Theoretical results concerning light absorption in a discrete medium,
and application to specific absorption of phytoplankton

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Abstract—The radiation absorption within a medium supposedly non-absorbing in itself but
containing an absorbing substance as particles is examined theoretically. Absorption by such
particles can be treated independently of (Mie) scattering under an assumption concerning the
complex refractive index that is reasonable in case of algal cells (index close to that of water and
weakly absorbing substance). The effect of discreteness on absorption properties is ruled by a
function of the dimensionless parameter that combines through their product the size \(d\) and the
absorption coefficient of the cell material \(a_m\). The limiting value of this function \((d \to 0)\) describes
the case of a true solution of the same material, whereas its variations with \(d\) and \(a_m\) imply that the
specific absorption coefficient, for a given substance, is variable in magnitude and in spectral
behaviour. Consequently, Beer's law, which rests on the existence of a constant specific coefficient,
generally cannot apply when canopy changes intervene in an algal population. Various cases of such
changes are studied along with their consequences on absorptive properties.

Theoretical conclusions are exemplified by some experimental results concerning algal
cultures. The absorption properties of the cell material for each species can be extrapolated from the
actual absorption spectra of intact cells.

Problems that originate from the non-constancy of the specific absorption coefficient (spectral
values or mean value) are examined in view of two kinds of applications: the photosynthetic
(quantum) yield evaluation and the algal biomass assessment by remote sensing, for which the
constancy is generally postulated.

INTRODUCTION

Radiation absorption in a discrete medium containing an absorbing substance as suspended
particles is different from absorption in a continuous medium containing an equal amount
of the same substance, supposedly dissolved. Mie theory for absorbing spheres of various
sizes can be used to account for this effect. The different behaviour of a suspension vis à vis
that of a solution was pointed out and explained by DUYSENS (1956) in his pioneer work.
More recently, KIRK (1975a, b, 1976), using a similar approach combined with some of
Duysens' results, presented a theoretical analysis of the contribution of algal cells to the
attenuation of irradiance within natural waters. In his study, he took into consideration the
size, shape, and the pigment content of the cells.

Surprisingly, these important results have not been fully explored in their consequences
and in particular they have not been extended to the concept of 'specific' absorption. A
specific absorption coefficient is defined as the absorption coefficient for unit concentration
of a specific substance, which may be present in a medium in dissolved or particulate state.
Application of the Beer—Lambert—Bouguer law depends on the existence of a well-defined

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specific absorption coefficient. Such coefficients are needed when attempting to give an analytical interpretation of the optical properties of a water body in terms of its content. With this aim, the actual absorption coefficient, \( a(\lambda) \), at a given wavelength, is partitioned into several terms:

\[
a(\lambda) = a_w(\lambda) + \sum a_x^*(\lambda) |x|.
\]

Each component, \( x \), contributes to the total absorption \( |x| \) times its specific absorption coefficient, where \( |x| \) is the concentration of \( x \), and the constant term \( a_w \) stands for the water itself. Among these components, phytoplankton is of particular importance. A specific absorption coefficient for phytoplankton is needed for a meaningful interpretation of the actual optical properties of ocean (and lake) waters with respect to their algal content. It is also required for studies of aquatic photosynthesis and algal biomass assessment by remote sensing.

A correct evaluation of the quantum yield efficiency in photosynthesis (see e.g., Bannister, 1974; Morel, 1978; Atlas and Bannister, 1980) requires knowledge of the absorptive capability of the algal cells in their natural radiative environment, i.e., of the spectral values of their actual specific absorption (which thereafter have to be combined with the spectral composition of the remnant light). The same holds true for the estimate of \textit{in vivo} fluorescence efficiency.

Remote sensing techniques, from spacecraft or aircraft, are now developed with the aim of estimating the phytoplankton concentration in the upper layers of the sea by measuring the color shift induced by the algal cells. In default of reliable spectral values for the specific absorption, \( a_x^*(\lambda) \), of algal cells, only statistical-empirical approaches are possible (Gordon and Clark, 1980; Morel, 1980; Morel and Gordon, 1980). With the knowledge of \( a_x^*(\lambda) \), an analytical approach would be possible. By inverting the radiative transfer equation, the subsurface reflectance of the sea, \( R(\lambda) \)—an "apparent property", according to Preisendorfer's (1961, 1976) definition—can be related to the inherent properties of the medium, namely to \( b_b \) and \( a \), through the ratio \( b_b/a \), where \( b_b \) and \( a \) are the backscattering and absorption coefficients (Gordon, Brown and Jacobs, 1975; Prieur and Morel, 1975; Morel and Prieur, 1977). Knowledge of \( a_x^*(\lambda) \) is required to analyse the spectral dependence of \( a(\lambda) \), and subsequently of \( R(\lambda) \), in terms of phytoplankton content.

Through a new theoretical approach, the purpose of this study is to reinvestigate the problem of absorption in a discrete medium, to examine the applicability of Beer's law in such a case, and finally to demonstrate how the concept of specific absorption is more complex than generally accepted and how it is modified when dealing with a suspended absorbing substance. The effect of discreteness is to render variable the specific absorption values of a given substance with the physical and geometrical parameters that characterize the suspension. It is studied with special reference to algal cells and possible change in canopy. Numerical predictions are also exemplified by some experimental results.

**THEORETICAL FRAMEWORK**

The algal cells are assumed to be spherical and homogeneous with respect to their absorptive properties, and their index of refraction is supposed to be close to that of the surrounding medium (water). So the relative index is \( m = n - in' \), where the real part, \( n \), is close to one and the imaginary part, \( n' \), remains small. In this case, \( Q_a \), the dimensionless efficiency factor for absorption, which is defined as the ratio of the energy absorbed within
the sphere to the radiant energy impinging on its geometrical cross-section \(s = \pi d^2/4\), if \(d\) is the diameter), is obtained by integration and expressed as:

\[
Q_a = 1 + \frac{2e^{-\rho}}{\rho'} + 2\frac{e^{-\rho'} - 1}{\rho'}
\]

(VAN DE HULST, 1957) (an equivalent relationship was also given by DUYSSENS, 1956), where \(\rho' = 4an'\). It is a pure number, which combines \(n'\) with the size parameter \(\alpha = \pi d/\lambda\), and \(\lambda\) is the wavelength in the surrounding medium. If at this wavelength \(a_{cm}\) is the absorption coefficient (dimension \(L^{-1}\)) of the supposedly homogeneous matter that forms the cells, hereafter called cell matter absorption coefficient, \(a_{cm}\) and \(n'\) are linked through \(n' = \lambda a_{cm}/4\pi\) and therefore \(\rho' = 4an'\) can also be expressed as \(\rho' = a_{cm}d\).

