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Light absorption by phytoplankton: development of a matching parameter for algal photosynthesis under different spectral regimes

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A spectral matching parameter (absorption efficiency, A_e) was developed to quantify the relationship between the light absorption spectra of phytoplankton communities and the spectral irradiance of their ambient light field. A_e was defined as the ratio between the amount of radiation absorbed by the phytoplankton in situ and the amount absorbed in a spectrally flat light regime. This approach was applied to our measurements of spectral absorption for the phytoplankton communities in six lakes in High Arctic Canada that spanned a range of bio-optical conditions. A_e values were calculated for the light spectrum down through the water column and for 11 types of artificial light source. Spectral matching varied among lakes and with depth. There was a significant linear relationship between the relative change in A_e with depth and the diffuse attenuation coefficient K_d ($r^2 = 0.52$, $P = 0.012$ for K_d for the 400–700 nm waveband; $r^2 = 0.78$, $P = 0.0003$ for K_d at 440 nm). The tabulated values for the matching parameter A_e allow the comparison of photosynthesis versus irradiance (P versus E) curves among studies using different light sources. A_e estimates also facilitate the evaluation of chromatic adaptation in natural waters, and the calculation of spectrally adjusted, in situ primary production down through a water column from P versus E relationships under a single spectral regime.

INTRODUCTION

The amount of light absorbed by phytoplankton depends on the spectral absorption characteristics of the cells and the spectral irradiance of their ambient light field. The spectral matching between these two sets of variables is a determinant of *in situ* photosynthesis and is, therefore, an important factor to incorporate within primary production models (Behrenfeld and Falkowski, 1997). Spectral matching has its greatest effect over the light-limited portion of the photosynthesis versus irradiance (*P* versus *E*) curve and contributes to the variations in primary productivity with depth, among water columns and among studies. These spectral effects are of particular concern when translating *P* versus *E* measurements obtained in standard shipboard or laboratory incubators into estimates of water column production (Harrison *et al.*, 1985). For example, Laws *et al.* concluded that by not correcting for spectral shifts down the water column, photosynthesis could be underestimated by >30% (Laws *et al.*, 1990). They recommended that the standard practice of *P* versus *E* incubations under white light should be abandoned in favour of more complex protocols that accurately simulate both the intensity and spectral characteristics of the underwater light field. More recent studies have noted that although the need to incorporate spectral dependencies in photosynthetic models is now well established, in practice this type of correction is often ignored for the sake of convenience and simplicity (Kyewalyanga *et al.*, 1997; Figueiras *et al.*, 1999).

Morel drew attention to the importance of spectral matching as a function of depth in the water column and

introduced the term photosynthetically usable radiation (PUR) (Morel, 1978). He defined PUR as the amount of light absorbed by the phytoplankton (E_a) normalized to the maximum absorption coefficient (a_{max}) for that community [see also (Sakshaug *et al.*, 1997)]. PUR has proven to be a valuable concept for marine and freshwater studies, e.g. in analysis of the ecophysiological effects of algal photoacclimation (Culver and Perry, 1999), development of models of UV photoinhibition of photosynthesis (Arrigo, 1994; Neale *et al.*, 1998), assessing light limitation in the ocean (Figueiras *et al.*, 1999) and for defining the habitat requirements of macrophytes (Gallegos, 1994). Our aim in the present study was to extend this approach by developing a spectral matching parameter that could be readily used to correct *P* versus *E* curves derived from incubators for *in situ* spectral effects and to compare studies using different light sources. The resultant parameter also allowed comparisons among depths and profiles, and provided a way of partitioning the initial slope (α) of the *P* versus *E* curve into components that are dependent on and independent of the spectral quality of the incident light field.

High-latitude lakes encompass a broad range of physical conditions, from clear ultra-oligotrophic fresh waters to turbid meromictic systems, and provide a useful span of environments for the development and evaluation of photosynthetic and bio-optical models [e.g. (Laurion *et al.*, 1997; Rae and Vincent, 1998; Markager *et al.*, 1999)]. In the present study, we determined the spectral irradiance in the water column and the spectral absorption properties of the phytoplankton in six optically contrasting lakes in the Canadian High Arctic. We then used this data set to develop and evaluate a spectral matching parameter.

THEORETICAL BACKGROUND

The amount of light absorbed by a phytoplankton community (E_a) is defined as:

$$E_a = \int E(\lambda) a(\lambda) d\lambda \quad (1)$$

where this integral (and those presented subsequently) is evaluated from λ = 400 nm to λ = 700 nm. E_a depends on the light level, the overall light absorption and the matching between the two spectra (Figure 1; all symbols are defined in Table I). It is, therefore, useful to decompose E_a into three unrelated parameters, which characterize: (1) the total photosynthetically active radiation (PAR); (2) the overall absorption coefficient of the population; and (3) a parameter that characterizes the matching between the two spectra. The total irradiance is defined as:

$$E_{PAR} = \int E(\lambda) d\lambda \quad (2)$$

and we can use the numerical mean of the measured absorption coefficients to characterize the overall phytoplankton absorption:

$$\hat{a}_{ph} = \frac{\sum a_{ph}(\lambda)}{n} \quad (3)$$

where *n* is the number of phytoplankton absorbance measurements over the PAR range. In the most simple case, where $E(\lambda)$ is the same at all wavelengths (i.e. a spectrally flat light field), the amount of light absorbed is given by:

$$E_{a}' = E_{PAR}\, \hat{a}_{ph} \quad (4)$$

A matching parameter (A_e, absorption efficiency) can therefore be defined as the ratio between the actual light absorption in the spectral irradiance *in situ* and the calculated light absorption under the same total irradiance but with a flat spectrum:

$$A_e = E_a / E_a' \quad (5)$$

An additional parameter of interest is the *in situ* absorption coefficient of the phytoplankton over the PAR range:

$$\bar{a}_{ph} = \frac{\sum_{\lambda=400}^{\lambda=700} a_{ph}(\lambda) E(\lambda)}{E_{PAR}} \quad (6)$$

