

Further Reading

- Buskey EJ (1992) Epipelagic planktonic bioluminescence in the marginal ice zone of the Greenland Sea. *Marine Biology* 113: 689–698.
- Harvey EN (1952) *Bioluminescence*. New York: Academic Press.
- Hastings JW and Morin JG (1991) Bioluminescence. In: Prosser CL (ed.) *Neural and Integrative Animal Physiology*, pp. 131–170. New York: Wiley-Liss.
- Herring PJ (1977) Bioluminescence in marine organisms. *Nature, London* 267: 788–793.
- Herring PJ (ed.) (1978) *Bioluminescence in action*. London: Academic Press.
- Herring PJ (1985) How to survive in the dark: bioluminescence in the deep sea. In: Laverack MS (ed.) *Physiological Adaptations of Marine Animals*, pp. 323–350. Cambridge: The Company of Biologists.
- Lapota D, Geiger ML, Stiffey AV, Rosenberger DE and Young DK (1989) Correlations of planktonic bioluminescence with other oceanographic parameters from a Norwegian fjord. *Marine Ecology Progress Series* 55: 217–227.
- Widder EA (1999) Bioluminescence. In: Archer SN *et al.* (eds) *Adaptive Mechanisms in the Ecology of Vision*, pp. 555–581. Leiden: Kluwer Academic Publishers.

BIO-OPTICAL MODELS

A. Morel, Université Pierre et Marie Curie,
Villefranche-sur-mer, France

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Introduction

The expression ‘bio-optical state of ocean waters’ was coined, in 1978, to acknowledge the fact that in many oceanic environments, the optical properties of water bodies are essentially subordinated to the biological activity, and ultimately to phytoplankton and their derivatives. More recently the adjective bio-optical has been associated with nouns like model or algorithms. At least two meanings can be distinguished under the term ‘bio-optical model.’

A bio-optical model can designate a tool used to analyze, and then to predict, the optical properties of biological materials, such as phytoplanktonic or heterotrophic unicellular organisms, the most abundant living organisms in the ocean. Such models are based on various fundamental theories of optics which apply to a single particle, and make use of a set of rigorous equations. The optical properties which can be ‘modeled’ belong to the category of the inherent optical properties (IOP, *see Radiative Transfer in the Ocean*). Defined at the level of a single cell, the extension of IOPs to a collection of cells (a population) or to an assemblage of populations is straightforward from conceptual and numerical viewpoints. The computation of IOPs are carried out by using some physical characteristics of the organisms, or of the population (such as cell size, size distribution, chemical composition which governs the complex index of refraction).

Bio-optical models can also refer to various ways of describing and forecasting the ‘bio-optical state’ of the ocean, namely the optical properties of a water body as a function of the biological activity within this water. Both the IOPs and the apparent optical properties (AOPs) of the water are aimed at in such approaches. In contrast to the first kind of theoretical models, these models are essentially empirical, descriptive, and actually derived from field measurements. They initially rest on observations of some regular variations in the oceanic optical properties along with its algal content in ‘Case 1 waters’ (see **Table 1**). The chlorophyll concentration, [Chl], is commonly used as an index to quantify the algal content, and more generally the bio-optical state of ocean water. Once identified, and if recognized as statistically significant, such empirical relationships (between optical properties and [Chl] can be inverted, and thereafter used as predictive tools or model.

It is worth remarking that regular trends generally vanish in so-called Case 2 waters (**Table 1**). Indeed, in these waters the optical properties are no longer influenced just by phytoplankton and related particles, as they are in Case 1 waters. They are also, and independently, determined by other substances of terrestrial origin, notably by sediments and colored dissolved (organic) matter, carried from land into coastal zones and not correlated to [Chl]. Therefore, bio-geo-optical models, that might be developed and locally useful in such areas, are not of general applicability.

The two kinds of models are not disconnected. To the extent that the IOPs at the level of particles are additive, the first models, in principle, may be utilized to reconstruct the IOPs of a water body containing any assemblage of organisms and other (living

Table 1 Concepts and quantities used in bio-optical models

Case 1/Case 2 water. Case 1 waters are those waters in which phytoplankton and their accompanying and covarying retinue of material are the principal agents responsible for the variations in optical properties of the water bodies. The accompanying material includes living heterotrophic organisms, such as bacteria or virus, various debris of biological origin, and dissolved organic matter excreted by organisms or liberated by decaying detritus. Such waters are typical of the open ocean, far from land influence. Conversely, Case 2 waters are influenced not only by unicellular algae and related particles or substances, but also by other optically significant components, from terrestrial origin, such as inorganic and organic particles in suspension, yellow substances resulting from land drainage, and sediments resuspended from bottom

| Quantity | Units | Symbol |
|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------|--------------------------|
| Absorption coefficient | m^{-1} | a |
| Scattering coefficient | m^{-1} | b |
| Volume scattering function | $m^{-1} sr^{-1}$ | $\beta(\theta)$ |
| Back-scattering coefficient | m^{-1} | b_b |
| Back-scattering efficiency (the ratio b_b/b) | — | \bar{b}_b |
| Attenuation coefficient ($c = a + b$) | m^{-1} | c |
| Chlorophyll-specific (absorption or scattering) coefficients of phytoplankton | $m^2 (mg\ Chl)^{-1}$ | a_{ϕ}^*, b_{ϕ}^* |
| Efficiency factors for absorption and scattering (subscripts a, b, respectively), defined as the ratios of energy absorbed within the particle, or scattered out from the particle, to the energy impinging onto its geometrical cross-section | | Q_a, Q_b |
| Relative size of a spherical particle, defined as $\alpha = \pi D n_w (\lambda_0)^{-1} D$ diameter, n_w refractive index of water, and λ_0 , wavelength <i>in vacuo</i> | — | α |
| Relative (complex) refractive index of the particle, defined as the ratio of the index of the substance forming the particle to the refractive index of water (n , real part, n' imaginary part) | — | $m = n - in'$ |
| Van de Hulst parameter, defined as $\rho = 2\alpha(n - 1)$ | — | ρ |
| Depth of the euphotic layer where PAR is reduced to 1% of its surface value | m | Z_{eu} |
| Photosynthetic available radiation (within the 400–700 nm range) | photons $s^{-1} m^{-2}$ | PAR |
| Attenuation coefficient for downward irradiance (also K) | m^{-1} | K_d |

or detritus) biogenic particles. Then these bulk IOPs can be combined through the radiative transfer equation (RTE) with the appropriate boundary conditions (the illumination conditions at the surface and the reflectance properties of the bottom, in particular), with a view to computing the AOPs at various depths within the water column. In this way, the result of the second category of models, the descriptive models, can be understood or interpreted.