There is a unique absorption curve, \(Q_a(\rho')\) (Fig. 1), for all absorbing spheres depending on the parameter \(\rho'\), as similarly there is only one scattering curve, \(Q_s(\rho)\), depending on the parameter \(\rho = 2\alpha(m-1)\), for all non-absorbing spheres and under the same assumption, i.e., \((m-1) \ll 1\). \(Q_s\) is the efficiency factor for scattering (ratio of the energy scattered by the sphere to energy impinging on its geometrical cross section), \(\rho\) is the phase lag for the central ray passing through the sphere, whereas \(\rho'\) can be seen as the ‘optical thickness’ due to absorption, also along the central ray. This assumption concerning \(m\) allows absorption to be treated independently of scattering even in the (Mie) domain of larger spheres. The converse is not true [see for instance MUELLER (1973) or MOREL and BRICAUD (1981) and Appendix 2].

The important properties of the monotonic function \(Q_a(\rho')\) that will be used later are \(Q_a \to 1\) when \(\rho' \to \infty\), that is to say for big and/or strongly absorbing spheres that tend to
act as perfect black bodies (‘perfect’ because, with the real part \( n \) assumed to be close to one, reflection vanishes). When \( \rho' \to 0 \), that is to say for small and/or weakly absorbing spheres, \( Q_a \to 0 \). If expanded, equation (1) gives

\[
Q_a(\rho') = 2 \sum (-1)^{n+1} \frac{n+1}{(n+2)!} \rho'^n,
\]

which reduces, for small \( \rho' \), to:

\[
Q_a(\rho') \approx (2/3) \rho' + \ldots \quad (1a)
\]

meaning that \( Q_a(\rho') \) becomes approximately a linear function of \( \rho' \).

If \( \rho' \) is increased by a factor \( k(k > 1) \) by increasing \( \alpha \) or \( n' \), or equivalently, by increasing the size \( d \) or the cell matter absorption \( a_{cm} \), \( Q_a(\rho') \) is changed into \( Q_a(k\rho') \). According to the properties mentioned above, the following situations may arise:

\[
\begin{align*}
Q_a(k\rho') &\approx kQ_a(\rho') \quad \text{in the quasi-linear domain (\( \rho' \) small)} \quad (2a) \\
Q_a(k\rho') &< kQ_a(\rho') \quad \text{in general} \quad (2b) \\
Q_a(k\rho') &\approx Q_a(\rho') \approx 1 \quad \text{in the ‘black body’ domain (\( \rho' \) high)} \quad (2c)
\end{align*}
\]

The consequences of these relationships upon the absorption coefficient for a suspension are straightforward. If \( N \) spherical cells of uniform size are in suspension in a volume \( V \), the absorption coefficient (dimension \( L^{-1} \)) of this medium, due to the presence of this discrete absorbing substance will be:

\[
a = NQ_a s/V. \quad (3)
\]

This equation is always locally valid, in the same way as an inherent property is always definable. Its applicability to a volume of finite thickness is discussed in Appendix 1.

When considering the three variables, \( a_{cm}, d \) (combined in \( \rho' \)), and \( (N/V) \) which intervene, three kinds of change in the algal population can ideally be imagined (see e.g., the “mental experiment” described by EDMONDSON, 1980).

(i) The cell number density, \( N/V \), changes but the cells remain the same. Since \( Q_a \) and \( s \) are unaffected, \( a \) is simply proportional to \( N/V \) (case 1 in Appendix 3).

(ii) The cell number density and cell size are assumed to be constant, but the intracellular pigment concentration, \( c_i \), and hence \( a_{cm} \), are supposedly increased by a factor \( k \) (case 2 in Appendix 3). Consequently, \( Q_a \) and \( a \) are modified. For small and weakly absorbing spheres, \( a \) will be multiplied by \( k \) (according to equation 2a). In general (equation 2b), \( a \) will be increased by a factor smaller than \( k \). In the limiting case (equation 2c), \( a \) will be almost unchanged.

(iii) \( N/V \) and \( a_{cm} \) being kept constant, the size \( d \) is increased by a factor \( k \) (case 3 in Appendix 3). The cross section \( s \) is multiplied by \( k^2 \), and \( Q_a \) is modified according to equation (2). In the quasi-linear domain, \( a \) is thus multiplied by \( k^3 \) and the absorption coefficient appears to be governed by the volume of the suspended material. Conversely, in the ‘black body’ domain, \( a \) is multiplied by \( k^2 \) and \( a \) is related to the surface area of the particles. Generally speaking, the factor that applies to \( a \) is \( k^n \), with \( 2 < n < 3 \). When considering the actual size range of algal cells and the corresponding \( \rho' \) values (Fig. 1), this intermediate situation is the general rule. Equation (1) allows exact computations to be made.
In the modifications inside the algal population, as envisaged above, the total pigment content, \( M \), in \( V \) is variable:

\[
M/V = C = (N/V)c_i;
\]  

(4)

\( C \) is the pigment concentration in the suspension (whereas \( c_i \) is the intracellular concentration) and \( v = (\pi/6)d^3 \). Beer’s law is currently invoked to account for the variation in absorption, \( a \), when \( C \) varies. However, this law should be valid for a discrete absorbing medium only if the variation in \( a \) is in any case strictly proportional to the change in \( C \), whatever is the cause of the change. According to equation (4), the change in \( C \) may result from separate or combined variations in \( N/V \), in \( v \), or in \( c_i \).

As seen above, the variations in \( a \) are strictly proportional to the variations in \( C \)—independently of the causes of these variations—in the quasi-linear domain only (true solution or solution-like suspension of very tiny particles), and only in this case Beer’s law holds true. Generally, it cannot be applied to phytoplankton populations unless it is ascertained that only the cell number density, \( N/V \), varies.

If the absorption coefficient (equation 3) is now expressed as the product \( a^*C \) of a specific absorption coefficient and the concentration, the departure from Beer’s law must be seen as a possible variation in that specific coefficient. This variation will be made explicit below.

**SPECIFIC ABSORPTION**

**General treatment**

The specific absorption coefficient, \( a^* \) (dimension \( L^2 M^{-1} \)), for an absorbing substance present in the medium as particles, is

\[
a^* = a/c_i c_v,
\]

where \( c_i \) is multiplied by \( c_v \) (dimensionless), the volume concentration of the suspended material: \( c_v = Nv/V \). Using equation (3), it follows that, for spherical particles

\[
a^* = Q_a c_i v = (3/2) Q_a c_i d',
\]

(5)

For sufficiently large and absorbing spheres, when \( Q_a \) approaches one asymptotically, \( a^* \) becomes simply proportional to the reciprocal of diameter (see Appendix 2). For the general case, it is more convenient to write equation (5) in another form by re-introducing the dimensionless parameters \( \alpha \) and \( n' \), so

\[
a^* = (3/8) a_{cm} Q_a (\alpha n') c_i
\]

or

\[
a^* = a_{cm} Q^*_a c_i,
\]

(5a)

where appears the dimensionless function \( Q^*_a \), defined as

\[
Q^*_a = (3/8) Q_a (\alpha n') = (3/2) Q(\rho') \rho'.
\]

(6)
The specific absorption coefficient, \( a^* \), is determined by the physical parameters, \( a_{cm} \) and \( c_i \), typical of the substance considered, and by the factor \( Q^*_a \). Thus, for a given dispersed absorbing substance (\( c_i, a_{cm} \), and consequently \( n' \) constant, at a given wavelength), \( Q^*_a \) becomes only a function of the size, and its value rules the evolution of \( a^* \) with changing size.