This parameter can also be expressed per unit of phytoplankton biomass, usually chlorophyll (Chl) *a*, and is then denoted $\bar{a}_{ph}^{*}$. The *in situ* absorption coefficient is an apparent parameter with a value that depends not only on the overall absorption per unit Chl, but also on how this absorption spectrum matches the *in situ* light spectrum. On the other hand, the value of $\hat{a}_{ph}$ [equation (3)] is independent of the incident spectrum and is, therefore, an inherent property of the phytoplankton population, which in turn depends on variables such as species composition, cell size, nutritional state and the extent of acclimation to PAR, UV radiation and temperature [e.g. (Berner *et al.*, 1989; Reynolds *et al.*, 1997; Roos and Vincent, 1998; Ciotti *et al.*, 1999)]. Since E_a is the product of the *in situ* irradiance and the *in situ* absorption coefficient, the matching parameter can also be expressed in terms of $\bar{a}_{ph}^{*}$ and $\hat{a}_{ph}$:

$$A_e = \frac{E_a}{E_a'} = \frac{\bar{a}_{ph}^{*}}{\hat{a}_{ph}} \quad (7)$$

The latter ratio of absorption coefficients is the inverse of the correction factor used by several authors to adjust for the spectral quality of incubation lamps in photosynthetic measurements [e.g. factor X in Kyewalyanga *et al.* (Kyewalyanga *et al.*, 1997)]. An A_e value >1 indicates that

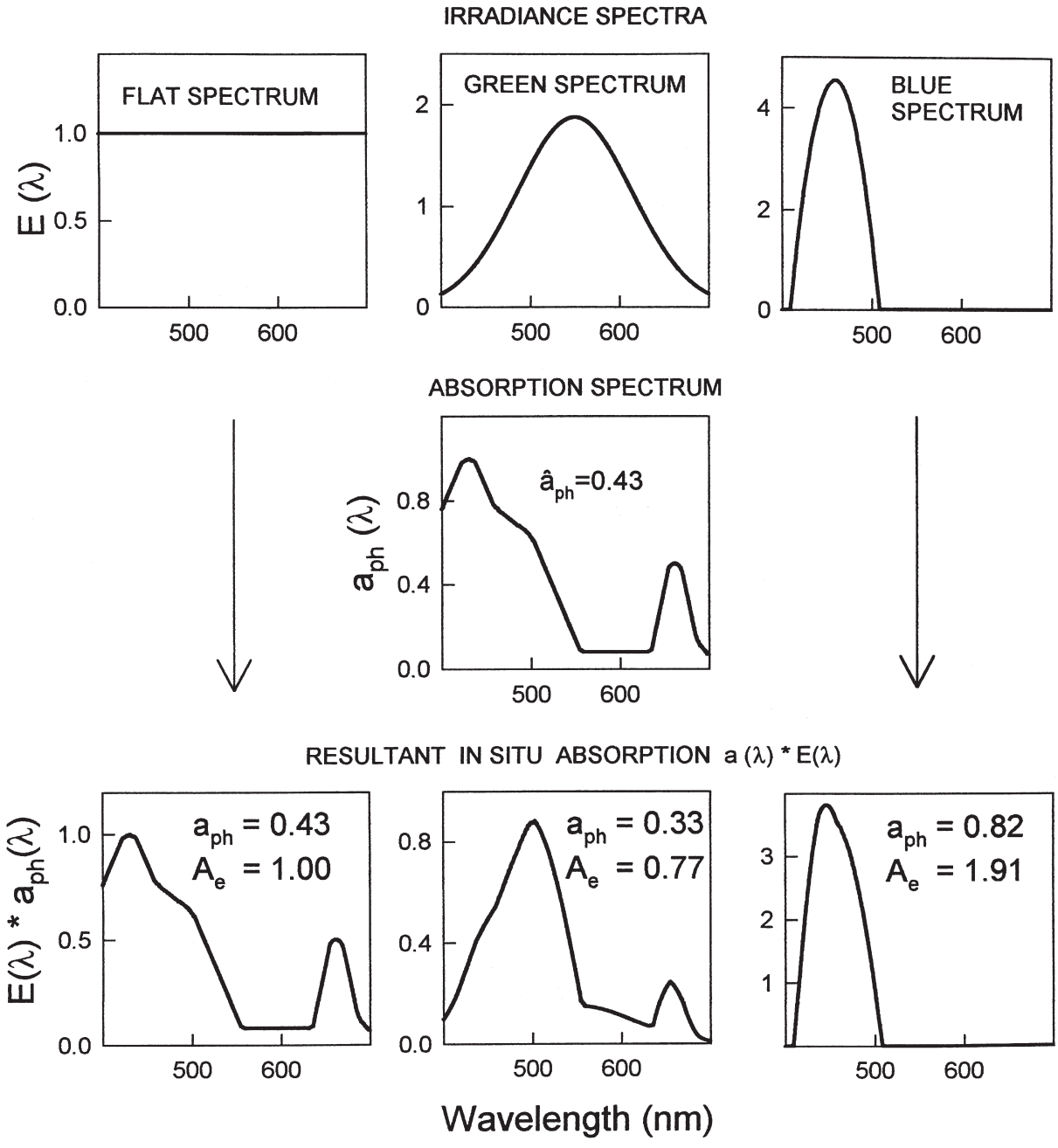

Fig. 1. Schematic illustration of the spectral matching concept. The upper panels show three hypothetical light spectra: a flat spectrum (same E at all wavelengths), a spectrum dominated by green light as found at depth in lakes and coastal waters, and a blue light spectrum. All spectra are adjusted to give the same integral PAR (E_{PAR}). The middle panel shows a typical light absorption spectrum for phytoplankton in schematic form and the value for $\bar{a}_{ph}$, which is independent of the light spectrum (maximum absorption set to one). The lower panels show E_a over the spectrum and the values for $\bar{a}_{ph}$ and A_e for the three *in situ* light regimes at the top.

the incident spectrum is enriched at wavelengths where the absorption coefficient is above the mean value. Similarly, an A_e value <1 indicates a spectrum rich in wavelengths that are poorly absorbed.

