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A Core Project of the International Geosphere-Biosphere Programme

JGOFS REPORT No. 27

PARAMETERS OF PHOTOSYNTHESIS: DEFINITIONS, THEORY AND INTERPRETATION OF RESULTS

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PARAMETERS OF PHOTOSYNTHESIS: DEFINITIONS, THEORY AND INTERPRETATION OF RESULTS

by

Egil Sakshaug, Annick Bricaud, Yves Dandonneau, Paul G. Falkowski, Dale A. Kiefer, Louis Legendre, André Morel, John Parslow and Masayuki Takahashi

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PARAMETERS OF PHOTOSYNTHESIS: DEFINITIONS, THEORY AND INTERPRETATION OF RESULTS

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ABSTRACT

A global assessment of carbon flux in the world ocean is one of the major undertakings of the Joint Global Ocean Flux Study (JGOFS). This has to be undertaken using historical *in situ* data of primary productivity. As required by the temporal and spatial scales involved in a global study, it can be conveniently done by combining, through appropriate models, remotely sensed information (chlorophyll *a*, temperature) with basic information about the parameters related to the carbon uptake by phytoplanktonic algae. This requires a better understanding as well as a more extended knowledge of these parameters which govern the radiative energy absorption and utilization by algae in photosynthesis. The measurement of the photosynthetic response of algae [the photosynthesis (*P)* versus irradiance (*E)* curves], besides being less shiptime-consuming than *in situ* primary production experiments, allow the needed parameters to be derived and systematically studied as a function of the physical, chemical and ecological conditions. The aim of the present paper is to review the significance of these parameters, especially in view of their introduction into models, to analyze the causes of their variations in the light of physiological considerations, and finally to provide methodological recommendations for meaningful determinations, and interpretation, of the data resulting from *P vs E* determinations. Of main concern are the available and usable irradiance, the chlorophyll *a*-specific absorption capabilities of the algae, the maximum light utilization coefficient (α), the maximum quantum yield (ϕ_m), the maximum photosynthetic rate (P_m), and the light saturation index (E_k). The potential of other, non-intrusive, approaches, such as the stimulated variable fluorescence, or the sun-induced natural fluorescence techniques is also examined.

1. INTRODUCTION

Although phytoplankton account for only 1-2% of the total global biomass, these organisms may fix between 35 and 45 Pg (petagrammes = 10^{15} grammes = gigatonnes) of carbon per year, *i.e.* no less than 30-60% of the global annual fixation of carbon on Earth (Berger *et al*. 1989, Falkowski 1994, Antoine *et al*. 1996).

When studying global carbon fluxes in the sea, primary productivity may be calculated on the basis of ocean color data provided by satellites (Platt and Sathyendranath 1988, Sathyendranath *et al*. 1989, Morel and André 1991, Lee et al. 1996, Behrenfeld and Falkowski 1997). Thus, whereas most ecological processes cannot be described at a global scale because the variables that should be observed are strongly undersampled, this is not so much the case for phytoplankton biomass. However, estimating marine primary productivity from remotely sensed information requires regional data on phytoplankton photosynthetic characteristics, which are still much undersampled (Longhurst *et al.* 1995).

In order to achieve a global synthesis of global carbon fluxes in the sea, mathematical models must be used, with light, temperature, nutrients and chlorophyll (Chl) *a* concentration as input variables. What is needed is not data for the net carbon fixation at a few given places, but a set of mathematical relationships between the above variables and the photosynthetic carbon flux, *i.e.* primarily the parameters of functions that relate the carbon fixation rate of phytoplankton to irradiance and chlorophyll Chl *a* concentration or light absorption.

The photophysiological responses of phytoplankton vary as a function of light regime, temperature and nutrient status. A major goal in understanding how phytoplankton photosynthesis affects carbon cycles, and is affected by ocean dynamics, is to determine how the photosynthetic processes respond to geochemical and physical processes. Understanding this is critical to developing prognostic models of the forcing and feedbacks between phytoplankton dynamics and ocean circulation. Even if there presently is a general understanding of photosynthetic responses to environmental variations, major difficulties remain regarding the application of this knowledge to specific oceanographic regimes. One strategy for developing reliable mathematical models to calculate photosynthetic rates under the present-day ocean forcing, as well as under climatically altered forcing regimes, is to exploit theoretical constructs of photosynthetic responses and apply these constructs to empirical measurements. Such an approach rests on the assumption that the behavior of composite variables can be related to geochemical and physical processes more readily than the complex variables derived from purely empirical approaches.

This paper, which is written by the JGOFS Task Team for Photosynthetic Measurements, presents definitions and theoretical considerations relevant to studies of the relationship between carbon uptake by phytoplankton and irradiance (*P vs E* curves) in phytoplankton, by means of the ^{14}C method (Steemann Nielsen 1952), and for estimating light absorption by phytoplankton. The paper also discusses methodological problems that may be encountered, and deals at length with the physiological interpretation of *P vs E* parameters. Although obtaining a satisfactory grid of observations is a major problem for estimating global marine productivity, this is not the focus of the

present paper. Therefore, the use of satellite observations, automated *in situ* instrumentation, etc., is cursorily treated.

2. DEFINITIONS AND THEORETICAL BACKGROUND

2A. General

In oxygenic photosynthesis, the term 'gross photosynthesis' is the rate of electron equivalents that have been photochemically extracted from the oxidation of water. Assuming the absence of any respiratory losses, it corresponds to the (gross) oxygen evolution rate.

If photosynthesis is measured as carbon uptake, the term 'gross carbon uptake rate' rate covers all photosynthetic carbon fixation, whether or not the organic carbon formed becomes part of the organisms or is excreted or secreted into the environment as dissolved organic or inorganic respiratory carbon (Williams 1993). This rate is generally lower than the gross oxygen evolution rate. The ratio of O_2 evolved per CO_2 fixed on a molar basis is called the photosynthetic quotient (PQ) and is larger than unity. This results from not all the energy captured by the photosystems being spent in the fixation of carbon. A fraction is used by the cells to reduce nitrate and, to a much smaller extent, reduce sulphate (Falkowski and Raven 1997). Thus high photosynthetic quotients are related to high nitrate utilization (Myers 1980, Langdon 1988, Laws 1991, Williams and Robertson 1991).

'Net photosynthesis' corresponds to the net evolution of oxygen following all autotrophic respiratory costs. In analogy, the 'net carbon uptake rate' is the carbon uptake rate following all losses of CO_2 due to oxidation of organic carbon in the cells in daylight. The net rates in terms of oxygen evolution and carbon uptake (assuming that production of extracellular organic matter is included) should be equivalent.

Primary productivity is a rate with dimensions mass (volume or surface area)$^{-1}$ time^{-1}. When dealing with phytoplankton, productivity is related to the cubic meter (m^3) as the unit of water volume and the square meter (m^2) as the unit of area.

The term 'gross primary productivity' is frequently used for the gross carbon uptake rate over a 24 h period. The term 'net primary productivity' is the organic carbon synthesized by phytoplankton that is subsequently available to the next trophic level (Lindeman 1942). Thus, 'net primary productivity' represents the carbon uptake rate following all daytime and nighttime respiratory losses. This term is therefore most successfully expressed over a 24 h period. Dissolved organic carbon (DOC) that is produced by the cells and subsequently released to the surrounding water is part of both net photosynthetic rate and net primary productivity, albeit not included in ^{14}C-based estimates of productivity if samples are filtered before analysis.

Net primary productivity is related to the 'growth rate', which can be defined as the net turnover rate for particulate carbon (not including production of DOC), provided that the cells are in steady-state (balanced) growth (Eppley 1981). In this definition, losses of matter/energy from the cells are included but not losses of cells due to external factors (*e.g.* grazing, sinking and horizontal transport). Among the external processes, grazing may represent a problem in incubation bottles (Eppley 1980). Although to some extent this may be eliminated, quite often estimates of the loss rate due to respiration reflect the community metabolism. It is therefore virtually

impossible to directly determine the contribution of algal respiration to the total respiratory losses in natural plankton communities (Williams 1993). The depth at which gross photosynthesis and respiration losses are equal is called the 'compensation depth' (zero net photosynthesis).

The 'euphotic zone' is the portion of the water column that supports net primary production. In this regard it is important to point out that the respiratory costs for the calculation of the compensation depth are for the autotrophs only and should be integrated over 24 hours. Above the compensation depth, net primary production is positive; below it, it is negative. Due to the impact of variations in environmental and other factors on gross photosynthesis and respiratory losses, the euphotic zone is easier to define than to measure. It is commonly assumed to be the water column down to the depth that corresponds to 1% of the photosynthetically available radiation at the surface. Serious problems are, however, associated with the 1% rule: It is now acknowledged that net photosynthesis may occur at depths down to 0.1% of PAR, and at high latitudes, because of the extreme daylength variation, net daily production may vary considerably with no change in the 1% level.

Assuming a mixed water column: at some depth, the gross carbon uptake rate, integrated over the above water column over 24 hours, will equal the diel, water column-integrated respiratory carbon losses above the same depth. This depth is called the 'critical depth' (Sverdrup 1953) and is always greater than the compensation depth. Although Sverdrup based his model on respiration as the only loss factor, the realized critical depth also depends on other loss factors, such as grazing, sinking and production of DOC (of which Sverdrup was aware). These losses are incorporated in many modern models that are extensions of Sverdrup's model.

P vs E parameters and bio-optical parameters are conveniently normalized to Chl *a*. This has been and still is the only pigment routinely measured at sea, using simple techniques. Because Chl *a* is the terminal photosynthetic pigment in light absorption (even if the energy has been captured by accessory photosynthetic pigments, it must be transferred to chlorophyll *a* before it can be utilized for the photochemical reactions), the amount of Chl *a* is generally used as an index of the living, photosynthetically active phytoplankton biomass. Because of the up to tenfold variation in the carbon to chlorophyll ratio in natural phytoplankton communities, chlorophyll *a* data should not be used without qualification for estimating algal carbon. Direct measurement of algal carbon in nature is impossible in most cases because it is inseparable from non-algal carbon by any convenient and reliable approach.