As shown in Fig. 1, \( Q^*_a \) reaches its maximum value, equal to one, for \( \rho' \) tending towards zero (according to equation 1a) and then decreases, becoming a hyperbolic function with zero as asymptotic value. When dealing with a discrete medium and as anticipated in the discussion about the applicability of Beer's law, the concept of specific absorption appears more complicated than is generally admitted. Its numerical value, unique for a solution, becomes for a suspension variable and size-dependent.

The limiting case corresponding to \( Q^*_a = 1 \), is obtained when \( \alpha n' \to 0 \) or when \( \alpha \to 0 \), because \( n' \) is constant for a given substance. This limiting case is simply a solution of the same absorbing substance, in which the size of the particles is reduced to the molecular size. Hence, \( a^* \) becomes \( a_{sol}^* \), so that

\[
a_{sol}^* = a_{cm}/c_i, \tag{7}
\]

which obviously could have been directly inferred. If the absorbing substance is no longer dissolved but is particulate, the specific absorption is lowered according to the ratio:

\[
a^*/a_{sol}^* = Q^*_a \tag{8}
\]

or alternatively:

\[
a^*/a_{sol}^* = \frac{3}{2} \frac{Q_a}{a_{cm}d} \tag{8a}
\]

It is a simple demonstration of the equivalent formula established by Duyvsehn (1956, equation 2a) through a somewhat different and more complicated approach.

The decrease in specific absorption with increasing size, as resulting from equation (8), may be illustrated as follows. The pigments contained in algal cells exhibit an absorption peak, in vivo, around 435 nm. According to experimental results partly reported here (Appendix 4), the cell matter absorption coefficient at this wavelength would be in the range \( 5 \times 10^3 \) to \( 5 \times 10^4 \) m\(^{-1}\). For the numerical example, \( a_{cm} \) is tentatively put equal to \( 2 \times 10^5 \) m\(^{-1}\) (which corresponds to \( n' = 0.0052 \) at \( \lambda = 435 \) nm). By using Strickland's (1960) relationships among chlorophyll, carbon, and weight of phytoplankton, an average value can be obtained for the total algal volume per unit of chlorophyll \( a \), which is \( 3.5 \times 10^{-7} \) m\(^3\) (mg Chl \( a \))\(^{-1}\). In turn, this value leads to intracellular chlorophyll \( a \) concentration \( c_i = 2.86 \times 10^6 \) (mg Chl \( a \)) m\(^{-3}\),†

If the cells were disrupted and the cellular pigment were so finely subdivided that it can be regarded as dissolved, it follows, with the values of \( a_{cm} \) and \( c_i \) adopted, that the specific absorption coefficient, at \( \lambda = 435 \) nm, would be (equation 7):

\[
a_{sol}^* = 0.070 \text{ m}^{-1} \text{ (mg Chl } a \text{ m}^{-3})^{-1} \text{ or m}^2 \text{ mg}^{-1} \text{ Chl } a. \]

† So far as we know, little information is available in the literature concerning \( a_{cm} \). A determination made by Duyvsehn (quoted in Latimer and Rabinyitch, 1959) leads to the value \( 3.28 \times 10^5 \) m\(^{-1}\) at 675 nm for Chlorella pyethroidosa. The cell volume to carbon content relationship is better documented (Strathmann, 1967) than the volume to pigment content relationship, which allows \( c_i \) to be inferred. Kirk (1975b) adopted the value \( 2.92 \times 10^6 \) (mg Chl \( a \)) m\(^{-3}\) as a representative mean value for green algal cells. This concentration is, in effect, highly variable with the species of phytoplankter (see Appendix 4).
If the same cellular matter \( (a_{cm} \text{ and } c_i \text{ unchanged}) \) is now included in spherical cells of supposedly variable size (case 3, Appendix 3), the specific coefficient will take the following values, according to the diameter (equation 5a):

\[
\begin{align*}
a^* & \quad 0.070 \quad 0.065 \quad 0.053 \quad 0.041 \quad 0.028 \quad 0.015 \quad \text{m}^2\text{mg}^{-1} \text{ Chl a} \\
\text{for } d & \quad "0" \quad 2 \quad 4 \quad 8 \quad 16 \quad 32 \quad \mu\text{m}.
\end{align*}
\]

*Consequences of the equivalent role played by size and cellular absorption*

As they intervene through their product in fixing the values of \( Q_a \) and \( Q^*_a \), the numbers \( a \) and \( n' \), or the quantities \( d \) and \( a_{cm} \), have an homologous effect. By virtue of this equivalence, \( Q_a \) and \( Q^*_a \) remain unchanged if the absorption coefficient \( a_{cm} \) is changed by a factor \( k \), whereas size is simultaneously changed by \( k^{-1} \).

According to equation (5a), the same rule holds true for the specific absorption coefficient. A reciprocal change in \( a_{cm} \) and \( d \) leaves \( Q^*_a \) unaffected. Moreover, a change in \( a_{cm} \) also leaves the ratio \( a_{cm} : c_i \) unaffected. By application of Beer's law (applicable for the cell matter), a variation in absorption by the cell matter \( (a_{cm}) \) implies a proportional change in intracellular concentration \( (c_i) \). Coming back to the numerical example, if the cell matter absorption is now assumed to be half of its previous value \( (1 \times 10^5 \text{ m}^{-1}) \), cells with \( d = 16 \mu\text{m} \) will behave as the former 8-\( \mu\text{m} \) cells, and \( a^* \) will be increased from 0.028 to 0.041 \( \text{m}^2\text{mg}^{-1} \text{ Chl a} \). In other words, when the cellular pigment concentration decreases, at constant cell size, the specific absorption increases (case 2, Appendix 3).