Because empirical bio-optical models generally refer to the trophic level, depicted by [Chl], they are in essence restricted to upper oceanic layers, where the photosynthetic activity takes place, where the vegetal biomass is confined, and [Chl] is measurable. In addition, a considerable effort in developing bio-optical models originates from the need to interpret the satellite ocean color data in terms of chlorophyll concentration, which is only detectable in the upper oceanic layer. Possible relationships between optical properties and heterotrophic activity (bacterial abundance), or particulate organic carbon and minerogenic contents in the interior of the ocean, are not examined here.

Finally, it must be added that the spectral domain encompassed by bio-optical models is that of visible (or photosynthetic) radiation, namely the

400–700 nm domain, occasionally slightly extended toward the near infrared and near ultraviolet regions.

Optical Models for Individual Particle or Population of Particles

In the open ocean Case 1 waters, phytoplankton with their accompanying retinue of living and detrital particles, are the principal agents responsible for the determination of the optical properties. The size of these particles extends from less than 0.1 μm (virus, colloids, debris), to less than 1 μm for heterotrophic bacteria and picoplanktonic algal species, and from 1 to tens or even several hundreds of micrometers for phytoplankton, protists, and large heterotrophic organisms (and actually up to tens of meters for whales). It is well known that the size distribution function of marine particles is rather monotonic, with numbers continuously increasing toward smaller sizes (Figure 1). A simple function, often sufficient to approximately describe the size distribution of oceanic particulate matter, is a power law (known as Junge distribution),

$$dn(x)/dx = N(x) = kx^{-i} \quad [1]$$

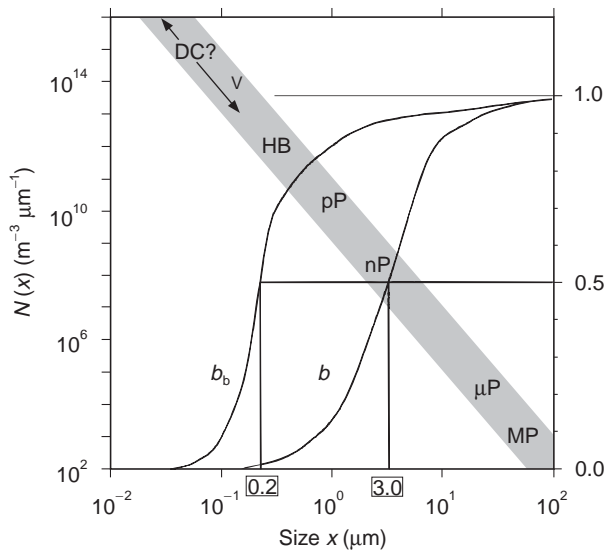


Figure 1 Schematic plot (shaded stripe, left-hand side ordinate log-scale) of the approximate numerical concentration of particles according to their size in oceanic waters (eqn [1] with $j = 4$). Approximate abundance versus mean size of major groups of microorganisms or particles are also indicated, with notations as follows: DC, debris and colloids; V, viruses; HB, heterotrophic bacteria; pP, picophytoplankton; nP nanoplankton; μ P microplankton; MP, large macroplankton. (Adapted from Stramski and Kiefer (1991) Light scattering by microorganisms in the open ocean. *Progress in Oceanography* 28: 343–383.) Linear plot (right-hand ordinate scale, from 0 to 1) of the progressive value of the scattering coefficient, b , when the upper limit of the integral (eqn [3]) is increasing; the progressive value is relative and normalized by its final value (unity). A similar curve is drawn for the backscattering coefficient, b_b . For these computations, the relative refractive index of the spherical particles is 1.05, and the wavelength is 550 nm. (Adapted from Morel A and Ahn Y-H (1991) Optics of heterotrophic nanoflagellates and ciliates: tentative assessment of their scattering role in oceanic waters compared to those of bacterial and algal cells. *Journal of Marine Research* 49: 177–202.)

where x is the size (e.g., the diameter, if the particles can be considered as spherical), $N(x)$ is the distribution function, i.e., the number of particles per unit of volume, having a given size x , and within a dx interval (around x), k is a scaling factor, and j is an exponent, with typical values around 4 for oceanic particles. Such a distribution means that an increase by a factor of 10 in size corresponds to a reduction in number (in frequency of occurrence) by a factor of 10 000.

As a consequence of this abruptly decreasing number of particles with size (combined with optical theories, see below), the particles which are the most optically significant are in the size range of 1–10 μm , and thus include most of the small heterotrophic organisms, phytoplanktonic cells, and various small debris. This is true for the scattering properties, but not for the back-scattering coefficient

predominantly due to smaller particles (Figure 1). It is also true for absorption, even if in this process heterotrophs play a minor role (they are rather colorless); in contrast, algal cells containing a variety of pigments (chlorophylls, carotenoids, and occasionally phycobilins) are strongly absorbing bodies.

The interaction between radiation and an optical object like a particle is conveniently described by dimensionless numbers, called efficiency factors for absorption and for scattering, and denoted Q_a and Q_b , respectively (Table 1). One advantage of these factors lies in the fact that theories are available by which their values can be predicted as a function of the relative size (α , defined in Table 1), and the relative complex index of refraction of the particle (m , see Table 1). The Mie-Lorenz theory provide for spherical particles accurate Q values, and the angular values of the volume scattering function (see **Radiative Transfer in the Ocean**). When the refractive index of the particle is close to that of the surrounding medium (as is the case for most of the watery oceanic particles in suspension in water), the so-called van de Hulst approximation can apply and provide Q -factors more rapidly than via Mie computations.