In the present paper, the term chlorophyll *a* is abbreviated Chl *a* and includes the divinyl-chlorophyll *a* of prochlorophytes. The Chl *a* concentration is denoted [Chl *a*], with units mg m^{-3} (or moles m^{-3}).

We generally suggest an asterisk (*) instead of the superscript B (with the general meaning of biomass) to denote the usual normalization of productivity-related parameters and variables to Chl *a* concentration (*e.g.* P^* instead of P^B for the Chl *a*-normalized photosynthetic rate). Other normalizations may be preferable and possible in some circumstances, *i.e.* per cell, per unit carbon, etc.

One should note that using mass units for some parameters and mol units for others may necessitate the use of molar weights in the derivation of parameters from other parameters. We recommend the use of mol units for carbon uptake and oxygen evolution, together with mol photons for irradiance, as the most consistent approach.

2B. Irradiance

Photosynthesis is a photochemical process. Because any absorbed photon with a wavelength in the range 350-700 nm may be equally effective in producing a photochemical charge separation, irrespective of wavelength, it is convenient (albeit not necessary) to express the amount of radiant energy which fuels photosynthesis in terms of photons (the quanta or "particles" of electromagnetic radiation) with a specified wavelength or frequency.

'Photosynthetic Available Radiation' ('PAR') has been defined in reference to the above spectral interval according to the SCOR/UNESCO Working Group 15 (Tyler 1966). For reasons related to the technical difficulty of measuring light in the near-ultraviolet region, this interval was reduced to 400-700 nm. Neglecting the near-UV (350-400 nm) domain usually does not entail a significant error because the contribution of this radiation range to the total (350-700 nm) is small, of the order of 5-7% for the incident radiation at the ocean surface. In the bluest, oligotrophic waters, however, in which the near-UV radiation may be more penetrating than light of wavelengths >500 nm (green, yellow, red), the UV proportion increases with depth and may represent up to 15% of PAR near the bottom of the euphotic zone.

The radiometric quantity to be considered and measured in studies of photosynthesis is the amount of radiant energy incident per of unit time and unit of area. This quantity is termed 'Irradiance'. It is represented by the symbol E and is expressed in energetic units (W m^{-2}) or quantum units (mol photons m^{-2} s^{-1}). The symbol '*I*', which is often used for irradiance, should be avoided as it can be confused with the same symbol used for 'Radiant Intensity' (units W sr^{-1}). 'Radiance', with the symbol '*L*', is the radiant flux in a given direction per unit angle per unit area, and expressed by W m^{-2} sr^{-1} (Morel and Smith 1982). Integrals of radiances over a finite solid angle and under specified conditions lead to the various irradiances (Table 1).

It is generally assumed that phytoplankton cells may collect radiant energy equally from all directions so that 'Scalar Irradiance' is the required quantity (WG-15, SCOR/UNESCO recommendations; see Table 1). It has the symbol $\overset{o}{E}$ (or E_o) according to IAPSO, the International Association for the Physical Sciences of the Ocean (Morel and Smith 1982). $\overset{o}{E}$ for a given wavelength is denoted (λ) and has also been termed PAR(λ) in the bio-optical literature. $\overset{o}{E}$ (λ) has the units W m^{-2} nm^{-1} or mol photons m^{-2} nm^{-1} s^{-1}. The total irradiance over the whole PAR range can be computed in either energetic (Eq 1) or quantum units (Eq 2):

$$\overset{o}{E}_{\mathrm{PAR}} = \int_{400\,\mathrm{nm}}^{700\,\mathrm{nm}} \overset{o}{E}(\lambda)\,\mathrm{d}\lambda \qquad [1]$$

[$\overset{o}{E}$ (λ) in W m^{-2} nm^{-1}]

$$\overset{o}{E}_{\mathrm{PAR}} = (1/hc) \int_{400\,\mathrm{nm}}^{700\,\mathrm{nm}} \overset{o}{E}(\lambda)\lambda\,\mathrm{d}\lambda \qquad [2]$$

[$\overset{o}{E}_{\mathrm{PAR}}$ in photons m^{-2} s^{-1}, $\overset{o}{E}$ (λ) in W m^{-2} nm^{-1}]

To obtain mol photons m^{-2} s^{-1}, the number of photons resulting from Eq 2 must be divided by Avogadro's number (N = 6.022 $\times$ 10^{23}). PAR represents roughly 40-45% of the total solar radiation at the sea level (Kirk 1994).
The energy of a photon (ε) is related to its wavelength (λ) by Planck's law: $\varepsilon = hc/\lambda$ where h is Planck's constant (6.626 $\times$ 10^{-34} Joule seconds) and c is the speed of electromagnetic radiation *in vacuo* (2.9979 $\times$ 10^8 m s^{-1}). Thus PAR measurements in terms of power cannot be accurately

transformed in terms of photons, and *vice versa*, unless the spectral distribution of the irradiance is known. Nevertheless, approximate conversions for incident solar radiation, as well as for in-water irradiance, are possible (*e.g.* Morel and Smith 1974).

As the air-water interface is essentially a plane, the rate of radiant energy able to enter the ocean is represented by the symbol E_d (Table 1), the downwelling irradiance at null depth (just beneath the interface). This irradiance is generally measured just above the surface and must be corrected for by the loss by reflection at the interface in order to provide the energy actually introduced into the water column (Section 3A).

In the following sections the term 'irradiance' is used. One should, however, bear in mind that scalar irradiance is assumed for under-water irradiance data that will be related to algal photosynthesis and growth ($\overset{o}{E}$ in equations).

2C. Chlorophyll *a*-specific absorption coefficient of phytoplankton

The 'Chl *a*-specific absorption coefficient' (cross section) is crucial for calculation of the impact of phytoplankton on the absorption coefficient of seawater and how much light is absorbed by the phytoplankton in bio-optical models of marine primary production. It has the symbol $a^*_\phi(\lambda)$ and units m^2 (mg Chl a)$^{-1}$.
The magnitude and the spectral shape of $a^*_\phi(\lambda)$ are not constant. Inter and intra-specific differences exist within rather wide intervals. They originate from chemical effects, *i.e.* pigment composition (Prézelin and Bozcar 1986) as well as physical effects, *i.e.* packaging. Both these effects usually result from physiological acclimation (Sections 2F.4 and 3E).
In the calculation of light that is actually absorbed by the phytoplankton, one needs the mean Chl *a*-specific absorption coefficient, a^*_ϕ defined in relevance to the actual spectral composition of light source used in a given experiment (*in situ* or *in vitro*):

$$\overline{a^*_f} = \left[\overset{o}{E}_{\mathrm{PAR}}\right]^{-1} \cdot \int_{400\,\mathrm{nm}}^{700\,\mathrm{nm}} a^*_f(\lambda)\overset{o}{E}(\lambda)\,\mathrm{d}\lambda \qquad [3]$$

The dimensionless algal absorption coefficient of phytoplankton, $A_\phi(\lambda)$, is needed to calculate 'Photosynthetically Usable Radiation' (PUR) that represents the fraction of PAR at such wavelengths that can be absorbed by phytoplankton. $A_\phi(\lambda)$ is defined in the 0-1 interval, according to:

$$A_f(\lambda) = a^*_f(\lambda)a^{*\,-1}_{f\,\mathrm{m}} \qquad [4]$$

$a^*_{\phi\mathrm{m}}$ is the maximum value of $a^*(\lambda)$, reached at the wavelength λ_m which is generally found at around 440 nm. PUR is computed as:

$$\overset{o}{E}_{\mathrm{PUR}} = \int_{400\,\mathrm{nm}}^{700\,\mathrm{nm}} A_f(\lambda)\overset{o}{E}(\lambda)\,\mathrm{d}\lambda \qquad [5]$$

From Eqs 3, 4 and 5, it follows that

$$\overline{a^*_f} \cdot \overset{o}{E}_{\mathrm{PAR}} = a^*_{f\,\mathrm{m}} \cdot \overset{o}{E}_{\mathrm{PUR}} \qquad [6]$$

TABLE 1. Recommended symbols and units relevant to aquatic photosynthesis. All the radiometric quantities (part A), except PAR, can be considered as spectral quantities, with the argument ë (wavelength) added. PAR is already integrated over a wide spectral range, 350 or 400 nm to 700 nm; see Section 2.B. Among the other quantities, a^*, A_ϕ, σ_{PSU}, σ_{PSII}, α^*, E_k, and β^* have spectral properties; ϕ_m is usually treated as spectrally independent. An asterisk (*) denotes normalization to the amount (mg) of chlorophyll *a*.

	Symbol	Units
A. RELEVANT RADIOMETRIC QUANTITIES		
Radiant energy	Q	J (= 1 Ws)
Radiant power or flux	Φ, F	W
Radiance	L	W m^{-2} sr^{-1}
[its directional character is often depicted by a zenith angle (Θ) and an azimuth angle (ϕ), *e.g.* $L(\Theta,\phi)$]		
Scalar irradiance[1]	$\overset{o}{E}$	W m^{-2}
[$\overset{o}{E} = \int_{\equiv} L(\Theta,\phi)\, d\Omega$; Ω is the solid angle and $\equiv$ ($=4\pi$ sr) the whole space] mol photons m^{-2} t^{-1}		
Plane irradiance		
Downward	E_d	W m^{-2}
Upward	E_u	W m^{-2}
[$E_d = \int_{\equiv d} L(\Theta,\phi)\cos\Theta\, d\Omega$; $\equiv_d$ ($=2\pi$ sr) represents the upper hemisphere, *i.e.* all downward directions. Similar integration over the lower hemisphere, $\equiv_u$ (all upward directions), provides E_u]		
Photosynthetically available radiation[1,2]	PAR	mol photons m^{-2} t^{-1} (or W m^{-2})
(as $\overset{o}{E}$, see Eqs 1 and 2)		
Irradiation (radiant exposure)	H	J m^{-2}
For a duration Δt, $H = \int_{\Delta t} E(t)dt$ where E is $\overset{o}{E}$, E_d or PAR		mol photons m^{-2}
Absorption coefficient	a	m^{-1}
Scattering coefficient	b	m^{-1}
Attenuation coefficient (= a + b)	c	m^{-1}
Vertical attenuation coefficient	K	m^{-1}
[for a radiometric quantity $x = L, \overset{o}{E}, E_d ..., K = -d\ln x/z$, where z is depth, measured positive downward]		
B. BIO-OPTICAL AND DARK-REACTION PARAMETERS AND VARIABLES		
Chl *a*-specific absorption coefficient	a^*	m^2 (mg Chl *a*)$^{-1}$ (Eqs 4, 5, 11)
Dimensionless algal absorption coefficient	A_ϕ	dimensionless (Eq 6)
Photosynthetically usable radiation	PUR	(as $\overset{o}{E}$, PAR) (Eqs 7, 8)
Number of photosynthetic units[3]	n	mol X (mg Chl *a*)$^{-1}$
Functional cross section of PSU[4]	σ_{PSU}	m^2 (mol X)$^{-1}$