When \( a^* \) is maintained constant by reciprocal variations in \( d \) and \( a_{cm} \), the absorption coefficient, \( a \), generally is variable (case 4a, Appendix 3). However, if the pigment concentration, \( C \), is kept constant by changing accordingly the cell number density, \( a \) may also be constant (case 4b, Appendix 3). Conversely, if \( C \) is kept constant by changing the intracellular concentration at \( N/V \) constant, \( a^* \) and \( a \) will be modified. This case (5, Appendix 3), represents a change in biomass due to a change in size at constant total pigment and cell number. In such a change, \( \rho' \) \( (= d a_{cm}) \) is divided by \( k \) so, if \( k > 1 \) (cells growing in size, biomass increasing), \( Q^*_a \) and \( a^* \) increase. For instance, if the previous 8-\( \mu\text{m} \) cells (with \( a_{cm} = 2 \times 10^5 \text{ m}^{-1} \)) grow to 16 \( \mu\text{m} \), \( c_i \) and \( a_{cm} \) are divided by 8, and \( \rho' \) by 4, and the new value for \( a^* \) is 0.0605 \( \text{m}^2\text{mg}^{-1} \text{ Chl a} \).

Similar conclusions were drawn by Kirk (1975a) through an approximate theory made initially with the proviso of “constant pathlength cells” (defined such that a ray passes through the same pathlength of all material, no matter at what point it traverses the cell) and then extended to cells of any shape and orientation (Kirk, 1976).

By considering equations (3, 4, and 5) and with the knowledge of the behaviour of \( Q^*_a \) and \( Q^*_a \) (equations 1 and 6), the consequences of various modifications taking place in the algal crop can be predicted. They are summarized in Appendix 3. The modifications may affect separately or simultaneously the cell number density, the diameter, and the intracellular concentration (or consequently the cell matter absorption) and lead to modify \( B \), the biomass concentration \( (B = N v/V) \), and \( C \), the pigment concentration in the medium. The correlative changes in absorptive properties, \( a^* \) and \( a \), are obtained through the variations of \( Q^*_a \) and \( Q^*_a \). The list is not exhaustive, and other cases can be imagined. However, the basic trends are given and from them, other results can be inferred.
Spectral values of specific absorption

Due to the non-linear effect of the function $Q_a^*$, the spectral specific values, $a^*(\lambda)$, appear also to be size dependent. In the preceding reasoning, it was assumed that a change in cell matter absorption can only result from a change in intracellular pigment concentration, as $\lambda$ was fixed. However, $a_{cm}$ can be modified, at $c_i$ constant, by changing the wavelength. The consequence of such a change, for a given population ($N/V$, $d$ and $c_i$ constant), is identical to that described as case 2 in Appendix 3. By considering equation (5a), $a^*$ would be increased by a factor $k$ when $a_{cm}$ is increased by this factor (by changing $\lambda$), only if $Q_a^* = 1$, that is to say only in the quasi-linear domain. Generally, $Q_a^* < 1$, and so the larger $d$ or $a_{cm}$, the greater the departure from one and the smaller the possible increase in $a^*$. In other words, compared to a solution of the same pigments, pigmented cells will tend to absorb less efficiently the radiations that normally are the most strongly absorbed (high $a_{cm}$). The $a^*(\lambda)$ spectrum will be lowered and flattened with respect to the $a_{cm}(\lambda)$ spectrum, as explained by Duyzens (1956).

For a given absorbing substance, i.e., for a given $a_{cm}(\lambda)$ spectrum, the flattening effect becomes more pronounced as the size increases, as exemplified by Fig. 2. Whatever the absorption, the limit, for sufficiently large size, will be a black body that has a completely flat absorption spectrum (when $Q_a^*$ varies as $k^{-1}$).

The importance of the flattening effect is evidenced by the difference between the absorption spectrum measured for intact cells and the corresponding spectrum computed

![Image](image-url)
(see below) for a hypothetical aqueous solution of the cell matter. Figure 3 provides examples of strong and weak flattening effects for three species of marine phytoplankters, grown in batches and harvested during the exponential growth phase. Relevant information concerning the cultures is given in Appendix 4.

*Platymonas suecica*, with \( d = 6.0 \mu m \) and \( c_i = 4.48 \times 10^6 \) mg Chl a m\(^{-3}\), possesses high \( \rho' \) values, particularly in the blue part of the spectrum, and so the flattening effect is pronounced. It is much weaker for the other algae. *Coccolithus huxleyi* exhibits lower \( \rho' \) values due to smaller size (3.8 \( \mu m \)) combined with a lower intracellular pigment concentration \((1.07 \times 10^6 \) mg Chl a m\(^{-3}\)). With a very low pigment concentration \((0.1 \times 10^6 \) mg Chl a m\(^{-3}\)), *Chaetoceros protuberans* also has low \( \rho' \) values in spite of its large size (the equivalent diameter of these almost cylindrical cells is, on average, 26.5 \( \mu m \)).

The procedure to derive \( a_{sol}^* \) from \( a^* \) is as follows: experimental values obtained for \( a^*, c_i, \) and \( d \) are used as input parameters in equation (5), which can be solved for \( Q_a \) at each wavelength considered. With \( Q_a(\lambda) \) and \( \alpha = \pi d / \lambda \) as input parameters, equation (1) is thereafter solved for \( n' \) (through \( \rho' = 4\pi n' \)). Finally, the \( n'(\lambda) \) values are converted into spectral values of the cell matter absorption coefficient, \( a_{sol}(\lambda) \). By assuming that \( Q_a^* = 1 \), the condition that allows equation (7) to be written and used, the specific spectral absorption for the hypothetical solution, \( a_{sol}^*(\lambda) \), can be straightforwardly computed. These \( a_{sol}^* \) spectra (dotted curves, Fig. 3) are directly comparable in magnitude as the disturbing influence of discreteness is eliminated.

**DISCUSSION**

*Validity of hypotheses*

Besides the reasonable assumption about the refractive index, the present theoretical approach postulates the homogeneity and the sphericity of the algal cells. The homogeneity should be approximated by cells packed uniformly with chloroplasts. More realistically, a cell can be regarded as having strongly absorbing parts (chloroplasts) embedded in an almost non-absorbing substance (cytoplasm and walls). The same theoretical treatment applies, with only a change in scale. Between a homogeneous absorbing sphere and a non-absorbing body containing an inner and smaller sphere, where the same amount of pigment would be concentrated, a difference that is just as described in case 5, Appendix 3 (with \( k < 1 \)) exists. The consequence of the actual granulation is a decrease in \( a^* \) and \( a \) values. This trend is counterbalanced if the same pigment quantity is distributed in several \( (n) \) chloroplasts, because the concentration in each chloroplast is then divided by \( n \). Conversely, from actual \( a^* \) values, the extrapolation toward \( a_{sol}^* \) leads to an underestimated value if the cell characteristics are used in computation instead of the chloroplast characteristics. This effect does not appear crucial as \( a_{sol}^* \) spectra obtained from different species of phytoplankter have coinciding red peaks (at 675 nm) in spite of the fact that the cell diameter was used for calculation (Fig. 3).

