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Introduction

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Without light there would be no life in the sea. Since the seas were the cradle for the evolution of all life forms, the theme of this book is central to our understanding of the interaction between living organisms and their environment. To express the breadth of research in this area, leading experts in topics as diverse as satellite imagery and molecular biology have contributed to this collection of essays on 'Light and Life in the Sea' so that it is unique in both its scope and its authority. The intention is not to provide a comprehensive textbook but rather to present the reader with a sampler of the exciting research that is underway and to provide an introduction to its broad compass.

The book opens with a series of chapters on the physics of light in the sea. Here the spectral characteristics of the incoming radiation are described and their modification by absorption, scattering, fluorescence and bioluminescence is explained. Microscopic drifting plants, the phytoplankton, intervene and modify the characteristics of light reflected and radiated from the surface layers of the ocean. The use and verification of remote sensing techniques for determining the distribution and productivity of phytoplankton in the oceans is described. The harvesting of light for photosynthesis provides the main topic for the following section of the book. The mean depth of the oceans is nearly four kilometres but photosynthesis is restricted to a thin layer, at most a few hundred metres thick. The factors controlling the depth of this shallow photic zone are described and the photosynthetic strategies for organisms ranging from bacteria to seaweeds are explained and the importance of light in controlling the development of plant cells is discussed.

The second half of the book explores the exploitation of light in the sea by marine animals, often at great depths. As well as providing the basic energy source for life in the sea, light is used by animals to provide information about their environment, through vision. The optics of the eyes of marine animals show great diversity but, where a particular structure provides optimal sensitivity or resolution it may evolve by a number of independent routes. A section on vision considers the physiology of vision and the functioning of the photoreceptors of vertebrates and of invertebrates. The following section explores the way in which animals use the visual information and the effects that this has on their behaviour. The impact on the vertical migration and schooling of fish

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and on the diurnal rhythms of animals in reef communities is described. The exploitation of such behavioural responses by man is discussed in an essay considering the use of light lures on fishing gear. Where sunlight can penetrate the oceans this is utilised, but at night or at greater depths the organisms must generate their own light. The final section of the book therefore considers the use of this biologically generated light (bioluminescence) for communication between organisms. The physiology, evolution and biochemistry of bioluminescence are described and examples are given of the exploitation of bioluminescent proteins for medical research.

The individual essays were originally presented as invited papers at the first Annual Scientific Meeting of the Marine Biological Association which was held at the Polytechnic South West in Plymouth in April 1989. The speakers, and their topics, were selected to provide a balanced view of the exploitation of light by life in the sea. The invited papers were augmented at the meeting by a diverse range of submitted papers and posters. The result was a meeting of extraordinary breadth that was greeted with great enthusiasm by those who participated, not least because it provided an opportunity for experts studying different aspects of the impact of light on life in the sea to understand the context of their investigations. It is our intention that this series of essays should provide an equally bracing stimulus to a much wider audience.

In closing this introduction I would like to express my thanks to all those who have contributed to the production of this book. Tony Campbell and Peter Herring developed the theme of the meeting and were responsible for assembling such an excellent and diverse set of authors. John Green, through his careful organisation and infinite patience, untiringly helped by Jane and Rebecca Green, ensured that the meeting itself ran smoothly so that we could all concentrate on enjoying the delightful variety of ideas that we hope this volume will convey to its readers. Finally, Linda Maddock carried out most of the detailed editorial work, ably assisted by Elwyn Harris, Jinny Rutherford and Robert Maddock, and shepherded the individual contributions into a well-organised volume.

