Reprinted from Canadian Bulletin of Fisheries and Aquatic Sciences 214

Photosynthetic Picoplankton

EDITED BY TREVOR PLATT AND WILLIAM K.W. LI

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Pages 561-583



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Introduction

Until recently, picoplankton was considered to be an unimportant component of marine phytoplankton, and consequently, it remained largely uninvestigated. Of late, many papers show that the contribution of picoplankton to the biomass as well as to production of phytoplankton is not negligible (Herbland et al. 1985; Johnson and Sieburth 1979; Joint and Pomroy 1983; Li et al. 1983; Platt et al. 1983; Takahashi and Beinfang 1983; Waterbury et al. 1979). It, therefore, seems an appropriate moment to re-examine procedures for phytoplankton remote sensing in the light of what we may call the "picoplankton discovery". I address the following questions:

How does picoplankton affect the remotely sensed signal?

Can remote sensing tell us anything about picoplankton? In the absence of remote sensing data on the effects of picoplankton, efforts to evaluate their implications for remote sensing will have to be based at this stage entirely on information available from theoretical, laboratory and *in situ* studies.

I have approached this problem by reviewing the capabilities and limitations of the present-day techniques for remote sensing of marine phytoplankton. This includes discussions on the various techniques for deriving phytoplankton biomass, as well as some emerging techniques for retrieving additional information on phytoplankton type and primary productivity. A persistent problem, in obtaining a phytoplankton biomass index through remote sensing, has been the variability of the phytoplankton absorption, scattering and fluorescence signatures. At each stage, the consequences of this variability in phytoplankton signatures (and whenever possible, that of picoplankton in particular) are examined. The gaps in knowledge of picoplankton optical signatures limit the conclusions that can be drawn, and these will be indicated.

The paper is organised as follows: We first derive the signal leaving the water surface from the signal received by a sensor on a remote platform. The diverse techniques of phytoplankton remote sensing (passive radiometry, passive fluorescence and active lidar techniques) are then examined. Finally, the limitations of the depths accessible by remote sensing are studied.

The Coastal Zone Color Scanner (CZCS), launched in 1978 on board the satellite NIMBUS-7, has remained the only satellite sensor ever launched that was specifically designed for ocean phytoplankton remote sensing. The CZCS orbits sun-synchronously at an altitude of about 955 km, and has a ground resolution of 825 m by 825 m. It picks up radiance at six channels, centred at 443, 520, 550, 670, 750 and 11,500 nm (the 750 nm channel has not been operational since launch). The sensor scans in a direction perpendicular to the orbit track. The scan plane can be tilted up to 20° north or south of nadir, to avoid sun glint. The swath width varies from 1300 to 2300 km, depending on the tilt. Each swath slightly overlaps the previous one. Thus the data from the satellite can be used to create contiguous mosaics of radiances or derived parameters that cover millions of square kilometres. The satellite track repeats every 6 days. All our practical experience on satellite remote sensing of phytoplankton is confined to this one sensor, and consequently, extra emphasis is given in this paper to interpretation of data from CZCS type of sensors.

A glossary of the radiometric terms and notations used in the text is given in Appendix I. All the optical quantities discussed here are wavelength-dependent. When wavelength is not specified, it implies that the statement holds for all wavelengths.

The Remotely Sensed Signal

The basic remote sensing problem posed here is to measure spectral variations in the light leaving the water surface, and to derive information on phytoplankton from them. In the case of passive remote sensing, the primary light source for the water-leaving radiance is the sunlight itself, whereas in active remote sensing, the source is a laser. Before the water-leaving signal reaches the remote sensor, it is distorted by the intervening atmospheric column. The first step in the study, therefore, is to evolve suitable schemes for correcting the total signal for atmospheric noise. This aspect is examined briefly next.

PASSIVE REMOTE SENSING

Consider a sensor at height Z above the sea surface, viewing the sea at an angle (θ', ϕ) , under cloud free conditions. Let the radiance received by the sensor be $L(Z, \theta', \phi)$. The following factors would influence L (see Fig. 1 also):

a) Attenuation of light emerging from the sea surface, by the atmospheric column between the sea surface and the sensor.

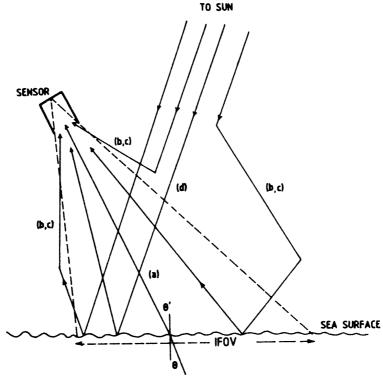


FIG. 1. Pathways of radiation reaching the remote sensor. (a) is upwelling radiation from within the water, and may consist of scattered light or fluorescence emission. This is the useful signal for the biological oceanographer. (b,c) consist of scattered light, which may or may not have been reflected at the sea surface. The atmospheric gases (b) or aerosols (c) may be responsible for the scattering process. It is convenient to treat the two types of scattering separately, because of the great differences in their volume scattering function. (d) reprensents specular reflection of sunlight into the sensor. IFOV is the Instantaneous Field of View.

- b) Rayleigh scattering of diffuse sky light into the sensor by atmospheric gases. The scattered light may include that reflected at the sea surface.
- c) Aerosol scattering of diffuse sky light into the sensor (Mie scattering). The scattered light may include that reflected at the sea surface.
- d) Reflection of direct sunlight into the sensor.

The specular reflection term is avoided by the CZCS by pointing the sensor away from the region of sunglint. Gordon (1978) expresses the dependence of L on the remaining processes as:

(1)
$$L(z, \theta', \phi) = L_w(\theta', \phi) t + L_R + L_A$$

The water-leaving radiance, L_w , consists of: (i) sunlight which penetrated the water, and was retransmitted into the atmosphere after scattering, and (ii) fluorescence emission from the water column, if any. This therefore, is the useful signal for the biological oceanographer.

The quantity t is the diffuse transmittance of the atmosphere defined by Gordon and Morel (1983) as:

(2)
$$t = \exp \left[-(T_R/2 + T_{O_2} + (1 - \omega_A F)T_A)/\cos\theta \right]$$

where, T_R , T_{Oz} and T_A are the optical thicknesses of the intervening atmosphere due to atmospheric gases, ozone and aerosols, respectively.

 ω_A is the aerosol scattering albedo.

F is the probability of forward scattering in the case of aerosol scattering.

The diffuse transmittance term allows for the fact that radiance from nearby pixels can be scattered into the sensor. If the direct transmittance were used, the exponent in Eq. 2 would have to be replaced by the sum of the three optical thicknesses. (When neighbouring pixels are sharply contrasted, contamination from the neighbours can become unacceptably high, and such areas would have to be rejected from analysis.)

 L_R is the contribution to L from scattering by atmospheric gases.

 L_A accounts for the contribution due to Mie scattering by aerosols.

Equation 1 assumes that the Rayleigh scattering and aerosol scattering events can be decoupled. Gordon has shown this to be a realistic and useful simplification, but it is strictly true only if there is no multiple scattering.

Gordon and co-workers, in a series of articles, have outlined practical ways of estimating $L_{\rm w}$ from L in the case of the CZCS (see review of Gordon and Morel 1983). Their method is based on the following assumptions: Aerosol scattering phase function and single scattering albedo are wavelength independent; Rayleigh scattering component does not depend on sea-surface roughness; and aerosol contribution is directly proportional to the aerosol optical thickness.