Table 1. continued

	Symbol	Units
Cross section of PSII	σ_{PSII}	m^2 (mol photons)$^{-1}$
Quantum yield	ϕ	mol X (mol photons)$^{-1}$
Maximum quantum yield (= $\alpha^*/a_f^* = \sigma_{PSII}/\sigma_{PSU}$)	ϕ_m	as ϕ (Eqs 9, 10)
Minimum turnover time for photons in PSII[1]	τ	t
Instantaneous rate of fluorescence	J_f	mol photons s^{-1}
Quantum yield of fluorescence	ϕ_f	photons emitted (photons absorbed)$^{-1}$
C. P-E PARAMETERS AND VARIABLES		
Photosynthetic rate[1,3]	P^*	mol X (mg Chl *a*)$^{-1}$ t^{-1}
Maximum photosynthetic rate[5] (= $n\,\tau^{-1}$)	P_m^*	as P^*
Maximum light utilization coefficient[3,6] (=$a_f^*\,\phi_m = n\,\sigma_{PSU}\,\phi_m = n\,\sigma_{PSII}$)	α^*	mol X m^2 (mg Chl *a*)$^{-1}$(mol photons)$^{-1}$ (Eqs 9, 10, 12, 14)
Light saturation parameter =[P_m^*/α^*, = $1/(\sigma_{PSII}\,\tau)$]	E_k	as $\overset{o}{E}$
Photoinhibition parameter	β^*	as α^*
D. WATER COLUMN PARAMETERS		
Water column light utilization index[7]	ψ_α^*	as α^* (Eq 17)
Water column photosynthetic cross-section[7]	ψ_E^*	as a^* (Eq 18)
Maximum Chl *a*-normalized photosynthetic rate within a water column maximum	P_{opt}^*	as P_m^*

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[1]the unit of time, t, should be the same for these variables and parameters; either second or hour.

[2]the terms photon flux or photon flux density should be avoided.

[3]X denotes C fixed or O_2 evolved; mol units are recommended, to avoid the use of conversion factors.

[4]or 'absorption cross section per unit of mass (mg) Chl *a*'; a_f^* refers to absorption by phytoplankton only; for decomposition of a^* and a of water, see section 2C and Eq. 3.

[5]also known as the 'assimilation number', not to be recommended because a 'number' implies a dimensionless quantity and, like P^*, as the 'photosynthetic capacity'.

[6]also known as the 'photosynthetic efficiency', not to be recommended because a 'number' implies a dimensionless quantity.

[7]per unit Chl *a* mass.

2D. Total and partial absorption coefficients

The 'total absorption coefficient' of seawater, a (m^{-1}) is an 'inherent' optical property of seawater (*sensu* Preisendorfer 1961). It can therefore be expressed as a sum of partial coefficients:

$$a(\lambda) = a_w(\lambda) + a_f(\lambda) + a_{NAP}(\lambda) + a_{DS}(\lambda) \quad [7]$$

The coefficient $a_\phi(\lambda)$ represents the contribution by algal pigments; $a_w(\lambda)$ that by the water itself, $a_{NAP}(\lambda)$ that by non-algal particulate matter, and $a_{DS}(\lambda)$ that by dissolved colored material. The coefficient $a_\phi(\lambda)$ is the sum of the absorption coefficients for photosynthetic pigments [$a_{PS}(\lambda)$] and algal non-photosynthetic pigments [$a_{NPS}(\lambda)$]. Absorption due to all kinds of suspended particles (phytoplankton, bacteria, heterotrophs, debris and various detritus, including minerogenic types) may be represented by the sum $a_\phi + a_{NAP} = a_P$.
By definition, $a_\phi(\lambda)$ can be predicted if $a^*_\phi(\lambda)$ and [Chl *a*] are known:

$$a^*_f(\lambda)[\text{Chl } a] = a_f(\lambda) \quad [8]$$

Phytoplankton pigments modulate, through $a_\phi(\lambda)$, the absorption coefficient of seawater considerably, thus modifying the submarine light field strongly (*e.g.* algal self shading in the water column, ocean color), and this effect provides the basis for remote sensing of the pigment concentration. Dissolved substances that are of organic origin (known as 'yellow substances', 'gilvin', or 'Gelbstoff') may affect the total absorption coefficient considerably in some coastal waters where river input is prominent. The coefficient for pure seawater, a_w, has been determined in laboratory experiments; some uncertainties remain because of the extremely low absorption by water in the blue part of the spectrum.

In aquatic systems, the bulk coefficient $a(\lambda)$ can, at least in principle, be measured *in situ*, and the absorption spectra of filtered particles, $a_P(\lambda)$, can be measured and to some extent partitioned into components (Sections 3A,B). Finally, $a_{DS}(\lambda)$ can be measured on filtered water samples, using an appropriate blank.

2E. Photosynthesis versus irradiance curves (*P vs E* curves)

Photosynthetic rates are related to irradiance in a non-linear fashion. To parametrize this relationship, *P vs E* data are needed. In a *P vs E* determination, a series of subsamples drawn from a single seawater sample with known [Chl *a*] is incubated in a gradient of artificial light, at a temperature as close as possible to natural conditions. The *P vs E* response should ideally refer to instantaneous light and provide information on the photoacclimational state of the phytoplankton at the moment of sampling. However, unless incubation time is only a few minutes, some acclimation will take place during incubation, especially in terms of the photoprotective apparatus of phytoplankton. Therefore "ideal" measurements fully relevant to the state of phytoplankton at the moment of sampling are not possible to carry out in the field.

If ^{14}C is used to estimate photosynthetic carbon fixation and if the duration of incubation is so short that newly incorporated carbon is not respired or recycled within the cell, it can be assumed that *P vs E* measurements would yield results that are close to the gross carbon uptake rate (Dring and Jewson 1982, Williams 1993). Therefore, commonly employed *P vs E* functions for carbon uptake rate pass through the origin.

There are at present no satisfactory methods for estimating the gross or the net carbon uptake rates accurately. Even short incubations may fail in yielding the gross uptake rate (Williams *et al.* 1996a,b). In terms of primary productivity, however, night-time respiratory losses may be more important than the daytime difference between gross and net carbon uptake rates. Incubations of 24 h duration or more using the ^{14}C method is unsatisfactory because of the artefacts that may be introduced. The oxygen method is not yet sensitive enough to resolve the variations caused by photosynthesis in the oligotrophic parts of the ocean.

The *P vs E* response typically can be described with three major regions:

i. At the lowest irradiances, photosynthetic rates are virtually linearly proportional to irradiance, *i.e.* the absorption of photons is slower than the capacity rate of steady-state electron transport from water to CO_2.
ii. As irradiance increases, photosynthetic rates become increasingly non-linear and rise to a saturation level, at which the rate of photon absorption greatly exceeds the rate of steady-state electron transport from water to CO_2.
iii. With further increase in irradiance, a reduction in the photosynthetic rate relative to the saturation level may take place (photoinhibition), dependent upon both the irradiance and the duration of exposure.

Several *P vs E* equations have been proposed through the years. Most of them fit *P vs E* data adequately. Because none of them are "theoretically" perfect, one particular formulation is not recommended above others. One should, however, be aware that different formulations may yield different parameter values when fit to the same set of data (Section 3F).

2F. *P vs E* Parameters

The *P vs E* parameters conventionally in use are α^* (the initial slope of the *P vs E* curve), P^*_m (the 'maximum photosynthetic rate'), E_k (the 'light saturation index', *i.e.* the ratio P^*_m/α^*), and β^* (the 'photoinhibition parameter'). The 'Maximum Quantum Yield' for photosynthesis, ϕ_m, is implicit in α^* (Section 2F.1). The photosynthetic rate in the lower part of the water column (low light) is determined largely by α^* and in the surface layers (strong light) by P^*_m; E_k representing the transition zone between the two regimes.

We propose some changes in the *P vs E* nomenclature relative to the aquatic sciences tradition, thus (i) *P vs E* instead of *P vs I* because *E*, as already explained, denotes irradiance. We also propose (ii) that the same units of time should be employed for both irradiance and the photosynthetic rate (either second or hour). Finally (iii), the term 'Maximum Light Utilization Coefficient' is suggested for the initial slope of the *P vs E* curve, α^*, because it represents a maximum value, in analogy with ϕ_m.

2F.1 The 'maximum light utilization coefficient', a^*, and the 'maximum quantum yield', ϕ_m

The parameters α^* and ϕ_m are related but differ in that α^* is defined in terms of ambient light (irradiance) whereas ϕ_m is defined in terms of light absorbed by the phytoplankton. Because the absorption of light by phytoplankton is variable and makes up but a small fraction of the total absorption of light in water, α^* differs greatly from ϕ_m. It would, however, approximate ϕ_m if all or most of the light shone on the sample were absorbed by the plant, such as in a thick leaf. To find the maximum quantum yield, α^* has to be divided by the Chl *a*-specific absorption coefficient of the phytoplankton, a^*_ϕ, or the *P vs E* data may be plotted against absorbed

irradiance instead of available irradiance.

Employing the same units of time for the photosynthetic rate and the irradiance, α^* should have the units mol O_2 evolved or CO_2 fixed m^2 (mg *Chl a*)$^{-1}$ (mol photons)$^{-1}$, whereas ϕ_m is in the units mole O_2 evolved or CO_2 fixed per mole absorbed photons (Myers 1980, Falkowski and Raven 1996; Table 1). The inverse value $1/\phi_m$ is called the 'minimum quantum requirement'.