If now the assumption of sphericity is also left out (for chloroplast or for cell) the general behaviour remains unchanged. For particles (or chloroplasts) of other shapes and uniformly oriented with respect to the beam direction, other \( Q_a \) and \( Q_a^* \) functions will appear. These new functions, however, have the same limiting values as the corresponding functions for spheres, both in the quasi-linear and in the black body domains (this can be seen, for instance, when \( Q_a = 1 - e^{-a_{sol}'} \) or \( 1 - e^{-4\pi n'} \), which is the function corresponding
Fig. 3. Spectral absorption values normalized to unit chlorophyll A concentration (1 mg m\(^{-3}\)). (A, B, C) Solid curves: values for intact cells in cultures, measured using a Perkin-Elmer 571 spectrophotometer. Dotted curves: absorption values computed for a hypothetical aqueous solution of the material forming the cells. (D) Actual absorption by acetone solution of extracted pigments for the same species and with the same normalization. Values for intact cells are obtained using the "scattered transmission accessory" of the spectrophotometer, implemented with an additional opal glass. With this accessory, the algal suspension can be set very close to the detector, allowing the scattered light to be received within a solid angle corresponding to about 40°. Mie computations of the volume scattering functions by the algal cells demonstrate that more than
99.5% of the scattered light enters the detector in the 700 to 750-nm range. The specific scattering, \( b^* \), is of the order of 0.2 m\(^2\) (mg Chl \( a \))\(^{-1}\), according to measurements not reported here. The recorded absorbance at 750 nm cannot therefore be accounted for by residual scattering (less than 0.2 m\(^{-1}\) \( \times \) 0.5% = 0.001 m\(^{-1}\)). In default of convincing reason this residual absorbance has not been subtracted. Measurements are carried out with reference to the medium where the algae were grown, filtered on Whatman GF/C glass fibre filters. In this way the absorption due to dissolved (yellow) organic substances, possibly created by algae, is eliminated. Relevant information concerning the cultures is given in Appendix 4.
to the cell with a constant pathlength, \( d \), as imagined by Kirk, see above). They can only differ from the spherical case in the intermediate domain. However, this difference is obviously reduced and nearly eliminated by virtue of the random orientation and, in nature, the diffuse light field.

When trying properly to reconstruct or interpret the absorption properties of an algal population, the approximations induced by the assumption discussed above are minor in comparison with the unavoidable uncertainties concerning the determination of \( c_1 \), \( a_{\text{os}} \), and \( d \) (and size distribution), which result from experimental limitations. For the sake of clarity, the general treatment presented is confined to monodisperse systems. Some unialgal cultures approximate such systems. In any case, there is no theoretical restriction in extending the results to polydisperse systems, but more computations are needed, when appropriate size distributions used as weighting functions are applied to the preceding equations. Some examples are provided elsewhere (Morel and Bricaud, 1981).

The divergence of the values of specific absorption by phytoplankton

The rather wide range of theoretically possible variations in specific absorption with size and cellular pigment concentration could be the origin of the scatter of values reported in literature. Theory demonstrates that concordance would have been surprising. However, other sources of discrepancy, including artifacts, are to be examined. When considering that the published data may concern natural populations or unialgal cultures, and recalling that they are reported in terms of "true" absorption, "diffuse" absorption, or irradiance attenuation (called "extinction" coefficient by many authors; see Appendix I for definitions), several reasons can be recognized for the scatter of the data.

Bannister (1974) and Dubinsky and Berman (1979) have reviewed the published values for the mean specific "extinction" coefficient, i.e., the averaged coefficient for the whole photosynthetic spectral domain, often referred to as \( \bar{a} \) (or \( a^* \), if true absorption is considered). These values range between 0.006 and 0.02 m\(^2\) mg\(^{-1}\) Chl \( a \), or even 0.09 when including Smith and Baker's results (1978a) obtained for low algal concentration. Large discrepancies also appear in the magnitude of the spectral specific coefficients. Around \( \lambda = 435 \) nm, where absorption exhibits a maximum, the values range from approximately 0.1 (Yentsch, 1960; Duntley, Wilson and Edgerton, 1974) to less than 0.009 m\(^2\) mg\(^{-1}\) Chl \( a \) when calculated from the data presented by Privoznik, Daniel and Incropera (1978)*. When examining these results, several kinds of measurements have to be distinguished.

In field measurements, disregarding the fact that \( K \) is a variable overestimate of \( a \) (Appendix 1), absorption by viable plant pigments cannot be easily separated from absorption by other absorbing materials insofar as they are co-varying. If \( a \) or \( K \) values are statistically studied along with pigment (Chl \( a \)) concentrations through any kind of correlation analysis, it results necessarily that the specific coefficient so obtained will inevitably include both living cells and their retinue. In lake studies, mostly in eutrophic conditions, linear regressions have been used (Dubinsky and Berman, 1979). In the ocean,

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* These authors show the spectral variations of absorption cross section (\( sQ_\lambda \)), together with the chlorophyll \( a \) content per cell (\( c_i v \) in our notation). So the ratio \( sQ_\lambda/c_P \) (see equation 5) gives \( a^* \) directly. At 440 nm, the calculated values lie around 0.01 m\(^2\) mg\(^{-1}\) Chl \( a \), instead of 0.0314 for the same phytoplankter (Chlorella pyrenoidosa) according to Bannister (1979). The bimodal size distribution observed by Privoznik et al. (1978), which results in a questionable mean diameter, presumably accounts for the disagreement.
Smith and Baker (1978a,b) showed that two separate linear regressions for waters with low and high concentrations phytoplankton, are more significant than a single one (Tyler, 1975). Others (e.g., Lorenzen, 1972; Morel, 1979) have chosen to fit this "non-linear" global biological effect on a power law. Such a law, \( a_{\text{phyto}} = a_0^* |c|^n \), where \( |c| \) is alternatively the (Chl \( a \)) or the (Chl \( a \) plus Phaeo \( a \)) concentration, and \( n < 1 \), must be more properly written as: \( a_{\text{phyto}} = a_0^* (c) |c|^n \), where the specific coefficient appears as a function of \( c \), continuously decreasing when the biomass increases. This decrease in \( a_0^* \) may signify that associated detrital matter is, as a rule, proportionally less abundant in eutrophic conditions than in oligotrophic ones. It may also reflect an ecological process leading the cells in oligotrophic areas to be more efficient in catching light, with smaller \( \rho' \) values and higher \( Q^*_s \) values (C. huxleyi could provide an example of this ability).

Unless special care is taken, laboratory measurements on algal cultures are not exempt from the influence of dead cells and debris, and the specific absorption increases and is spectrally modified with the age of the culture, as shown by Kiefer, Olson and Wilson (1979). This artifact can only be avoided by using healthy cultures in exponential growth. In this respect, the specific spectral values published by Bannister (1979) for C. pyrenoidosa or by Kiefer et al. (1979) for Monochrysis lutheri and Thalassiosira pseudonana, in active growing state, are probably free from this artifact. As long as phaeopigments have not significantly appeared (see Appendix 4), debris is scarce, as is corroborated by microscopic examination. It can reasonably be assumed that it has a negligible optical effect, so that the actual absorption is only due to living and healthy cells. Moreover, the measurements were made on dilute suspensions in order to respect the conditions imposed by equation (3) and the definition of \( a \) (see Appendix 1). For concentrations up to 5 times those of Appendix 4, the relationships between absorption and cell number do not depart from linearity (Sathyendranath, 1981), which means that multiple absorption (mutual-shading) and multiple scattering remain negligible. For these reasons, the results presented here are expected to be representative of true absorption for these species.