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Chapter 1

THE LIGHT FIELD IN THE OCEAN: ITS MODIFICATION AND EXPLOITATION BY THE PELAGIC BIOTA

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INTRODUCTION

Life in the sea is intimately linked to the quality and quantity of light available there. Primary production, upon which the entire trophic economy of the sea depends, is controlled by the spectral and angular distribution of underwater light. At the same time, the marine organisms themselves modify the submarine light field by absorption and scattering, and through the processes of fluorescence and bioluminescence. The light produced underwater by marine organisms through fluorescence and bioluminescence is but a minute fraction of the sunlight reaching the sea surface, and is therefore safely neglected in most energy budget calculations for the pelagic ocean. On the other hand, it carries the spectral signature of the organisms that generate it, and thus has potential significance as a diagnostic marker for them. Variations in the pigmented biota usually dominate variations in ocean colour as seen by an observer outside the ocean, a phenomenon which is now being exploited for estimation, by remote sensing, of phytoplankton biomass and primary production.

Here, we describe the light field at the surface and in the interior of the oceans. Light emission within the sea by fluorescence is briefly discussed. We describe how the expected rate of photosynthesis depends on the characteristics of the submarine light field, and how this information can be used in remote sensing applications.

Our discussion is confined to the visible spectrum. Light penetration in water, marine photosynthesis, fluorescence by phytoplankton, and bioluminescence all show strong wavelength dependence, and within the spectral range of interest it is therefore important to consider the spectral distribution, rather than just the total flux available. The terms and notations used in this paper are described in the Glossary in Appendix 1.

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LIGHT REACHING THE SEA SURFACE

The extra-terrestrial solar irradiance spectrum is now fairly well known. Changes in the distance between earth and sun introduce a seasonal variation of just ±3.4% around the mean extra-terrestrial irradiance. If, however, we compute the flux per unit area on the surface of the earth (neglecting atmospheric effects), it is seen to vary markedly with latitude and with season, the seasonal variation being most pronounced at the poles and weakest at the equator. The daily path of the sun across the sky, which determines both the day length and the daily maximum in solar flux per unit surface area, is also a function of latitude and season. In addition to these effects, which can be computed on purely geometrical considerations, we also have to take into account the consequences of variable transmission through the atmosphere. Atmospheric transmission changes not only the quantity and spectral quality of light reaching the sea surface, but also its angular distribution: part of the light reaching the sea surface arrives from the direction of the sun (direct sunlight), and the remainder (diffuse sky light) has a complex angular distribution, from scattering by the atmospheric constituents.