The maximum quantum yield, ϕ_m is, together with a^*_ϕ, frequently used as a parameter in "light-chlorophyll" models of primary productivity and growth rate (Bannister 1974, 1979; Kiefer and Mitchell 1983, Bidigare *et al.* 1987, Sakshaug *et al.* 1989, Sathyendranath *et al.* 1989, Smith *et al.* 1989, Cullen 1990, Morel 1991, Platt *et al.* 1992, Bidigare *et al.* 1992, Lee et al. 1996).

α^* is quantitatively related to ϕ_m and to a^*_ϕ, the Chl *a*-specific absorption coefficient for the algae; in a spectral notation:

$$\alpha^*(\lambda) = f_m(\lambda) a^*_f(\lambda) \qquad [9]$$

Although the quantum yield at times has been defined in terms of available radiation (PAR; Odum 1971, Dubinsky 1980), the quantum yield relevant to photobiological models should be referenced to absorbed light. Because $\overset{o}{E}$ and a^*_ϕ are spectrally dependent, the realized value for α^*, $\overline{\alpha^*}$, is:

$$\overline{a^*} = \left[\overset{o}{E}_{\mathrm{PAR}} \right]^{-1} \left[\int f_m(\lambda) a^*_f(\lambda) \overset{o}{E}(\lambda) \mathrm{d}\lambda \right] \qquad [10]$$

The maximum quantum yield, ϕ_m is in principle is spectrally dependent, as in Eq 10. In practice, however, it is usually treated as a non-spectral parameter. Because studies of $\alpha^*(\lambda)$ are few, there are few accurate spectral estimates of $\phi_m(\lambda)$ of photosynthesis in natural phytoplankton communities (Lewis *et al.* 1985, Schofield *et al.* 1993, 1996, Carder *et al.* 1995).

Photosynthetic processes have been studied thoroughly in the last 20 years using flash techniques, measuring oxygen and fluorescence yields and employing target theory for modelling (Ley and Mauzerall 1982, Dubinsky *et al.* 1986 and Falkowski *et al.* 1986). Essentially, target theory describes the photosynthetic rate as a function of irradiance on basis of the probability that an open reaction center of a photosystem is hit by one or more absorbed photons (excitons). [The *P vs E* function published by Webb *et al.* in 1974, identical to that of Platt *et al.* (1980) without a term for photoinhibition, is equivalent to target theory formulation.] These investigations have shed light on the physiological nature of the *P vs E* parameters. In the following, α^* and ϕ_m is discussed in view of these investigations.

The light-absorbing pigments of phytoplankton ("antennae") may be regarded as an arrangement of photosynthetic units, each containing a number of Photosystem I (PSI) and Photosystem II (PSII) reaction centers that mediate the transformation of the absorbed energy into a chemically usable form. According to the Emerson and Arnold (1932) definition, a photosynthetic unit (PSU) is the functional, oxygen-producing entity.

The concentration of PSUs per unit Chl *a* is denoted *n* and has the units mol O_2 (mg Chl *a*)$^{-1}$. In the terminology of target theory, the PSU has a functional cross section, σ_{PSU}, that relates oxygen evolution to the light absorbed by the entire PSU (PSII and PSI). The parameter σ_{PSU}, which is spectrally dependent, has units m^2 (mol O_2)$^{-1}$.
The light absorption coefficient a^*_ϕ is the product of σ_{PSU} and *n*, thus (in a non-spectral notation):

$$a^*_f = n\sigma_{\mathrm{PSU}} \qquad [11]$$

Substitution of Eq 11 into Eq 9 gives:

$$a^* = n\sigma_{PSU} f_m \qquad [12]$$

The maximum quantum yield, ϕ_m, can also be related to the absorption cross section of PSII, σ_{PSII}. This parameter is related to PSII (not the whole PSU) and has the units m^2 (mol photons)$^{-1}$, *i.e.* the inverse of the measured moles of photons delivered per square meter during a flash of light. Like σ_{PSU}, it is a spectrum. The maximum quantum yield is (in non-spectral notation) the ratio of σ_{PSII} to σ_{PSU}:

$$\phi_m = \sigma_{PSII} (\sigma_{PSU})^{-1} \qquad [13]$$

Substituting Eq 13 for ϕ_m in Eq 12 yields

$$\alpha^* = n\, \sigma_{PSII} \qquad [14]$$

Eq 13 implies that ϕ_m is spectrally neutral only if σ_{PSII} and σ_{PSU} have the same spectral shape. This, however, is unlikely in the presence of non-photosynthetic pigments because these pigments, which absorb mainly blue light, affect σ_{PSU} more than σ_{PSII}.

Being spectra, σ_{PSII} and σ_{PSU}, like α^*, should be spectrally weighted in analogy with Eq 10 or given for a defined wavelength and compared at the same wavelength. Moreover, the parameters σ_{PSU} and n may be calculated in terms of gross carbon fixation instead of oxygen evolution, with the units m^2 (mol C)$^{-1}$ and mol C (mg Chl *a*)$^{-1}$, respectively. The resulting values will, however, not be the same (Section 2F.4).

2F.2. The 'maximum photosynthetic rate', P_m^*

The light-saturated photosynthetic rate P_m^* (also known as the 'assimilation number') is independent of the absorption cross section of the photosynthetic apparatus. It is therefore, in contrast to α^*, not spectrally dependent. This implies that the maximum photosynthetic rate cannot be derived from knowledge of light absorption, except by employing empirical statistical relationships, such as in the studies of P_m^* and α^* by Harrison and Platt (1980, 1986).

The maximum photosynthetic rate at steady-state is related to the number of photosynthetic units, *n*, and the minimum turnover time for electrons (τ; Dubinsky *et al.* 1986):

$$P_m^* = n t^{-1} \qquad [15]$$

The inverse of the minimum turnover time, *i.e.* the maximum turnover rate, τ^{-1}, of a photosynthetic unit, represents the highest electron transfer rate for the entire photosynthetic electron transport chain from water to CO_2. Both τ and *n* can be measured: τ may vary from 1 to >50 ms or, correspondingly, τ^{-1} from 1000 to <20 s^{-1}.

The rate-limiting step in the overall photosynthetic pathway has been the subject of discussion and debate. Early on it was found that the slowest step in electron transport was the reoxidation of plastoquinol, taking up to 10 ms. This suggestion ignored, however, the processes on the acceptor side of PSI related to carbon fixation. In higher plants, P_m could be related to the concentration of leaf Rubisco, indicating that carboxylation or a step closely associated with carboxylation (*e.g.* the regeneration of ribulose biphosphate) was the overall rate-limiting reaction under light saturation.

Sukenik *et al.* (1987) followed changes in the pool sizes of a number of electron transport components and Rubisco in nutrient-saturated cultures of the marine chlorophyte *Dunaliella tertiolecta* at constant temperature and found that τ increased with

decreasing growth irradiance, from 3.5 to 14 ms, in parallel with increases in the contents of Chl *a*, PSII, PQ, cytochrome b_6f, PSI and thylakoid surface density. The ratios between these components were independent of growth irradiance whereas τ^{-1} increased linearly with the ratio of the electron transport components to Rubisco, suggesting that carbon fixation rather than the electron transport chain is rate-limiting for photosynthesis at realistic irradiances.

2F.3. The 'light saturation index', E_k

The light saturation index is the intercept between the initial slope of the *P vs E* curve, α^* and P^*_m and is denoted E_k ($=P^*_m/\alpha^*$). This ratio was introduced in the analysis of photosynthetic responses of freshwater phytoplankton by Talling (1957). E_k indicates the irradiance at which control of photosynthesis passes from light absorption and photochemical energy conversion to reductant utilisation. E_k may be a convenient indicator of photoacclimational status (Section 3E).

Substitution of Eq 14 for α^* and Eq 15 for P^*_m, shows that:

$$E_k = (\sigma_{PSII}\,\tau)^{-1} \qquad [16]$$

Thus, E_k can vary by changes in either σ_{PSII} or τ. Like α^*, it is spectrally dependent.

2F.4. Causes of variations in the maximum quantum yield, f_m, and other photosynthetic parameters

According to well-known the 'Z' scheme, that describes photosynthetic electron transport through PSII and PSI, and a yield of unity for each photochemical reaction, 8 photons are required to derive one molecule of O_2 (Kok 1948), hence ϕ has an upper threshold of 0.125. Common values of ϕ_m for laboratory cultures of phytoplankton may be 0.10-0.12 for oxygen evolution (Myers 1980, Ley and Mauzerall 1982). Values for ϕ_m of gross carbon uptake are, however, typically as low as 0.06-0.08 (Laws 1991, Sakshaug 1993). In natural communities, values of ϕ_m based on measurements of α^* and a^*_ϕ, or derived from measurements of variable fluorescence, are highly variable and can be <0.005 in prominently oligotrophic areas - oligotrophy in combination with strong light may cause particularly low values (Lewis *et al*. 1988, Cleveland *et al*. 1989, Bidigare *et al*. 1990b, Schofield *et al*. 1993, Babin *et al*. 1996b).

Generally lower ϕ_m (and ϕ) values for carbon uptake relative to those for oxygen evolution reflect that the photosynthetic quotient is generally >1 (Section 2A). Because this is mainly due to energy costs involved in uptake of nitrate, cells near the base of the nutricline in oligotrophic waters may have lower ϕ_m values for carbon uptake than cells utilizing ammonium or urea higher up in the water column. The lower ϕ_m for carbon uptake than for oxygen evolution implies different sets of values for every parameter that has O_2 or C (X in Table 1) in its units. Thus, α^*, β^*, P^*_m (and P^*), and *n* are also lower for carbon uptake than for oxygen evolution, while σ_{PSU} is higher.

