Primary Production from Ocean Colour

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The Photosynthesis Equation

available energy

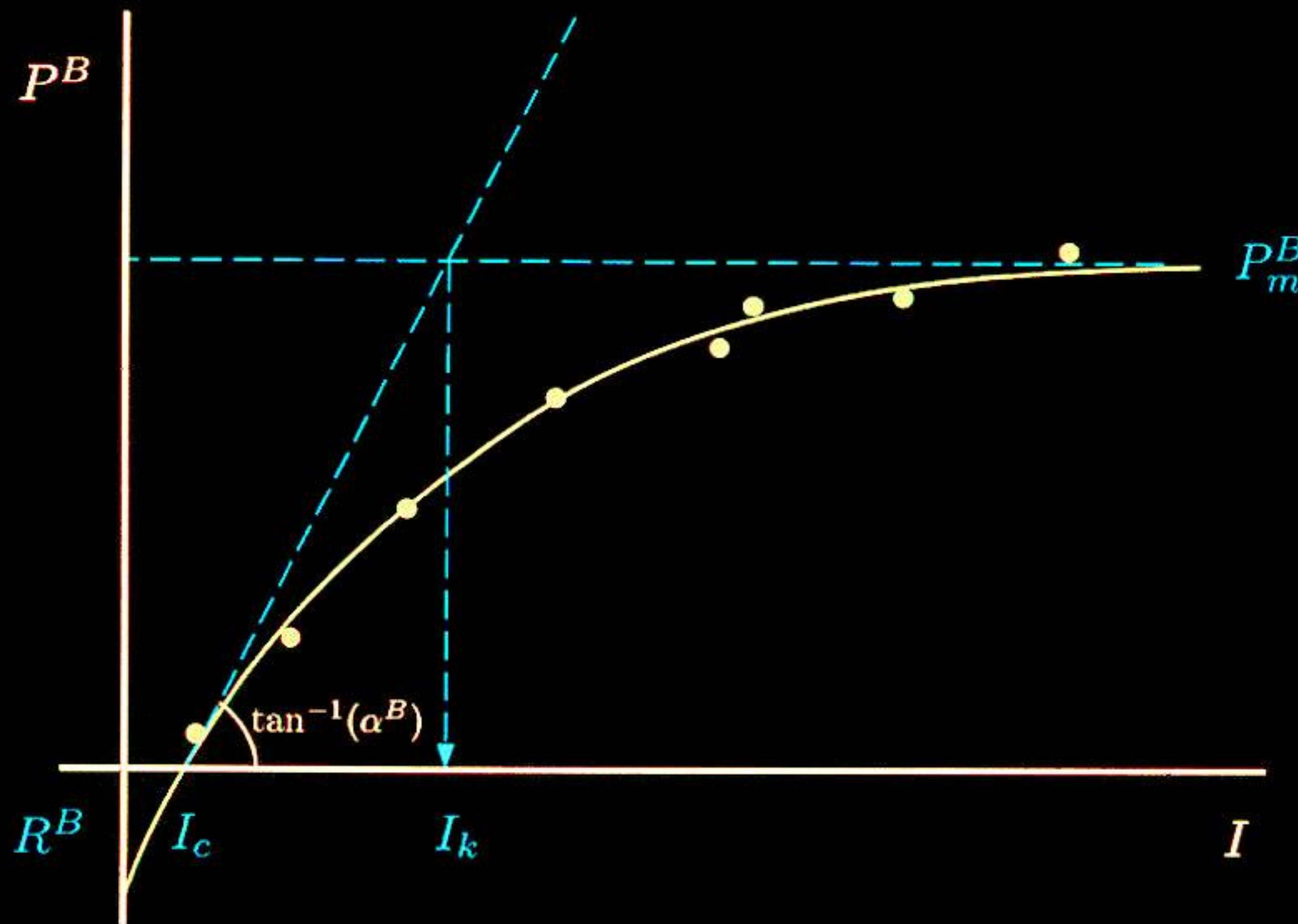
$$\Downarrow$$

$$H_2O + CO_2 + \text{utilised energy} \rightarrow CH_2O + O_2 + \text{dissipated energy.}$$

$$\Downarrow$$

stored energy

Photosynthesis-Irradiance Curve



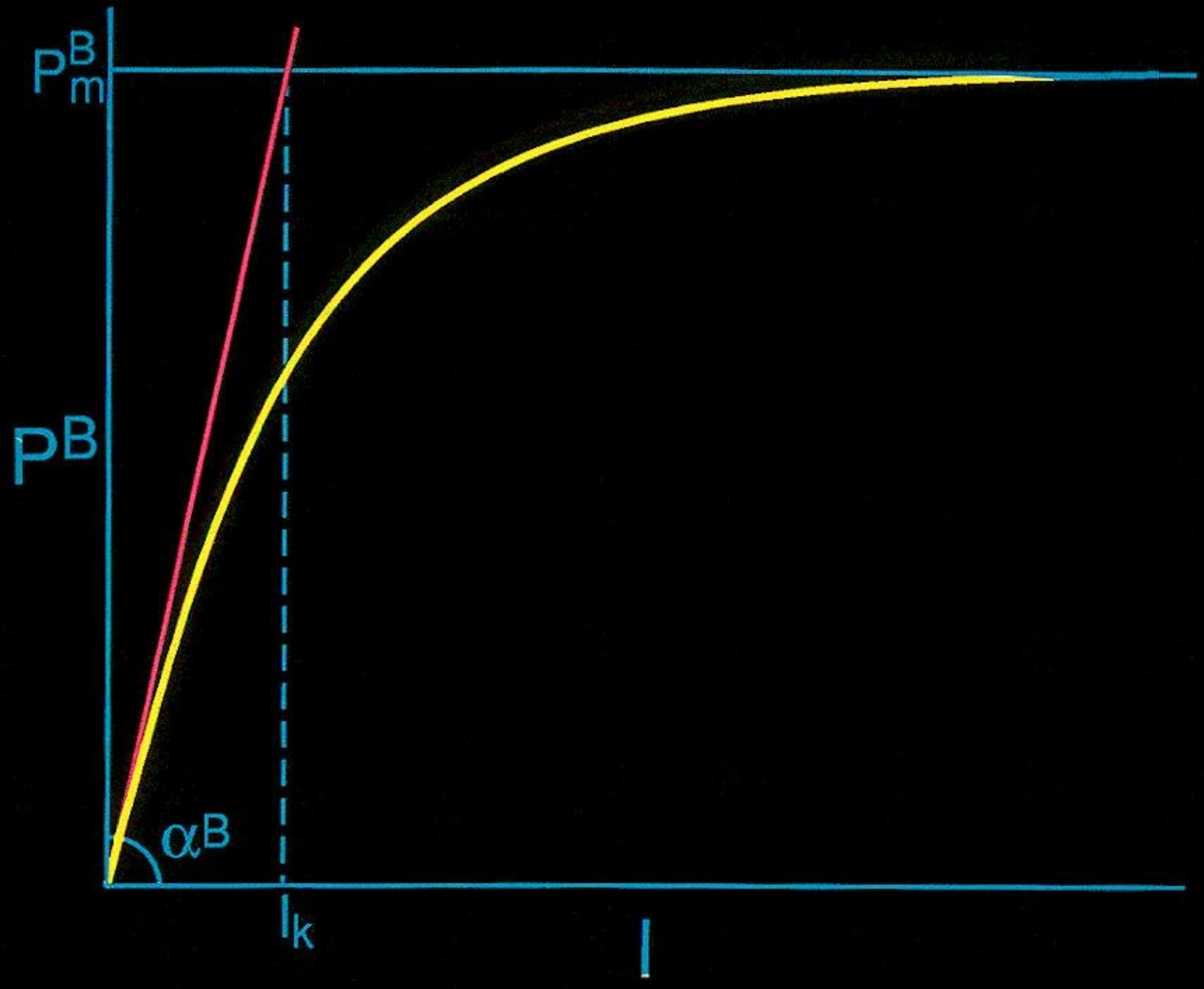
Variables and Parameters

It is crucial to recognise that when an equation is written out in terms of variables and parameters it describes not just one line on a graph, but an entire *family* of them. The different members of the family are distinguished by the particular values of their parameter sets. Although one sees many examples to the contrary, the correct usage of the word "parameter" is to signify the label that differentiates members of a family of relationships specified by a given model. For example:

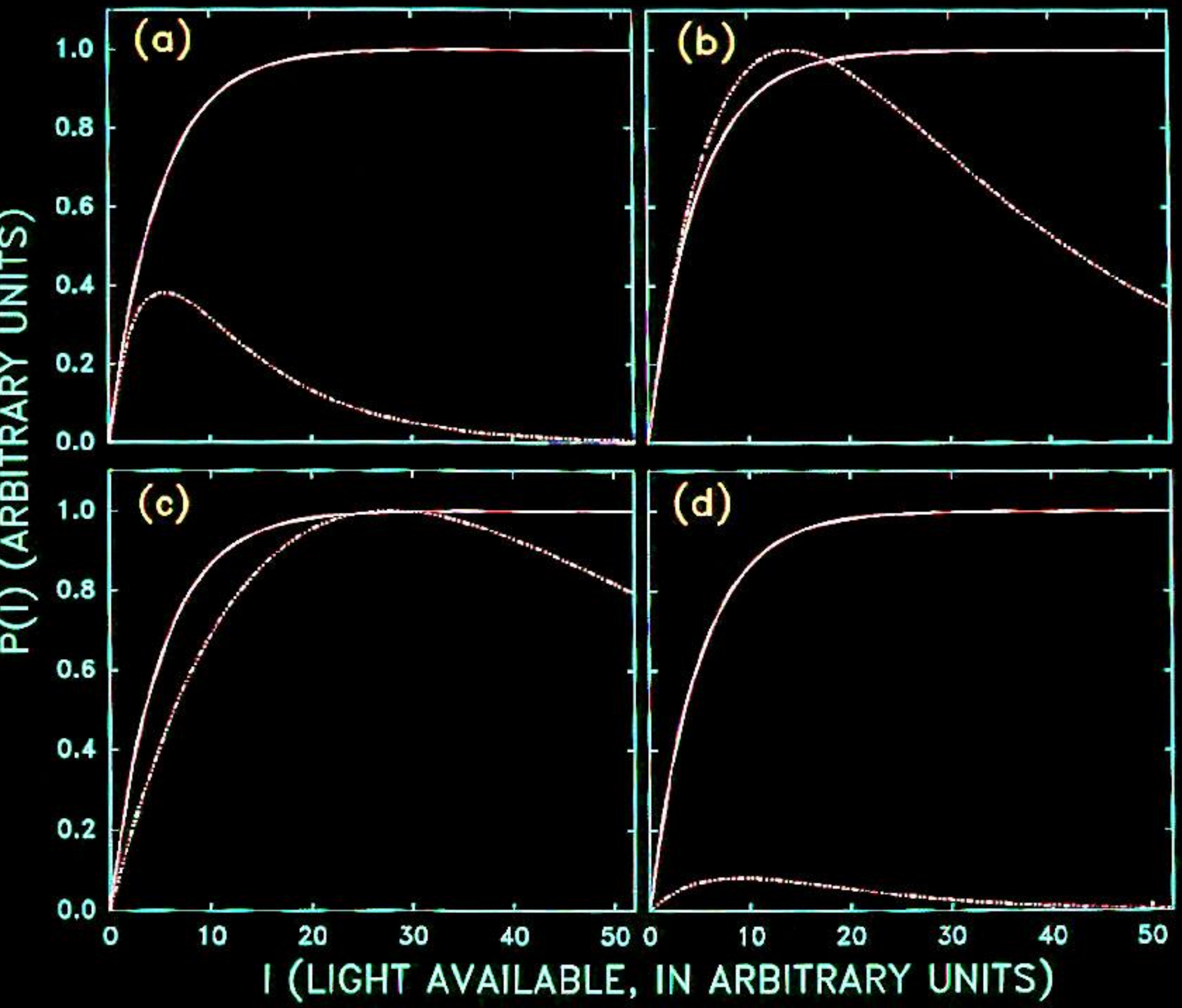
$$\text{Straight lines}: \qquad y = mx + c$$

$$\text{Circles centred at the origin}: \qquad x^2 + y^2 = r^2$$

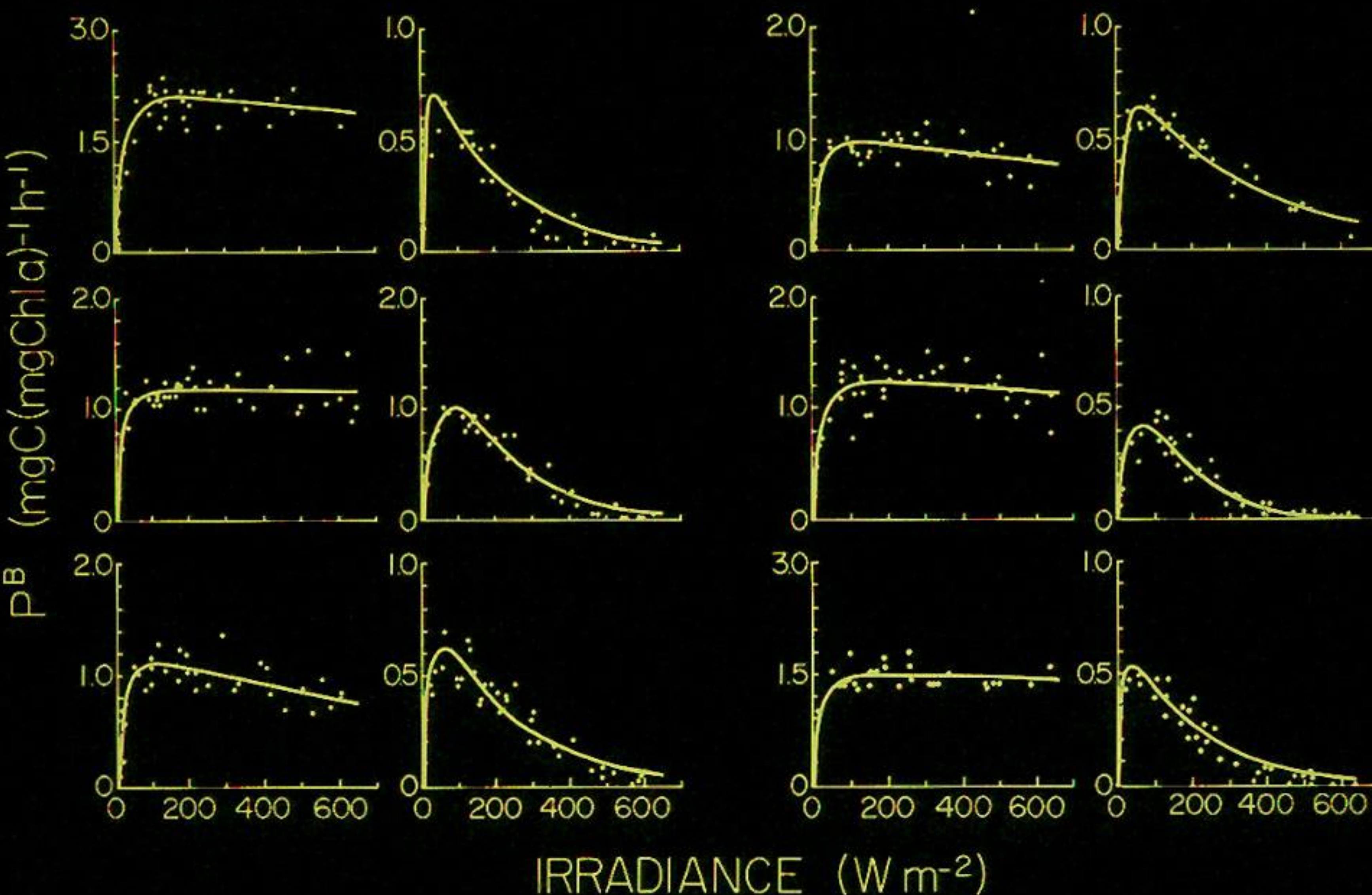
For the straight line, x is the independent variable, the slope m and intercept c are parameters. We can change the slope (and/or the intercept), so that the plot of y on x will change, but the underlying model (a straight line) will still be the same. Similarly, for the circle, an infinite variety exists, depending on the value assigned to the radius parameter. But they all conform to the same model.



P_m^B
P^B
α^B
I_k
I



(a)
(b)
(c)
(d)
P(I) (ARBITRARY UNITS)
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
50
I (LIGHT AVAILABLE, IN ARBITRARY UNITS)