The matching parameter A_e allows a direct comparison of α values between studies. α is equal to the product of quantum yield (Φ) and $\bar{a}_{ph}$, and from equation (7) can be expressed as:

$$\alpha = \Phi \bar{a}_{ph} = \Phi \hat{a}_{ph} \cdot A_e \quad (8)$$

The matching parameter can thus be used to correct a

Table I: List of symbols

$a_{ph}(\lambda)$	m^{-1}	Absorption coefficient of pigmented particles at a given wavelength
$a_{ph}(max)$	m^{-1}	The maximum value of a_{ph} over the spectrum
$\bar{a}_{ph}$	m^{-1}	In situ absorption coefficient for pigmented particles over the PAR spectrum
$\hat{a}_{ph}$	m^{-1}	Mean value for a_{ph} over the PAR spectrum
A_e	dimensionless	*In situ* absorption efficiency (spectral matching parameter)
α	g C m^{-1} mol^{-1} quanta	Initial slope of the *P* versus *E* curve
α'	g C m^{-1} mol^{-1} quanta	α corrected for spectral effects, $\alpha' = \alpha/A_e = \hat{a}_{ph}\Phi$
$E(\lambda)$	µmol m^{-2} s^{-1} nm^{-1}	Irradiance at a given wavelength
E	µmol m^{-2} s^{-1}	Irradiance from 400 to 700 nm
E_0	µmol m^{-2} s^{-1}	Irradiance just below the surface
E_a	µmol m^{-3} s^{-1}	Irradiance absorbed by pigmented particles over the PAR spectrum
E_a'	µmol m^{-3} s^{-1}	Irradiance absorbed by pigmented particles in a flat light spectrum
[Chl *a*]	mg Chl *a* m^{-3}	Chl *a* concentration
Φ	mmol C mol^{-1} quanta	Quantum yield of light-limited photosynthesis
K_d	m^{-1}	Downwelling attenuation coefficient
P	mg C m^{-3} h^{-1}	Volume photosynthesis rate
P_m	mg C m^{-3} h^{-1}	Light-saturated photosynthesis rate
z	m	Depth

The superscript asterisk denotes that the parameter is expressed per unit algal biomass measured as Chl *a*.

given ambient α value to the value in a flat spectrum (α'):

$$\alpha' = (\alpha)_{fl} = \frac{\alpha}{A_e} \quad (9)$$

In studies where α values are compared between investigations, part of the variation can stem from different spectral composition of the light fields used to generate *P* versus *E* curves. Part of this variation can be eliminated by comparing α' values instead of α values. This requires knowledge of A_e or its source terms for each measurement. These are seldom provided, but a good approximation can be made if the A_e values for the light source are known for a common phytoplankton absorption spectrum. One of the aims of the present study was to obtain such values. Another potentially important application of A_e is for the calculation of *in situ* primary production at depth. By calculating A_e as a function of depth, α values can be corrected for the changes in light spectrum down the water column to provide an *in situ* measure of α:

$$\alpha(z) = \alpha' A_e(z) \quad (10)$$

This can then be used in *P* versus *E* equations to provide an estimate of photosynthesis corrected for the spectral regime at that depth. For example, using the relationship of Webb *et al.* (Webb *et al.*, 1974), *in situ* photosynthesis is calculated as:

$$P(z) = [\text{Chl } a]\, P_m^*\,(1 - \exp - (\alpha^*(z)\, E_{PAR}(z)/P_m^*)) \quad (11)$$

where [Chl *a*] is the Chl *a* concentration and P_m^* is the light-saturated value of photosynthesis per unit Chl *a* obtained from a *P* versus *E* assay. In the present study, we illustrate some of these applications by way of data from a set of optically contrasting lakes and additional data from the literature.

METHOD

Six lakes were sampled during late summer (open-water conditions) in High Arctic Canada, in the vicinity of Resolute Bay at latitude 74°N, longitude 94°W. Five of the lakes had a well-mixed water column, while the sixth, Lake Sophia, was meromictic and had a Chl maximum in the pycnocline. Spectra of ambient irradiance at the surface and at depth were made with a Li-Cor 1800 spectroradiometer deployed from a helicopter at a mid-lake site. The diffuse attenuation coefficients for downwelling irradiance [$K_d(\lambda)$] were then calculated over the spectrum at 1 nm intervals according to Markager and Vincent (Markager and Vincent, 2000).

Light absorption by seston was measured with the filter-pad technique of Yentsch (Yentsch, 1962). Subsamples of 350 and 550 ml of water were filtered through GF/F filters, and the transmission of light through the filter was measured in an integrating sphere connected to the

Li-Cor 1800 spectroradiometer via a fibre optic cable. Blank filters through which pre-filtered water was passed were used as a reference. Volume-specific absorption coefficients were calculated according to Bricaud and Stramski (Bricaud and Stramski, 1990) with a variable β-factor:

$$\beta = 1.22(\mathrm{OD})^{-0.22} \quad (12)$$

where OD is the optical density. The absorption coefficients where then separated into absorption due to phytoplankton pigments and a background component by the numerical method developed by Bricaud and Stramski (Bricaud and Stramski, 1990). The background absorption includes absorption by detritus and non-pigment compounds in the cells. Samples for Chl *a* were filtered through GF/F filters, and the filters were kept frozen until they were extracted with 90% acetone and analysed fluorometrically (Strickland and Parsons, 1972) with a Shimadzu RF5000 spectrofluorometer calibrated with standard Chl *a* (Sigma Chemical Co.).