Other causes of variation in ϕ_m and the *P vs E* parameters include:

i. Increased absorption of light by pigments (*i.e.* the xanthophyll cycle) that dissipate the absorbed energy as heat instead of transferring it to the photosynthetic reaction centers (antenna quenching), lowering σ_{PSII} (Demmig-Adams 1990, Olaizola *et al*. 1994), thus decreasing ϕ_m and α^* and increasing E_k. These non-photosynthetic pigments are often produced at high irradiances during nutrient deprivation.
ii. Loss of functional reaction centers, lowering *n*, thus also α^* and P^*_m (Eqs 11

and 15). However, if the energy transfer between PSII reaction centers is small but finite, σ_{PSII} may be enhanced, increasing α^* and E_k. According to studies of the quantum yield of fluorescence of cultures of phytoplankton, *n* is at its maximum value when cells are nutrient-replete. These studies also indicate that *n* may be remarkably independent of species and low in nutrient-deprived cells, presumably corresponding to the growth rate in steady state (Kolber *et al*. 1988, Falkowski 1992, Vassiliev *et al.* 1995). In the upper portion of the nutrient-impoverished central gyres of the oceans, values may be reduced by 40-70%; in the nutricline (100-125 m depth) by about 25% (Falkowski and Kolber 1995).

iii. Cyclic electron flow. This increases σ_{PSU} both for O_2 evolution and C uptake and thus lowers ϕ_m and α^* while increasing E_k. In cyanobacteria, cyclic electron flow around PSI, that generates ATP, is essential to support metabolism (especially nitrogen fixation). Such a cycle utilizes photons but does not lead to the reduction of CO_2 and, hence, appears as a reduced overall photosynthetic quantum yield. At high irradiances, electrons can cycle around PSII, bypassing the oxidation of the water-splitting complex (Prasil *et al*. 1996). This cycle is protective because it dissipates excess excitation, accounting for about 15% of the loss of quantum yield.

iv. Photorespiration. The major carbon-fixing enzyme, Rubisco, can accept O_2 as a substrate, leading to the formation of two carbon molecules, especially glycolate. This increases the photosynthetic quotient, thus lowering the values of α^* and P^*_m for carbon uptake. Photorespiration has not been quantified for marine phytoplankton but is known to lower the quantum yield for carbon fixation on the order of 25% in higher plants. Photorespiration is presumably high at elevated oxygen levels.

v. Packaging. The packaging of pigments inside the cell may reduce the absorption efficiency of pigments. Thus the Chl *a*-normalized parameters a^*_ϕ and σ_{PSII} may be somewhat smaller for shade-acclimated than for light-acclimated cells. Because α^* is Chl *a*-normalized it behaves similarly, while E_k may increase. This effect is physical: pigments packed into chloroplasts are less efficient in absorbing light per unit pigment mass than when in an optically thin solution. The packaging depends both on the cell size and pigment concentration/ratios in the cell (Kirk 1975, Morel and Bricaud 1981) and is wavelength-dependent, being most pronounced where absorption is highest. It is generally most pronounced in large and pigment-rich (shade-acclimated) cells; this may cause lower α^* in shade-acclimated than light-acclimated cells. This loss of efficiency per unit pigment mass is, however, smaller than the absorption gain through increased cellular pigment content. Thus shade-acclimated cells in the end absorb more light per cell or unit carbon than light-acclimated cells.

2G. Water column productivity

The ability to derive basin-scale maps of the distribution of phytoplankton Chl *a* in the upper ocean from satellite color sensors (Lewis 1992) has progressively led to the development of models relating biomass to primary productivity (Falkowski 1981, Platt and Sathyendranath 1988, Morel 1991, Bidigare *et al*. 1992, Cullen *et al*. 1993, Behrenfeld and Falkowski 1997). The amount or concentration of Chl *a*, however, represents a state variable. Therefore, to calculate primary productivity, which is a flux, a variable that includes the dimension

time^{-1} is needed. Such models relating carbon fixation to Chl *a* incorporate irradiance and a

normalized to the amount of Chl *a* (ψ^*) and is a bulk yield function for the whole water column, valid for a lapse of time, *e.g.* one day. These so-called "light-chlorophyll" models (Ryther and Yentsch 1957, Cullen 1990) are difficult to verify in the ocean, hence, their usefulness lies in understanding the underlying biological processes and how those processes are regulated.

The transfer function ψ includes the physiological response of phytoplankton to light, nutrients, temperature, etc (Falkowski 1981). It merges both the absorption and the photosynthetic response of the entire population exposed to decreasing irradiance from the surface down to the bottom of the euphotic zone. Thus, understanding ψ^* requires the knowledge of each level of the spectral absorption capacity of phytoplankton, of their photosynthetic (*P vs E*) responses, etc., as well as the spectral composition and amount of available energy.

If PAR is expressed as photons, the coefficient ψ^*, then denoted ψ^*_α (the 'water column light utilization index'), has the same units as α^*, *i.e.* mol C m^2 (mg Chl *a*)$^{-1}$ (mol photons)$^{-1}$. It is smaller for carbon uptake than for oxygen evolution (*cf.* the photosynthetic quotient, Section 2A). Water column production (P_{tot}) may be related to the amount of Chl *a* in the water column and incident irradiance via the factor ψ^*_α ,thus:

$$P_{tot} = (\mathrm{PAR}_s)\mathrm{Chl}\cdot a_{tot}\psi^*_\alpha \qquad [17]$$

Traditionally, P_{tot} is in the units g C m^{-2} and for a given period (*e.g.* one day), and PAR_s is PAR at the ocean surface during the same period. The fraction of PAR which is absorbed by phytoplankton depends on the amount of Chl *a* within the water column, Chl a_{tot} (g m^{-2}), and on the absorption characteristics of the algae in question.

Phytoplankton biomass may be expressed in energy units (Platt and Irwin 1973). Thus, if PAR_s is expressed in energy units, the realized P_{tot} during the same period can be transformed into its energetic equivalent PSR_{tot} ('Photosynthetically Stored Radiation') by assuming an energetic equivalent for the fixed carbon and using a transfer function, ψ^*_E, with the same units as the Chl *a*-specific absorption coefficient *a**, *i.e.* m^2 (mg Chl *a*)$^{-1}$:

$$\mathrm{PSR}_{tot} = \mathrm{PAR}_s\,\mathrm{Chl}\,a_{tot}\,\psi^*_E \qquad [18]$$

Here, both PAR_s and PSR_{tot} are in energy units, *e.g.* J m^{-2}, for a given duration (Morel 1978, 1991). The quantity ψ^*_E may be termed the 'Water Column Photosynthetic Cross Section' per unit of Chl *a* mass for the water column.

Assuming an annual global phytoplankton carbon fixation of 40 Pg (a midpoint of the range given in the Introduction), a conversion factor of 4.3 mmol photons (kJ)$^{-1}$ (Morel and Smith 1974), an energy density of 39 kJ (g C)$^{-1}$ in phytoplankton (actually a value for carbohydrate; Morel 1978) and PAR over the oceans averaging 9.76×10^{20} kJ yr^{-1}, the global ratio of PSR:PAR is 0.16%, or about 1370 photons per fixed carbon atom on an annual basis (Morel 1991, Behrenfeld and Falkowski 1997). This estimate is about 1/3 of the apparent conversion efficiency of land plants.

3. METHODOLOGICAL CONSIDERATIONS

The vertical distribution of Chl *a* in the euphotic zone and the penetration of light are assumed to be known. At each depth, the radiant energy absorbed by the photosynthetic pigments in phytoplankton is usually represented by the product of [Chl *a*], $\overset{o}{E}$ and *a**, the latter two being spectral

variables. PUR may be computed by integrating Eq 5 from 400-700 nm. The calculation of PUR takes into account the spectral distribution of the light and requires that $a^*(\lambda)$ be measured (see below). The maximum quantum yield, ϕ_m, over the PAR region is then calculated as $\phi_m = \alpha^*/a^*_\phi$ the factor α^* being weighted for the spectral distribution of the incubator light.

3A. Penetration of photosynthetically available radiation

Above the surface, measurements of irradiance have to be made in terms of downwelling irradiance, E_d, *i.e.* with an instrument equipped with a flat (cosine) collector. Use of a spherical collector always implies an overestimate of the penetrating radiant flux. The magnitude of this overestimate is considerable and mainly depending on solar altitude. It may, for instance, reach a factor of about 2 for a zenith-sun angle of 60° and a dark-blue sky.

Because scalar irradiance, $\overset{o}{E}$, is the sought quantity in the water column (Section 2B), a spherical (4π collector must be used for the in-water measurements. Both $\overset{o}{E}(\lambda)$ and $\overset{o}{E}_{PAR}$, *i.e.* the integrated irradiance over the 400-700 nm range (Eq 1), are considered and measured as function of depth. Because of the fluctuations (originating from wave-induced "lens effects" and from variations in immersion depths), the measurements in the upper layers are unreliable and their extrapolation toward the "null depth" very uncertain. As a consequence, the origin (100%) of the vertical irradiance profile remains poorly determined, so that all the relative irradiances (such as the 1% depth, which is much used to fix the depth of the euphotic zone) are inaccurately known. The commonly adopted solution consists in measuring the incident irradiance in air, above the surface (E_d), and in correcting the measured value for the loss due to reflection. This loss amounts to only 3-5%, and more than 10% of incident irradiance for low solar elevation, slightly depending on the sea state and on the sky radiation (Morel and Antoine 1994).

Historically, and because of instrumental limitations (now overcome), in-water data for $\overset{o}{E}$ have been replaced by measurements of E_d. This is not crucial in terms of relative irradiance profiles, as the attenuation coefficients for both kinds of irradiance are close. It is, however, important in terms of absolute values of available energy: the $\overset{o}{E}:E_d$ ratio, always >1, can be as high as about 2 in some instances, *e.g.* in highly scattering waters with low absorption. Phytoplankton blooms are relevant examples (Morel 1991). By relying on exact calculations of radiative transfer (*e.g.* Mobley 1994), or on approximations, E_d can be transformed into $\overset{o}{E}$ with reasonable accuracy. Approximations have been developed by Kirk (1984); a method is presented in Morel (1991).

If penetration of light into the sea cannot be measured, it may instead be predicted from data for incident PAR radiation recorded above the surface, and from the vertical distribution of Chl *a*, at least in Case I waters (Baker and Smith 1982, Morel 1988). The prediction in Case II waters is more complicated and requires additional information, that is generally not available, on the other optically active constituents.