If the particles are made of the same substance (same refractive index, m), and are assumed to be spherical, with the same diameter, D , the absorption and scattering coefficients, a and b , of the medium which contains these particles, are simply expressed as

$$a \text{ or } b = N\pi(D^2/4) \cdot Q_{a \text{ or } b} \quad [2]$$

where N is the number of particles per unit volume, $\pi(D^2/4)$ represents the geometrical cross-section of a single (spherical) particle. The Q factors are simultaneously functions of D and m , through the parameter ρ (see Table 1).

For perfectly transparent particles ($n' = 0$), a and Q_a are obviously 0. In this case, Q_b after oscillations tends asymptotically toward 2 for increasing size (Figure 2); such a particle is able to remove from the radiative field by scattering twice the amount of radiation intercepted by its geometrical cross-section (this is often called the ‘extinction paradox’). For absorbing particles, Q_a increases with increasing size, and Q_b , after some oscillations tends toward 1, like Q_a (Figure 2).

If the particles are not uniform in size, and the population is characterized by a size distribution function, $N(D)$ the eqn [2] must be integrated over the appropriate size interval, according to

$$a, \text{ or } b = (\pi/4) \int N(D)D^2 Q_{a \text{ or } b}(D, m) d(D) \quad [3]$$

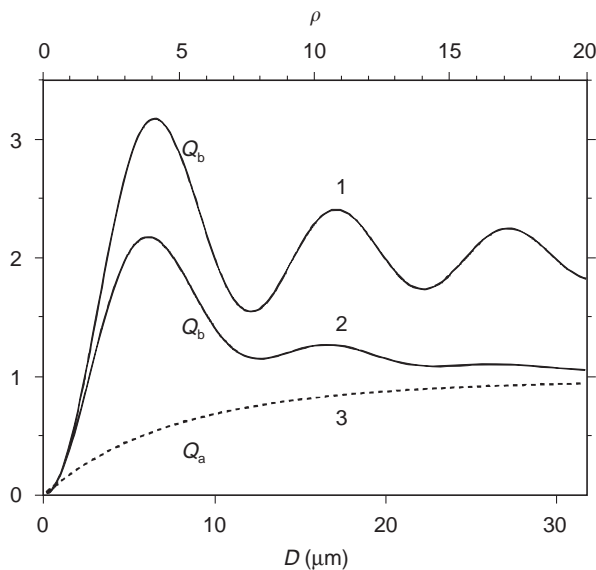


Figure 2 Efficiency factor for scattering, Q_b , as a function of the parameter ρ (defined in **Table 1**), or of the diameter, D , when the relative index of the particle is set equal to 1.05, and the wavelength λ is 675 nm. Curve 1 represents Q_b for a non-absorbing particle. Curve 2 represents Q_b for an absorbing particle, with $n' = 0.0075$, $n = 1.05$, and $\lambda = 675$ nm. Curve 3 represents the efficiency factor for absorption Q_a for the same n , n' , and λ values as for curve 2. Note that when the size increases, Q_b oscillates around, and tends asymptotically, toward 2, if the particle is not absorbing, or toward 1 when it is absorbing; Q_a tends also toward 1.

The same parameters (size, complex refractive index) are used in the frame of the rigorous Mie theory, to compute the volume-scattering function (VSF, see **Table 1**) of any individual particle. The VSF for the entire particle population is simply obtained by adding the individual VSF with the appropriate weight, as derived from the distribution function $N(D)$. All the bio-optical models of the scattering properties of marine particles rest on such an approach. Their limitations do not originate from theory, but from the present lack of accurate information about the sizes and composition of the suspended material (in Case 1, and even more in Case 2 waters). If the actual pattern of the particle VSF is globally understood and can be reconstructed, the predictive skill of the models (actually the available information used as inputs) are still insufficient to allow the evolution of the back-scattering coefficient to be safely parameterized as a function of the bio-optical state (see reflectance modeling). What can be predicted, however, is the extremely low back-scattering efficiency exhibited by most of the unicellular organisms with low refractive index (such as algal cells, for instance). Also that this efficiency increases with the decreasing particle size is a theoretical evidence; as a consequence, the par-

ticles responsible for the formation of the scattering and back-scattering coefficients do not belong to the same size range (**Figure 1**).

In summary, theoretical models are available which account very well for most of the observed optical properties. They have been validated in particular through *in vitro* experiments and by using various cells grown in culture (heterotrophic or photo-autotrophic organisms). Several phenomena, predicted through theories and subsequent bio-optical models, are worth mentioning.

- Scattering by small (0.4–2 μm) organisms depends on the wavelength according to a λ^{-2} law. This spectral dependency is perfectly verified for heterotrophic bacteria (almost nonabsorbing bodies); for small phytoplanktonic cells (such as *Prochlorococcus* and *Synechococcus*), the presence of pigments results in localized features (minima) superimposed onto the general λ^{-2} spectral pattern.
- For larger organisms, the scattering spectrum may exhibit various shapes, including a ‘flat’ (λ^0) shape when the size exceeds approximately 10 μm . For algal cells, the various absorbing pigments always influence the scattering spectrum, by introducing minima and maxima in scattering throughout the absorption bands of these pigments.
- Absorption by pigmented cells in suspension differs from that of a ‘solution’ of the same material, if the pigments were homogeneously distributed. This ‘packaging’ effect, and its corollary, the ‘flattening’ of the absorption spectrum, both originate from the behavior of the Q_a factors with varying size and n' . These effects are well understood, described by simple equations and accurately modeled.

The above models, which address the optics of individual cells, or ultimately deal with populations, allow the properties observed in oceanic waters containing assemblages of these particles to be interpreted. In this sense, they are able to support the second category of bio-optical models, which are examined below.