The effect of size and intracellular concentration partly accounts for the difference in specific values observed for the various species. It is eliminated by comparing the \( a_{\text{sol}}^* \) spectra (Fig. 3), which reveal only the difference in pigment composition. By virtue of normalization with respect to chlorophyll \( a \), the amplitude of the 675-nm peak must be, and approximately is, the same for these absorption curves (about 0.022 \( \text{m}^2 \ \text{mg}^{-1} \ \text{Chl} \ a \)), whereas other values and features throughout the spectrum appear different. The normalization to a single pigment may induce a biased representation of the actual absorption capability. It also leads to a variable mean specific absorption coefficient, \( \bar{a}^* \), from one phytoplankter to another, owing to the variable amount of other absorbing components, i.e., the other photosynthetic and accessory pigments, and to a lesser extent, the cytoplasm and walls. C. huxleyi, for instance, with a high carotenoid to chlorophyll \( a \) ratio (see Appendix 4), exhibits a high \( \bar{a}^* \) value due to its enhanced "blue" absorption capability.

**Summary and Conclusions**

Absorption by particulate absorbing substances, as algal cells in suspension, is governed by the size of the particles \( (d) \) and the absorption coefficient \( (a_{\text{om}}) \) of the cellular material forming the particles. These quantities are combined through their (dimensionless) product. This number, \( \rho' = da_{\text{om}} \), appears as a variable in equation (1) (combined with equation 3), which governs the absorption coefficient of the discrete medium.
Equation (1) reduces to a linear one when $\rho'$ is small (small and/or weakly absorbing particles). In this case, absorption is related to the volume concentration of particles, or alternatively to the mass concentration of absorbing substance, hence the corresponding specific absorption coefficient is constant. Beer's law is strictly valid in this ideal case, which tends to resemble that of a true solution.

The same equation becomes independent of $\rho'$, for sufficiently high $\rho'$ (large and/or strongly absorbing particles acting as black bodies). In that case, absorption in the medium is related to the concentration of cross-sectional area. Between these two limiting cases, and practically for most of the algal cells, absorption is linked to an intermediate geometrical parameter (between volume and surface), and thus is no longer proportional to the mass concentration. In other words, the specific absorption coefficient is not constant, and Beer's law cannot apply. There is, however, one theoretical exception if the change in canopy is only a change in cell number density, whereas everything in the algal population, i.e., size distribution and intracellular pigment composition and concentration, remains unchanged.

The non-applicability of Beer's law results from the variability in specific absorption. This coefficient, in its magnitude and its spectral distribution, varies with $\rho'$. For given absorptive properties of the cell material, the efficiency in absorbing radiation decreases with increasing cell size. Reciprocally, for a given size, the efficiency decreases when the intracellular pigment concentration increases. The absorption properties of the substance forming the cells, free from the effects of discreteness and size, can be computed if the size and the pigment content per cell (or absorption per cell) are known. The computation—an extrapolation for $\rho' \to 0$—leads to the absorption by a hypothetical solution of the cell matter. The pigment identification can thus be made on a firm basis, because the spectral features, variably smoothed and even masked in actual cell absorption, are enhanced when the cellular material is ideally dispersed in solution. The comparison of the spectral absorption values for this 'solution' with those obtained after extraction in organic solvents, can provide information about absorption by other cellular components than chloroplasts, such as walls and cytoplasm.

Because of the effect of discreteness, the true absorption to be considered in photosynthesis studies differs from what could be directly inferred from the chlorophyll (or, if available, from total pigment) content. This remark holds for the quantum yield evaluation and the interpretation of the initial slope of the "P vs I" curve, as pointed out by Platt and Jassby (1976) and evidenced in the results of Taguchi (1976). Actual absorption by intact cells is measurable in culture experiments and in this way, light utilization efficiency can be properly established. In field measurements, the solution does not appear so simple, as examined below.

For a given amount of chlorophyll $a$, the only pigment routinely determined, the effect of an algal biomass upon the optical properties of a water body depends on and varies with (i) the amount of biogeneous detritus associated with living cells, which (in the open sea) seems to covary with them through likely non-linear correlations, (ii) the photosynthetic and accessory pigment composition, within the cells, and (iii) the effect of discreteness, which combines the influence of size and of pigment concentration in the cells.

For these reasons, the specific absorption attributed to phytoplankton is expected to vary, when expressed with respect to a single pigment (Chl $a$), or even if expressed with respect to the sum (Chl $a$ + Phaeo $a$) as in remote sensing applications. These possible variations are reflected in the dispersion of the published values. In absence of a knowledge of the dominant local species and their optical properties, mean specific absorption values
are generally adopted, which inevitably leads to a large uncertainty when estimating light uptake efficiencies.

The same limitations arise in remote sensing assessment of phytoplankton. At least in oceanic conditions, when the influence of land runoff and resuspended material becomes negligible, the shift in ocean color results from the "blue" absorption caused by the algal biomass with its retinue. For the three reasons mentioned above, this shift, remotely detectable, cannot be simply proportional to the (Chl a + Phaeo a) concentration and closely linked to this index. The phytoplankton content, in terms of this index, is at present expected to be derived from satellite measurements to within a factor of two under favourable conditions (see e.g., Morel and Gordon, 1980). This accuracy appears to be an upper limit, unless local and diversified algorithms are developed and an improved index, more representative of the blue absorption by the algal biomass, is used.

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**APPENDIX 1**

The absorption coefficient, $a$, is defined for an infinitesimally thin layer, $dx$, of the medium, normal to the beam by:

$$a = -(d\phi_\omega/d\omega)(1/dx);$$

$d\phi_\omega/d\omega$ is the ratio of the radiant flux absorbed within the layer to the incident flux. It is an inherent
optical property according to Preissendorfer's (1961, 1976) definition. When \( a \) is expressed as in equation (3), valid for a discrete medium, it is implicitly understood that (i) incident photons cannot reach more than one particle when travelling through \( dx \) and (ii) scattered photons escape from the layer without impinging on a particle. These provisos are the same as those made when defining the scattering coefficient, \( b \), (i.e., dilute suspension, small volume) to ensure that single scattering occurs.