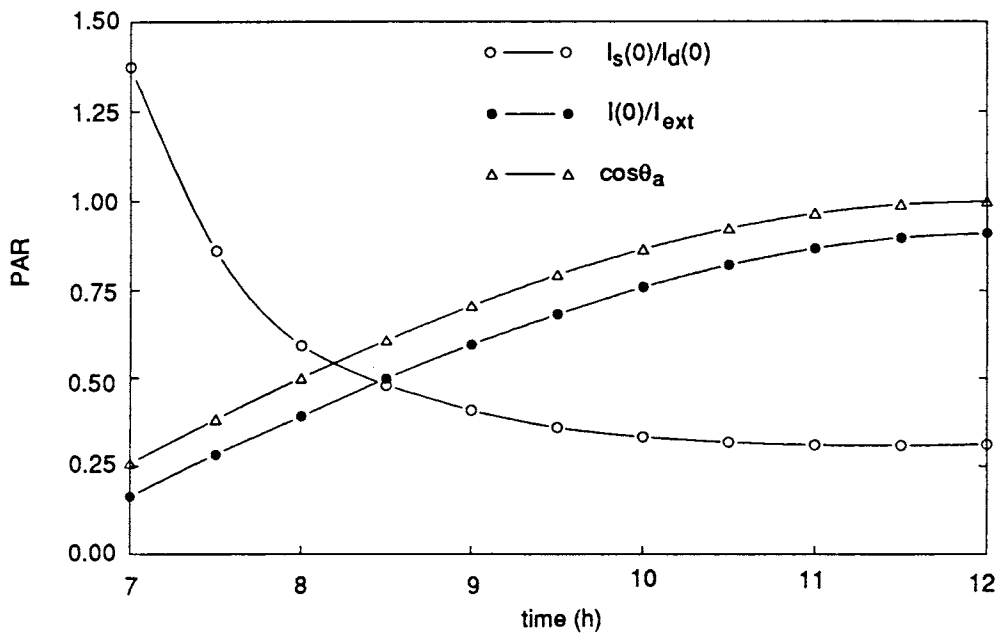

Figure 1.1. This figure shows an example of changes in the Photosynthetically Active Radiation (PAR) at the surface of the ocean, as a function of local apparent time. These are results of computations for a clear day at the equator, when the sun is directly overhead at noon. Computations were carried out using the spectral transmittance model of Bird (1984), and the results integrated to obtain PAR (400-700 nm). The ratio ($I(0)/I_{ext}$) is plotted, where I_{ext}(= 8.66 E m^{-2} h^{-1} in these computations), is the extra terrestrial PAR normal to the sun's rays. The ratio of diffuse to direct irradiance, on a horizontal plane facing upwards, at the sea surface ($I_s(0)/I_d(0)$) is also plotted. Notice that the increase in total irradiance $I(0)$ at the sea surface corresponds closely to changes in cos θ_a where θ_a is the zenith angle of the sun (in air).

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Under clear-sky conditions, atmospheric transmission is determined primarily by the zenith angle of the sun, which is a function of latitude, date and local time (see Figure 1.1 for an example). Models of varying degrees of complexity are now available that compute spectral transmission through a cloud-free atmosphere for a given zenith angle, starting with the extra-terrrestrial solar irradiance (Brine & Iqbal, 1983; Bird, 1984). The computations for the visible part of the spectrum have to account for Rayleigh scattering by atmospheric gases, for aerosol extinction, and for absorption by ozone and water vapour.