Modeling the Optical Properties of Ocean Waters in Relation to Their Biological State

In oceanic Case 1 waters, far from significant terrigenous influences, the origin of all materials present is necessarily to be found in the first link of the food chain, namely in photosynthesizing phytoplanktonic organisms. Heterotrophic organisms, as

well as inanimate detritus or dissolved organic matter are related to algal biomass, and to the initial creation of organic matter (and particles) through photosynthesis. Therefore, the water optical properties are logically studied as a function of this vegetal biomass.

Because chlorophyll *a* is the single ultimate photosynthetic pigment, the most abundant in all living plants, and because it is easily determined, its concentration in the water is a convenient, albeit imperfect, index of the bio-optical state. It is worth recalling that the chlorophyll concentration in oceanic waters, used as descriptor of the bio-optical state, and to which the optical properties are to be related, varies within about 3 orders of magnitude (say 0.02 and 20 mg m⁻³, between oligotrophic zones and eutrophic conditions in upwelling areas).

In practice, [Chl] and the optical properties within the upper layers must be measured simultaneously at sea to examine if statistically significant correlations can be found between some IOPs or AOPs and [Chl]. When such correlations are expressed mathematically (in general through nonlinear laws, and with a certain confidence interval), the corresponding expression can be used as a model or an algorithm. In contrast to what occurred for the previous category of bio-optical models (which are based on exact physical laws), the models examined below are in essence ‘empirical’. Varying uncertainties are therefore attached to each model; depending on inclusion of new data, the numerical formulation or the input parameters of these models are still liable to further evolution.

Inherent Optical Properties and [Chl]

The absorption coefficient of oceanic water Beside the fixed contribution of water itself (a_w) to this coefficient, the varying biological contribution (sometimes denoted a_{bio}) can itself be partitioned into a component due to particulate material, a_p , and another due to colored dissolved organic matter, a_{cdom} (all these coefficients are spectral quantities, even if the symbol λ is omitted, when not necessary)

$$a = a_w + a_{cdom} + a_p \quad [4]$$

In turn, a_p can be divided according to

$$a_p = a_\phi + a_{nap} \quad [5]$$

where a_ϕ and a_{nap} are the partial absorption coefficients by phytoplanktonic cells, and ‘nonalgal’

particles, respectively. This nonalgal compartment includes colored debris and all kinds of heterotrophic organisms. Techniques are available to discriminate between a_p and a_{nap} and to determine their spectra; such measurements are performed with particles retained on a filter, before and after methanol extraction. The algal absorption a_ϕ spectrum is indirectly obtained by difference. Typical shapes of these spectra are shown in Figure 3(A), when [Chl] is 1 mg m⁻³.

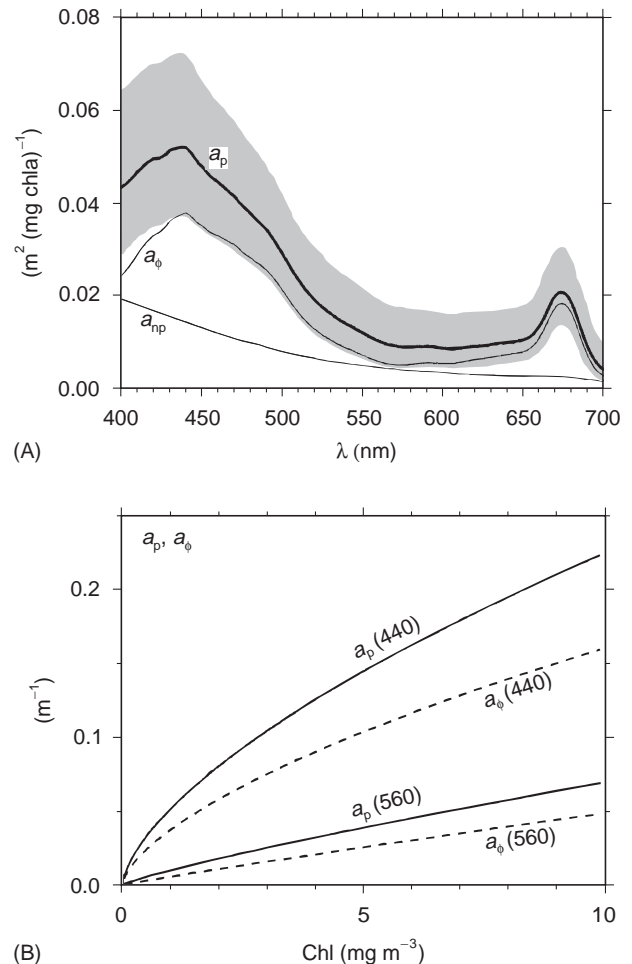


Figure 3 (A) Mean spectral absorption values, as they result from statistical analyses, when the chlorophyll concentration within the water body is 1 mg m⁻³. The curves represent $a_p(\lambda)$, plotted inside a shaded area which represents ± 1 SD, the nonalgal particle absorption spectrum, $a_{nap}(\lambda)$, and phytoplankton absorption spectrum, $a_\phi(\lambda)$ (see eqn [4]). (B) Nonlinear evolution of the mean absorption coefficients $a_p(\lambda)$ and $a_\phi(\lambda)$, with increasing chlorophyll concentration (see also eqns [2.1] and [2.2] in Table 2); the two selected wavelengths correspond to the maximum (440 nm), and the minimum (560 nm) of algal absorption. (Adapted from Bricaud A, Morel A, Babin M *et al.* (1998) Variation of light absorption by suspended particles with chlorophyll *a* concentration in oceanic (case 1) waters: analysis and implications for bio-optical models. *Journal of Geophysical Research* 103: 31033–31044.)