3B. Light absorption measurements

Methods that separate light absorption into components have been much discussed in recent years. The present section deals with measurements of total particulate absorption

(a_P), absorption by phytoplankton only (a_ϕ), and photosynthetically relevant absorption only (a_{PS}).

Spectral absorption by total particulate matter, $a_P(\lambda)$, represents a major methodological problem because of the low concentration of particulate matter in seawater (Yentsch 1962). To overcome this, the most widely used technique over the past years has been the glass filter technique first proposed by Trüper and Yentsch (1967). It involves measuring the absorption spectrum of particles retained on a glass-fiber filter (with a blank filter as a reference), using a spectrophotometer equipped with an integrating sphere or another optical arrangement for collection of light scattered by particles. This simple, rapid, and convenient measurement for routine use in the field is, however, strongly affected by pathlength amplification, induced by multiple scattering within the filter and between the filter and particles. The pathlength amplification factor (β *sensu* Butler 1962), varies with optical density, and therefore with wavelength, and with filter type (Mitchell 1990). Although previous studies (Mitchell 1990, Cleveland and Weidemann 1993) proposed species-independent algorithms, a recent study (Moore *et al*. 1995) suggests that these algorithms may lead to significant errors for some phytoplankton groups such as prochlorophytes and cyanobacteria.

An alternative technique, based on a modification of the filter-transfer-freeze (FTF) technique used for microscopic observations (Hewes and Holm-Hansen 1983), has been recently proposed (Allali *et al*. 1995). It involves concentrating particles onto a Nuclepore filter, transferring the filtered material to a glass microscope slide. After removing the filter, the absorption spectrum of particles is measured directly on the slide. Thus, the pathlength amplification effect is avoided.

Because the quantum yield is classically defined by reference to light absorption by living phytoplankton, $a_\phi(\lambda)$, the factor a_P must be corrected for absorption by non-algal particles, a_{NAP} (biogenous and non-biogenous detrital particles, heterotrophic bacteria, etc). Various techniques have been suggested, *e.g*. washing the sample with a mixture of organic solvents, applying UV radiation in the presence of hydrogen peroxide (Konovalov and Bekasova 1969), bleaching the cells with peracetic acid (CH_3CO_3H; Doucha and Kubin 1976) or with sodium hypochloride (Tassan and Ferrari 1995). The most frequently used procedure at present is that proposed by Kishino *et al*. (1985). It involves immersion of the filter in methanol for extracting pigments, measuring residual absorption on the bleached filter, yielding $a_{NAP}(\lambda)$, and subtracting this residual absorption spectrum from $a_P(\lambda)$ to obtain $a_\phi(\lambda)$. A modified procedure has been described in the case of measurements with the "glass-slide" technique. The Kishino method, although convenient, has some obvious limitations: the absorption spectrum of living phytoplankton is only approximated because (i) the $a_{NAP}(\lambda)$ spectrum may include absorption by depig-mented phytoplankton cells in addition to that by non-algal particles; (ii) $a_{NAP}(\lambda)$ also includes water-soluble pigments such as phycobilins, only weakly extracted or not at all by methanol, and (iii) $a_\phi(\lambda)$ erroneously includes detrital pheopigments and carotenoids that were extracted by the methanol. Therefore, numerical or statistical decomposition methods, based on various assumptions (Morrow *et al*. 1989, Roesler *et al*. 1989, Bricaud and Stramski 1990, Cleveland and Perry 1994) have been proposed as alternatives to Kishino's chemical method.

To gain insight into the variability of ϕ_m that is due to algal non-photosynthetic pigments, it is desirable to partition $a_\phi(\lambda)$ into

absorption by photosynthetic pigments, $a_{PS}(\lambda)$, and that by non-photosynthetic pigments, $a_{NPS}(\lambda)$. The factor $a_{PS}(\lambda)$ can be approximated, using the detailed pigment composition (Bidigare *et al*. 1990a, Johnsen *et al*. 1994, Sosik and Mitchell 1995). The *in vivo* absorption spectra of phytoplankton are, however, affected also by the packaging of pigments, so that accurate reconstruction is possible only for very small and weakly pigmented phytoplankton cells in which this effect can be neglected. Besides, variations in energy transfer efficiency among the various pigments may cause difficulties.

In many cases, a good proxy for the absorption coefficient of photosynthetic pigments, $a_{PS}(\lambda)$, is the fluorescence excitation spectrum (emission measured at around 730-740 nm); it is very similar in shape to the action spectrum for oxygen release (Haxo 1985, Neori *et al*. 1986). Such spectra, however, are usually measured on a relative scale, so they have to be scaled to the units of $a^*_\phi(\lambda)$. Maske and Haardt (1987) and Sakshaug *et al*. (1991) scaled the fluorescence excitation spectrum to the red absorption peak at 676 nm where the absorption is almost exclusively caused by Chl *a*, to distinguish $a_{PS}(\lambda)$ from $a_\phi(\lambda)$ in cultures. An underlying assumption for doing this is that the scaled fluorescence should be smaller than $a^*_\phi(\lambda)$ at any wavelength because the fraction of light energy which is transported to PSII cannot be larger than the total energy absorbed. Johnsen and Sakshaug (1993) noted that three main problems in this scaling technique: (i) the cells should be treated with DCMU under actinic light to avoid variable fluorescence; (ii) the light energy received by PSII relative to PSI, which is dependent on the pigment composition of the two systems and their respective light-harvesting complexes (LHCs), affects the scaling; and (iii) the light energy transfer efficiency at 676 nm therefore may be considerably less than 100%.

On the basis of studies on dinoflagellates, Johnsen and Sakshaug (1993) suggested a 80-85% scaling against the red peak of a^*_ϕ at 676 nm for chromophytes. As an alternative, however, scaling may be carried out to 100% at a wavelength chosen so that no "overshoot" relative to $a^*_\phi(\lambda)$ occurs at the other wavelengths. For dinoflagellates, a scaling to 100% at around 545 nm (the shoulder of the peridinin spectrum) fulfils this requirement and implies a 80% scaling at 676 nm (Johnsen *et al*. 1994). For phycobiliprotein-containing organisms, 100% scaling at around 570 nm may be appropriate. This scaling corresponds, however, only to a 15% scaling at 676 nm (*e.g*. *Synechococcus*; Johnsen and Sakshaug 1996), reflecting the small amount of Chl *a* bound in the highly fluorescent PSII relative to PSI which is virtually non-fluorescent at room temperature. The "no overshoot" approach may be the more general and recommendable procedure for scaling of fluorescence excitation spectra to a^*_ϕ.

3C. Carbon *vs* oxygen

In algal cultures, carbon uptake must be lower than rates for oxygen evolution (Section 2F.4). For natural communities, however, the oxygen budget of a *P vs E* sample, or a body of water, is related to the net community production, *i.e*. the gross photosynthesis minus respiratory losses in all organisms, heterotrophs included. This makes it difficult to detect the small changes that arise, due to photosynthesis, in oxygen concentration after short (<24 h) incubations, except under bloom conditions (Williams *et al*. 1983). We therefore concentrate here on guidelines which refer to measurements of carbon uptake.

3D. Gains and losses of POC and DOC during incubation

In some of the methods used to estimate phytoplankton productivity or to determine photosynthetic parameters, cells are retained on a filter and DOC is in the filtrate (the traditional ^{14}C technique for estimating marine carbon uptake rates - *e.g.* linear incubators) whereas in other methods, measurements are conducted on whole seawater samples (*e.g.* photosynthetrons). Radioactivity retained on filters is related to particulate production, whereas analysis of whole seawater samples ideally yield estimates for the production of both dissolved (DOC) and particulate organic carbon (POC). The production of dissolved organic carbon may, however, be underestimated for short incubation times (few hours) because $DO^{14}C$ increases with time until isotope equilibrium is reached. The distinction between POC (particulate organic carbon) and DOC is arbitrary and depends on the filter used to separate the two size fractions. However, all organic matter synthesized by phytoplankton, whether particulate or dissolved, is part of the primary production. Estimates of phytoplankton production and/or photosynthetic parameters may sometimes differ significantly if they are derived from carbon fixed in POC only or in both DOC and POC.

The various pathways through which carbon fixed by phytoplankton is transformed to DOC and DOC is oxidized to CO_2 (respired) include:

i. Photorespiration, which leads to production of glycolate and oxidation of part of it into CO_2. Some glycolate is exuded into the surrounding water; ^{14}C taken up by phytoplankton may appear in the exuded glycolate within 5-10 minutes.
ii. Exudation of various polysaccharides, from low to high-molecular weight. This may be particularly important at high latitudes, *e.g.* blooms of the prymnesiophyte *Phaeocystis* (Wassmann *et al.* 1991) and some diatoms (*e.g. Chaetoceros socialis* and *C. affinis* var. *willei*) that release abundantly carbohydrates, especially when nutrient-deficient (Myklestad 1974, Zlotnik and Dubinsky 1989).
iii. Spontaneous lysis of cells, which would release cellular material in the water. This may occur when cells are nutrient-deficient at the conclusion of a bloom (von Boekel *et al.* 1992), but the likelihood of spontaneous autolysis during incubations is not documented.
iv. Lysis of cells following viral attacks, which releases cellular material into the water (*e.g.* Cottrell and Suttle 1995).
v. Grazing by mesozooplankton ("sloppy feeding"), which is accompanied by release of cell material (*e.g.* Roy *et al.* 1989). In most cases, however, this problem is minimized by screening out the mesozooplankton before incubation (possibly causing stronger nutrient limitation than in the natural environment).
vi. Grazing by microzooplankton, which does not generally transfer phytoplankton carbon to the DOC pool because autotrophic organic matter becomes included in heterotrophic organisms. Hence, there is little loss of tracer from the particulate phase. Respiration by heterotrophs following grazing causes, however, loss of carbon.

Uptake by heterotrophic bacteria of DOC released by phytoplankton during the course of incubation could result in transferring dissolved tracer back to the particulate phase. The actual rate of re-incorporation of tracer into POC through this pathway will depend on the relative concentrations of POC and heterotrophic bacteria. Depending on the duration of the incubation, some of the tracer taken up by bacteria could be respired before the end of the incubation.