RESULTS

Chlorophyll *a* concentrations in the Arctic lakes ranged from 0.04 to 1.24 μg l^{-1} at the time of sampling. The highest values were recorded in the pycnocline region of Lake Sophia. The underwater light field differed among lakes in terms of overall attenuation of PAR as well as the spectral changes with depth. K_d(PAR) ranged from ~0.14 m^{-1} in ultra-oligotrophic Char Lake and Lake Sophia to 0.29 m^{-1} in North Lake. All of the waters showed the typically sharp attenuation of wavelengths >600 nm with depth, with peak underwater irradiance in the green (e.g. Eleanor Lake, 556 nm) or blue (e.g. Lake Sophia, 497 nm) wavebands (Figure 2). Further background details concerning the six lakes at the time of sampling are given in Markager *et al.* (Markager *et al.*, 1999).

The light absorption coefficient of pigmented particles varied over the spectrum, as shown in Figure 3. Maximum values were at 430–450 nm with a shoulder at 485 nm and a secondary peak at 676 nm. Minimum values were recorded between 560 and 590 nm. The mean values over PAR normalized to Chl *a* ($\hat{a}_{ph}^*$) ranged from 13.5 m^2 g^{-1} Chl *a* in the deep sample from Lake Sophia to 30.0 m^2 g^{-1} Chl *a* in the surface sample from Lake Sophia. Surface values were always higher than those from the deep samples and the differences were significant when tested with a *t*-test for both the mean over the full PAR range ($\hat{a}_{ph}^*$) and values at 440 and 675 nm [$\hat{a}_{ph}^*$: $P = 0.012$; a_{ph}^* (675): $P = 0.040$; a_{ph}^* (440): $P = 0.042$].

Figure 4 shows the A_e profiles for four of the lakes, with comparative values for the lamp used in this experiment and for two light sources that are commonly used in photosynthetic experiments elsewhere. The values for surface light were close to 0.9 for all samples (Figure 4; Table II). The value is less than one because daylight is slightly depleted in blue light, which is strongly absorbed by phytoplankton (Figures 2 and 3). The

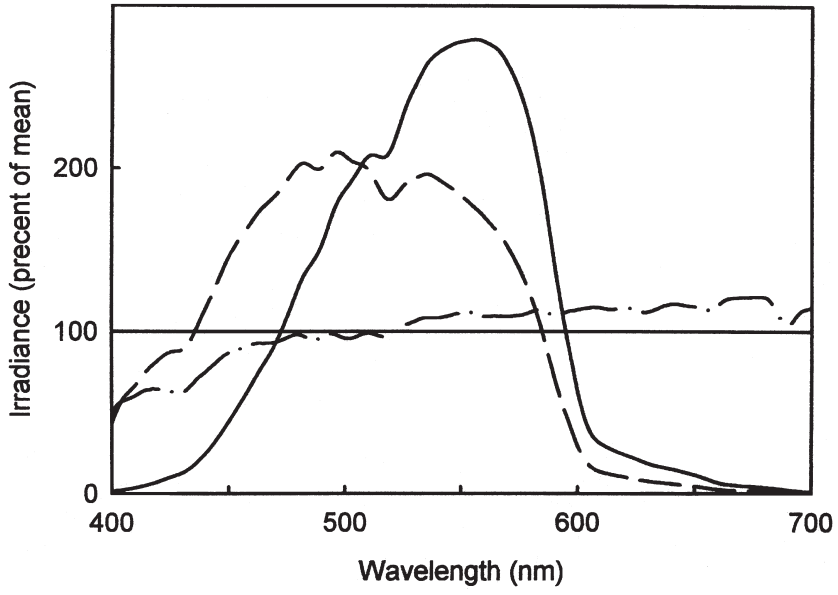

Fig. 2. Spectra of light at the depth of 10% of surface PAR irradiance in Eleanor Lake (solid line) and Lake Sophia (dashed line). A surface irradiance spectrum is also shown (dash–dot–dash).

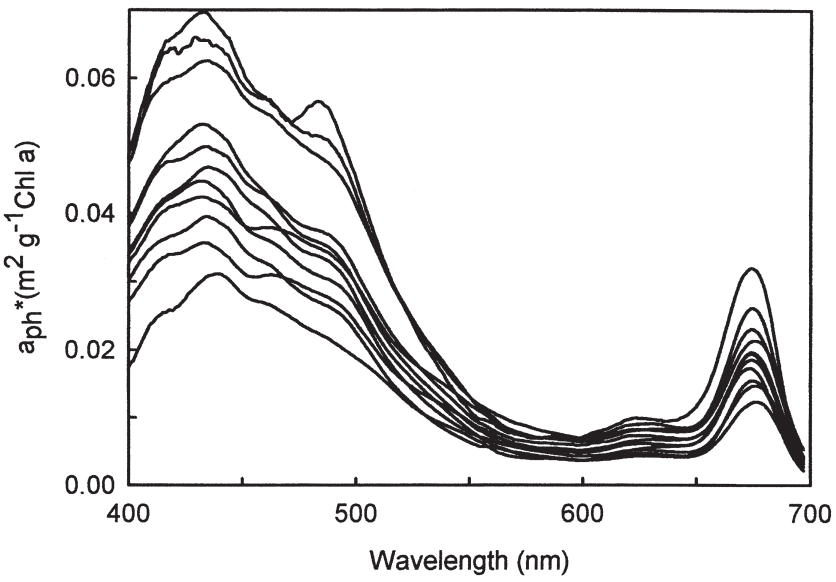

Fig. 3. Chlorophyll-specific absorption spectra for pigmented particles in this study.

values of A_e increased with depth in lakes with low K_d(PAR) (Char Lake, Resolute Lake and Lake Sophia), increasing to a maximum of 1.22 in Lake Sophia. A_e decreased with depth in Eleanor Lake, with a minimum value of 0.77 at 19.5 m. For the overall data set, there was a significant negative relationship (Figure 5a; r^2 = 0.52, P = 0.012) between the change in A_e down the water column [A_e(surface) – A_e(deep)] and K_d(PAR); this relationship was substantially improved by using K_d at 440 nm (Figure 5b; r^2 = 0.78, P = 0.0003). The equilibrium point, i.e. the K_d at which A_e does not change with depth, was estimated as 0.28 m^{-1} [K_d(PAR)] or 0.38 m^{-1} [K_d(440)].