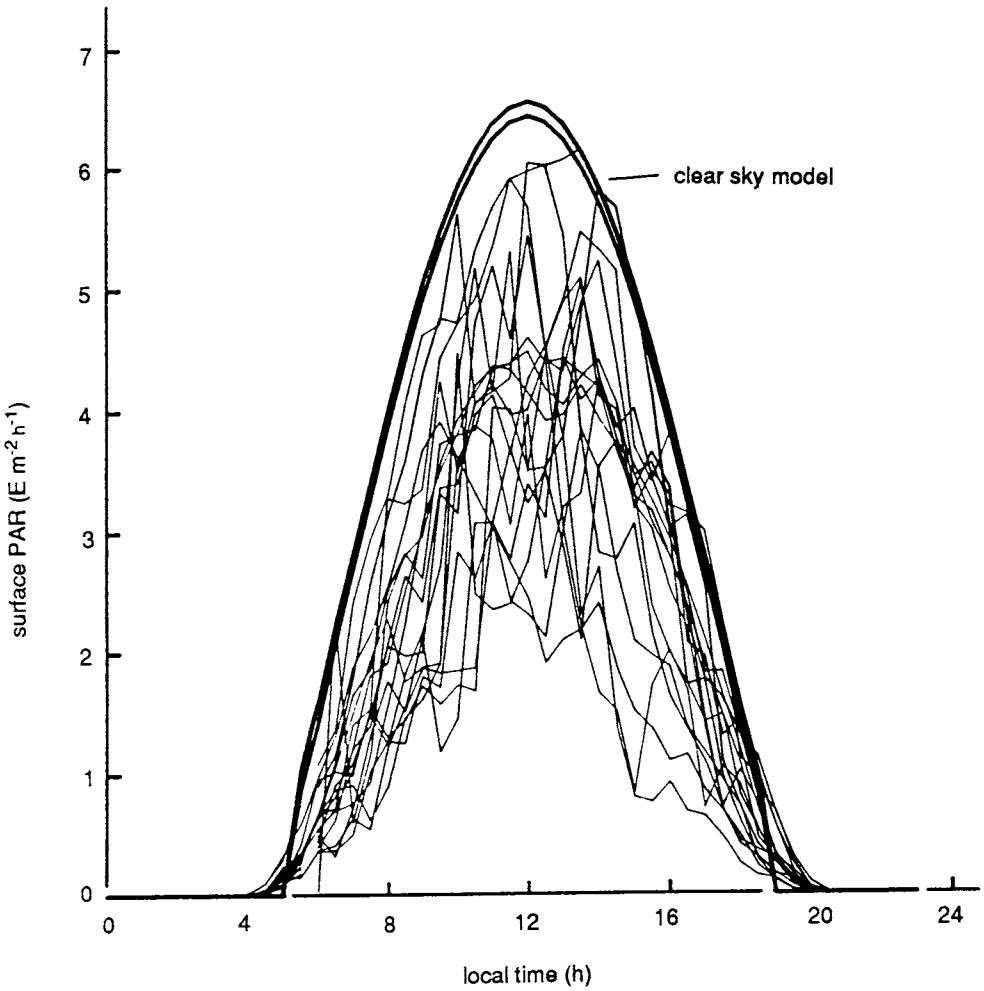

Figure 1.2. Comparison of surface irradiance (PAR) obtained using the clear-sky model with direct observations at the sea surface during a cruise in the Celtic Sea on board RRS 'Darwin' from 18 May to 7 July 1986. The two thick curves correspond to clear-sky computations for the first and last days of observation. The thin jagged lines represent all observations. The clear-sky computations envelope the upper limit of the observations. The discrepancies are mostly due to clouds, and the figure gives a good indication of the complex effect of clouds on the surface irradiance. We are indebted to Dr M. J. R. Fasham for use of the data.

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In the visible, water vapour has an absorption band at 593 nm, but it is a weak one. The Rayleigh scattering component can be computed very accurately, given atmospheric pressure. Aerosol extinction depends on the concentration of aerosols, their size spectrum, refractive index and distribution with altitude. This component is therefore the most difficult one to model for routine computations treating clear skies. But some parameterisations are available (Paltridge & Platt, 1976; Brine & Iqbal, 1983; Bird, 1984) that allow reasonable approximations of their spectral extinction, given the aerosol turbidity at one wavelength (defined as the aerosol optical depth τ_a at that wavelength, and for the total vertical atmospheric column). These computations are usually easier for the sea than for the land, because of low concentrations of aerosols over the sea.

Modelling spectral transmission under cloudy skies has proved to be extremely difficult (see Figure 1.2 for an example). In the first place, the computations, which depend on the types and vertical height distributions of clouds, are very complex; in the second place, cloud data are rarely available in sufficient detail for such computations. By scattering more light in the direction of the sea, certain fields of small, loosely-distributed clouds can even cause an increase (5-10%) in radiation at sea level, compared to that under a clear sky. Extensive and thick clouds, on the other hand, can reduce the surface flux to about 20% of the clear-sky value (Kirk, 1983). Clouds also alter the partition of the total flux between direct and diffuse components. Paltridge & Platt (1976) have discussed parameterisation of the cloud effect. Most parameterisations now in use account for changes in the total flux and in the relative size of the direct and diffuse fractions, but do not offer any indication of the change in spectral shape.

THE AIR-SEA INTERFACE

The light reaching the sea surface is modified by refraction and reflection at the interface. Reflection (which can be computed according to Fresnel's Law) remains very low (≈2%) for angles of incidence down to 45°, and then increases steadily to total reflection at grazing incidence. Note that, at Brewster's angle (53·1°), reflection drops to zero for light polarised parallel to the plane of incidence. The effect of refraction (computed according to Snell's Law as a function of incident angle), is to change the angular distribution of light under water. In the case of a flat sea surface, it limits the light field to a cone of semi-vertical angle of 48° (the critical angle). A rough sea surface diffuses the edge of this cone.