If inside a layer of finite thickness, \( \Delta x \), the concentration of cross sectional area, \( NS/V \), is such that self-shading (multiple absorption) and multiple scattering occur significantly, the 'diffuse' absorption that would be measured is no longer an inherent property and differs from that given by equation (3). This equation, however, remains locally valid, in the same way as \( a \) can always be defined as a local inherent property. Practically, a currently accepted criterion to decide if interactions remain weak is \( \tau < 0.3 \) (Van de Hulst, 1957), where \( \tau \) is the optical thickness of the layer (\( \tau = (a + b)\Delta x \)).

The interests in studying such an inherent property, which can be seen as a property valid in the limiting case of microscopic scale, are (i) it depends only on the substance, whatever is the light field, and respects the additivity principle; (ii) with other inherent properties, it is an input parameter in radiative transfer computations dealing with various lighting conditions and extended thicknesses (conversely, it is the goal of inversion techniques); and (iii) it governs directly the energy uptake at the scale of each algal cell.

Measurements of \( a \) imply that all the scattered radiation around the collimated beam be collected by the receiver. Spectrophotometers, equipped with integrating sphere or "scattered transmission accessory" allow "true" absorption to be obtained (at least approximately) if suspensions are sufficiently dilute. If they are dense (high values of \( \tau \)), only a "diffuse" absorption coefficient is obtainable (Kiefer, Olson and Wilson, 1979), unless the equation of radiative transfer, in its one-dimensional form, is inverted to derive \( a \), as done by Privoznik, Daniel and Incropera (1978).

At sea, new instruments (Høegh-Sørensen, 1975; Spitzer and Wernand, 1979a,b) measure both scalar and vector irradiances from which \( a \) can be straightforwardly deduced. Most in situ measurements, however, deal with irradiance on a horizontal plane and lead to an apparent property, \( K \), the vertical attenuation coefficient for (downward or upward) irradiance (often called "extinction coefficient" in marine biology literature). \( K \) differs from and always exceeds \( a \). Moreover, the ratio \( K : a \) depends on the radiance distribution and consequently varies even in a homogeneous water body. This ratio is also wavelength dependent. It is possible to retrieve \( a \) from \( K \) if a complete set of measurements is available (upward and downward irradiances at several depths) and under some assumptions necessary to solve the transfer equation (Morel and Prieur, 1975, 1977).

The coefficient \( a \) can be considered rigorously as the sum of independent terms. Strictly speaking, it is no longer true for \( K \), whilst the partition of \( K \) is often done, and Beer's law wrongly invoked (see e.g., Tyler, 1976). It may be a suitable approximation, but only an approximation. The concept of \( k_b \), the so-called specific "extinction" coefficient of phytoplankton, suffers an uncertainty resulting from the variable and non-additive character of \( K \).

Symbols and definitions used here are those recommended by the IAPSO Committee on Radiant Energy in the Sea (Jerlov, 1968) and then by the IAPSO Working Group on Optical Oceanography (Morel and Smith, 1981).

**APPENDIX 2**

A reasoning similar to that developed for absorption can be made for scattering by sufficiently large particles, for which \( Q_b \) becomes almost constant and equal to 2 for non-absorbing particles (\( Q_a = 0 \)), or to one for absorbing particles (\( Q_a \approx 1 \)). The scattering coefficient, \( b \), due to the presence of \( N \) particles in \( V \) is:

\[
b = (N/V) s Q_b = (N/V) \frac{\pi d^2}{4} Q_b.
\]

The mass concentration of the suspended matter is \((N/V) v \delta\), where \( \delta \) is the mass density of the matter. Hence, the 'specific' scattering coefficient, \( b^* \), will be:

\[
b^* = \frac{3}{2} \frac{1}{d \delta} Q_b \quad \text{(dimension: length}^2 \text{mass}^{-1}).
\]
For a given mass of suspended matter and if $Q_s$ can be regarded as constant, the scattering is simply proportional to the reciprocal of the diameter, as experimentally shown by Jerlov and Kullenberg (1953) without theoretical proof. The specific scattering coefficient is $3/d\bar{d}$ for non-absorbing material. For absorbing particles, scattering is reduced to one-half its value for non-absorbing equivalent particles under the assumption that they are large enough. This ratio $1:2$ is an upper limit. The depressive effect of absorption on scattering is less for smaller size and weaker absorption and full computations are needed (Morel and Bricaud, 1981) to establish this effect accurately.

### APPENDIX 3

**Modifications (5 cases) in algal population and correlative changes in absorptive properties**

It must be assumed that an initial ‘reference’ algal population exists with given values for the cell number density, $N/V$, the diameter of the cells, $d$ (volume $v$), and for the intracellular concentration in pigment, $c_i$. The absorption coefficient for the cell material, $a_{cm}$, is proportional to $c_i$. $B$ is the biomass (volume) concentration in the suspension, $B = Nv/V$, and $C$ the pigment (mass) concentration, $C = Bc_i$. $Q_a$ and $Q_a^*$ are the dimensionless functions (equations 1 and 6) governing the absorption coefficient due to the presence of algae in the medium, $a$ (equation 3), and the specific absorption coefficient, $a^*$ (equations 5 and 5a).

<table>
<thead>
<tr>
<th>Cases (No.)</th>
<th>$N/V$</th>
<th>$d$</th>
<th>$c_i$</th>
<th>$B$</th>
<th>$C$</th>
<th>$Q_a$</th>
<th>$Q_a^*$</th>
<th>$a^*$</th>
<th>$a$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>$\times K$</td>
<td>$\times 1$</td>
<td>$\times K$</td>
<td>$\times K$</td>
<td>$\times K$</td>
<td>$\times 1$</td>
<td>$\times 1$</td>
<td>$\times 1$</td>
<td>$\times K$</td>
</tr>
<tr>
<td>2</td>
<td>$\times 1$</td>
<td>$\times K$</td>
<td>$\times 1$</td>
<td>$\times K$</td>
<td>$\times 1$</td>
<td>$\left{ \begin{array}{ll} K &gt; 1 \ K &lt; 1 \end{array} \right.$</td>
<td>$\sim (K, 1)$</td>
<td>$\sim (1, K^{-1})$</td>
<td>$\sim (1, K^{-1})$</td>
</tr>
<tr>
<td>3</td>
<td>$\times 1$</td>
<td>$\times K$</td>
<td>$\times 1$</td>
<td>$\times K$</td>
<td>$\times K^3$</td>
<td>$\times 1$</td>
<td>$\sim (K, 1)$</td>
<td>$\sim (1, K^{-1})$</td>
<td>$\sim (1, K^{-1})$</td>
</tr>
<tr>
<td>4 (a)</td>
<td>$\times 1$</td>
<td>$\times K^{-2}$</td>
<td>$\times K^3$</td>
<td>$\times K$</td>
<td>$\times 1$</td>
<td>$\times 1$</td>
<td>$\sim (K^{-2}, 1)$</td>
<td>$\sim (1, K^2)$</td>
<td>$\sim (1, K^2)$</td>
</tr>
<tr>
<td>4 (b)</td>
<td>$\times 1$</td>
<td>$\times K^3$</td>
<td>$\times K^{-3}$</td>
<td>$\times K$</td>
<td>$\times 1$</td>
<td>$\times 1$</td>
<td>$\sim (K^3, 1)$</td>
<td>$\sim (1, K)$</td>
<td>$\sim (1, K)$</td>
</tr>
</tbody>
</table>