Statistical analyses of absorption measurements performed systematically in Case 1 waters with increasing [Chl] have demonstrated that the partial coefficients (a_ϕ and a_{nap}) increase with [Chl] in a nonlinear manner (Table 2, examples in Figure 3B). As a consequence, the chlorophyll-specific absorption coefficient of phytoplankton (a_ϕ , Table 1) is not a constant and decreases when [Chl] increases. Such a trend is, at least partly, due to the above-mentioned packaging effect. In addition, a regular change in the pigment composition is also at the origin of this decrease; recall that algal absorption originates from all accessory pigments, while normalization is made with respect to the sole chlorophyll a .

Most of the recent studies in oceanic waters have shown that algal cells are the dominant term in forming a_p . On average, a_ϕ would represent about 70% of a_p within the absorption blue maximum of algae (around 440 nm), and even more in the red

peak (around 675 nm). The spectral a_ϕ and a_p patterns in Figure 3(A) are slightly changing with [Chl], as a consequence of the differences between the spectral values of the exponents (in eqns [2.1] and [2.2], Table 2). In comparison, nonalgal particles are less absorbing, and their absorption, regularly increasing toward the short wavelengths, is well modeled with an exponential function (Table 2, eqn [2.3]).

The measurements of a_{cdom} (performed on filtered water) are rather scarce in oceanic waters; they have not yet provided a clear relationship (if any) between this term and [Chl], but have shown that the spectral shape, namely a monotonous (exponential) increase of a_{cdom} toward the short wavelengths, is rather stable (eqn [2.4]). It is worth noting that this spectral dependency is close to that typical of a_{nap} , apart from a small difference in slope. All models presently proposed in the literature have the same exponential structure.

Table 2 Bio-optical models for Case 1 waters, and corresponding equations by which the main inherent optical properties (IOP) of a water body can be related to its chlorophyll concentration^a

$$a_p(\lambda) = A_p(\lambda)[\text{Chl}]^{\text{Ep}(\lambda)} \quad [2.1]$$

$$a_\phi(\lambda) = A_\phi(\lambda)[\text{Chl}]^{\text{E}\phi(\lambda)} \quad [2.2]$$

Note that the terms A_p and A_ϕ are displayed in Figure 3(A), as $a_p(\lambda)$ and $a_\phi(\lambda)$ are shown when [Chl] is set equal to 1 mg m^{-3} ; the exponents $\text{Ep}(\lambda)$, and $\text{E}\phi(\lambda)$ are similar in magnitude but not equal, and they vary within the range 0.6–0.9, approximately.

$$a_{\text{nap}}(\lambda) = a_{\text{nap}}(\lambda_0) \exp[-S_{\text{nap}}(\lambda - \lambda_0)] \quad [2.3]$$

$$a_{\text{cdom}}(\lambda) = a_{\text{cdom}}(\lambda_0) \exp[-S_{\text{cdom}}(\lambda - \lambda_0)] \quad [2.4]$$

Note that in these two last expressions, the reference wavelength (λ_0) is arbitrary (often 440 nm is adopted), and the slopes (S) of the exponential decrease are approximately $S_{\text{nap}} = 0.012 \text{ nm}^{-1}$ and $S_{\text{cdom}} = 0.015 \text{ nm}^{-1}$.

$$b(\text{Chl}, \lambda_0) = b_w(\lambda_0) + b_p(\text{Chl}, \lambda_0)$$

and

$$b_p(\text{Chl}, \lambda_0) = B_p(\lambda_0)[\text{Chl}]^x \quad [2.5]$$

with the exponent x in the range 0.6–0.7, approximately; with $B(\lambda_0)$, at $\lambda_0 = 550 \text{ nm}$, statistically found to vary between 0.15 and $0.45 \text{ m}^2 (\text{mgChl})^{-1}$ (see also Figure 4).

$$b_p(\text{Chl}, \lambda) = b_p(\text{Chl}, \lambda_0)(\lambda/\lambda_0)^y \quad [2.6]$$

with the exponent y between -0.5 and -2 (the value -1 is commonly adopted).

$$b_p(C, \lambda_0) = B'_p(\lambda_0)[C]^{x'} \quad [2.7]$$

with the exponent x' close to 1 (see also Figure 4).

^aSubscripts: w, water; p, particles; ϕ , phytoplankton; nap, nonalgal particle; cdom, colored dissolved organic matter.

The scattering coefficient In open ocean waters, the scattering coefficient, $b = b_w + b_p$, is the sum of the constant molecular scattering (b_w), and of a varying contribution, b_p , resulting from the presence of all kinds of particles, living organisms, and detritus. Unlike a_p , b_p cannot be split into algal and nonalgal contributions, as there is no experimental technique allowing such a discrimination.

Bio-optical models aim at relating this bulk coefficient b_p to [Chl]. *In situ* measurements of $b_p(\lambda)$, at fixed wavelength, λ_0 (or indirect determination via the particle attenuation coefficient $c_p(\lambda)$, from which $a_p(\lambda)$ is subtracted), have led, through least-squares analyses, to a nonlinear dependence upon [Chl] of the form

$$b_p(\lambda_0) = B_p(\lambda_0)[\text{Chl}]^\times \quad [6]$$

$B_p(\lambda_0)$ (which represents the value of b_p when $\text{Chl} = 1 \text{ mg m}^{-3}$) has been found to vary within a factor 3 for Case 1 waters (see also Figure 4; and eqn [2.5]).

The nonlinearity in eqn [6] (a power law with $\times < 1$) is such that when the algal biomass increases, b_p increases more slowly. This effect is generally attributed to a change (i.e., a decrease) in the

relative contribution of detritus and of heterotrophic organisms to scattering when [Chl] increases (in eutrophic waters). This explanation is corroborated by the following observation: when b_p is studied as a function of the particulate organic carbon concentration, [C], instead of [Chl], it varies linearly with [C] (see Table 2, eqn [2.7]).