The A_e values were almost identical whether calculated

Table II: Chlorophyll-specific absorption coefficients (m^2 g^{-1} Chl)

Sample	Depth (m)	a_{ph}* 440 nm	a_{ph}* 675 nm	$\hat{a}_{ph}$*	$\bar{a}_{ph}$* (E_0)	$\bar{a}_{ph}$* (10% E_0)	$\bar{a}_{ph}$* (1% E_o)
Char Lake	0.5	66.9	26.4	29.1	26.0	33.9	33.4
	15	48.7	19.7	21.9	19.7	25.4	25.1
Eleanor Lake	0.5	41.2	23.3	20.8	19.1	19.2	17.8
	20	34.3	18.6	17.0	15.6	15.5	14.2
Meretta Lake	0.5	43.1	14.7	18.2	16.2	16.5	15.0
	6	38.6	12.1	15.8	14.0	14.3	12.8
North Lake	0.5	61.7	21.4	27.7	24.8	27.5	25.7
Resolute Lake	0.5	51.7	19.4	21.3	18.9	21.3	19.7
	12	46.1	15.7	18.9	16.8	19.5	18.1
Lake Sophia	0.5	63.8	31.9	30.0	27.1	38.9	41.6
	12	31.1	17.2	13.8	12.7	17.4	18.4
Mean values		47.9	20.0	21.3	19.2	22.7	22.0

$\hat{a}_{ph}$*, numerical mean over the 400–700 nm spectrum; $\bar{a}_{ph}$*, coefficient in the ambient light spectrum; E_o, mean for $\bar{a}_{ph}$* in 12 surface light spectra obtained at different times of the day during the study period; 10% E_o, mean for $\bar{a}_{ph}$* at the depth of 10% surface PAR irradiance; 1% E_o, mean for $\bar{a}_{ph}$* at the depth of 1% surface PAR irradiance.

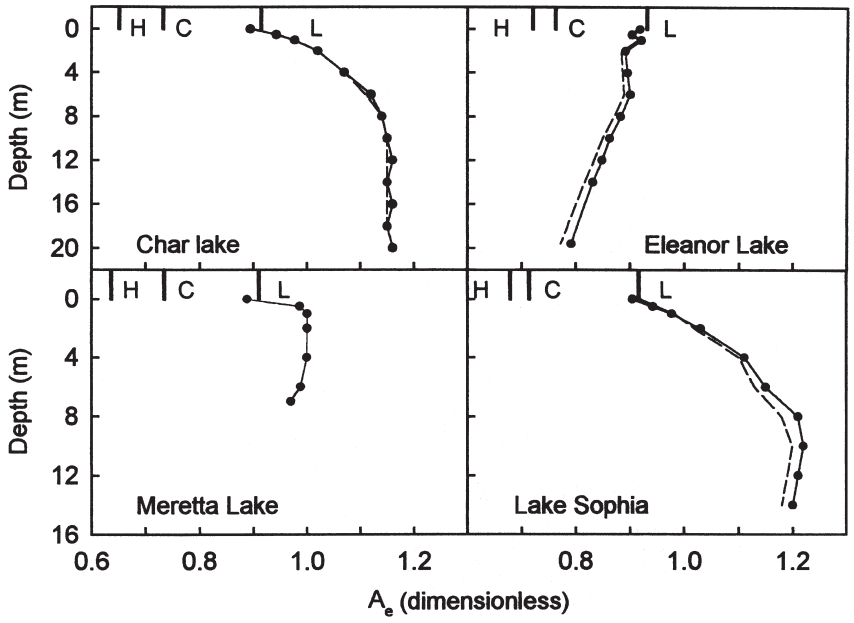

Fig. 4. Vertical profiles of A_e calculated for measured spectral irradiance fields down each water column. The solid line and closed circles are derived from spectral absorption values for surface phytoplankton, and the dashed lines represent deep samples. A_e values are also given for three different artificial light sources (vertical lines at the top): the lamp used in this experiment (L), cool-white fluorescence tubes (C) and a 12 V tungsten halogen lamp (H).

Table III: Mean values and statistics for absorption efficiency values [A_e; for definition, see equation (5)] with spectra from different artificial light sources and in situ

Lamp	Mean	SD	CV	Range
Cool-white fluorescent tubes				
Sanyo FL4022.W/37	0.75	0.014	1.9%	0.72–0.78
Sylvania F72T12/CW/VHQ	0.74	0.015	2.0%	0.71–0.77
Incandescent lamps				
Light bulb, 110 V, 60 W (2790 °K)	0.57	0.050	8.9%	0.51–0.64
Tungsten halogen spot, General Electric, 110 V, 90 W	0.60	0.046	7.6%	0.55–0.67
Tungsten halogen lamp, Osram, 12 V, 50 W (3100 °K)	0.67	0.038	5.6%	0.62–0.72
High-pressure metal halide lamps				
Osram, HQI-T, M80PN-R 250 W	0.92	0.009	1.0%	0.91–0.94
Duro-test, Optimarc, 400 W	0.85	0.015	1.7%	0.84–0.88
Sylvania metal arc, M47 R, 1000 W	0.84	0.010	1.2%	0.82–0.86
Miscellaneous				
Lamp combination used in the present study[a]	0.92	0.011	1.2%	0.91–0.95
Blue fluorescent tube, Phillips TLD18	1.93	0.093	4.8%	1.77–2.05
High-pressure sodium lamp	0.44	0.033	7.5%	0.39–0.50
Natural light fields				
Surface light, Resolute Bay	0.90	0.019	2.1%	0.89–0.94
Depth at 10% surface irradiance	1.02	0.123	12%	0.86–1.21