P^B (mgC(mgChl a)^-1 h^-1)
IRRADIANCE (W m^-2)
0
200
400
600
3.0
2.0
1.5
1.0
0.5

Utility of remote sensing for estimation of oceanic primary production

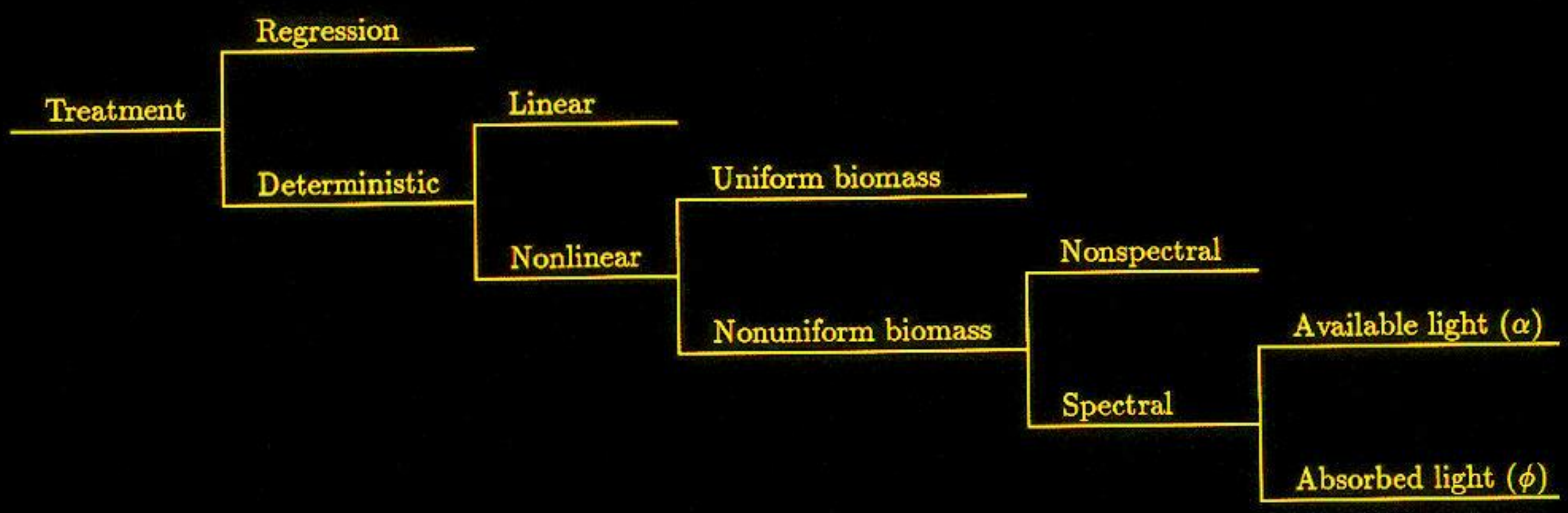
$$P = \frac{P}{B} \times B$$

- B has dynamic range of more than four decades
- Remote sensing gives synoptic view of this variation

The remote sensing method

- Uses all the available ship data
- In addition, uses the rich satellite archive
- Sees the ship and the satellite as complementary tools
- Is the method of choice

Hierarchy of Primary Production Models



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

$$P = P(I)$$

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

$$I_0 = I_0(t)$$

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

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

Dependence of result on second-order effects

$$P_{Z,T} = f(I_0^m, B; \alpha, P_m)$$

- α can be an explicit function of temperature and/or nutrients.
- P_m can be an explicit function of temperature and/or nutrients.

Alternatively, α and P_m can be prescribed, based on observations. In this case, the second-order effects will have contributed indirectly to the prescribed values of the parameters.

The basic equations

Light-saturation curve

$$P^B(I) = P_m^B \left(1 - e^{\alpha^B I / P_m^B}\right)$$

Light penetration

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

Diurnal variation of incident irradiance

$$I_0(t) = I_0^m \sin\left(\frac{\pi t}{D}\right)$$

Dimensional Analysis (1)

We expect that the solution for $P_{Z,T}$ will be a function of the variables B, D, I_0^m, and the parameters α^B and P_m^B. The most general statement of this expectation is

$$\int_{Z,T} P \sim B^q \, (\alpha^B)^u \, (P_m^B)^v \, D^w \, (I_0^m)^x \, K^y,$$

where q, u, v, w, x and y are exponents that remain to be determined. Let us take the basic dimensional set for the problem to be $[B]$, $[C]$, $[L]$, $[T]$, and $[F]$, respectively, the mass of pigment, the mass of carbon, length, time and photon flux. For dimensional consistency between the left- and right-hand sides of the equation above we must then have

$$[CL^{-2}] = [BL^{-3}]^q \, [CB^{-1}T^{-1}F^{-1}]^u \, [CB^{-1}T^{-1}]^v \, [T]^w \, [F]^x \, [L^{-1}]^y,$$

or, collecting terms

$$[CL^{-2}] = [B]^{q-u-v} \, [C]^{u+v} \, [T]^{w-u-v} \, [F]^{x-u} \, [L]^{-3q-y}.$$

Matching exponents on either side leads to the following set of simultaneous equations:

$$1 = u + v$$

$$0 = q - u - v$$

$$0 = w - u - v$$

$$0 = x - u$$

$$-2 = -3q - y.$$

Dimensional Analysis (2)

The simultaneous equations cannot be solved completely as the number of unknowns exceeds the number of equations (by one). If we choose x to be the indeterminate exponent, we have $q = 1$; $y = -1$; $w = 1$; $u = x$; and $v = 1 - x$. We conclude therefore that the general form of the solution is

$$\int_{Z,T} P \sim \frac{BP_m^B D}{K} \left(I_0^m \alpha^B / P_m^B\right)^x .$$

The terms in parentheses on the right hand side form a dimensionless group whatever the value of x. From Buckingham's theorem we are led to expect one such dimensionless group for each undetermined exponent. It is conventional to rewrite statements such as the equation above in the form

$$\int_{Z,T} P \sim \frac{BP_m^B D}{K} f\left(\frac{I_0^m \alpha^B}{P_m^B}\right),$$

where f is an undetermined function of the dimensionless group $(I_0^m \alpha^B / P_m^B)$.

Dimensional Analysis (3)

The solution is instructive. It implies that the quotient P_m^B/α^B, (which has the dimensions of irradiance and is designated by I_k) is the natural irradiance scale for the problem under discussion. That is to say, we may generalise the analysis further by working in terms of a normalised irradiance I_* obtained by scaling irradiance to I_k. In other words, we define a dimensionless, surface irradiance at local noon as

$$I_*^m = I_0^m / I_k .$$

We may then write

$$\int_{Z,T} P \sim \frac{BP_m^B D}{K} f\left(I_*^m\right).$$

The elements $(BP_m^B D/K)$ and $f(I_*^m)$ may be regarded as separate parts of the solution to $P_{Z,T}$. The factor $BP_m^B D/K$ is, to within a numerical constant, the scale factor for the solution. It has the same dimensions as daily, water-column production. The function $f(I_*^m)$ is dimensionless and may be tabulated, once and for all, over a suitable range of the normalised variable I_*^m at a particular value, say unity, of the scale factor. This is the most general and economical way to state the solution for $P_{Z,T}$.

Daily, watercolumn, primary production

Dimensional analysis shows that

$$P_{Z,T} = (BP_m^B D/K) f(I_0^m \alpha / P_m)$$

$$P_{Z,T} = (BP_m^B D/K) f(I_0^m / I_k)$$

$$P_{Z,T} = (BP_m^B D/K) f(I_*^m)$$

Regardless of the formulation of the photosynthesis-light curve

Reduction of models to canonical form

Dimensional analysis informs us that all the models can be reduced to the common format

$$P_{Z,T} = A \times f(I_*^m),$$

which we may refer to as the canonical form. It will show us how they relate to each other without our invoking or accessing any field data. This approach makes clear the assumptions, implied or expressed, associated with the use of each of the models.

The general approach for a given model is to factor out the quantity $A = BP_m^B D/(\pi K)$. The other factor, when expressed as a function of I_*^m, must then be $f(I_*^m)$.

Measurement of instantaneous rates

Dimensions

The dimensions of a rate quantity include time in the denominator

Applicability

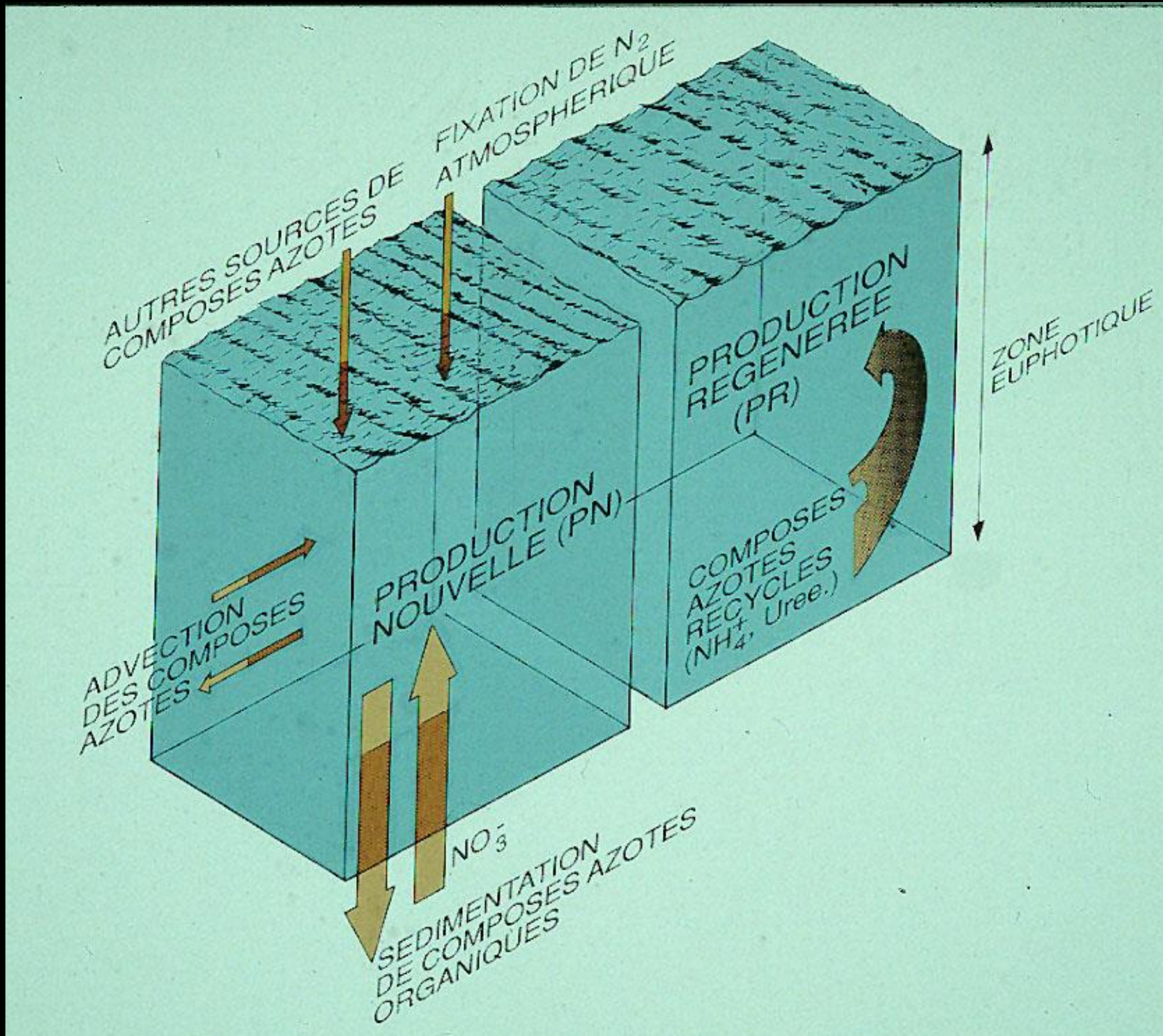
The intrinsic time scale for the method, or the time scale on which the results can be expected to apply, is related to the duration of measurement