The above considerations stress that

comparison of photosynthetic parameters determined using different methods, or comparison of carbon uptake rates determined at sea using the conventional ^{14}C method with estimates derived from *P vs E* measurements, should take into account the following differences in approaches:

i. Duration of incubation: short incubations (order of 1 hour) provide estimates that are (with qualification) closer to the gross carbon uptake rate than long incubations, because the likelihood of labelled carbon to be respired to CO_2 increases and/or recycled within the cell with the duration of incubation (Dring and Jewson 1982).
ii. Filtered *vs* whole samples: this problem might be resolved if uptake of tracer in the DOC and POC fractions were both determined in cases involving filtration. This, however, is generally not done in the field.

Both points suggest that estimates of photosynthetic parameters from a photosynthetron, an incubator that that uses small whole- water samples (Lewis and Smith 1983) should lead to higher estimates of productivity than those from linear incubators which involve filtering of samples and no determination of DOC (although some DOC may be adsorbed on the filter Maske and Garcia-Mendoza 1994), and that they should be higher than those resulting from long incubations at sea. It should be noted that mitochondrial respiration may occur simultaneously with photosynthesis, thus causing too low values for gross oxygen evolution rates (Weger and Turpin 1989, Weger *et al.* 1989).

3E. Physiological acclimation

Physiological acclimation of the photosynthetic apparatus during incubation may cause *P vs E* curve variability, *i.e.* as a result of variations in light, temperature and nutrients. This is another reason, in addition to respiratory loss of labelled carbon mentioned above, to keep incubation times as short as possible, or using non-interfering methods (Section 4A).

The acclimation strategies appear to have common molecular biological causes that are signalled by the redox status of specific elements in the photosynthetic electron transport chain (Escoubas *et al.* 1995). In essence, physiological acclimation serves to minimize variations in the growth rate when environmental growth-controlling factors vary (Sakshaug and Holm-Hansen 1986); this is reflected in, at times major, changes in the pigment contents and composition of the cells, and in the *P vs E* parameters.

Phytoplankton strive to maintain an optimum balance between light and dark reactions of photosynthesis, *i.e.* a balance between the rate of photon absorption by PSII and the rate of electron transport from water to CO_2. This balance happens at the irradiance indicated by the light saturation parameter, E_k (Escoubas *et al.* 1995). At lower irradiances, the quantum yield of photosynthesis is higher, but the photosynthetic rate is lower; at higher irradiances, there is no major increase in the photosynthetic rate and, hence, nothing to be gained, and potentially much to be lost. Consequently, if the irradiance increases, the algae adjust their E_k upwards, and *vice versa*. Thus, E_k is a convenient indicator of the photoacclimation state of phytoplankton. Because irradiance in the field is fluctuating and acclimation takes some time, E_k (like other acclimation-sensitive parameters) is continually changing and in principle never entirely matching the instantaneous irradiance. This is particularly true for phytoplankton in well-mixed waters.

The changes in acclimation state are due to

different processes that have evolved on a number of time scales. To one extent or another, they affect either σ_{PSII} or τ, *i.e.* the two factors that determine E_k. For example, the xanthophyll cycle affects σ_{PSII} within a time scale of <60 minutes in a highly reversible fashion (Olaizola *et al.* 1994). As described before, changes in τ are related to the ratio of Rubisco to the electron transport components. *In situ* observations (Falkowski and Kolber 1995) suggest that both non-photochemical quenching of fluorescence due to photoprotective mechanisms and damage to reaction centers may occur simultaneously in the marine environment.

On time scales of tens of minutes, non-photochemical quenching by photoprotective pigments may lower σ_{PSII} (hence α^* decreases and E_k increases) while damage to photosynthetic units may lower *n* (hence both α^* and P^*_m), as mentioned earlier (Maxwell *et al.* 1994, Olaizola *et al.* 1994, Vassiliev *et al.* 1994).

On time scales of hours to days, the redox-signalling pathways can lead to the generation of specific signal molecules that can repress or enhance the expression of chloroplast and/or nuclear encoded genes. These alterations are responsible for (*e.g.*) the light-dependent changes in cellular Chl *a* content and the C:Chl *a* ratio and similarly forced changes in response to thermal changes (Escoubas *et al.* 1995). In the diatom *Skeletonema costatum*, there appears to be a virtually linear relationship between the C:Chl *a* ratio and the number of absorbed photons per unit Chl *a*, irrespective of the spectral composition of light (Nielsen and Sakshaug 1993).

In the oligotrophic upper ocean, low photochemical energy conversion efficiencies typically resulting from photoinhibition can often be restored within two days to near-maximum values by incubating subsamples under moderate irradiance (adding supplemental inorganic nitrogen if the cells are also nutrient-deficient; Falkowski and Kolber 1995). Such restoration occurs naturally in the open ocean in conjunction with an increase in the nutrient supply when eddies and storms are passing. Eddy and storm-enhanced productivities may be indicated in transects of variable fluorescence and seem to be correlated with temperature changes as low as ca 0.1°C.

3F. Curve fitting

Problems related to the fitting of mathematical functions to *P vs E* data to estimate α^*, β^* and P^*_m have been adressed by Frenette *et al.* (1993). The user has several choices at this step but, according to the approach that is adopted, the resulting *P vs E* parameters can be markedly different.

A first problem is the dark fixation of carbon, which is related to β-carboxylation (Geider and Osborne 1991). The dark bottle values may constitute a significant fraction of light bottle values, especially in oligotrophic waters (Banse 1993). It is generally admitted that fixation in clear bottles minus dark fixation represents the effect of photosynthesis. Therefore, the dark fixation rate, which is typically not null, is subtracted from the light bottle readings and the *P vs E* curve is forced through the origin, as for commonly used *P vs E* formulations, such as those of Webb *et al.* (1974) and Platt *et al.* (1980). This may be the most reasonable approach; however, the difference between values from a dark and a clear bottle does not necessarily exactly represent photosynthesis. There are some indications that the non-photosynthetic carbon fixation rate is not the same in the dark as in the light (Legendre *et al.* 1983, Li *et al.* 1993).

Knowledge of the dark fixation rate is important in *P vs E* determinations because ϕ_m for carbon uptake occurs at vanishing

irradiances (derived from α^*). The carbon fixation rates in the dark bottle and at the lowest irradiances have the largest weight in the determination of this slope. Using functions that allow the curve to have a non-null intercept at the origin, may lead to wide dispersion of α^* values.

A second problem concerns the choice of a *P vs E* model. Several models or mathematical representations exist (Webb *et al*. 1974, Jassby and Platt 1976, Jamart *et al*. 1977, Platt *et al*. 1980), which include or not a term for photoinhibition. At present, it is premature to recommend one model above another as long as they fit the data reasonably well - a theoretically "correct" function would yield a curvature anywhere between those of the Michaelis-Menten and Blackman functions. One should, however, be aware of this source of variation and therefore take care to follow a protocol that include archiving of the original data (*i.e*. the carbon fixation at each irradiance) so that these could be fitted to other models for purposes of comparison. As stressed by Frenette *et al*. (1993), systematic differences in α^* and P^*_m are found between the models of *e.g.* Webb *et al*. (1974), Jassby and Platt (1976) and Platt *et al*. (1980), α^* being particularly sensitive. This results from the regressions forcing mathematical functions with different curvatures to the data. One also has to be aware of this when comparing data in the literature.

Published protocols usually contain recommendations concerning precision and accuracy of the results. This cannot be achieved for the photosynthetic parameters, which are estimated from several different measurements and thus lack an absolute reference.

4. SPECIAL INSTRUMENTATION

4A. Variable fluorescence

Considering all the artefacts in determinations involving incubations, emphasis should be put on developing non-manipulative methods, preferably profiling methods that do not require water sampling at all. The variable fluorescence yield of photosystem II (Falkowski and Kiefer 1985), together with the development of new bio-optical instruments, are possible approaches which permit new insights into the physiology of the phytoplankton and do not require filtration, thus avoiding a time-consuming and error-generating step in operations at sea.

The usefulness of variable fluorescence methods to studies of photosynthetic rates in the sea lies not so much in the quantitative value of the measurements but in understanding the parameters that influence the photosynthetic behavior of phytoplankton. The changes in variable fluorescence can be extremely helpful in interpreting or apportioning causes of variations in ϕ_m. While such measurements can be made using specialized instruments, such as the fast-repetition rate fluorometer (FRRF), the pump and probe fluorometer (PPF), and the pulse-amplitude-modulated-fluorescence meter (PAM), similar measurements can be made using simple fluorometers by determining the fluorescence yields prior to and following the addition of the electron transport inhibitor, DCMU. Yields of stimulated fluorescence can be used, in addition to the above, to determine the functional absorption cross section of PSII (σ_{PSII}) *in situ* and to derive E_k in the water column.

The FRRF, PPF and PAM instruments are based on the progressive closure of photosystem II reaction centers and subsequent increase of fluorescence, by a brief series of strong (pump) and weak (probe) excitation flashes. The characteristics

and evolution of the fluorescence yield during this brief series of flashes is then used to estimate [Chl *a*], the fraction of open reaction centers, the maximum change in the quantum yield of fluorescence, and the absorption cross section of PSII (Falkowski and Kolber 1993). These parameters can be entered in models of photosynthesis and used to estimate the primary productivity. The great advantages of the FRRF and PPF fluorometers is their great sensitivity and that they are profiling, *i.e*. they can be attached to a CTD and provide vertical profiles of photosynthetic parameters at the same rate as vertical profiles of temperature and salinity, making it possible to study the response of primary production to physical forcing at small space and time scales. A hand-held PAM instrument for divers is available and offers new possibilities for *in situ* studies of photosynthesis of both phytoplankton and seaweeds.