The values for the lamps are based on measurements of spectra of each source and a_{ph} spectra from 11 phytoplankton samples; both sets of data were obtained with the same Li-Cor 1800 spectroradiometer. The values for surface irradiance are mean values for 12 spectra taken at different times of the day at Resolute Bay, 74°N. Underwater values are mean values for the six lakes investigated calculated from the absorption spectra (surface or deep samples) and the corresponding *in situ* irradiance spectra for the lakes near the surface (0.5 m) and at the depth of 10% surface PAR irradiance.
[a]Described in Markager *et al.* (Markager *et al.*, 1999).

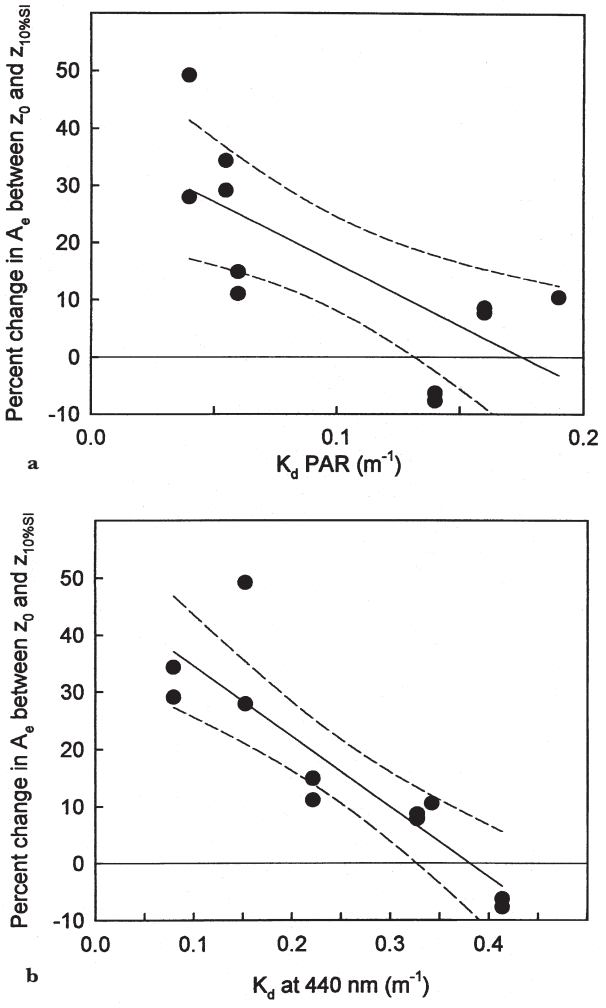

Fig. 5. The relative change in A_e versus attenuation coefficients (K_d) for the six lakes. In the upper panel, K_d is for the full PAR spectrum; in the lower panel, K_d is for blue light at 440 nm. Regression lines and 95% confidence intervals were obtained by least squares regression (see the text for statistics).

from the absorption spectra of a surface sample or a deep sample (Figure 4). Even the values from Lake Sophia were quite similar despite the permanent stratification in this lake, which could have led to the development of a phytoplankton community with different absorption spectra. Interestingly, the A_e value for the deep sample in Lake Sophia, calculated with the light spectrum at the pycnocline, was lower than for the surface sample (also calculated with the spectrum at the pycnocline), indicating that the deep phytoplankton community was not chromatically adapted to its *in situ* spectral regime.

Values for A_e for different lamps are shown with vertical lines in Figure 4 and mean values for a wider range of lamps are provided in Table III (representative lamp spectra are given in Figure 6). The lamp combination used in the present study (Markager *et al.*, 1999) had a spectrum that resembles daylight (Figure 6A and B) and A_e was, therefore, close to daylight values. In contrast, A_e was significantly lower for cool-white fluorescent light (0.71–0.78) and incandescent lamps (0.51–0.72; Table III). High-pressure metal halide lamps have a spectrum that is relatively flat overall, but with several sharp peaks (Figure 6C), and A_e values for this lamp type range from 0.82 to 0.94. Coloured light sources, such as blue fluorescence tubes (similar to spectra using blue filters) or sodium lamps (Figure 6D), have very high or low A_e values, respectively. The variability in A_e varies between the lamps depending on the overall shape of the spectrum. For relatively flat spectra such as daylight, high-pressure lamps and the combination of lamps used in the present study, the range of A_e is low (0.04), whereas it is higher for other lamp types (up to 0.28). With a more even spectrum, $\overline{a}_{ph}$ will approach $\hat{a}_{ph}$, and the ratio, A_e, will approach unity (Figure 1). Thus, A_e and thereby α will be less sensitive to variations in the spectral shape of a_{ph} between samples.

DISCUSSION

The matching parameter A_e builds upon previous formulations [specifically those based on PUR; (Morel, 1978)] and provides a convenient approach towards incorporating spectral effects in a broad range of applications. For example, the parameter α in P versus E determinations can be corrected to a spectrally flat light field by selecting an A_e value from Table III according to the type of lamp used in the incubator and then using equation (9). If spectral irradiance profiles are available for the water column, then these data can be used in combination with spectral absorption estimates for the phytoplankton [from filter determinations as in Roesler (Roesler, 1998); *in vivo* fluorescence excitation spectra as in Neori *et al.* (Neori *et al.*, 1986); or average shape of the photosynthetic action spectrum as in Kyewalyanga *et al.* (Kyewalyanga *et al.*, 1997)] to determine $A_e(z)$. The latter values are used in equation (10) to adjust the flat-spectrum α' for the spectral irradiance at specific depths within the water column. The resultant $\alpha(z)$ then allows the *in situ*, spectrally corrected photosynthetic rate to be estimated using equation (11).

