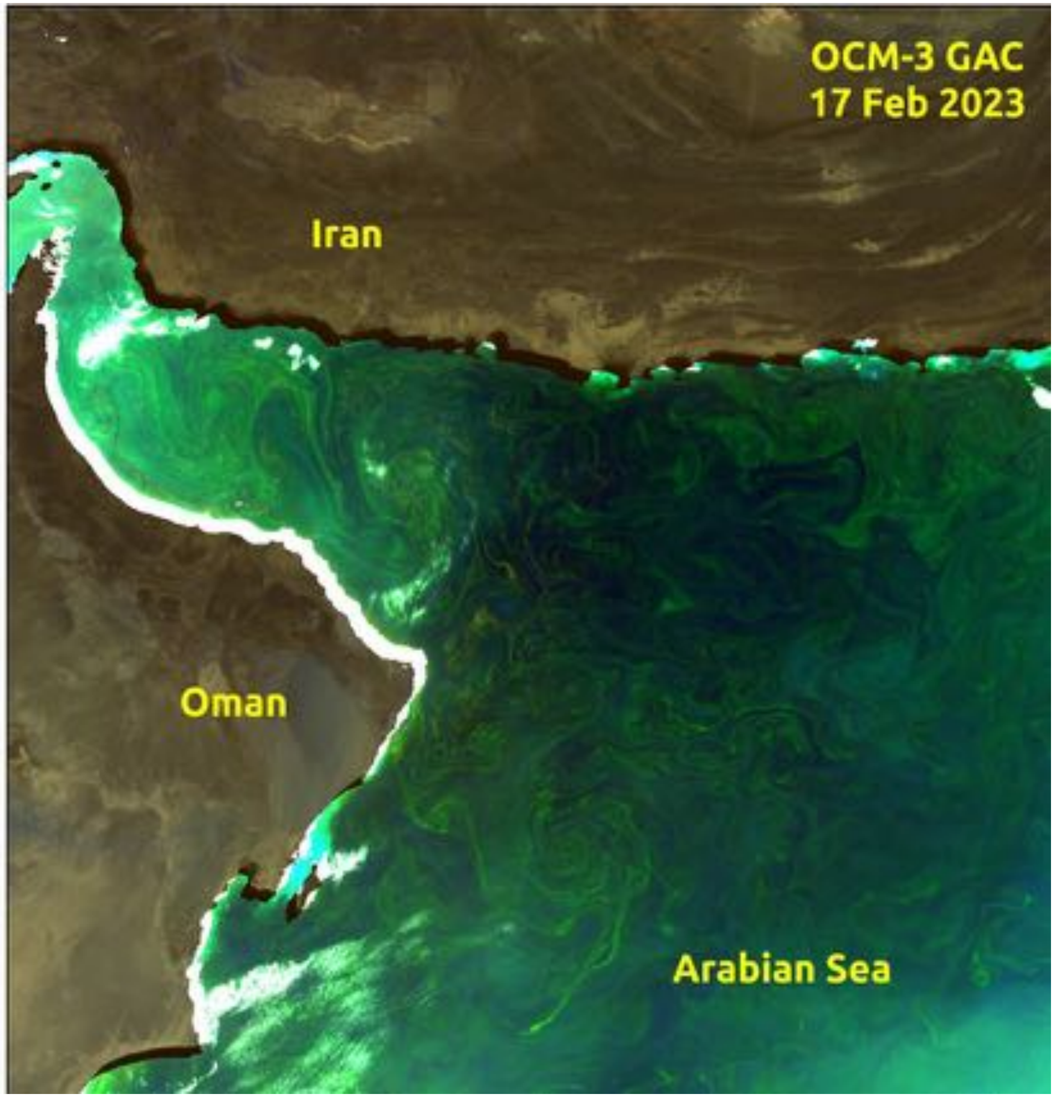
Platt et al. (1992); Sathyendranath et al. (2019)

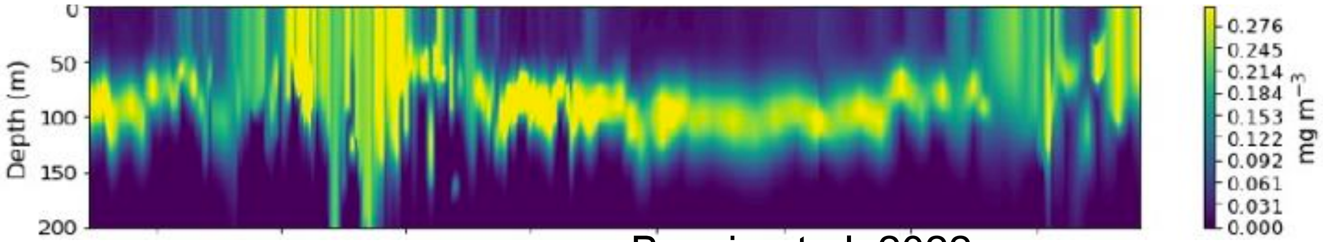
Scales of Time and Space

In aquatic systems, time and space scales are inextricably linked. For diffuse systems, the scales are related through the diffusion coefficient. For advective systems, they are related through the mean flow velocity.

Key Messages

- *In situ* databases have been central to the work.
- Many of the scientific questions that have emerged require products at higher temporal (daily) and spatial (1km) products to resolve.
- Uncertainties are of paramount importance.
- **Gaps:**
- Lack of photosynthesis-irradiance parameters
- Dynamic assignment of parameters.
- Comparisons between models and satellite-based observations.
- Closer links to physical oceanography: for example to define phytoplankton profiles (e.g., Brewin et al. 2022).
- An ocean carbon for ocean stewardship
- Implications of a noisier environment
- Do phytoplankton have a role in air-sea carbon flux
- Increasing and extensive occurrences of unusual algal blooms





Brewin et al. 2022

Bob Brewin has put together a simple version of a primary production model on Jupyter Notebook for the TPSF training last year, and he has just put it on GitHub for this course:

https://github.com/rjbrewin/TPSF_PP

If you click the launch-binder button at the bottom of the readme file (displayed on the home page) you should be able to run the notebook in Jupyter Binder (it can take a little while to load).

Thank you, Bob.