Computation of reflection and refraction requires a knowledge of the angular distribution of the light field reaching the sea surface. For diffuse sky light, it is common to assume either a uniform or a cardioidal distribution in air (see Jerlov, 1976). Reflection is also a function of polarisation, but computations are usually made assuming the light to be unpolarised (note however, that clouds have a depolarising effect; see Jerlov, 1976).

Another complication is that refraction and reflection are functions of sea surface roughness. It has been shown that the slope distribution at the sea surface approximates a Gaussian distribution when the sea surface is ruffled by winds, and that there is only a small difference between the along-wind and across-wind slope distributions (Preis-

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endorfer, 1976*a*). Computations and observations have shown that wind-induced roughness has a noticeable effect on reflection only at solar elevations less than 30°, with reflection decreasing with increased wind speed (Preisendorfer & Mobley, 1986; Apel, 1987).

LIGHT TRANSMISSION UNDER WATER

The equation of radiative transfer

A complete description of the underwater light field would require that the flux be described for every angle, and for every wavelength. In other words, if one assumed the horizontal divergence of light flux to be zero, it would be necessary to specify the radiance L for every depth z, wavelength λ, zenith angle θ, and azimuth angle ϕ. Neglecting light sources within the water, the equation of radiation transfer, which describes the rate of change of radiance with distance r, can be written as (Jerlov, 1976):

$$\frac{dL(z,\lambda,\theta,\phi)}{dr} = -c(z,\lambda)L(z,\lambda,\theta,\phi) + L_*(z,\lambda,\theta,\phi) \tag{1.1}$$

where c is the total volume attenuation coefficient and L_*, known as the path function, accounts for the light scattered into the direction (θ,ϕ) from all other directions (θ',ϕ'):

$$L_*(z,\lambda,\theta,\phi) = \int_{\phi'=0}^{2\pi}\int_{\theta'=0}^{\pi} \beta(z,\lambda,\theta,\phi;\theta',\phi')\, L(z,\lambda,\theta',\phi')\sin\theta'\, d\theta'\, d\phi' \tag{1.2}$$

where $\beta(z,\lambda,\theta,\phi;\theta',\phi')$ is the volume scattering function at depth, z, for the wavelength, λ, and for the angle defined by the directions (θ,ϕ) and (θ',ϕ').

These equations imply that a complete description of the radiance field requires that we specify all the inherent optical properties of the medium: the volume scattering function β, whose integral over all angles yields the volume scattering coefficient b, and the volume absorption coefficient a (note that $c = a + b$). Integration of Equation 1.1 over long distances also has to take into account the effects of multiple scattering and the depth dependence of the inherent optical properties. Even if the inherent optical properties of the water column and the incident light field at the ocean surface are known with the necessary detail (which is often not the case), finding complete solutions to the radiative transfer equation represents a monumental task in computing. Fortunately, most applications do not require such a complete description of the light field.

For biological applications, such as the estimation of the light absorbed by phytoplankton, computations can be simplified considerably by dealing with the irradiance field rather than with the radiance field. The vector irradiance I, which defines flux per unit area, is given by:

$$I(z,\lambda) = \int_{\phi=0}^{2\pi}\int_{\theta=0}^{\pi} L(z,\lambda,\theta,\phi)\cos\theta\,\sin\theta\, d\theta\, d\phi \tag{1.3}$$

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In addition to the saving in computational time that results from dealing with the integrated flux, irradiance also offers the added advantage of relative ease of measurement at sea.

Parameterisation of the irradiance field

In computations, as well as in measurements, it is common to split the total irradiance into two parts: the downwelling irradiance, which represents the integration of radiance over the upper hemisphere, and the upwelling irradiance, which represents the integration over the lower hemisphere. Note that downwelling irradiance is that fraction of irradiance measured by a flat horizontal collector facing upwards, and that upwelling irradiance is measured by a similar collector facing downwards. The upwelling irradiance arises primarily from scattering, and also from biological activity, such as fluorescence and bioluminescence.