Several authors have used the ratio:

$$\frac{E_{\mathrm{PUR}}}{E_{\mathrm{PAR}}} = \frac{E_{\lambda}}{E_{\mathrm{PAR}}\,a_{\mathrm{ph}}(\lambda)_{\mathrm{max}}} \qquad (13)$$

as an index of absorption efficiency. This ratio is analogous to A_e, except that the amount of light absorbed is normalized to the maximum absorption at one wavelength rather than the mean over the spectrum, as is the

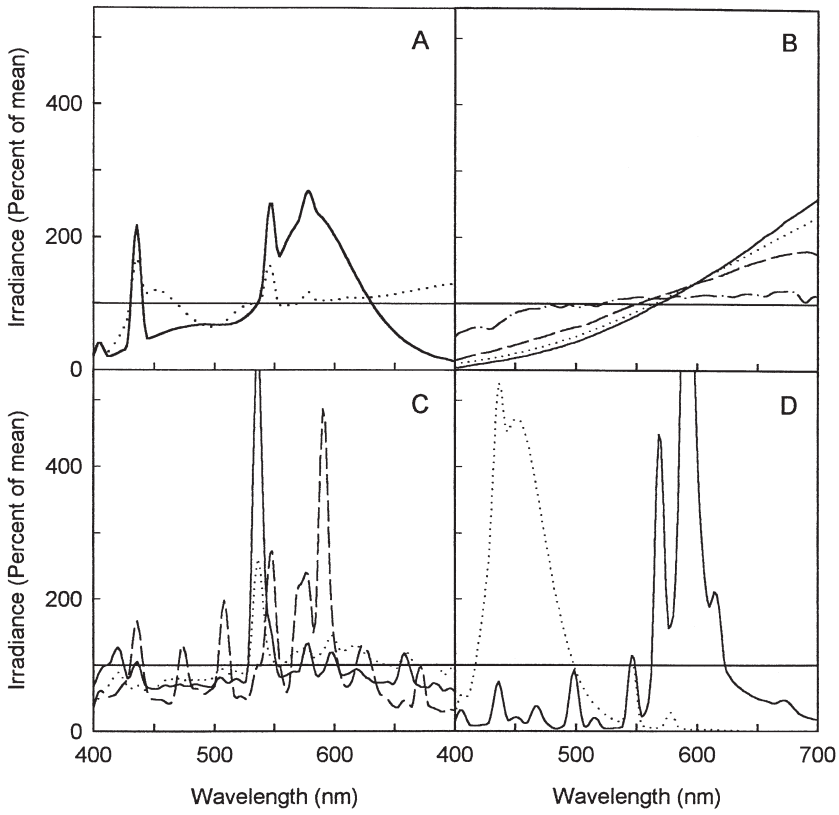

Fig. 6. Spectra of lamps that are commonly used in photosynthetic experiments. (**A**) Solid line: Sanyo cool-white fluorescence tube (FL4022.W/37); dotted line: combination of lamps used in this study (Markager *et al.*, 1999). (**B**) Solid line: 60 W light bulb; dotted line: 90 W halogen garden spot; dashed line: 12 V tungsten halogen spot; dash–dot–dash: surface irradiance at Resolute Bay. (**C**) Solid line: Osram HQI-T daylight, 250 W; dotted line: high-pressure halogen lamp, 400 W; dashed line: Sylvania metal halide lamp, 1000 W. (**D**) Solid line: Phillips sodium lamp, 430 W; dotted line: Phillips blue fluorescence tube, 18W-18.

case for A_e. However, by using the maximum a_{ph} for the PUR calculation, this ratio compares the actual absorbed irradiance to the situation where the entire irradiance is received at the wavelength of maximal absorption. E_{PUR}/E_{PAR} is thus always much lower than unity. In contrast, when E_a is normalized to E_a' [equation (7)], the ratio A_e is generally closer to one in most cases (see Figure 1). Values of A_e above one indicate a closer matching to the *in situ* spectrum than to white light, while values below one indicate a lesser matching.

The ratio E_{PUR}/E_{PAR} can be used to decompose α into an inherent component and an apparent component similar to equation (8):

$$\alpha = \phi\overline{a}_{ph}^{*} = \phi a_{ph}^{*}(\max)\,\frac{E_{PUR}}{E_{PAR}} \qquad (14)$$

However, we suggest that equation (8) is a better formulation than equation (14), since it makes use of $\hat{a}_{ph}$, which contains information about the absorption capacity over the entire spectrum [incorporated in E_{PUR} in equation (14)] instead of $a_{ph}(\max)$, which depends only on one wavelength.

Direct comparisons of a_{ph}^* are generally limited to the wavelengths 430–440 and 675 nm, since these are usually the only values provided in the literature. This means that comparisons between studies are restricted to the absorption due to Chl, which dominates the absorption spectrum at those wavelengths. The absorption due to other pigment is most pronounced at wavelengths between 450 and 550 nm. Analyses based on $\hat{a}_{ph}^*$ would incorporate this latter component and would allow a more detailed comparison of Chl-specific absorption among species and as a function of growth conditions. Analyses based on $\overline{a}_{ph}^*$ are unsatisfactory because they are dependent on the ambient light spectrum. Values of $\hat{a}_{ph}$ would seem to be useful to report routinely, given that this parameter contains information about absorption over the entire spectrum, is independent of the incident light spectrum and is readily calculated.