The measurement of variable Chl *a* fluorescence can also be done in a survey mode on a ship by diverting a stream of near-surface sea water from the hull pump into a flow-through cuvette of the FRRF, configured with a blue excitation source and a red emission detector (Kolber *et al*. 1994). In this instrument, the excitation pulse is provided as a burst of subsaturating flashes in the microsecond time domain. The cumulative excitation provided by the flashes leads to saturation of PSII within ca 75 μs; the saturation profile can be used to derive the initial fluorescence yield, F_o, the maximum fluorescence yield, F_m, and, importantly, σ_{PSII} (Greene *et al*. 1994). These measurements can also be made *in situ* with a submersible version of the FRRF, equipped with 2 excitation channels. The FRRF is much more efficient than the formerly used PPF, as σ_{PSII} can be derived virtually instantly (within 150 μs), instead of over a period of minutes. Moreover, in a vertically profiling configuration, the submersible FRRF can be used to derive the fraction of open reaction centers at any instant. From knowledge of the cross sections, the quantum yield of photochemistry, and the simultaneously measured instantaneous spectral irradiance, which provide an estimate of the absolute rate of linear photosynthetic electron transport, can be derived and translated into a *P vs E* curve after calibration against oxygen evolution or carbon uptake rate (Kolber and Falkowski 1993).

Finally, the FRRF can be mounted on an undulating platform that permits both vertical and horizontal profiling. All three types of sampling strategies can be used to derive vertical and horizontal sections of fluorescence parameters along shiptracks (Falkowski and Kolber 1995). In conjunction with satellite images, these *in situ* measurements can be used to infer how changes in the physical environment affect photosynthetic energy conversion efficiency.

4B. Natural fluorescence

The contribution of phytoplankton fluorescence to the upward irradiance was first documented by Morel and Prieur (1977) and Neville and Gower (1977). Since then, natural fluorescence (also known as passive, solar or sun-induced phytoplankton fluorescence) has been used to estimate sea surface [Chl *a*] (Gordon 1979, Topliss 1985, Gower and Borstad 1990) and photosynthetic activity in the water column of marine environments (Kiefer *et al*. 1989, Chamberlin and Marra 1992, Abbott *et al*. 1995). A large variety of instruments containing passive fluorescence sensors have been developed; some for water column profiling and some for drifters (Chamberlin *et al*. 1990, Marra *et al*. 1992). By the end of this century, three satellites in orbit (MODIS, MERIS, GLI) will measure sea-surface sun-stimulated fluorescence rates.

The underlying theory for predicting the

photosynthetic rate on the basis of natural fluorescence, has been elaborated by Kiefer *et al.* (1989) and Kiefer and Reynolds (1992). The instantaneous rate of fluorescence (J_f, mol photons s^{-1}), as well as the gross rate of photosynthetic carbon fixation (P, mol C m^{-3} s^{-1}), can be approximated as the product of the rate of energy absorbed by the photosystem and the fraction of this energy re-emitted as fluorescence or stored as photosynthetic carbon, respectively. These fractions are determined by the probability that energy harvested by the photosystem be channeled into carbon fixation or fluorescence:

$$P = f \int_{400\ \mathrm{nm}}^{700\ \mathrm{nm}} \overset{o}{E}(\lambda) a_f \, \mathrm{d}(\lambda) \qquad [19]$$

$$J_f = f_f \int_{400\ \mathrm{nm}}^{700\ \mathrm{nm}} \overset{o}{E}(\lambda) a_f \, \mathrm{d}(\lambda) \qquad [20]$$

ϕ is the quantum yield of photosynthesis and ϕ_f the fluorescence quantum yield. The use of natural fluorescence to estimate gross photosynthetic rates is appealing because it is a non-intrusive method. Because rates of solar-induced fluorescence and photosynthetic carbon fixation in the water column appear to be equally dependent on the energy harvested by photosynthetic pigments, the estimates may be assumed to be independent of spectral variation in irradiance and light absorption coefficient of phytoplankton (reabsorption of emitted light may constitute a problem, see Collins *et al.* 1985). It is, however, necessary to know the variability in the ϕ:ϕ_f ratio in order to calculate accurate photosynthetic rates from measurements of natural fluorescence:

$$P = (\phi{:}\phi_f)\, J_f \qquad [21]$$

Chamberlin *et al.* (1990) used an empirical approach based on field observations to describe the variability in the ϕ:ϕ_f ratio due to changes in PAR. Their observations suggest that, when combining the results from a variety of ecosystems and light regimes (from 2-150 m depth), the variability in measurements of natural fluorescence accounts for 84% of the observed variability in photosynthetic rates; *i.e.* J_f and P as expected, are largely dependent on the irradiance. However, they found that the ϕ:ϕ_f ratio increases with increasing temperature and may decrease almost two orders of magnitude with increasing irradiance; a similar result was also obtained noted by Stegmann *et al.* (1992). By taking this variation into account, Chamberlin *et al.* (1990) were able to account for 90% of the variability in photosynthetic rate related to natural fluorescence.

One must be careful when extrapolating results to various seasons and oceanic regimes (Stegmann *et al.* 1992). For example, species composition may play an important role in the variability in the ϕ:ϕ_f ratio; *e.g.* this ratio may be higher in communities dominated by *Synechococcus*, as a result of its low PSII:PSI ratio, than in other communities. Moreover, there is strong evidence of deviations between photosynthetic rates estimated at sea and those predicted on the basis of natural fluorescence under the high-light conditions often observed in the upper ocean (Stegmann *et al.* 1992), emphasizing the need to account for photoprotective pigments (*i.e.* the xanthophyll cycle).

In summary, variations in the gross photosynthetic carbon fixation rate, P, may be strongly correlated with variations in J_f (Babin *et al.* 1996a) over a wide range of irradiances, suggesting that the rate of light absorption by the phytoplankton, *i.e.* the product of a_ϕ and irradiance, is the main variable controlling J_f and P. This correlation may, however, be considerably weakened in the upper part of the water column where photosynthesis is light-saturated.

4C. *In situ* absorption meters

In situ spectral absorption meters are now available (Moore *et al*. 1992, Zaneveld *et al*. 1992). These are 25-cm path length transmissometers that have been modified to include a reflecting tube and a large area detector, so that most of the scattered light is collected by the detector (residual scattered light is estimated using an infra-red channel). One version of this instrument, called the "chlam", measures light absorption in the chlorophyll red peak region, at 676, 650 and 712 nm; the measurement at 676 nm provides the necessary absorption value, and the other two wavelengths allow correction for the absorption by degraded chlorophylls. Such an absorbance meter operated on vertical profiles, coupled to fluorescence excitation spectra at discrete depths, would allow scaling of fluorescence excitation spectra measured at discrete depths. A similar scaling can also be achieved with another version, the AC-9®, that measures absorption and attenuation at 9 user-defined wavelengths. Although this instrument yields more complete spectral information than the "chlam", at all wavelengths except in the red part of the spectrum, measurements of absorption of light by phytoplankton is not straight-forward: absorption by dissolved matter has to be corrected for, *e.g.* using a second AC-9 with a filter as well as particulate detrital absorption, *e.g.* by numerical methods.

5. OPEN QUESTIONS

In principle, light-photosynthesis models provide estimates for the gross rate of photosynthesis if irradiance and the quantum yield for photosynthesis are known. By subtracting the daily rates for respiration and production of DOC, net daily production of phytoplankton can be calculated. Results from such models can be expressed in terms of oxygen, nitrogen or carbon, using Redfield ratios (assuming that nutrient deficiency does not skew the ratio in the cells relative to this ratio). In prognostic models, *i.e.* if we want to use the predicted increase in biomass as the basis for the next-step prediction of the model, the increase in biomass (*e.g.* C) must be converted into an increase in [Chl *a*] which is the input of the *P vs E* function; for that, we need the C:Chl *a* ratio (as in calculations of carbon biomass). The C:Chl *a* ratio, however, is highly variable and a potential source of error. Similarly, the ratio between carbon fixed and oxygen evoluted (*i.e.* the photosynthetic quotient) and the role played by respiration, need to be better understood.

Experiments, and especially incubations in artificial conditions, modify the environment of the phytoplankton, which immediately, and more or less rapidly, start to acclimate themselves to the new conditions, whereas the results of the experiment often are referred to initial physiological conditions. The parameter σ_{PSII} may, for instance, change in the course of a few minutes (Falkowski *et al*. 1994), with consequences for ϕ_m and α^* (Mitchell and Kiefer 1988, Morel *et al*. 1987). The effect on community production estimates may, however, be slight (Falkowski *et al*. 1994).

Not all the light absorbed by the phytoplankton is transferred to photosynthesis, the remaining fraction being absorbed, especially by the photoprotective pigments. This fraction is included in the determination of a_ϕ^* but does not contribute to photosynthesis, thus not to α^* (Sakshaug *et al*. 1991, Sosik and Mitchell 1995). Hence, if the cells have large concentrations of photoprotective pigments (*i.e.* are high-light acclimated), the estimate of ϕ_m ($= \alpha^*/a_\phi^*$) will be low and necessarily spectrally dependent because the photoprotective pigments absorb mainly in the blue region

(Sakshaug *et al*. 1991, Morel *et al*. 1996). Once again, as much information as possible concerning the lamp emission spectrum and the phytoplankton absorption spectra should be given in published papers and recorded in data bases.

Over the past decade, phytoplankton ecologists have tended to develop ever more elaborate models to relate the photosynthetic rate to [Chl *a*] via irradiance. In so doing, the importance of P^*_m or its analogue, the maximum Chl *a*-normalized photosynthetic rate within a water column (also known as P^*_{opt}, in the same units as P^*_m), tends to be neglected. P^*_m varies by more than one order of magnitude in the ocean. It cannot in principle be predicted from a^*_ϕ or ϕ_m, hence not from α^*. While, to a first order, P^*_m is related to temperature, the simple Arrhenius-type of relationship described by Eppley (1972) does not appear to describe the variations in P^*_m in the ocean (Balch and Byrne 1994, Behrenfeld and Falkowski 1997). Certainly, much more attention needs to be paid to the sources of variation in P^*_m and P^*_{opt}, if global scale productivity models are to be developed with an acceptable degree of physiological representation of photosynthetic processes *in situ*.

Finally, the *P vs E* parameters and the pigment content of phytoplankton, and thus the C:Chl *a* ratio - which are essential in models of algal growth rate - are continuously changing as a result of the fluctuations in environmental conditions, because they are subjected to acclimation, typically with delayed responses at different time scales. This implies a need for models in which the *P vs E* parameters and pigment content are dynamical variables. The development of such models has already begun (Geider *et al*. 1996).

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