Spectral measurements of b_p in the open ocean are rather scarce. If the size distribution function obeys a Junge distribution (eqn [1]), the spectral dependency of the scattering coefficient can be theoretically predicted as being a power law, with an exponent (γ , in Table 2, eqn [2.6]) which is related to j (eqn [1]), simply by: $\gamma = 3 - j$. With typical values for j around 4, γ would be around -1 , as roughly observed, and generally adopted in bio-optical modeling. Such a monotonic decrease of b_p throughout the spectrum is probably oversimplifying, particularly at high algal concentration; indeed, phytoplankton scattering spectra are, as mentioned before, featured in reponse to the pigment absorption.

Apparent Optical Properties and [Chl]

Downwelling irradiance The downwelling and upwelling irradiances (radiant flux per unit of area, *see Radiative Transfer in the Ocean*) are convenient measurements to make at sea to characterize the penetration of daylight into the water column. The depth variations of these quantities are quantified by diffuse attenuation coefficients (**Radiative Transfer in the Ocean**). When dealing with downward irradiance, E_d , the corresponding coefficient is K_d (simply written K). It depends on the IOPs of the water and on the geometrical structure of the light field. Only by approximation, it can be seen as the sum of a term due to the water itself and a varying contribution of all materials (particulate and dissolved) originating from biological activity, so that

$$K(\lambda) \cong K_w(\lambda) + K_{\text{bio}}(\lambda) \quad [7]$$

The first term can be (again approximately) expressed as a function of the IOPs of optically pure seawater (a_w and b_w), whereas $K_{\text{bio}}(\lambda)$, resulting from the presence of all kinds of biological materials, can be related to [Chl].

On the basis of many field measurements in oceanic waters, it has been shown that the spectral $K_{\text{bio}}(\lambda)$ values do not vary at random but are interrelated. The proposed optical classification is based on the realization that such a rather regular change affects simultaneously all the wavelengths and progressively modifies the entire spectrum. Bio-optical algorithms derived from statistical analyses of these

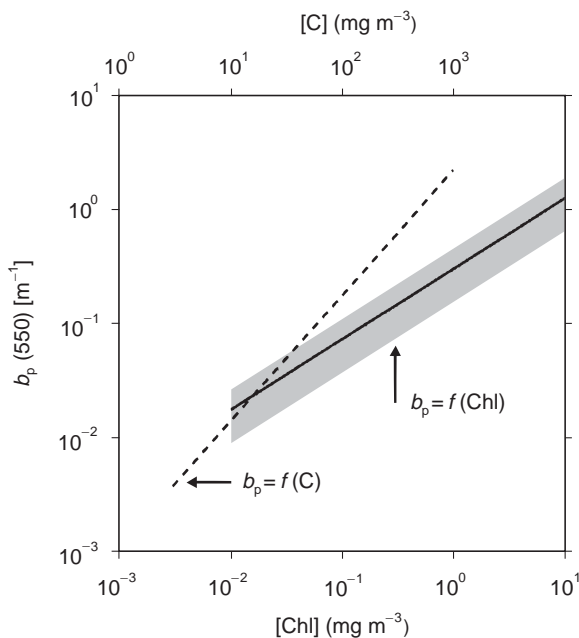


Figure 4 Particle-scattering coefficient as a function of the chlorophyll concentration in Case 1 waters, and at $\lambda = 550 \text{ nm}$ (eqn [2.5] in Table 2); the natural variability in this relationship for Case 1 waters is represented by the shaded band. The dashed line represents the empirical relationship statistically obtained between b_p and the organic carbon concentration (upper abscissa scale).

field data allow the entire $K(\lambda)$ spectrum to be specified, as soon as $K(\lambda_0)$, at a reference wavelength λ_0 is known (Table 3, eqn [3.1]).

A second way of analyzing the field data consists of relating the $K_{\text{bio}}(\lambda)$ values to [Chl]. In Case 1 waters, the diffuse attenuation coefficients appear to be highly correlated to [Chl], and the statistical relationships (linear regression on log-transformed quantities) are expressed as

$$K_{\text{bio}}(\lambda) = \chi(\lambda)[\text{Chl}]^{e(\lambda)} \quad [8]$$

with exponents $e(\lambda)$ are always < 1 , whatever the wavelength. The corresponding $K(\lambda)$ bio-optical model consists of a set of such nonlinear expressions based on eqns [7] and [8] (eqn 3.2, Table 3; Figure 5). More complex models have also been used (eqn [3.4]).

To the extent that K is largely determined by absorption, the nonlinear character of the correlation between K and [Chl] is not surprising and resembles that observed for a (Figure 3B). By integrating over the whole visible domain (the photosynthetic available radiation (PAR) domain, see Radiative Transfer in the Ocean, a relationship between Z_{eu} , the depth of the euphotic zone (cf. Table 1), and [Chl] can be obtained. This nonlinear relationship can also be derived through a direct analysis of the column-integ-

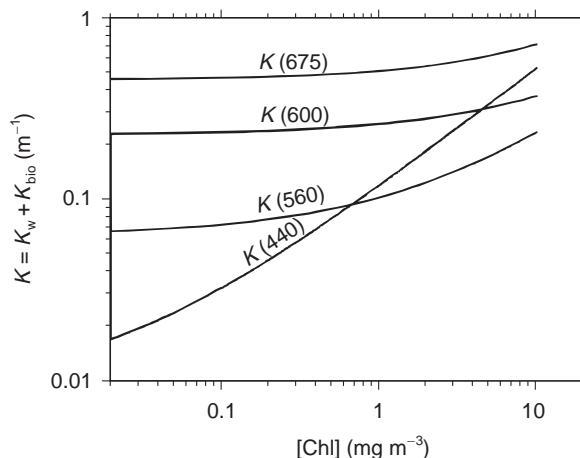


Figure 5 Diffuse attenuation coefficient for downward irradiance, at selected wavelengths, as a function of the chlorophyll concentration in Case 1 waters. The initial values (the ordinates when [Chl] = 0.02 mg m⁻³) are almost the pure sea water values (K_w in eqn [7], see also eqn [3.1], in Table 3, for the term K_{bio}).

rated chlorophyll content and of Z_{eu} , observed at sea by using a photometer able to determine the vertical PAR profile. This bio-optical algorithm is useful to predict, in Case 1 waters, the depth of the euphotic zone when the vertical chlorophyll profile has been determined (eqn [3.3], Table 3).