When L_w is zero at λ_o , Eq. 1 reduces to:

(3)
$$L(\lambda_o) = L_R(\lambda_o) + L_A(\lambda_o)$$

In the case of the CZCS, λ_o is taken to be 670 nm. The quantity L_R is wavelength-dependent, but its value for any wavelength can be calculated theoretically from a knowledge of the atmospheric pressure, solar elevation and the look angle of the sensor. Therefore, $L_A(\lambda_o)$ can be estimated from $L(\lambda_o)$ and L_R . We now define the ratio

(4)
$$S(\lambda, \lambda_0) = L_A(\lambda)/L_A(\lambda_0).$$

Here L_A is a function of T_A , the extra-terrestrial solar irradiance after correction for ozone absorption (F_o) , and other terms which are assumed wavelength-independent in the model. We therefore have:

The quantity F_o can be calculated. To be able to evaluate $L_A(\lambda)$, we therefore have to estimate $T(\lambda, \lambda_o)$. Initially, this was done through ground measurements. If a direct measurement of T_A is available at ground level for any one pixel in the satellite imagery, for the time of the satellite overpass, $S(\lambda, \lambda_o)$ can be determined for that pixel from Eq. 5. The rest of the scene is processed on the assumption that this ratio remains constant over the entire scene. The assumption is only valid if the aerosol type remains constant over the area, though the total aerosol concentration may change. The quantity S can also be determined from in situ measurement of L_w and evaluation of tL_w , through Eqs. 1 and 4.

To calculate the term t from Eq. 2, it is assumed that the term involving the aerosol optical thickness T_A is negligible. This assumption is not considered to be critical, since T_A is typically of the order of 0.1 and $(1 - \omega_A F)$ is generally less than 1/6. The major effect of aerosols on L is through the L_A term. The optical thicknesses due to atmospheric gases and ozone can be calculated theoretically.

An alternate method, proposed by Gordon and Clark (1981) does not require ground measurements for estimating S. In this method, atmospheric correction over the entire scene is first carried out assuming

$$S(\lambda, \lambda_o) = F_o(\lambda)/F_o(\lambda_o).$$

This permits identification of pixels with very clear waters. For these pixels, L_w values are assumed to be known, which permits recalculation of S. The atmospheric effects are now recalculated for the whole scene using the S values derived for clear water pixels. Bricaud (personal communication) uses an interation scheme which re-identifies clear water pixels in the case of the new S values (these new clear water pixels may turn out to be different from the original ones). The process is repeated until it becomes stable.

The assumption that $L_{w}(670)$ is zero is not valid for all waters. Smith and Wilson (1981) have proposed an iterative scheme for correcting errors arising from this assumption. Their method relies on statistical relationships between L_{w} values for different wavelengths taken in pairs. Guan et al. (1985) have proposed a scheme based on error analysis, for reducing the calculation time.

The atmospheric correction described here is critical, when we consider that only 20% or less of the signal received by the satellite is useful. Even though the present methods make several assumptions, they have nevertheless yielded good results.

The atmospheric correction scheme outlined here is valid for other sensors on aircraft or satellite. In the case of aircraft, the F_o terms in Eq. 4 will have to be replaced by the values of downwelling irradiance at the aircraft altitude, and the ozone optical thickness would drop to zero. In the case of low flying aircraft, naturally, atmospheric correction will be less important.

ACTIVE REMOTE SENSING

In the case of active remote sensing, the quantity we are interested in measuring is the laser-induced scattering and fluorescence signals leaving the water surface. All ambient light, therefore, constitutes noise. By operating the laser in pulses, it is possible to monitor the background and apply suitable corrections. Though this appears easy in principle, in practice, difficulties are introduced by the high level of background noise in the case of daytime operations, which calls for stringent instrumental requirements on sensitivity and range. (It is interesting to note that, when the active system is monitoring the background, it is in fact acting as a passive sensor.) It is also necessary to account for the atmospheric attenuation in both directions. Suitable methods can be devised for this correction, but at the present state of art, this is not

a critical problem as laser techniques have so far only been tried from aircraft flying at very low altitudes (about 150 m).

Ocean Colour

I now examine how the satellite signal, after correction for atmospheric effects, can be related to the phytoplankton biomass and type.

RELATIONSHIP BETWEEN COLOUR AND UPWELLING RADIANCE AT THE WATER SURFACE

The water leaving radiance $L_u(\theta, \phi)$ is related to the upwelling radiance $L_u(\theta, \phi)$ just below the water surface through the equation:

(6)
$$L_w(\theta,\phi) = L_u(\theta,\phi) \left[1 - \varrho(\theta,\phi)\right]/m^2$$

where m is the refractive index of water, $m \sin \theta = \sin \theta'$, and ϱ is the Fresnel reflectivity. The $[1 - \varrho(\theta, \phi)]$ term accounts for reflection at a calm sea surface (the reflectivity does not change much in the case of a rough sea, for small nadir viewing angles), and the $1/m^2$ term arises due to the spreading of the beam because of refraction. For nadir viewing angles of about 40° or less, the latter term is dominant, and the radiance distribution is generally found to be insensitive to changes in θ and ϕ . Therefore, for small nadir viewing angles, it is possible to simplify Eq. 6 to:

$$L_w(\theta', \phi) \cong 0.544 L_u$$

where L_u is the radiance in the upward direction (see Austin 1974, 1980; Kirk 1983). Let Q be the ratio of E_u (the upwelling irradiance at depth zero) to L_u .

$$L_u = E_u(0)/Q.$$

For a perfectly diffuse medium, $Q = \pi$. Experimental and theoretical results (Austin 1980; Kirk 1983) suggest that for oceanic waters, the value of Q is close to 5 for nadir and near-nadir angles.

Now, the "intrinsic colour" of seawater is determined by the spectral form of reflectance R at depth zero, defined by:

$$R(0) = E_u(0)/E_d(0)$$

where E_d is the downwelling irradiance. The reflectance ratio at 2 wavelengths can now be expressed in terms of the water leaving radiance at those wavelengths:

(7)
$$\frac{R(\lambda_1)}{R(\lambda_2)} = \frac{L_w(\lambda_1) \ Q(\lambda_1) \ E_d(\lambda_2)}{L_w(\lambda_2) \ Q(\lambda_2) \ E_d(\lambda_1)}$$

It is clear from Eq. 7 that the ratio of reflectances is proportional to the ratio of water leaving radiances if $E_d(\lambda_2)/E_d(\lambda_1)$ and $Q(\lambda_1)/Q(\lambda_2)$ are constants. Neglecting the slight variability of these parameters, the radiance ratios may be assumed equal to the reflectance ratios. Theoretically, it is possible to estimate E_d from satellite data, thereby eliminating one source of uncertainty, though generally this is not done. As we will see later, most remote sensing algorithms use radiance or reflectance ratios for phytoplankton estimations. When trying to interpret and understand these algorithms, it is convenient to think in terms of reflectance, because: (i) fluctuations in incoming solar irradiance do not affect it, as it is normalized to this variable, and (ii) reflectance can be expressed in terms of the inherent optical properties of sea water, as shown in the next section. Inherent optical properties have the advantage of being independent of variations in the angular distribution of ambiant light.

COLOUR IN TERMS OF INHERENT OPTICAL PROPERTIES

Gordon and Morel (1983) have reviewed the recent theoretical results relating R to the inherent properties b_b (backscattering coefficient) and a (absorption coefficient). For oceanic waters they reduce to a simple relationship of the form:

$$(8) R \cong 0.33 \ b_b/a.$$

Equation 8 assumes that there is no fluorescence emission at the wavelength considered. It is valid for waters where b_b/a is less than 0.3. The coefficients a and b_b obey the principle of superposition.