The Chl-specific absorption coefficients in this study

(Table II) are similar to those measured previously in other systems. For example, the range and the means of $a_{ph}^*(440)$ and $a_{ph}^*(675)$ correspond closely to the values given by Moisan and Mitchell (Moisan and Mitchell, 1999) for *Phaeocystis antarctica*. Values for $a_{ph}^*(675)$ are somewhat higher than those given in Culver and Perry (Culver and Perry, 1999) for four species of marine phytoplankton. Both studies showed an increase in a_{ph}^* with increasing growth irradiance, corresponding to a decrease in self-shading and packing of pigment with a decrease in the pigment content per cell. This pattern is in agreement with our results, which showed higher values for surface samples than for the deep samples and the lowest absolute values in the pycnocline of Lake Sophia, which had a stable shaded environment.

The data for A_e for the Arctic lakes illustrate the large variability in how *in situ* light absorption by phytoplankton communities changes with depth. This change was positive in lakes with low K_d values, but decreased with increasing K_d and become negative when K_d(PAR) was >0.28 m^{-1} or $K_d(440)$ was >0.38 m^{-1} (Figure 5). This is because light absorption by phytoplankton is lower in the red than in the blue region of the spectrum. Since water is responsible for most of the light attenuation when K_d is low and preferentially absorbs red wavelengths, the light shifts towards the blue end of the spectrum with depth (Figure 2; Char Lake), and is therefore absorbed with higher efficiency by phytoplankton. In most lakes with high K_d values, the absorption of blue light is high, either because of high dissolved organic carbon (DOC) concentrations (Laurion *et al.*, 1997) or because of high Chl concentrations. The spectrum is therefore depleted in blue light with depth, causing A_e to decrease down the water column (Figure 2, Eleanor Lake). This blue light effect is underscored by the stronger relationship between the relative A_e shift with depth and K_d for 440 nm than for the full PAR waveband (Figure 5).

Decreasing spectral matching (A_e) with depth is probably the normal pattern in subarctic and temperate lakes where DOC concentrations are higher than in the high Arctic lakes around Resolute Bay (Pienitz and Smol, 1993; Vincent and Pienitz, 1996). DOC (more specifically chromophoric dissolved organic matter, CDOM) is thus a factor that may limit integrated water column production in oligotrophic systems by competing with phytoplankton for photons, particularly in the strongly absorbed blue part of the spectrum. An interesting corollary is that we should expect higher values of primary production per unit surface area in oligotrophic marine systems where CDOM concentrations are often lower [~1 mg DOC l^{-1} (Guo *et al.*, 1995)] and less coloured than in freshwater systems with similar Chl *a* concentrations.

The light utilization efficiency (α) will follow the changes in A_e [equation (8)], assuming that the effect of any spectral dependency of quantum yield is small (Schofield *et al.*, 1996). Estimated this way, the changes in the *in situ* α values with depth relative to the surface value ranged from –22% in Lake Eleanor to +27% in Lake Sophia and Char Lake. Similarly, we can calculate the difference between the measured α values and the *in situ* values from A_e-lamp/A_e-*in situ*. The light source used in this experiment was a combination of lamps designed to produce a flat spectrum (Markager *et al.*, 1999). This is reflected in the low mean difference between our measured α values and the calculated *in situ* values; for 0.5 m, the mean difference was +1%, with the largest deviation of –8% for Meretta Lake. However, A_e values for most other artificial light sources are much lower than *in situ* values (Table III). For example, if we had used cool-white fluorescent tubes, the average α value in the incubator would have been 28% lower than the average *in situ* value, and for the deep sample from Lake Sophia the difference would have been as high as 65% [$100 \times (1.22 - 0.74)/0.74$]. This error could be even larger under oceanic conditions (Johnsen and Sakshaug, 1993) in which there are greater spectral changes with depth. On the other hand, our results show that A_e values decrease with depth in lakes with high DOC concentrations, and α values estimated with a spectrum that resembles surface irradiance will therefore overestimate *in situ* photosynthesis at depth. These observations underscore the conclusion that spectral effects must be taken into account for accurate estimates of *in situ* primary production based on an incubator approach, and that the parameter A_e provides a convenient way to model and correct for such effects.

The effect of spectral quality must also be taken into account for intersystem comparisons of α values. An α value measured with irradiance from cool-white fluorescent tubes would be ~82% of the value measured in daylight ($100 \times 0.74/0.90$; Table III). Such a correction can only be an approximation in the absence of spectral measurements for phytoplankton absorption and the irradiance for the incubator. However, the general similarity among phytoplankton absorption spectra [Figure 3 in Bricaud and Stramski (Bricaud and Stramski, 1990); Figure 6 in Culver and Perry (Culver and Perry, 1999); Figure 2 in the present study] means that the effect of different light sources on α will be reasonably uniform among many types of phytoplankton communities. Kyewalyanga *et al.* similarly found that the use of an average absorption spectrum in combination with α gave a good approximation of the photosynthetic action spectrum for marine phytoplankton communities, and that the error caused by non-photosynthetic pigments was relatively minor (Kyewalyanga *et al.*, 1997).

Using data from a literature survey including 134 α values for marine phytoplankton from seven sources (Markager *et al.*, 1999), we found that the correction for differences in A_e reduced the coefficient of variation in α by ~14%. A similar result was obtained for culture values. This reaffirms that spectral quality can explain part of the variation in α values in the literature. A_e values for most of the lamps listed in Table III are lower than A_e for daylight. This means that α values for surface conditions overall are underestimated when measured with artificial light sources. The magnitude of this error is about –18% (assuming an average A_e of 0.75 for artificial light and of 0.90 for daylight), but the exact value will vary depending on the actual *in situ* absorption properties of the phytoplankton under test.

Underwater irradiance, phytoplankton absorption coefficients and most artificial light sources all share the feature of being highly wavelength dependent. The matching parameter developed here, A_e, allows these effects to be placed on a common scale by reference to a flat PAR spectrum. This approach allows direct comparisons among experiments using different light regimes and it provides a spectral correction for calculations of *in situ* absorption and photosynthesis. Our A_e analysis of Arctic lakes illustrates how spectral matching varies among water bodies, and also as a function of depth down the water column.

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