Scales of Time and Space

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

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


AUTRES SOURCES DE
COMPOSES AZOTES
FIXATION DE N_2
ATMOSPHERIQUE
PRODUCTION
REGENEREE
(PR)
ZONE
EUPHOTIQUE
PRODUCTION
NOUVELLE (PN)
COMPOSES
AZOTES
RECYCLES
(NH_4^+, Uree.)
ADVECTION
DES COMPOSES
AZOTES
NO_3^-
SEDIMENTATION
DE COMPOSES AZOTES
ORGANIQUES

Primary Production at Regional Scale

Computation of primary production at regional scale has two components:

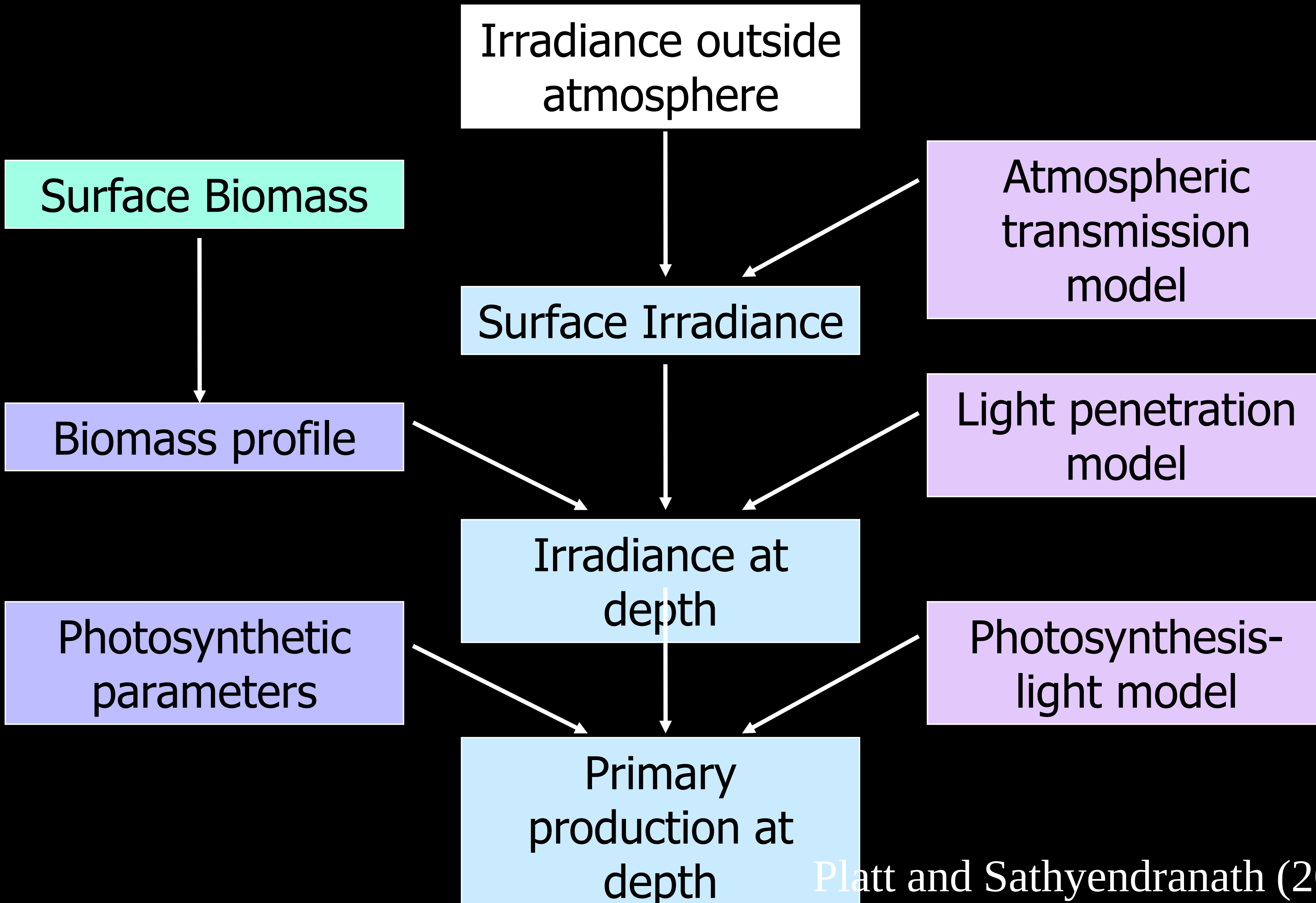
1. Construct local algorithm, assuming all necessary information will be available.

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

Basic Methodology For Computation of Primary Production

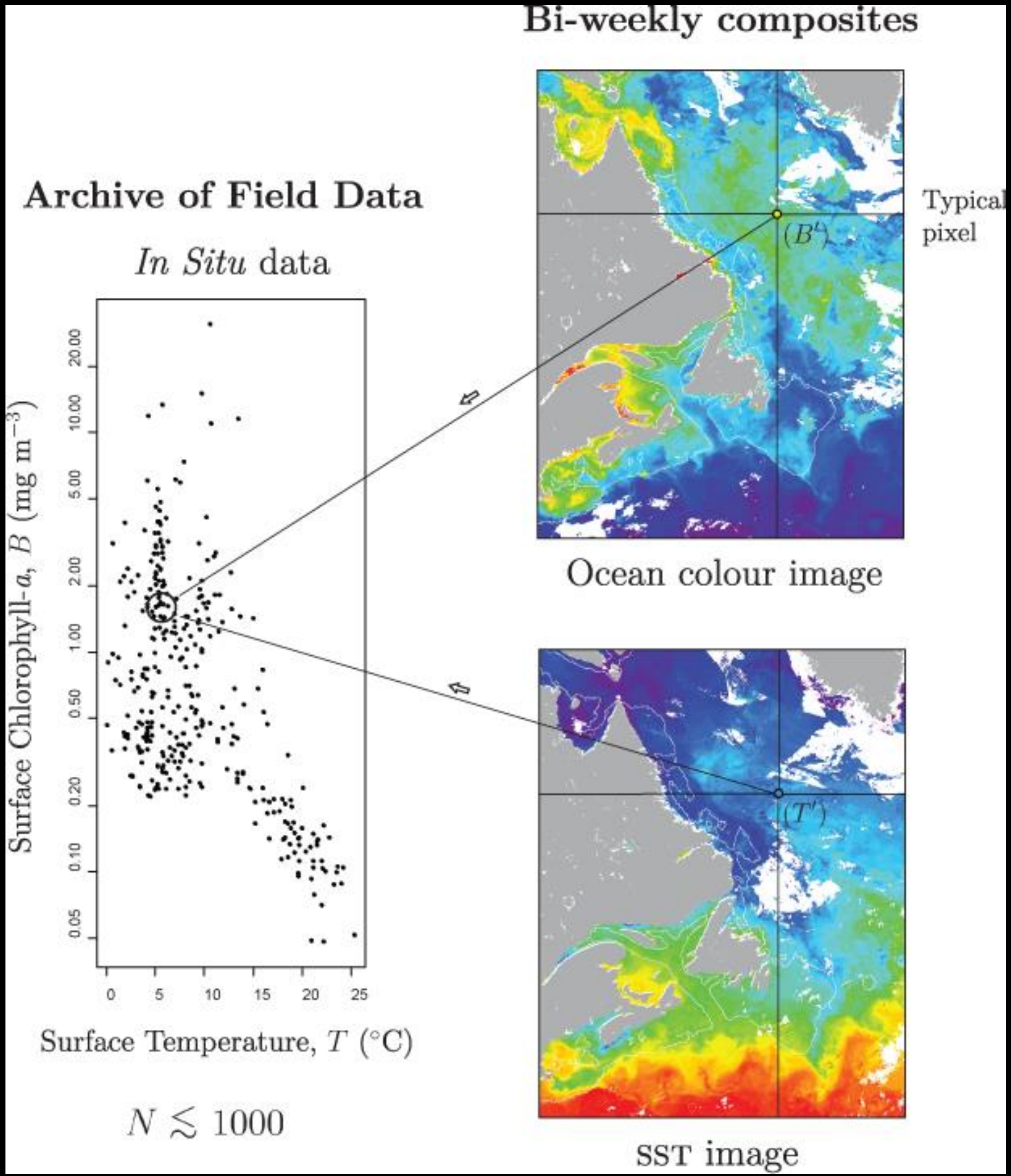
1. Compute light just below the sea surface
2. Estimate biomass at the surface
3. Define the biomass profile
4. Estimate parameters of the photosynthesis- light model
5. Compute parameters of light transmission underwater
6. Compute water-column primary production