Scattering in sea water is of two kinds: molecular scattering by pure sea water, and particle scattering by suspended material in the sea water. An important property of molecular scattering is that forward scattering equals backward scattering: it is symmetrical about the plane of incidence. Particle scattering in sea water, which falls in the domain of Mie scattering, is characterised on the other hand by very pronounced forward scattering. It is strongly asymmetrical. In the oceans, scattering by particles always dominates molecular scattering. An important consequence is that the upwelling irradiance is usually only a small fraction of the downwelling irradiance, and can safely be neglected for many applications. We adopt this simplifying assumption here, and equate I with the downwelling irradiance.

The rate of decrease of the downwelling irradiance is determined by the attenuation coefficient for irradiance K, defined by:

$$K(z,\lambda) = \frac{-1}{I(z,\lambda)} \frac{dI(z)}{dz} \tag{1.4}$$

The parameter K is a function of the inherent optical properties of the sea water and of the angular distribution of the light field. Because it is dependent on the ambient light conditions, it is classed as one of the apparent optical properties. It is interesting to see how K can be expressed as a function of the inherent optical properties. For light incident normally, and for single scattering approximation,

$$K(z,\lambda) = a(z,\lambda) + b_b(z,\lambda) \tag{1.5}$$

where b_b is the backscattering coefficient, defined by

$$b_b(z,\lambda) = 2\pi \int_{\pi/2}^{\pi} \beta(z,\chi) \sin\chi \, d\chi \tag{1.6}$$

where χ is the scattering angle with respect to the initial direction of the light ray. Now, for light incident at zenith angle θ, $K(z,\lambda)$ becomes:

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$$K(z,\lambda) = \frac{a(z,\lambda) + b_u(z,\lambda)}{\cos\theta} \tag{1.7}$$

where b_u is the upward scattering. The $\cos\theta$ term accounts for the increased path length of light per unit vertical distance for oblique incidence. Sathyendranath & Platt (1988) have used b_b as an approximation of b_u. Because of the asymmetry in the volume scattering function of particles, b_u for particles is greater than b_b. But Sathyendranath & Platt (1989) have argued that it is a reasonable approximation for most open ocean waters, where a dominates over b_u, such that K is largely determined by a. For a diffuse light field, the $\cos\theta$ term has to be replaced by μ, the mean path length of the light rays per unit vertical distance. In this case, with the approximate expression for upward scattering, we have:

$$K(z,\lambda) = \frac{a(z,\lambda) + b_b(z,\lambda)}{\mu} \tag{1.8}$$

To account for multiple scattering, we have to admit the possibility that some of the light scattered in the upward direction may be scattered downwards again. But here once again, due to the pronounced forward scattering by particles, the correction would be only minor. Another consequence of multiple scattering is that the angular distribution of light underwater, and therefore the average cosine μ, changes with depth. It has been established both experimentally and theoretically that, a few attenuation depths (1 attenuation depth = $1/K$) below the sea surface, the angular distribution approaches an asymptotic state, which depends only on the inherent optical properties of the medium (Preisendorfer, 1959). However, change in μ with depth is generally not more than ±10% for open ocean waters (Preisendorfer, 1976*b*; Prieur, 1976).

One of the primary sources of variability in $K(z,\lambda)$ is phytoplankton, the other sources being suspended sediments and dissolved organic matter. In fact, in open-ocean waters, phytoplankton can be considered to be the single independent variable controlling the magnitude of K. Parameterisations of the spectral values of K fall into two classes: (1) those that are based on statistical correlations between K and the phytoplankton concentration C (Smith & Baker, 1978*a*; Morel, 1988), and (2) those based on expression of a and b as functions of C, combined with parameterisation of μ (Dirks & Spitzer, 1987; Sathyendranath & Platt, 1988). Examples of results from the model of Sathyendranath & Platt (1988) are given in Figures 1.3 and 1.4.