Morel (1980) proposed that for the simplest case of oceanic waters with little land influence (no land drainage, river runoff or bottom sediments brought into resuspension by wave action), it may be reasonably assumed that the variations in a and b_b are completely determined by the optical properties of the phytoplankton present in it (this is the case 1 waters). Then a and b_b can be rewritten as:

$$(9) a = a_w + a_c$$

$$(10) b_b = b_{bw} + b_{bc}$$

where subscripts w and c stand for contributions due to pure seawater and phytoplankton respectively. In turn, a_c and b_{bc} can be expressed in terms of the specific coefficients (coefficients per unit concentration) a^*_c and b^*_{bc} , and the concentration of phytoplankton in water, C. i.e.,

$$(11) a_c = C a^*_c$$

$$(12) b_{bc} = C b^*_{bc}.$$

By common practice, the concentration of chlorophyll-a is taken as the index of phytoplankton biomass, and the specific values are expressed per unit concentration of chlorophyll-a.

Equations 9 and 10 assume simple, ideal conditions where variations by other substances like dissolved organic matter and suspended material other than phytoplankton can be accommodated provided they covary with phytoplankton. The contribution from pure seawater is invariant, and the spectral values of a_w and b_{bw} are well known (Morel 1974; Smith and Baker 1981). Therefore, if the spectral values of a_c^* and b_{bc}^* were invariant with species composition and the physiological state of the population, variations in ocean colour would be solely determined by C. It would then be a relatively simple matter to retrieve C from the magnitude and spectral form of R. This however, is not the case, and the variability in phytoplankton optical signatures merits careful examination to evaluate the consequences in remote sensing.

BACKSCATTERING BY PHYTOPLANKTON

Theoretical and experimental results of Morel and Bricaud (1981a) and Bricaud et al. (1983) indicate that backscattering and absorption by phytoplankton have approximately complementary spectral forms. Phytoplankton backscattering spectra are generally characterised by two minima at around 440 and 675 nm, corresponding to the chlorophyll-a absorption at these wavelengths. Superimposed on this general form there is considerable variability. The magnitude of specific backscattering is also highly variable, but generally extremely low. Theoretically (Morel and Bricaud 1981a), the specific backscattering by picoplankton could be up to an order of magnitude or so higher than that of larger cells with the same refractive indices. Thus, the remotely sensed signal would have a higher component due to backscatter in

picoplankton-rich waters. In spite of this, variations in b_{bc} would remain small compared to b_{bw} for low phytoplankton concentrations, and this effect would only be of secondary importance in contributing to variations in R, when compared to the effect of the variability in a^*_c .

SPECTRAL SPECIFIC ABSORPTION OF PHYTOPLANKTON

In vivo spectral specific absorption of phytoplankton has been the subject of several laboratory studies. These spectra are generally characterised by a maximum at 440 nm and a secondary maximum at 675 nm, both of which are associated with chlorophyll-a absorption bands. Additional peaks due to the auxiliary pigments chlorophylls b or c and carotenoids are superimposed on the chlorophyll-a absorption bands. Generally, there is a broad minimum in the 550-620 nm range. But in the case of phytoplankton with biliproteins (cyanobacteria, cryptophytes and rhodophytes), this zone is occupied by the absorption bands of phycoerythrin (500-565 nm) and phycocyanin (610-645 nm). The phytoplankton specific absorption at 440 nm per unit chlorophyll-a concentration is seen to vary by a factor of three. Besides the variations in the pigment composition, the "flattening effect" is another factor causing variations in the spectral form and magnitude of specific absorption. Duysens (1956), Kirk (1983) and Morel and Bricaud (1981b) have examined the effect of particle size on absorption, and noted that when the absorbing material is concentrated within suspended particles in the medium, there is a decrease in absorption, and a flattening of the spectrum, as compared to absorption by the same material in solution. Sathyendranath et al. (1987) studied the specific absorption spectra of selected monospecific cultures, and concluded that pigment composition and flattening effect account for practically all the variability in the spectra. They assumed spherical, homogeneous particles for calculating the flattening effect.

Reverting to Eq. 11, the variable a_c^* can therefore be calculated if the concentration of all the auxiliary pigments and the size distribution of the phytoplankton cells are known, using the following equations:

If *n* pigments with concentration C_i (i = 1 to n) are present in the phytoplankton population in addition to chlorophyll-a at concentration C, then a parameter a^*_{sol} can be calculated, which represents the absorption that the medium would have in the absence of flattening effect (absorption by a hypothetical equivalent solution):

(13)
$$a^*_{sol} = \sum_{i=1}^n \frac{C_i}{C} a^*_{soli} + a^*_{solc}$$

where a^*_{solc} and a^*_{soli} represent specific absorption by the chlorophyll-a and the auxiliary pigments, respectively, in the absence of all other pigments, and if there is no package effect. The first term on the right hand side of Eq. 13 accounts for changes in specific absorption due to changes in the relative concentrations of the auxiliary pigments, with respect to chlorophyll-a.

The flattening effect can now be calculated as follows. We first calculate the specific absorption coefficient of the cellular material, a_{cm} , given by:

(14)
$$a_{cm} = (6a^*_{sol})/(\pi Nd^3)$$

where N is the number of particles per unit chlorophyll-a concentration, and d is the diameter of the equivalent sphere with the same volume as an individual particle. Then, with $\varrho' = d a_{cm}$, the efficiency factor for absorption, Q_a , is calculated:

(15)
$$Q_a = 1 + (2e^{-\varrho'})/\varrho' + 2(e^{-\varrho'} - 1)/\varrho'^2.$$

Then,

(16)
$$a^*_c = \pi N d^2 O_a / 4$$
.

The flattening effect is given by $a^* c/a^*_{sol}$, which is always less than one, but tends to one when ϱ' tends to zero. This ratio decreases non-linearly, but monotonically, with increase in ϱ' . Since ϱ' is greater at absorption maxima than at the minima, $a^* c/a^*_{sol}$ will be less at absorption maxima. Consequently, the spectrum will appear flattened when compared to the corresponding a^*_{sol} spectrum.

Clearly, the size of the particle influences the form and magnitude of the specific absorption spectrum. But it is to be noted that an increment in a_{cm} has an identical effect on Q_a as a similar increment in d. Obviously, picoplankton, with their small size, will tend to have higher specific absorption than larger cells with the same pigment characteristics.

We do not have much information on whether picoplankton have intracellular pigment concentrations similar to larger phytoplankton. Li et al. (1983) report chlorophyll-a concentrations of the order of 0.5 fg/cell for cyanobacteria from a tropical upwelling ecosystem. This yields a value of about 106 mg of chlorophyll-a per cubic metre of cell material, if we assume the cell size to be of the order of $1\mu m$. This is comparable to values obtained for larger cells in cultures (Sathyendranath et al. 1987) and is favourable for high specific absorptions in picoplankton. However, the data from Li et al. (1983) for another tropical station, from Smith et al. (1985) and from Platt et al. (1983) yield cell chlorophyll concentrations of about one or two orders of magnitude higher. Such cells, obviously, would tend to have very low specific absorption values! (One possibility, of course, is that, as suggested by Li et al. for their data, the cell numbers are underestimated. This is supported by the fact that the reported photosynthetic parameters of these picoplankton suggest high specific absorptions.) Prezelin et al. (1985) report concentrations ranging from 2 to 100 fg/cell, with the lower values at the surface, and the higher values at the bottom of the euphotic zone. (The data from Platt et al. (1983) also refer to data from the deep chlorophyll maximum.) There is a marked dearth of data on the pigment composition of picoplankton also. So the question of what a_{cm} values to attribute to picoplankton remains unsolved at present. However, the available limited data suggest that, at least for remote sensing purposes, where we are mostly concerned with surface waters, low intra-cellular pigment concentrations may be a reasonable assumption.