Computation of primary production field



Platt and Sathyendranath (20

Assignment of Parameters for Computation of Primary Production



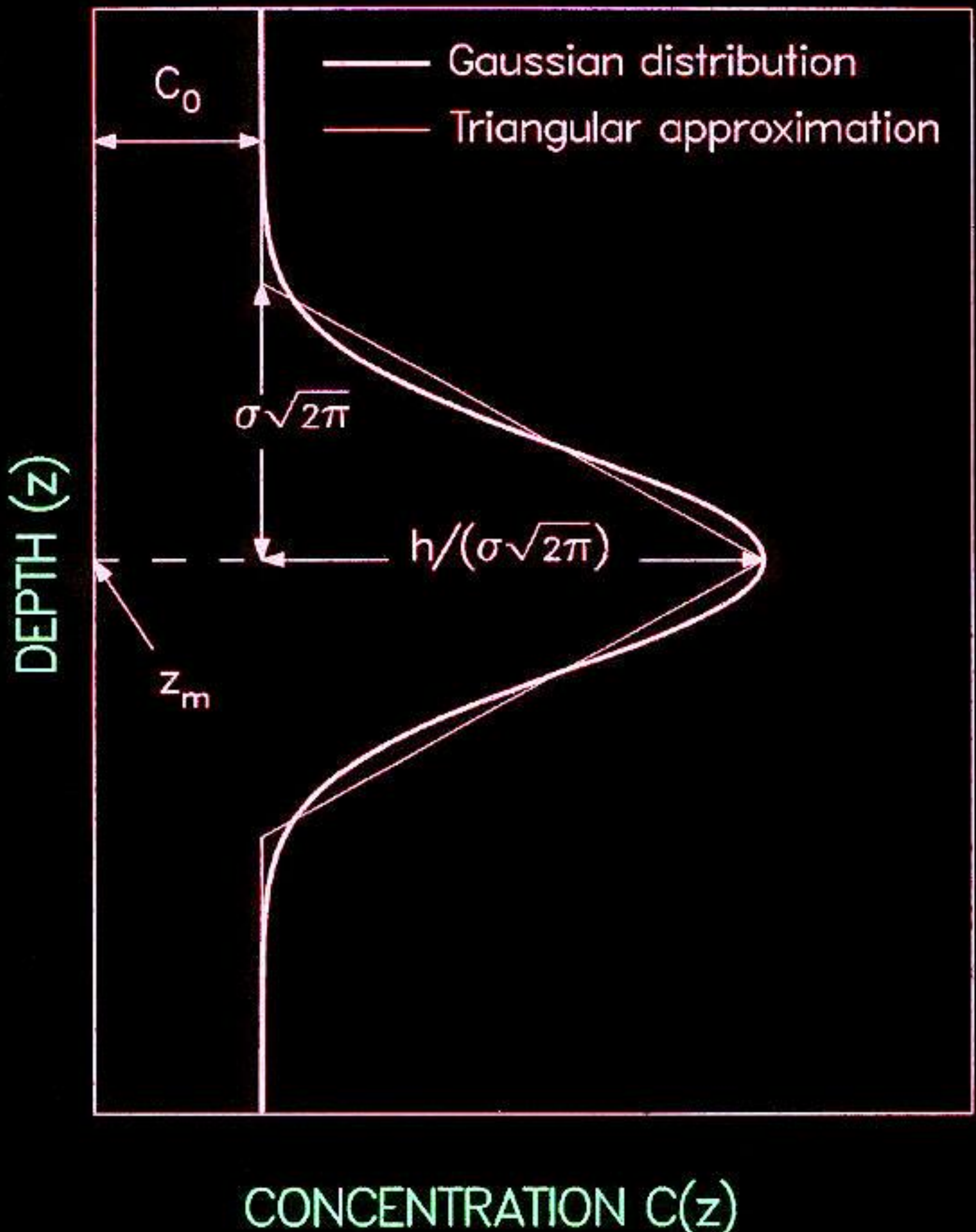
The model is robust, but needs a protocol for assignment of parameters relating to

(1) photosynthetic response; and

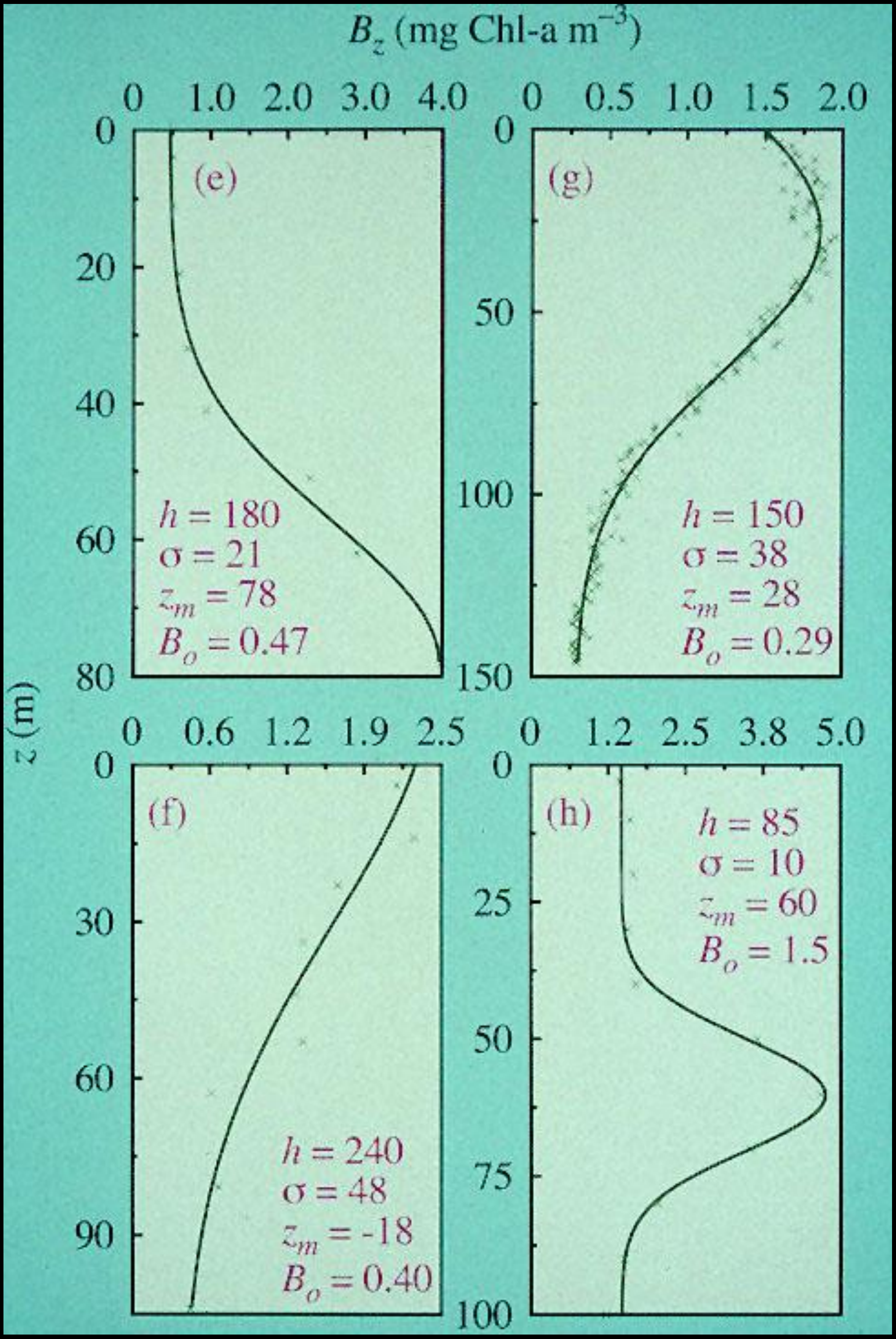
(2) vertical structure.