The first class makes uses of the 'quasi-inherent' nature of K: that is, according to many observations in the open oceans, K is not strongly dependent on the underwater light distribution (partly explained by the fact that refraction at the sea surface limits maximum θ to 48° for a flat sea surface, and by the fact that light measurements at sea are usually made at high light-levels, that is, when solar elevation is high). The second approach offers some flexibility. For example, separation of absorption and scattering effects makes it relatively easy to compute the fraction that has been absorbed by phytoplankton, and is therefore available for photosynthesis. But on the other hand, it requires that μ be specified explicitly.

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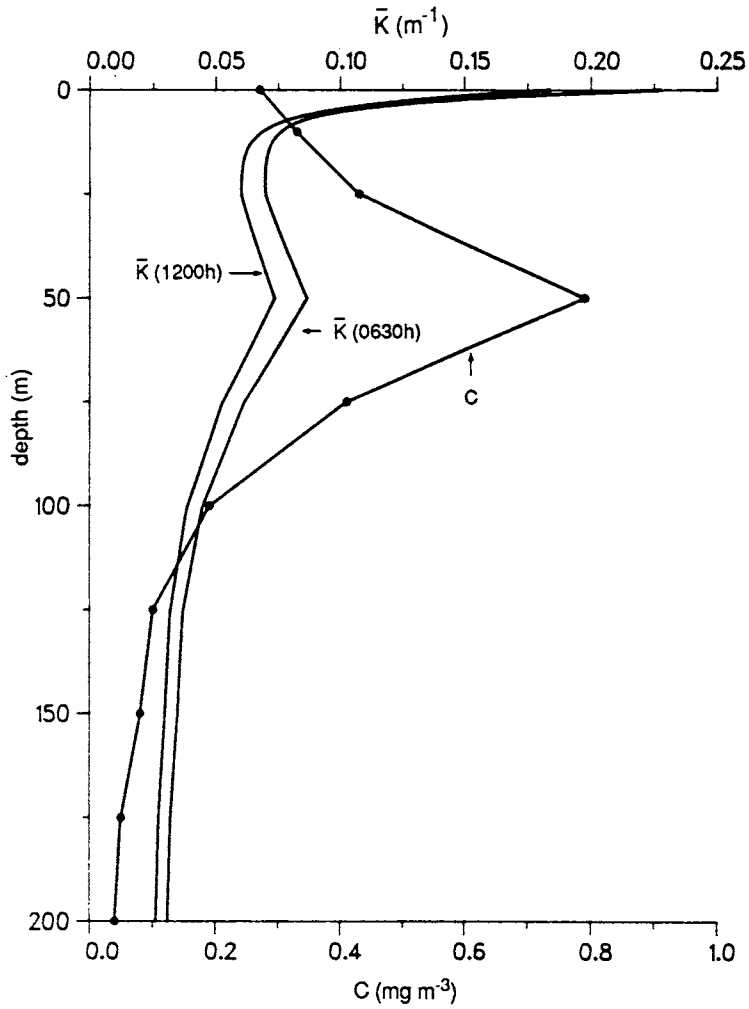

Figure 1.3. An example of computations of $\bar{K}$, the attenuation coefficient for total PAR, for a given vertical distribution of pigments C (from Sathyendranath & Platt, 1988; copyright by the American Geophysical Union). The computations of $\bar{K}$ were carried out for early morning (0630 h) and noon (1200 h) and the curves are labelled accordingly. Note that the changing angular distribution of incident light from morning to noon does introduce a significant effect on the attenuation coefficient. Also significant is the fact that in the surface layers, the attenuation coefficient does not covary with the concentration of pigments; instead, it is dominated by the high attenuation of the red wavelengths by pure sea water.

In the first approach, $K(z,\lambda)$ is expressed as:

$$K(z,\lambda) = K_w(\lambda) + C(z)\,k_c(\lambda) \tag{1.9}$$

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