CASE 2 WATERS

Thus far only case 1 waters have been considered. In case 2 waters (see Gordon and Morel 1983), which are mostly encountered in coastal regions, yellow substances (dissolved organic matter) and suspended sediments may vary independently of chlorophyll-a concentrations, thereby rendering the system more complex.

The absorption coefficient in this case will contain additional terms a_y and a_x representing contributions from yellow substances and suspended matter (other than phytoplankton) respectively, while the backscattering coefficient will contain the extra term b_{bx} which accounts for backscattering by suspended sediments.

Bricaud et al. (1981) have expressed the absorption by yellow substances by an equation of the form:

$$a_y(\lambda) = a_y(440)\exp[-0.014(\lambda - 440)]$$

(see Fig. 2). The constant 0.014 is a mean value, as it has a slight variability.

Yentsch (1962) has observed a neutral absorption spectrum for suspended sediments from Woods Hole waters, and a spectrum similar to that of yellow substances for samples from waters below 100 m. Prieur and Sathyendranath (1981) have proposed an "U-shaped" absorption curve for suspended particles based on *in situ* results. Further studies are needed to determine the variability of absorption and back-scattering characteristics for different types of suspended sediments.

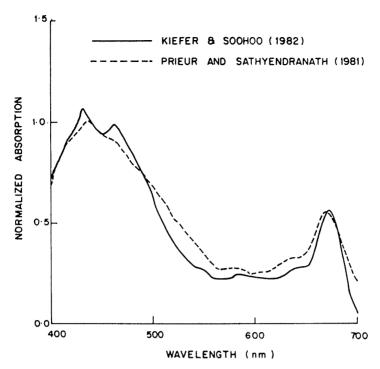


FIG. 2. Absorption spectra associated with phytoplankton, for *in situ* conditions, from Prieur and Sathyendranath (1981) and Kiefer and SooHoo (1982). Both spectra are normalized at 440 nm, in order to compare the spectral form.

In situ absorption and reflectance spectra

We examine now the in situ observations in the light of the theoretical and laboratory results described above. Prieur and Sathyendranath (1981) have shown that the absolute values of in situ specific absorption of phytoplankton in fact vary with region (at 440 nm, the value was found to vary by more than a factor of 3). The highest specific absorptions were noted in oligotrophic open ocean waters with a possibly high fraction of picoplankton. However, these specific absorptions are probably overestimates, since no special precaution was taken to retain the picoplankton fraction during filtration for chlorophyll-a estimation. Their study, on the other hand, did not reveal any variations in the spectral form of specific absorption and they pointed out that this would require more exhaustive and accurate data than was available, since spectral variability apparently introduced only minor changes around the average spectral form. Kiefer and SooHoo (1982) identified the in situ specific absorption spectrum associated with chlorophyll-a after correction for the effects of pheopigments. Their spectral form compares well with that proposed earlier by Prieur and Sathyendranath (1981) (see Fig. 3). Under non-bloom conditions when several types of phytoplankton would be present in the population, the mixing of types would tend to wash out the marked variations in spectral signatures which are observed in the case of single species cultures in the laboratory.

Sathyendranath (1981) showed that a model of absorption with a single spectral form for phytoplankton specific absorption, with variable efficiencies, can explain

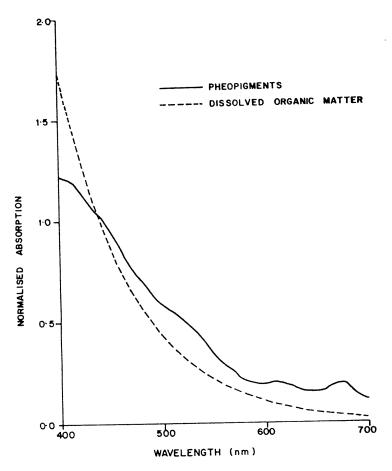


FIG. 3. Absorption spectra of dissolved organic matter, according to the Eq. of Bricaud et al. (1981). The absorption spectrum associated with pheopigments, proposed by Kiefer and SooHoo (1982) is also presented. The two spectra show considerable similarity. When spectral signatures of different substances have similar characteristics, it becomes difficult to distinguish them by remote sensing.

observed reflectance spectra, with certain additional hypotheses regarding b_b (Fig. 4). As a first approximation, the b^*_{bc} spectrum proposed had a form inversely proportional to the a^*_c curve, and a constant backscattering ratio of 0.5%. Comparison with observed values was good, which once again implies that b^*_{bc} variability is of secondary importance in determining the reflectance spectra. For case 2 waters, this model uses the "U" shaped absorption spectrum for suspended sediments and a b_{bx} spectrum which follows a λ^{-n} law. The parameter n was found to vary from station to station over a range of 0 to 2. The backscattering ratio was also found to vary over the range 0.3 to 2%.

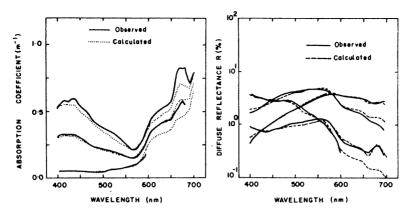


FIG. 4. *In situ* absorption and reflectance spectra compared with the spectra calculated from absorption and reflectance models (from Prieur and Sathyendranath 1981 and Sathyendranath 1981).

ALGORITHMS FOR CHLOROPHYLL RETRIEVAL FROM OCEAN COLOUR

When the phytoplankton characteristics affecting the R spectra are understood, the various techniques to solve the inverse problem of recovering phytoplankton information from the R spectra can be examined against this background. Some of the algorithms are developed directly from models of R. But the most commonly used algorithm, especially for CZCS data, is an empirical relationship of the form:

$$(17) C = A r_{ij}^{-B}$$

where r_{ij} stands for the ratio of radiances or reflectances at wavelengths i and j, and the coefficients A and B are determined by least square fit on log transformed data. In the case of the CZCS data, the wavelength pairs taken are (443, 550) and (520, 550). The 443 channel on CZCS corresponds to the absorption maximum of chlorophyll-a, while 550 corresponds to the minimum. For high phytoplankton concentrations, the signal at 443 becomes very low, and then the 520 signal is used instead. The method has been found to yield reasonable results, particularly for case 1 waters. However, the coefficients A and B appear to be subject to certain variability. Suitable coefficients are normally selected on the basis of sea truth data. Chlorophyll retrieval accuracies of \pm 40% have been reported for this method. Algorithms of different forms, but essentially based on the same principle (i.e., the change in the blue-green ratio of reflectance with change in chlorophyll concentration) have also been proposed by various authors (see review of Sathyendranth and Morel 1983).