Our protocol uses remotely-sensed data as input

Platt et al. (2008)



Gaussian distribution
Triangular approximation
C_0
$\sigma\sqrt{2\pi}$
$h/(\sigma\sqrt{2\pi})$
z_m
DEPTH (z)
CONCENTRATION C(z)



B_z (mg Chl-a m^{-3})
z (m)
(e)
$h = 180$
$\sigma = 21$
$z_m = 78$
$B_o = 0.47$
(g)
$h = 150$
$\sigma = 38$
$z_m = 28$
$B_o = 0.29$
(f)
$h = 240$
$\sigma = 48$
$z_m = -18$
$B_o = 0.40$
(h)
$h = 85$
$\sigma = 10$
$z_m = 60$
$B_o = 1.5$

The $P-I$ curve

The light dependence of photosynthesis implies that:

$$P^B(z,t) = p\left(I(z,t);\, \alpha^B, P_m^B\right)$$

Light I and α^B always appear as products. Therefore we define a new quantity Π, given by:

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

The $P-I$ equation may then be written as:

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

Spectral and Non-Spectral Models

The light dependence of photosynthesis:

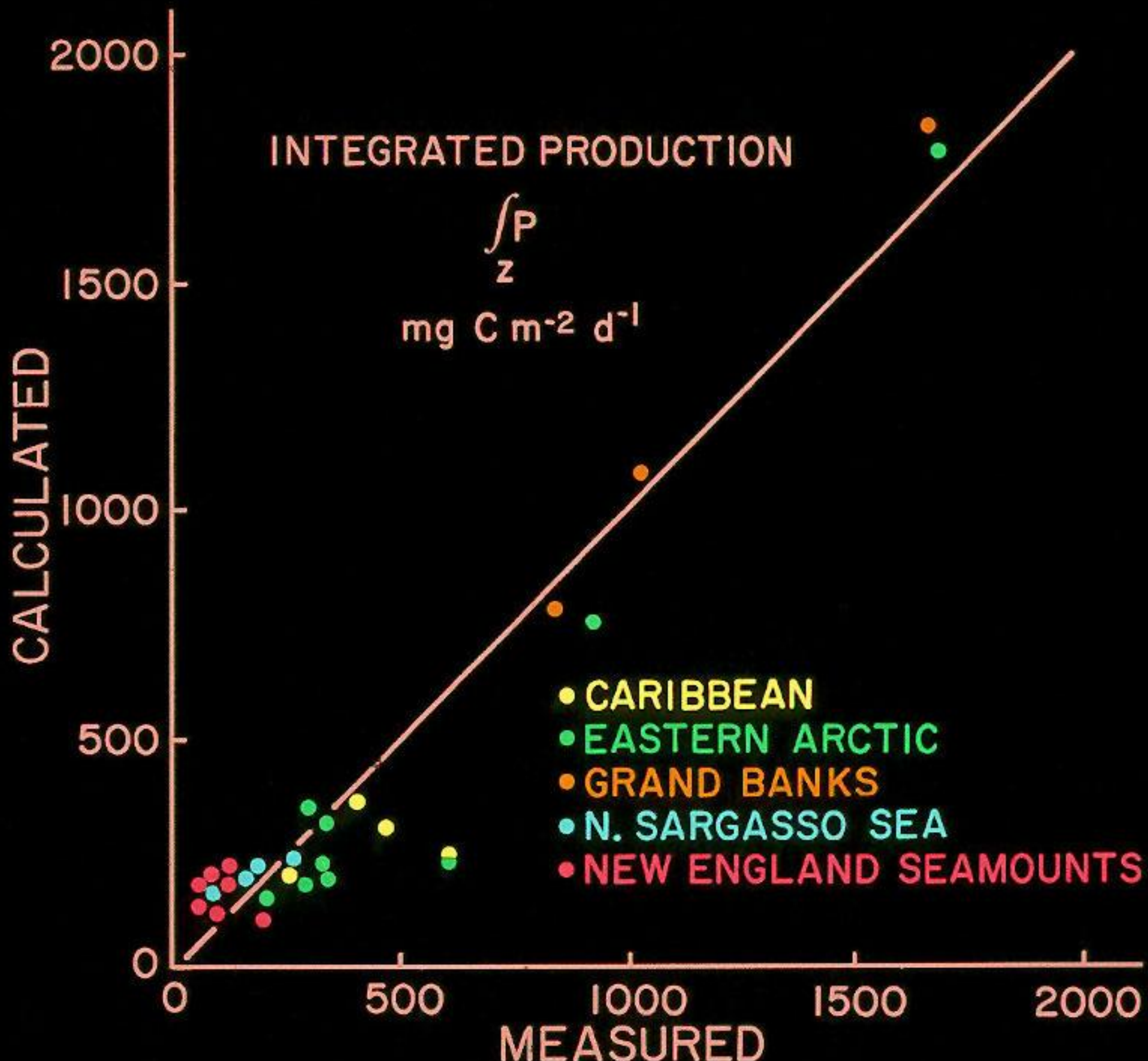
$$P^B(z,t) = p\left(\Pi(z,t), P_m^B\right)$$

Non-Spectral Model:

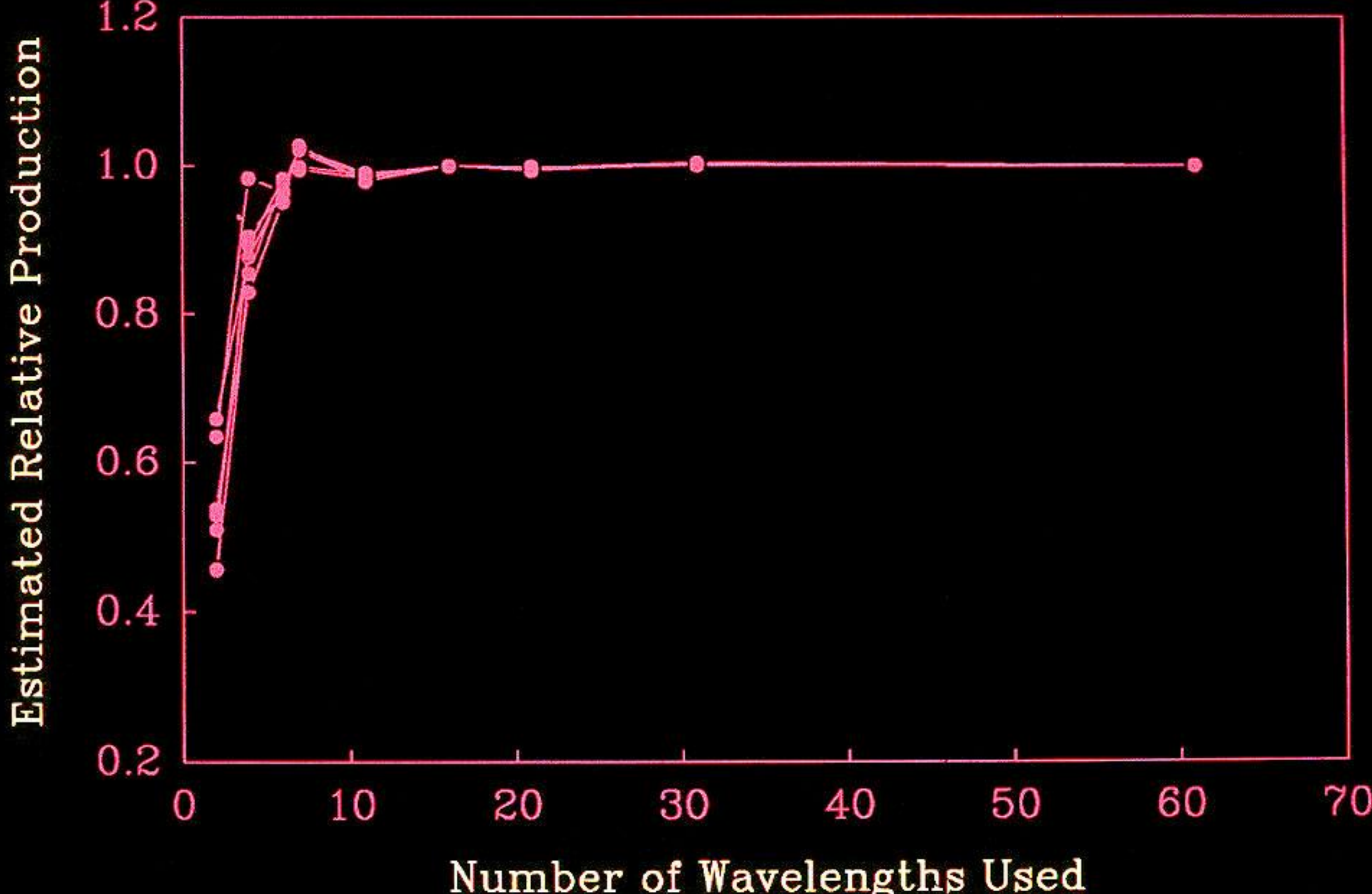
$$\Pi(z,t) = I(z,t)\alpha^B(z)$$

Spectral Model:

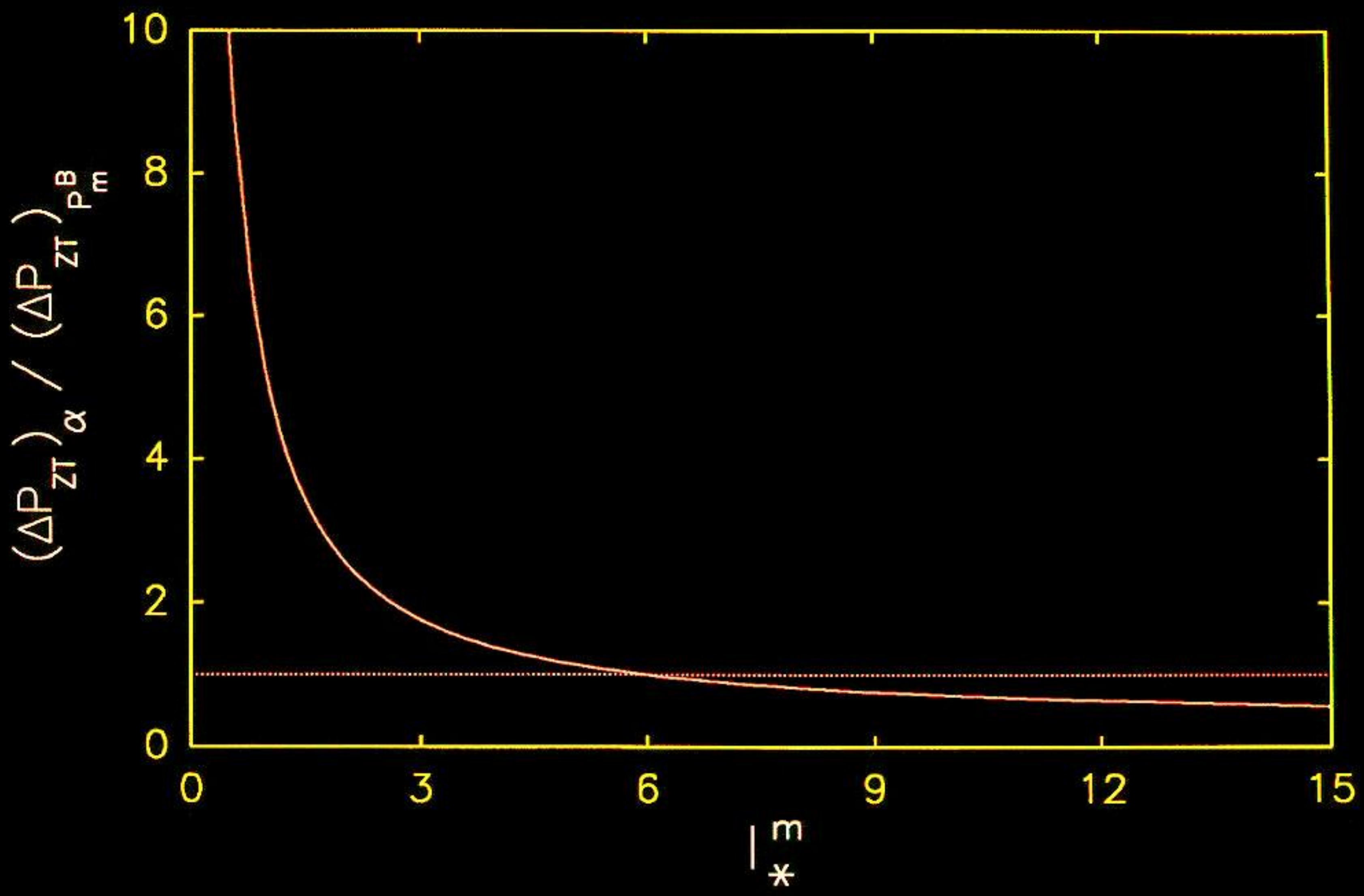
$$\Pi(z,t) = \int I(\lambda,z,t)\alpha^B(\lambda,z)\,d\lambda$$



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



Estimated Relative Production
1.2
1.0
0.8
0.6
0.4
0.2
0
10
20
30
40
50
60
70
Number of Wavelengths Used



10
8
6
4
2
0
0
3
6
9
12
15
$(\Delta P_{ZT})_\alpha / (\Delta P_{ZT})_{P_m^B}$
l_*^m

Available Light vs Absorbed Light Models

Available light model

$$\alpha = \lim_{I \to 0} \frac{dP}{dI}$$

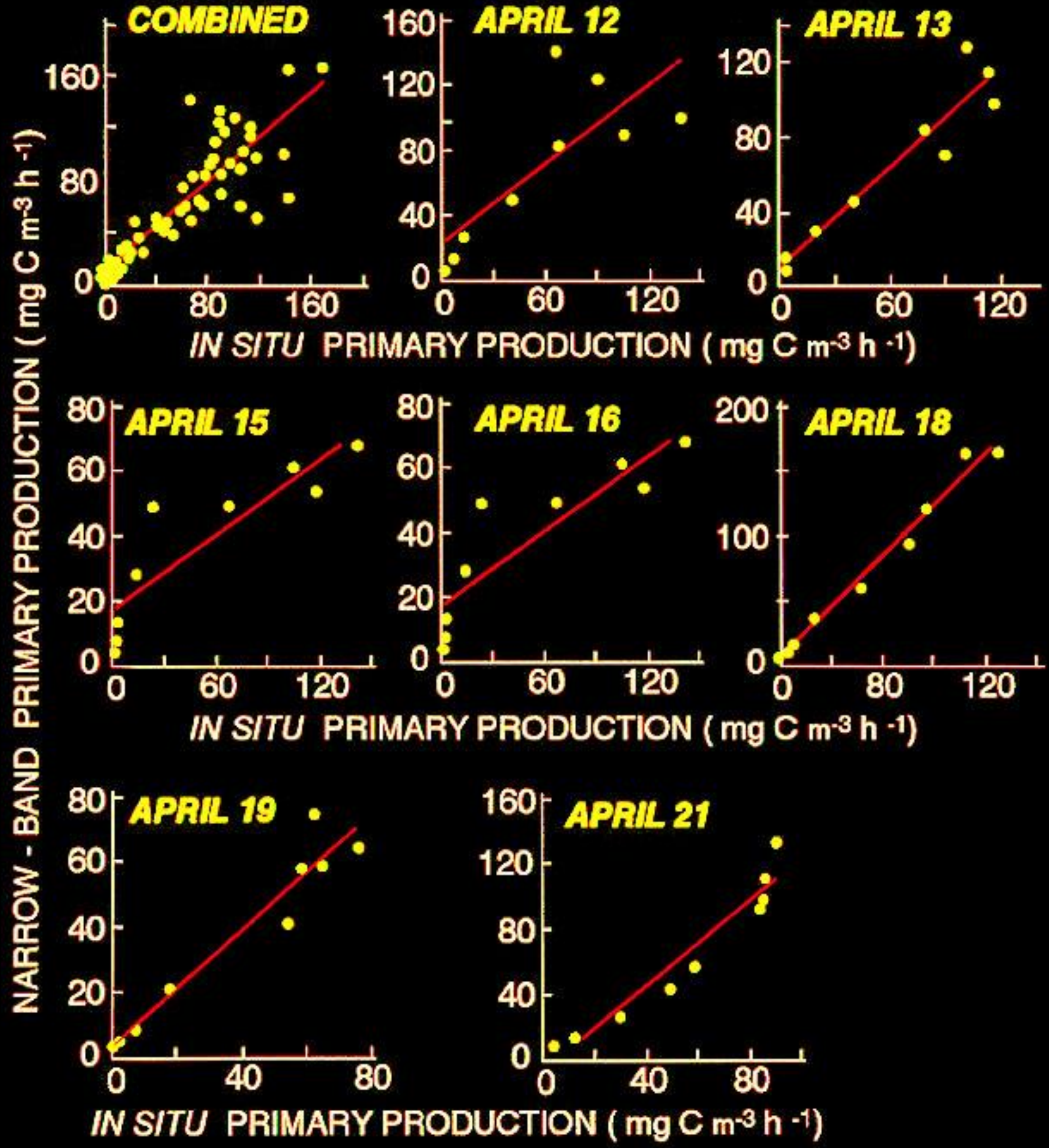
α is the initial slope of the photosynthesis-light curve. It characterises the efficiency of photosynthesis at low light.