Table 3 Bio-optical models, and corresponding equations by which the main apparent optical properties (AOP) in Case 1 waters can be related to the chlorophyll concentration [Chl]

$$K(\lambda) = K_w(\lambda) + M(\lambda)[K(\lambda_0) - K_w(\lambda_0)] \quad [3.1]$$

where $K_w(\lambda)$ is the attenuation coefficient for downwelling irradiance in pure water, $M(\lambda)$ are statistically derived coefficients and λ_0 a reference wavelength.

$$K(\lambda) = K_w(\lambda) + \chi(\lambda)[\text{Chl}]^{e(\lambda)} \quad [3.2]$$

$\chi(\lambda)$ and $e(\lambda)$ are empirical wavelength-dependent factors and exponents, derived from statistical analysis.

$$Z_{\text{eu}} = z[\text{Chl}]^\zeta \quad [3.3]$$

z is about 38 m, and the exponent ζ is close to $\frac{1}{2}$; this expression is computed by using eqn [3.2], combined with a standard spectrum of solar radiation at sea level.

$$K(\lambda, [\text{Chl}]) = k(\lambda) \exp \{ -k'(\lambda) \log_{10} ([\text{Chl}]/[\text{Chl}_0]^2) \} + 0.001[\text{Chl}]^2 \quad [3.4]$$

$[\text{Chl}_0]$ is a reference concentration (0.5 mg m⁻³), and $k(\lambda)$ and $k'(\lambda)$ are empirical spectral parameters derived from statistical analysis.

$$\log_{10}([\text{Chl}]) = a_0 + a_1 r + a_2 r^2 + a_3 r^3 \quad [3.5]$$

where $r = \log_{10} [R(\lambda_1)/R(\lambda_2)]$ is the decimal logarithm of a ratio of reflectances at two wavelengths; the cubic polynomial is an example (first order polynomials have also been proposed). The inverse relationships, which express various r ratios as a function of $\log_{10}([\text{Chl}])$, also have the same polynomial structure.

Irradiance reflectance This apparent optical property, $R(\lambda)$, is crucial in the interpretation of the remotely sensed ocean color. It is defined as the ratio of upwelling irradiance, E_u , to downwelling irradiance at the same depth (actually just beneath the surface in remote sensing applications)

$$R(\lambda) = E_u(\lambda)/E_d(\lambda) \quad [9]$$

Other expressions involving upward radiance (instead of E_u) are also in use in ocean color remote sensing; they are geometrically related to $R(\lambda)$ as defined, and physically modeled in a similar way.

Historically, purely empirical models were the first to have been developed. As for K_d , quasi-simultaneous field measurements of $R(\lambda)$ and of [Chl] were carried out, and then statistically analyzed. The relationships obtained through such regression analyses were used as algorithms when processing ocean color data. Most of these algorithms consider the ratios of reflectance at two wavelengths, λ_1 and λ_2 . Statistical analyses have demonstrated that these ratios vary regularly with [Chl]. Therefore, they can be operated as predictor of [Chl], through a certain function F :

$$[\text{Chl}] = F[R(\lambda_1)/R(\lambda_2)] \quad [10]$$

When such ratios of reflectances (called band ratio in ocean color science) and [Chl] are plotted in log-log space, the scatterplot is sigmoid. In the so-called empirical ‘chlorophyll-algorithms’ in use in ocean color remote sensing, the functional dependency is expressed through a polynomial with respect to the log-transformed quantities (Table 3; linear approximations have also been employed).

Thanks to radiative transfer studies, it has been shown that (to a first approximation) $R(\lambda)$ can be expressed as a function of two inherent properties, a and b_b , through

$$R(\lambda) = f \cdot b_b / (a + b_b) \quad [11]$$

where f is not a constant factor (because R is not an inherent property), but depends in a complex manner on the structure of the light field, and on the VSF of the particles. Its value (between about 0.3 and 0.5 for common cases in oceanic waters) can only be computed by solving the RTE with the appropriate boundary conditions. As a consequence of eqn [11], a bio-optical model for reflectance reduces to a combination of models for a and b_b , separately considered. Because a and b_b are inherent properties, the additivity principle applies (eqns [4] and [5], for a). Therefore a purely analytical model would be built if a and b_b (actually each term

forming a and b_b) could be completely parameterized in terms of [Chl].

Such a model is not yet available. Modeling the back-scattering coefficient is presently an unresolved problem. This coefficient is generally expressed as being the product $b \cdot \tilde{b}_b$, of the scattering coefficient (which can be related to [Chl] through eqn [6]), and the dimensionless back-scattering efficiency \tilde{b}_b . The latter quantity is not presently well documented, and rather divergent hypotheses (including a constant value) have been proposed to express its dependency on [Chl] and on λ .

When dealing with absorption, the role of a_{cdom} in open ocean is largely unknown, or more precisely its magnitude has not yet been successfully related to [Chl]. For this reason, in particular, a can advantageously be replaced by its proxy, K_d , which cumulates the influence of all absorbing substances, and is easily modeled (see above). Some manipulations of the RTE, however, are necessary to derive a from K_d . Such models are called ‘semianalytical’ (see Figure 6). They are also used to predict the ratios of reflectances as a function of [Chl], and reciprocally (as through eqn [10]); they result in algorithms having the same structure as those derived from the empirical approach (eqn [3.4], Table 3, and Figure 7). Other bio-optical models, involving