The influence of picoplankton on this type of algorithm is evaluated next, in the light of the nature of variability of phytoplankton spectral signatures:

- 1) Picoplankton, with their small size, would be least subjected to the flattening effect (pigment composition and intracellular concentration remaining the same) and would have maximum specific absorption values. If this factor is not taken into account in picoplankton-rich waters, it would result in an overestimation of chlorophyll-a concentration. It may be noted that the coefficient B in Eq. 17 takes higher values in the open ocean case 1 waters than in the coastal regions. It is probable that this higher rate of change in the blue-green ratio with change in chlorophyll concentration is related to a higher absorption efficiency associated with picoplankton.
- 2) Since R and a are inversely related, the rate of change of R will be higher for lower concentrations of phytoplankton. Given the relative importance of picoplankton

in oligotrophic waters, ocean colour changes provide a sensitive method for mapping

small gradients in their concentration.

3) The algorithm type presented in Eq. 17, which relies on the change in the bluegreen ratio of reflectance with change in chlorophyll-a concentration, can be invalidated in an area rich in blue-green algae with possible prominent absorption peak in the green due to phycoerythrin. The four CZCS channels are inadequate to cope with such problems, and the validity of the derived results in such cases will depend on the availability of sea truth in the study area at the time of the satellite overpass.

More complex algorithms have been devised for case 2 waters, in order to separate the chlorophyll signal from those of non-phytoplanktonic material. Morel and Prieur (1978) and Pelevin (1978) have proposed analytical algorithms which make use of three wavelengths. Jain and Miller (1976) and Miller et al. (1977) have used a model of R with optimization techniques, to derive C. The approach has been extended by Bukata et al. (1981) for case 2 type of waters. They also established "duo-isopleths" of chlorophyll-a and suspended mineral concentrations. The concentrations could be read off from the graphs, if radiance values of 2 wavelengths were known. (However, this method uses only 2 wavelengths, and was found to be less accurate than the multispectral optimization technique.) Carder and Steward (1985) have also used a case 2 reflectance model of R. Chlorophyll concentration is taken to be that value which yields the best comparison between theoretical and observed spectra. The problem of passive radiometric remote sensing in case 2 waters has also been examined in detail by Sathyendranath et al. (1982, 1983). Their results indicate that the role of suspended sediments is basically to enhance the magnitude of the waterleaving signal in a more or less neutral manner, while changes in the concentration of phytoplankton and yellow substances result in alteration in the spectral form of reflectance. The presence of yellow substances tends to lower the level of outgoing signal monotonically towards the blue part of the spectrum, while the phytoplankton signal can be distinguished from it primarily by the presence of the minimum at 440 nm due to the chlorophyll absorption maximum at this wavelength. The non linear interactions between the signals of these substances make it difficult to arrive at a single algorithm that will be equally satisfactory in the case of all possible combinations of these substances. Best results will probably be achieved in such waters by adjusting the algorithms to suit local conditions. Many of these multispectral algorithms are not suitable for CZCS, since they make use of different or additional wavelengths from those available on this sensor. Sathyendranth et al. (1982, 1983), for example, point out that the use of 400 nm in addition to the CZCS channels considerably enhances the possibility of separating out chlorophyll signal from that of yellow substances.

ADDITIONAL INFORMATION ON PHYTOPLANKTON FROM OCEAN COLOUR

Since we now have a working hypothesis on the causes of variation in phytoplankton absorption efficiency with respect to chlorophyll-a, and its effect on ocean colour, we can examine the inverse problem of using this variability to extract additional information on phytoplankton.

An important, if not dominant, fraction of picoplankton is cyanobacteria or the blue-green algae (Johnson and Sieburth 1979; Waterbury et al. 1979; Li et al. 1983; Platt et al. 1983). In laboratory measurements of the absorption spectra of blue-green algae, the additional absorption bands due to the biliproteins show up clearly (Yentsch and Yentsch 1982; Lazzara 1983; Jeffrey 1980; examples of blue-green algal absorption spectra from Yentsch and Yentsch (1982) are shown in Fig. 5). We may surmise from this, that it should be easy to identify the blue-greens from other phytoplankton through these distinctive absorption bands, if complete spectral information on R

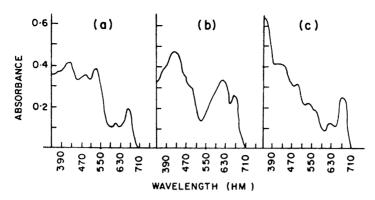


FIG. 5. The absorbance spectra of some blue-green algae, from Yentsch and Yentsch (1982). (a) Phycoerythrin containing picoplankton *Synechococcus* sp. "DC-2". (b) Phycocyanin containing picoplankton *Synechococcus* sp. "Syn". (c) Large filamentous algae *Oscillatoria erythraea*. Spectra (a) and (b) are based on laboratory cultures, while (c) is from a natural seawater sample.

is available. But there are certain problems that need to be solved before we can ascertain whether this is possible or not:

- (i) The absorption spectra of blue-greens show great diversity, depending on the type of biliproteins present, and their relative importance. This variability may be attributed to some genetic differences, as well as to chromatic adaptation of cyanobacteria to the light and nutrient environment (Lazzara 1983; Prezelin and Boczar 1986). Spectral signatures for remote sensing purposes will therefore have to be carefully selected, based on the forms these spectra are likely to take *in situ*.
- (ii) The *in situ* absorption spectra from surface waters of various marine regions studied by Prieur and Sathyendranath (1981) did not show clear traces of biliprotein absorption. Considering the ubiquitous nature of cyanobacteria, this can probably be explained by the fact that, in mixed populations, the differences in spectral signatures would tend to get smoothed out. Also, as noted by Prezelin and Boczar (1986), the biliproteins in surface waters may be 5 to 6 times less than in subsurface chlorophyll maxima.
- (iii) Blooms of non-picoplanktonic blue-green algae are known to occur in certain areas of the world oceans (see Carpenter 1983; Devassy et al. 1978; Ulbricht 1981). Distinguishing the picoplanktonic blue-greens from their larger counterparts or the cryptophytes and rhodophytes may require some prior knowledge on the type of phytoplankton commonly occurring in the study area during different seasons.

In fact, a systematic study needs to be undertaken, to evaluate the possibilities of extracting pigment composition from ocean colour, if complete spectral information is available. Some possibilities for doing this should exist, at least for case 1 waters. A difficulty in undertaking such a study has been the lack of a data bank of spectral reflectance, together with complementary data on concentrations of all pigments, necessary for testing various retrieval techniques. Even a theoretical approach would require reliable values of the coefficient a^*_{soli} in Eq. 13. Very little information is available on this parameter, beyond the preliminary results presented by Sathyendranath et al. (1987). Certain difficulties in such a study could arise because the mixing of different classes of phytoplankton in the natural environment would tend to smooth out the differences in spectral form, necessitating working with minor changes around a mean value. This problem would be less acute in single-species bloom conditions. Furthermore, the nonlinearity of the system, coupled with the fact that the spectral signatures of the intervening variables often show similar characteristics, would make

resolution of the signal into each of their components difficult. In case 2 waters, the problem is further complicated by noise from suspended sediments and dissolved organic matter, and at a first glance, the problem appears to be intractable for such waters.