Each case in Table 1 represents a modification with respect to the initial population. One or several of the initial parameters are multiplied by the factors given in the three first columns ($1 =$ unmodified). The arrows $\sim$ and $\sim$ mean an increase or a decrease. The first and the second number in parentheses correspond to the quasi-linear domain and to the black body domain and are the factors to be applied to the quantity under consideration in these limiting cases. As an example, $\sim (K, 1)$ must be read as: this quantity is increased by a factor $K$ in the quasi-linear domain, by a factor less than $K$ in general, and is no longer increased as the factor approaches 1 in the black body domain.

Cases 1 and 3. Proportional changes in biomass ($B$) and pigment ($C$) concentrations, by changing the cell number density ($N/V$) or the cell size ($d$) at constant intracellular concentration ($c_i$).

Case 4. Reciprocal change in size and intracellular concentration, at constant cell number (case 4a) or at constant total pigment (case 4b).

Case 2. Change in pigment, with constant biomass and cell number.

Case 5. Change in pigment, constant biomass and cell number.

Note that Beer’s law applies only in cases 1 and 4.
APPENDIX 4

Table 2. Relevant information concerning the three species of phytoplankters grown in batch cultures (a) and their optical properties (b)

<table>
<thead>
<tr>
<th>Species</th>
<th>Age (days)</th>
<th>Chl ( a ) (mg m(^{-3}))</th>
<th>Chl ( b ) (mg m(^{-3}))</th>
<th>Chl ( c ) (mg m(^{-3}))</th>
<th>Carot (mg m(^{-3}))</th>
<th>Phaeo ( a ) (mg m(^{-3}))</th>
<th>( N/V ) (m(^{-3}))</th>
<th>( d ) (( \mu )m)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Platymonas suecica</em></td>
<td>3</td>
<td>137.9</td>
<td>42.2</td>
<td>0.0</td>
<td>114.0</td>
<td>5.0</td>
<td>2550 ( \times ) 10(^{8})</td>
<td>6.0</td>
</tr>
<tr>
<td><em>Coccolithus huxleyi</em></td>
<td>7</td>
<td>89.6</td>
<td>0.0</td>
<td>53.4</td>
<td>129.2</td>
<td>5.5</td>
<td>29200 ( \times ) 10(^{8})</td>
<td>3.8</td>
</tr>
<tr>
<td><em>Chaetoceros protuberans</em></td>
<td>5</td>
<td>142.8</td>
<td>0.0</td>
<td>81.5</td>
<td>73.4</td>
<td>6.1</td>
<td>1355 ( \times ) 10(^{8})</td>
<td>26.5</td>
</tr>
</tbody>
</table>

(b) \( c_i \) (mg Chl \( a \) m\(^{-3}\)) \( a_m \) (435 nm) \( n' \) (435 nm) \( sQ_a \) (435 nm) \( Q_a \) (435 nm) \( a_{380-700}^{*} \) (m\(^{2}\) mg\(^{-1}\) Chl \( a \))

<table>
<thead>
<tr>
<th>Species</th>
<th>( c_i ) ( (10^6) )</th>
<th>( a_m ) (435 nm) ( \times 10^2 )</th>
<th>( n'(435 nm) )</th>
<th>( sQ_a(435 nm) )</th>
<th>( Q_a(435 nm) )</th>
<th>( a_{380-700}^{*} ) ( (m^2 \text{mg}^{-1} \text{Chl} \ a) )</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pl. suecica</em></td>
<td>4.48</td>
<td>2.86</td>
<td>0.00745</td>
<td>1.84 ( \times ) 10(^{-11})</td>
<td>0.651</td>
<td>0.0180</td>
</tr>
<tr>
<td><em>C. huxleyi</em></td>
<td>1.07</td>
<td>1.15</td>
<td>0.00300</td>
<td>2.82 ( \times ) 10(^{-12})</td>
<td>0.249</td>
<td>0.0397</td>
</tr>
<tr>
<td><em>Ch. protuberans</em></td>
<td>1.06</td>
<td>0.61</td>
<td>0.00016</td>
<td>5.58 ( \times ) 10(^{-11})</td>
<td>0.101</td>
<td>0.0305</td>
</tr>
</tbody>
</table>

The medium was aged seawater, filtered through Sartorius membrane filters (0.2-\( \mu \)m pore size), to which Provasoli’s ES enrichment was added, and refiltered under sterile conditions. Cells were grown in Erlenmeyer flasks, maintained at 18°C under continuous irradiation of about 2.5 \( \times \) 10\(^{16}\) quanta cm\(^{-2}\) s\(^{-1}\) (fluorescent tubes Silvania Grolux and Mazda). All measurements were made in active growing phase, when the cell number is sufficiently high for significant absorption measurements and before debris and phaeopigments appear. Cells were counted with a Fuchs-Rosenthal haemacytometer and appropriate magnification. Size distributions were obtained microscopically for *C. protuberans* or with a Coulter counter (type ZB) for the other species. Distributions were unimodal, and, for *P. suecica* and *C. huxleyi*, very narrow (\( \sigma_g \approx 400 \)). A tissue grinder was used to disrupt the cells before extraction.

Chlorophyll \( a \) and phaeophytin \( a \) concentrations were determined using Lorenzen’s method (1967), chlorophyll \( b \) and \( c \) concentrations were calculated using the SCOR–UNESCO equations, and total carotenoids using Richards’ equation (Strickland and Parsons, 1968).

The intracellular concentration is obtained from \( c_i = [\text{Chl} \ a](N/V)^{-1} \), where \( v = \pi d^3/6 \). The absorption coefficient of the cell matter, \( a_m \), and the imaginary part of the index of refraction, \( n' \), are computed (for \( \lambda = 435 \) nm), according to a scheme described in the text. The absorption cross section corresponding to one cell, \( sQ_a \), is obtained through \( sQ_a = a^* [\text{Chl} \ a](N/V)^{-1} \). The efficiency factor for absorption, \( Q_a \) (dimensionless), is also given. The mean specific absorption, \( a^* \), is computed for “pure white” irradiance according to:

\[
\bar{a}^* = \left( \lambda_2 - \lambda_1 \right)^{-1} \int_{\lambda_1}^{\lambda_2} 2 \bar{a}^*(\lambda) d\lambda,
\]

where \( \lambda_1 \) and \( \lambda_2 \) are 380 and 700 nm, respectively.