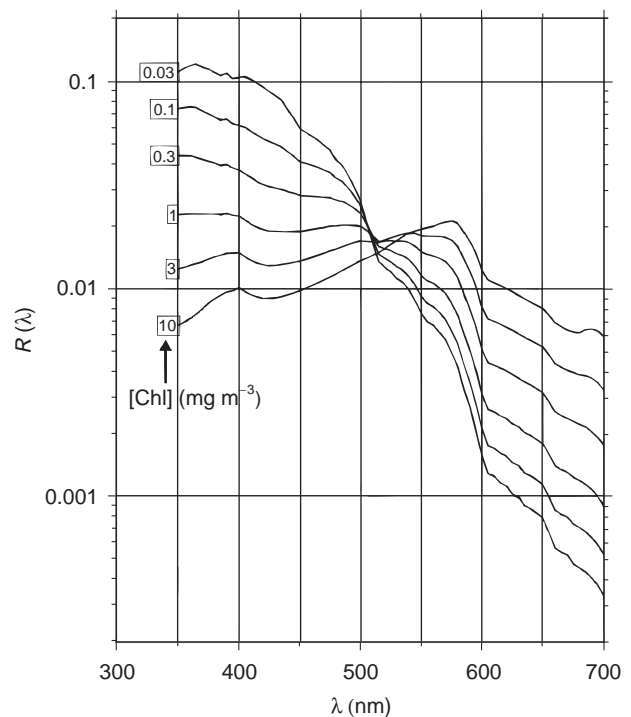


Figure 6 Example of a spectral model for reflectance as a function of [Chl] and for Case 1 waters; the various bio-optical models presently in use are not identical but very similar.

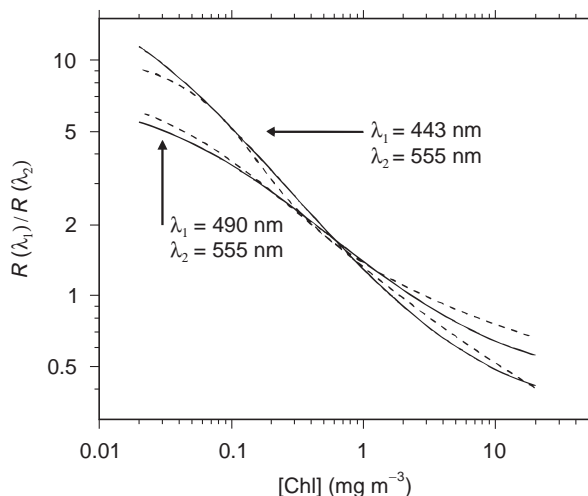


Figure 7 Example of outputs of models for Case 1 waters providing the evolution with [Chl] of ratios of reflectances at two wavelengths (as indicated) (see eqn [3.2], **Table 3**).

reflectances at more than two wavelengths, have also been proposed.

Reasonable agreements have been reached between such semi-analytical approaches, empirical approaches, and independent data sets (not used when developing the models). The sigmoidal shape is well understood if not analytically reproduced with accuracy.

Conclusions

In terms of accuracy or predictive capabilities, the first category of bio-optical models, dealing with the properties of individual organisms, are robust particularly because they rest on firm theoretical bases. The second category, dealing with bio-optical properties of oceanic water bodies, in essence empirical, cannot be as accurate, especially because they also reflect the 'natural' variability around mean laws.

This variability is expected to the extent that various substances, dissolved and particulate, living or inanimate, which are optically significant, are not strictly covarying with [Chl]. Therefore, the links between bulk optical properties and [Chl] cannot be tight. Actually, most of these properties may vary within a factor 2 or 3 (or more) around the mean value provided by the (nonlinear) models. This remark holds true for coefficients like a_p , a_ϕ , b_p , and K . The situation is somewhat better when ratios of optical coefficients are involved, and when covariations of these coefficients reduce the amplitude of fluctuations around the mean (as for reflectance and band ratios, for instance). In summary, the predictive skill of such models is inevitably limited by the tightness of the regressions on which they are based.

It is necessary to bear in mind that further studies at sea will likely change the result of the regression analyses, and thus the numerical values of the tabulated parameters entering into the models. For this reason, only equations are given in **Tables 2** and **3**, the provisional numerical information to be found in the literature, is likely amenable to modification in the future).

Most of the bio-optical models, by which optical properties and [Chl], are related, rely on nonlinear relationships, and often on power laws of [Chl], with exponents below 1. As a result, the optical properties vary within a narrower interval than does [Chl] in Case 1 waters, and do not span more than 2 orders of magnitude (instead of 3), which is still considerable. It can be envisaged that for Case 1 waters 'regional' bio-optical models, encompassing a less wide chlorophyll concentration range, and accounting for local biological activity with its specific assemblages, will be more efficient in the future. For Case 2 waters, bio-optical models based on [Chl], are insufficient and must be supplemented by accounting for the presence of mineral and organic sediments, and dissolved colored substance, not covarying with the algal biomass.

See also

Ocean Color from Satellites. Optical Particle Characterization. Radiative Transfer in the Ocean.

Further Reading

- Demers S (1991) *Particle Analysis in Oceanography*. NATO-ASI Series, vol. G 27. Berlin Heidelberg: Springer-Verlag.
- Gordon HR, Brown OB, Evans RH *et al.* (1988) A semi-analytical radiance model for ocean color. *Journal of Geophysical Research* 93: 10909–10924.
- Gordon HR and Morel A (1983) Remote sensing of ocean color for interpretation of satellite visible imagery: a review. *Lecture Notes on Coastal and Estuarine Studies*. New York, Berlin, Heidelberg, Tokyo: Springer-Verlag.
- Jerlov NG and Nielsen ES (1974) *Optical Aspects of Oceanography*. London, New York: Academic Press.
- Morel A (1988) Optical modeling of the upper ocean in relation to its biogenous matter content (Case 1 waters). *Journal of Geophysical Research* 93: 10749–10768.
- Morel A and Smith RC (1982) Terminology and units in optical oceanography. *Marine Geodesy* 5: 335–349
- Smith RC and Baker KS (1978) The bio-optical state of ocean waters and remote sensing. *Limnology and Oceanography* 23: 247–259.
- Van de Hulst HC (1957) *Light Scattering by Small Particles*. New York: Wiley.