Some recent results indicate the possibility of estimating primary productivity, through remote sensing. Smith (1981) and Platt and Herman (1983) showed that satellite-derived chlorophyll concentration is correlated with the total column chlorophyll concentration and the total column productivity. However, the constant of proportionality is site-specific, and for some ecosystems (eg. Peruvian shelf waters), the proportionality may not even be a reasonable assumption (Platt and Herman 1983). Platt (1986) has shown analytically that the column production, normalized by the column pigment concentration, should be a linear function of the surface irradiance E(0). i.e.:

(18)
$$\int P dz / \int C dz = \psi E(0)$$

where P is the primary production. E(0) is the total photosynthetically available radiation (integral over 400 to 700 nm). He has also shown that, the slope ψ can be proportional to α , the initial slope of the photosynthesis-light curve for phytoplankton. Empirical data from various sources show ψ to be consistent over a factor of two $(0.31-0.66 \text{ g Carbon (g Chla})^{-1} \text{ m}^2/\text{Einstein})$. The quantity E(0) can be estimated from satellite data (see Gauthier et al. 1980; Gauthier 1982; Gauthier and Katsaros 1984). Initial evidence (Platt et al. 1983; Smith et al. 1985) indicates that the picoplankton α values are significantly different from those of larger phytoplankton. Therefore, the relative importance of picoplankton in a given area could have a definite role in determining the slope ψ in Eq. 18.

Passive Fluorescence Technique

Determination of chlorophyll-a via its in vivo fluorescence peak in the red (at around 685 nm) from passive, remotely sensed signals was initiated by Neville and Gower (1977) and Gower (1980). This may be considered an extension of the in vivo technique for in situ monitoring of chlorophyll-a introduced by Lorenzen (1966), with the following main differences:

- 1) Excitation for the *in situ* experiments is provided by a source emitting known flux at a given wavelength, while in passive remote sensing, sun light is the source.
- 2) In situ fluorescence is measured at a fixed wavelength, while in remote sensing, it is necessary to measure the radiation at 3 or 4 wavelengths at least, to provide correction for background noise.
- 3) In situ fluorescence is measured from a small, known volume of water, while in passive remote sensing, the total water-leaving fluorescence signal is the measured quantity.

Good correlation has been observed between the height of the fluorescence peak and chlorophyll concentration (Neville and Gower 1977; Gower 1980; Doerffer 1981; Gower and Borstad 1981). But, as in the *in situ* experiments, in remote sensing too, the fluorescence efficiency per unit chlorophyll-a, F_c , has been found to vary from region to region. Gower and Borstad (1981) report variations by a factor of 2 or 3 in remote sensing experiments from aircraft.

Various studies which have thrown light on the causes of variation of *in vivo* fluorescence efficiency of phytoplankton have been reviewed by Sathyendranath et al. (1982). The main factors which are relevant to passive remote sensing experiments may be summarized as follows:

1) In vivo fluorescence is a complementary function of photosynthesis, and so F_c will decrease as photosynthetic rate increases.

- 2) F_c can be subject to a circadian rhythm, reaching a maximum at night and minimum at around mid-day (which is in concordance with the theory of *in vivo* fluorescence as a complementary function of photosynthesis). Some results indicte that the circadian rhythm is controlled by a biological clock rather than by light availability.
 - 3) High light intensities may inhibit fluorescence efficiency.
 - 4) Nutrient stress can introduce changes in fluorescence efficiency.
- 5) F_c may also vary with phytoplankton species (the species effect may in turn be related to changes in absorption efficiency).
- 6) The wavelength of the peak value of fluorescence may shift a few nanometers around a mean value of 685 nm. This can result in an apparent change in F_c if it is measured at a fixed wavelength. Phycoerythrin fluorescence from cyanobacteria has a maximum at around 610 nm, and phycocyanin at about 660 nm (Yentsch and Yentsch 1984).
- 7) F_c varies with change in wavelength of excitation, and the excitation spectrum differs with different algal types.
- 8) Background fluorescence from other substances may be significant, and failure to apply suitable corrections can introduce apparent changes in F_c .
- 9) At high chlorophyll-a concentrations, re-absorption of fluoresced light by the other cells can introduce a quenching effect and nonlinearity in the fluorescence height and chlorophyll-a relationship.

This variability implies that, as in the case of *in situ* continuous monitoring of phytoplankton fluorescence, in remote sensing too, discrete calibration points would be necessary to convert the fluorescence signal into chlorophyll-a concentration. In the absence of these calibration points, passive fluorescence technique can still be used as a very useful search tool for locating phytoplankton fronts, gradients and patchiness.

A priori, it would appear difficult to see how the passive fluorescence technique can yield information on the phytoplankton type. However, laboratory results indicate that fluorescence from phycocyanin-containing cyanobacteria peaks at 660 nm (Yentsch and Yentsch 1984), while chlorophyll-a fluorescence peak is normally observed at 685 nm. Consequently, in natural populations with phycocyanin-containing cells, one can expect the red fluorescence peak to occur somewhere in between 660 and 685 nm. The position of the red fluorescence peak could therefore be an indicator of the presence of these blue-greens. But this has yet to be confirmed by observations.

Methods are now emerging for primary productivity estimates from these fluorescence signals. From the theory postulating fluorescence as a complementary function of photosynthesis, it follows that fluorescence efficiency would decrease with increasing photosynthetic rate (other factors being negligible). Topliss and Platt (1986) tested this hypothesis in 2 different types of marine environments and found it to hold true generally. To calculate fluorescence efficiency from fluorescence emission, we also have to know the light absorbed by phytoplankton. This can be obtained through surface irradiance, pigment concentration and attenuation coefficient derived from passive radiometric techniques. (Total attenuation coefficient at different wavelengths can be determined from changes in ocean colour. See Austin and Petzold, 1981. The algorithm has the same form as Eq. 17. In case 1 waters, the residual attenuation after substracting the contribution of pure sea water, may be attributed to phytoplankton, as a first approximation. In case 2 waters, the attenuation due to suspended sediments and dissolved organic matter would also have to be substracted from the total.) Topliss and Platt (1986) have shown the fluorescence efficiency to be inversely related to α , the initial slope of the photosynthesis-light curve. It may be noted that α derived in this manner may be used to fix the coefficient ψ in Eq. 18. This holds out the promises of a new, non-destructive technique for measuring primary production rates either in situ or by remote sensing.

So far we have only considered passive fluorescence from a low flying aircraft. In the case of a high flying aircraft or spacecraft, certain additional factors would have to be taken into account. Gower and Borstad (1981) have demonstrated that, with increasing altitude of aircraft, the fluorescence maximum shifts from 685 nm towards 675 nm, due to the effect of the oxygen absorption band at 688 nm. It therefore follows that from a high aircraft, chlorophyll-a fluorescence is best measured at 675 nm. They have also pointed out that the increase in reflectance at 685 nm is of the order of 0.02% with an increase of one mg/m³ in chlorophyll-a concentration. It would be still smaller at 675 nm. As this signal will be superimposed on a background noise of the order of 5% (Sathyendranath et al. 1982), atmospheric correction becomes a very critical factor. However, atmospheric correction is easier in the red than at shorter wavelengths. Still, this demands a highly sensitive detector which would probably limit applications of this technique in waters of low chlorophyll-a concentrations.

Laser Fluorometry

Airborne lasers for ocean remote sensing have been described by Hoge and Swift (1981), Yentsch (1983) and Yentsch and Yentsch (1984). In the version described by Yentsch and Yentsch (1984), excitation is provided by short pulses at 532 nm with an Nd: Yag (garnet crystal) laser. The return signals are measured by 40 photomultiplier tubes. In the LIDAR mode, the 40 channels are tuned to the same wavelength, but are time gated so that the signal at each channel represents a different depth. In the fluorosensor mode, the 40 channels are set to different wavelengths, to measure the upwelling spectrum. A variation of this instrument allows excitation at 427 nm also, alternating with the pulses at 532 nm. In between pulses, the 40 receivers can act as a passive spectral radiometer.