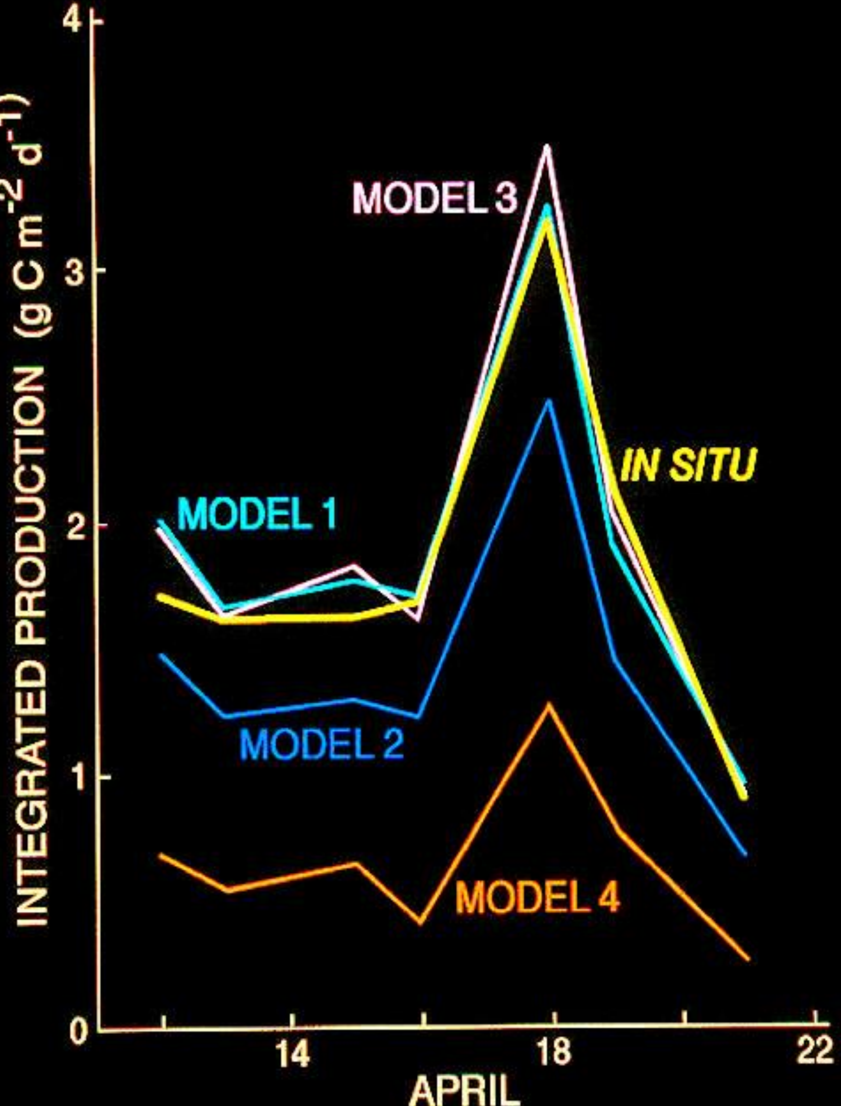
Absorbed light model

$$\alpha = \phi_m a_B^* B$$

ϕ_m is the maximum realised quantum yield.

The two models are entirely equivalent


COMBINED
APRIL 12
APRIL 13
APRIL 15
APRIL 16
APRIL 18
APRIL 19
APRIL 21
NARROW - BAND PRIMARY PRODUCTION (mg C m-3 h -1)
IN SITU PRIMARY PRODUCTION (mg C m-3 h -1)



INTEGRATED PRODUCTION (g C m-2 d-1)
4
3
2
1
0
MODEL 3
MODEL 1
IN SITU
MODEL 2
MODEL 4
14
18
22
APRIL

CONCLUSIONS

1) Primary production calculated by the spectral model is a good estimator of *in situ* production.

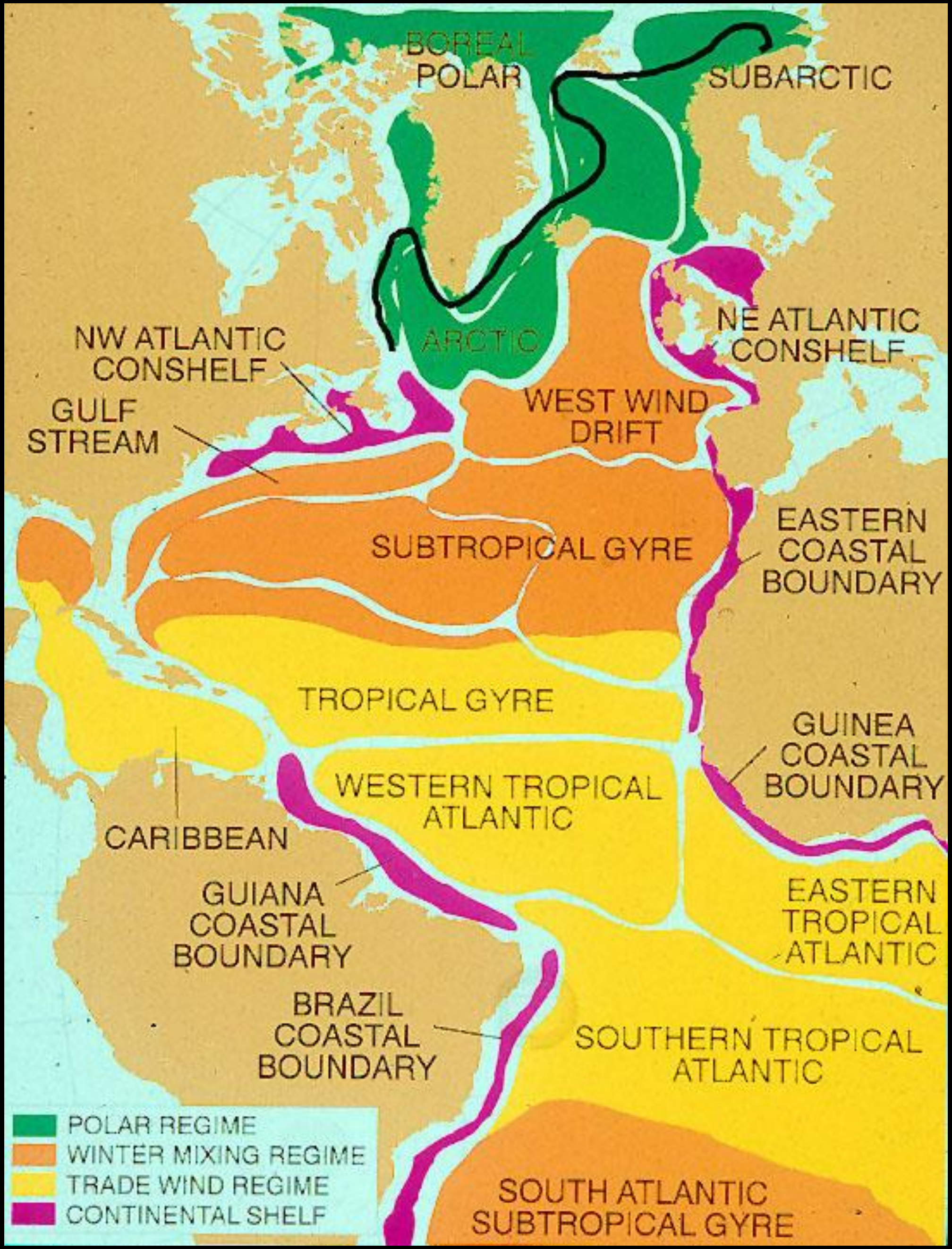
2) The broad-band model can underestimate primary production by over 60% when both the light and α are treated as wavelength-independent.

3) When the light is fully-spectral but α is not, the error is relatively low: less than 30%.

4) If light is computed using an average K, the results give a good estimate of *in situ* production, even when α is broad-band.

Biogeochemical provinces

1. Few in number for a given ocean.
2. Dynamic: Boundaries may vary with season and between years.
3. Instantaneous boundaries should be accessible to remote sensing.
4. Within seasons, have predictable properties (vertical structure; biogeochemical rate constants).
5. Provide templates for application of province-specific rules.


BOREAL
POLAR
SUBARCTIC
ARCTIC
NW ATLANTIC
CONSHELF
NE ATLANTIC
CONSHELF
GULF
STREAM
WEST WIND
DRIFT
SUBTROPICAL GYRE
EASTERN
COASTAL
BOUNDARY
TROPICAL GYRE
GUINEA
COASTAL
BOUNDARY
WESTERN TROPICAL
ATLANTIC
CARIBBEAN
GUIANA
COASTAL
BOUNDARY
EASTERN
TROPICAL
ATLANTIC
BRAZIL
COASTAL
BOUNDARY
SOUTHERN TROPICAL
ATLANTIC
POLAR REGIME
WINTER MIXING REGIME
TRADE WIND REGIME
CONTINENTAL SHELF
SOUTH ATLANTIC
SUBTROPICAL GYRE