Exton et al. (1983a) describe the return signal in terms of three components: (1) The elastically backscattered component at the excitation wavelength, (2) the spectrally shifted Raman scatter signal due to non-elastic scattering by water molecules, and (3) the fluorescence signal. For excitation at 532 nm, the predominant return signals, in addition to the backscattered light, are at 580 nm (due to phycoerythrin fluorescence), at 645 nm (Raman scattering) and at 685 nm (chlorophyll-a fluorescence).

The differential power dP received by the receptor due to fluorescence from a small volume of water at depth z can be expressed as follows (expression modified from Exton et al. 1983a):

(19)
$$dP = \frac{ACF_c(L) \exp [-(K(L) + K(U))z]dz}{(z + mZ)^2}$$

where K(L) and K(U) are the effective attenuation coefficients at laser and upwelling wavelengths, respectively, z is the depth within the water column, Z is height of the sensor above the water column, M is the refractive index of water, C is the concentration of fluorescing pigment and $F_c(L)$ is the fluorescence efficiency at the laser excitation wavelength. The instrumental parameters and atmospheric transmission terms are contained in A.

In the case of Raman scattered light, the equation remains effectively the same, except that the CF_c term has to be replaced by the product of N_R and σ_R representing the number of water molecules accessed by the laser, and the Raman scattering cross sections, respectively. The elastically scattered light will consist of components from molecular scattering by pure seawater and the Mie scattering component from particles. For the polidisperse suspension common to seawater, the Mie scattering term will be an integral of the form $N_M \sigma_M dM$ where N_M is the number of particles with scattering cross section σ_M .

The water Raman signal is a measure of the loss of signal due to attenuation, and thus provides an internal calibration. The fluorescence and scattering signals are

usually normalized by the Raman signal to correct for changes in water transmissivity.

The backscattered signal at the excitation wavelength, similarly normalized by the Raman signal, can be a rough measure of the seston concentration.

Laser techniques provide certain advantages over the passive techniques: (1) They can pick up phycoerythrin fluorescence in addition to chlorophyll-a fluorescence. (2)

They can monitor depth-wise variations in concentrations (subject to limitations due to loss of energy while penetrating and escaping the water column. This aspect is

discussd further in the next section).

Laboratory results indicate possibilities of further improvements in detection capabilities. Brown et al. (1977) studied variation in fluorescence intensity at 685 nm with variation in excitation wavelength, and found that the excitation spectra were significantly different for the four main phytoplankton taxonomic groups. They used excitation at 4 wavelengths (454, 539, 598 and 617 nm) using a tuned dye laser, and the fluorescence response at 685 nm in each case. In the case of a phytoplankton population comprising a mixture of all four groups, the term $CF_c(L)$ in Eq. 19 has to be replaced by a sum $C_1F_{c1}(L_i) + \ldots + C_4F_{cd}(L_i)$ where C_j represents the concentration of chlorophyll-a belonging to phytoplankton of group j, and L_i is the excitation wavelength. By solving the four simultaneous equations resulting from excitation at four wavelengths, they found that they could isolate the concentration of each group of phytoplankton in a mixture. Obviously, this method ignores all the causes of variation in fluorescence efficiency listed in the previous section, other than the species effect. Further studies in this direction are needed to determine the extent of the validity of these results for *in situ* conditions.

Active remote sensing offers the best possibility at present to monitor blue-green algae by remote sensing. Biliproteins of different types of phytoplankton have characteristic differences in their absorption and fluorescence signals (see Prezelin and Boczar 1986). For example, Exton et al. (1983b) report that cyanobacterial phycoerythrin fluorescence peaks at 576 nm, while that of cryptophytes peaks at 586 nm. A Lidar with high spectral resolution could use such differences to distinguish different types of phytoplankton. Though there are some problems in measuring the fluorescence height accurately due to overlap of neighbouring peaks in the return signal (Hoge and Swift 1981) and due to background noise from fluorescence by dissolved organic matter (Exton et al. 1983a), these problems are easily overcome. Once the fluorescence height is correctly determined, the algorithm for conversion to concentration would be a simple linear relationship. But the problem lies elsewhere. Lidar techniques have only been successfully carried out from rather large airplanes flying at very low altitudes. The limiting factors that preclude higher altitude flights and use of smaller aircraft, are the prohibitive power requirements for the laser and the bulky instrumentation (Hoge and Swift 1981 used laser with 3 MW peak power from an altitude of 150 m). From Eq. 19, it is evident that a 10 fold increase in aircraft altitude would call for a 100 fold increase in laser power (neglecting increased atmospheric attenuation), to obtain the same performance, if the instrumental parameters remain the same. So it appears that until some technological break-through lowers the operational costs, it may not be possible to use laser fluorescence remote sensing techniques extensively and routinely.

Limitations to the Depths Accessible by Remote Sensing

Gordon and McCluney (1975) have shown theoretically that approximately 90% of the upwelling light leaving the water surface emanates from a water column of depth z_{90} (called penetration depth) at which the incident light reduces to 1/e of its surface value. If we denote the diffuse attenuation coefficient for downwelling irradiance by K, then,

As this is about 1/4.6 of the euphotic depth, this implies that the top 22% of the total euphotic zone accounts for 90% of the signal for the remote sensor. As K is wavelength dependent, the depth of water column sampled will be different for different wavelengths. Also, due to attenuation of light during penetration and escaping, the "effective concentration" as seen by the remote sensor would be a weighted average over the water column of depth 1/K. Gordon and Clark (1980) defined the effective concentration X_i as:

$$X_i = \int_{0}^{1/K} X_i(z) f(z) dz / \int_{0}^{1/K} f(z) dz$$
$$f(z) = \exp - \int_{0}^{z} 2K(z') dz'$$

where

and $X_i(z)$ is the concentration of the substance at depth z.

Sathyendranath (1981) and Sathyendranath et al. (1983) studied theoretically the case of remote sensing in waters where the chlorophyll-a concentration is variable with depth. Four non-uniform depth distributions of chlorophyll, each with an average chlorophyll-a concentration of 1 mg/m³ were considered. The results indicated that the maximum z_{90} values were around 8 m in the 500 to 550 nm range, while in the red (560 to 700 nm range), the penetration depth was only around 2 m (see Fig. 6).

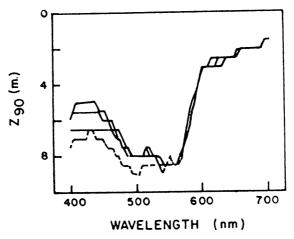


FIG. 6. Theoretically calculated wavelength dependence of penetration depth for 4 vertical distributions of chlorophyll-a (from Sathyendranath 1981). The curve in dashed line represents a uniform distribution of 1 mg/m³ of chlorophyll-a in the top 10 m. For the other 3 curves, mean chlorophyll concentration over the top 10 m remains the same, but vertical distributions are non-uniform.

The maximum observed efficiency factors for chlorophyll absorption were used in the study; using lower efficiency factors would have the effect of increasing z_{90} for the same chlorophyll-a concentrations. In this case too, the penetration depth is smaller for the red than the blue. Results of Smith (1981), based on similar calculations show that, when C varies from 0.01 to 10 mg \cdot m⁻³, z_{90} varies from about 58 to 2 m at 443 nm, and from about 15 to 4 m at 550 nm. At 670 nm, z_{90} is insensitive to changes in chlorophyll concentration (the dominant factor here is the absorption due to pure seawater itself).

Consequently, the fluorescence technique samples a much smaller volume of water than the ocean-colour based technique which uses the blue and green part of the spectrum. Comparison of the chlorophyll values yielded by the two methods could therefore give an indication of the vertical distribution of chlorophyll. Though laser techniques permit in principle the depth profiling of chlorophyll fluorescence, in practice, the maximum sampling depths have been limited to about 4 m (Yentsch and Yentsch 1984). Cyanobacteria are known to adapt well to very low light levels, and survive well in deep waters. At the present state of the art, these picoplanktonic forms will go undetected by remote sensing techniques.

In case 2 waters, the presence of suspended sediments and dissolved organic matter would tend to increase the attenuation coefficient of the water, thereby reducing the penetration depth still further.

However, statistical results of the sort derived by Lorenzen (1970), Smith (1981) and Platt and Herman (1983), which link surface chlorophyll and satellite-derived chlorophyll to total column chlorophyll and column primary production, can be used to map these additional variables using satellite data.

Summary and Conclusion

In this paper I have evaluated the implications of picoplankton in remote sensing as it stands today, with the hope that it will help us to be suitably cautious when interpreting remotely sensed data, as well as encourage further research in this area to improve existing techniques.

Where passive radiometric techniques based on changes in ocean colour are concerned, there seems to be no doubt that the picoplankton will leave their imprint on the water-leaving radiance, which serves as signal for remote sensing. Their small size favours higher specific absorption, and so their effect on the signal may be more important than warranted by considerations of the concentrations alone. The special pigment composition of the blue-green algae which makes their absorption spectra very distinct from the other types of phytoplankton is also an important factor to be considered while interpreting spectral radiometric data from waters rich in this type of picoplankton. Since the relative abundance of picoplankton appears to be higher in oligotrophic waters, a suitable method is needed that can monitor small changes in their concentration on a synoptic scale. Passive radiometric methods seem to be suitable for such applications. The possibility of employing variations in spectral signatures of different types of phytoplankton to separate the signals from various taxonomic groups of phytoplankton remains to be explored. This would require working with much higher spectral and radiometric resolution than is currently available.

Active fluorescence techniques have demonstrated the capability of picking up the phycoerythrin fluorescence signal, thereby making it possible to monitor a blue-green fraction of picoplankton at least, if not all the picoplankton. In this case, however, investigators will have reliance on alternate supporting data to ensure that the phycoerythrin being monitored is in fact contained in picoplankton, and not the larger blue-greens such as *Oscillatoria*, which appear in bloom conditions in the tropical areas, or even cryptomonads or rhodophytes.

It is clear that the ocean-colour technique, and the emerging active and passive fluorescence techniques do not bring redundant information. By combining the methods suitably, it is becoming possible to obtain more accurate estimates, particularly in the case of primary productivity. Fluorescence technique seems to be best suited for monitoring area of high phytoplankton concentration, while the ocean colour method is more sensitive at lower pigment concentrations. Lastly, the depth of the water column sampled by the two techniques differ significantly, and this fact could be used for deriving some information on the vertical distribution of pigments.

While it appears easier to understand the role of picoplankton in affecting the remote signal, the inverse problem of inferring direct and specific information on

picoplankton from the remote signal poses greater problems. There appears to be no optical method at present which would allow us to derive information on the size distribution of suspended material by remote sensing. So information pertaining to picoplankton has to be obtained indirectly, such as through the knowledge that a large fraction of picoplankton belongs to the group of cyanobacteria. As mentioned earlier, this leaves room for doubt, which can only be clarified by discrete in situ observations in addition to the remotely obtained data.

The power of remote sensing lies in its capability to obtain synoptic scale pictures of the ocean, and at time scales comparable to the rate of processes related to phytoplankton. The trade off is a decrease in the accuracy of estimates as compared to laboratory or *in situ* techniques. However, a point worth noting, which is often ignored, is that, when ship data are used for studying large areas, errors are introduced due to spatial variabilities in the fields, comparable to those inherent in satellite derived data (Platt and Herman 1983). At any rate, the accuracies can be increased considerably if *in situ* data points are used to validate and calibrate the output from remote sensing techniques.

Acknowledgements

The author wishes to thank Dr. H. N. Siddiquie, Director, National Institute of Oceanography, and Dr. J. S. Sastry, Head, Physical Oceanography Division, for making available the facilities, and Dr. André Morel and Dr. John T. O. Kirk for their comments on the manuscript.

Appendix 1. Radiometric Quantities.

Symbol	Quantity	Definition, Remarks	Unit
ф <i>I</i> Е	Radiant flux Radiant intensity Irradiance	Energy per unit time Flux per unit angle. $I = d\Phi/d\omega$. Flux per unit surface. $E = d\Phi/dA$. E_d and E_u are irradiances with	Watt. Watt/steradian. Watt/m².
L	Radiance	respect to a surface facing upward, or downward, respectively. Flux per unit angle per unit projected area of a surface. $L = d\Phi/dA \cos d\omega$.	Watt/m²/sr.
а	Absoprtion coefficient	$E_d = \int_0^{2\pi} a \int_0^{\pi} \frac{2}{a} L(\theta, \phi) \cos \theta \sin \theta d\theta d\phi$. $E_u = \int_0^{2\pi} a \int_0^{\pi} \frac{2}{a} L(\theta, \phi) \cos \theta \sin \theta d\theta d\phi$. The energy $d\Phi$ absorbed by a medium when a parallel, monochromatic flux Φ passes through distance dr in the medium, is given by $d\Phi = a\Phi dr$.	m ¹
β(θ)	Volume scattering function	Integration over distance r yields $\phi = \phi_n \exp(-ar)$, where ϕ_n is the incident flux. Radiant intensity scattered in the direction θ with respect to the incident direction, per unit volume and unit irradiance.	m [†]
b	Scattering coefficient	$\beta(\theta) = dI(\theta)/\text{Edv}$. Total scattered energy per unit volume and unit irradiance.	m ¹
b_b	Backscattering coefficient	b = $\int_0^{2\pi} \beta(\theta) d\omega = 2\pi \int_0^{\pi} \beta(\theta) \sin \theta d\theta$. Total scattered energy within the angles $\pi/2$ to π . $b_h = 2\pi \int_{-2}^{\pi} \beta(\theta) \sin \theta d\theta$.	m ¹
\tilde{b}_{b}	Backscattering ratio	$ \frac{\partial_h}{\partial b} = b_h/b. $	1
F "	Forward scattering ratio	$[2\pi]_0^{\pi/2}\beta(\theta)\sin\theta \ d\theta]/b.$	l 1
c	Attenuation coefficient	c = a + b	m ¹

m	Refractive index	Ratio of phase velocity of radiant energy in free space to that of the same energy in the given medium. If i is the angle of incidence, and j the angle of refraction, then $m = \sin i/\sin j$.	ı
K	Irradiance attenuation coefficient	Rate of decrease of irradiance, defined by: $K = -d \ln E/dz$. K_d and K_u define attenuation for downwelling and upwelling irradiances respectively.	m ¹
R	Reflectance	Ratio of upwelling to downwelling irradiance at a given depth. $R(z) = E_{\nu}(z)/E_{\nu}(z)$.	1
Q,,	Efficiency factor for absoprtion by a particle	Ratio of flux absorbed by a particle to flux incident on it.	1
T	Optical thickness	Product of attenuation coefficient and distance.	1
ω	Single scattering albedo	Ratio of scattering coefficient to attenuation coefficient.	$\omega = b/c$

Here, dr, dA, $d\omega$, and dv refer to infinitesimally small distance, area, solid angle, and volume, respectively.

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