Remote sensing of water-column primary production

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Satellite observations of ocean colour at selected wavelengths have made it possible to map near-surface distribution of phytoplankton pigments at the global scale. While the advantage of remote sensing in providing synoptic coverage of large-scale surface features is incontestable, the estimation of primary production from these data requires additional information inaccessible to present-day satellite remote sensing, such as the parameters for conversion of biomass to growth rates, and the parameters describing the vertical structure of biomass. The value of remote sensing would therefore be enhanced considerably if the satellite data could be combined with in situ data to provide the missing information. Since satellite and in situ data are collected at very different time and space scales, conceptual schemes are necessary to render the two data sets compatible. The idea of bio-geochemical provinces has proved to be very useful in this context. Both empirical and analytic approaches have been used to address the problem of estimating primary production from satellite-derived biomass estimates. The various analytic models that have been proposed can be classified according to their level of complexity. In any application, a suitable model has to be selected, based on: (1) validity of the model assumptions in the particular context, (2) computational requirements, (3) availability of auxiliary data, and (4) acceptable levels of error.

Introduction

Remote sensing of primary production is a science in its infancy: it has a very short history, and it is in a state of rapid growth. A review of the field today is likely to be soon outmoded. Nevertheless, a clear philosophy of approach has been emerging in this area, which will probably have a longer life span than many of the details regarding its implementation. In this paper, therefore, we will try to outline the philosophy, which will in turn suggest a basic methodology. We will then examine the progress to date on the implementation of various aspects of the methodology.

In the late 1960s and the 1970s, it was shown that changes in ocean colour, observed from aircraft or from ship, are related to variations in phytoplankton pigment concentrations (Morel and Prieur, 1977). The Coastal Zone Color Scanner (CZCS), the first satellite to be launched to monitor ocean colour from space, was operational from November 1978 to May 1986, and proved the feasibility of monitoring chlorophyll distributions from space (Gordon and Morel, 1983). Even as algorithms for chlorophyll retrieval from ocean colour were being developed in the early 1980s, biological oceanographers were quick to realize that empirical relationships which often exist between surface biomass and water-column primary production could be exploited to estimate oceanic production by remote sensing (Smith et al., 1982; Platt and Herman, 1983; Eppley et al., 1985). The latter half of the last decade saw further developments in this area, with a number of analytical or semi-analytical models being proposed. In any field that is in a state of rapid development, analytical models are to be preferred over purely empirical
ones, since the former give better insights into problems when models fail to perform well. Besides, with analytical models, it is easier to make intelligent extrapolations of results from one region to another. Analytical and semi-analytical models are therefore the focus of this paper.

Basic approach and methodology

The analytical models suggest that remote sensing of primary production can be posed as a problem in classical plant physiology: the study of the photosynthetic response of plants to available light. According to photosynthesis–light models, primary productivity can be expressed as a function of biomass (B) and available light (I). Of all the indices that may be chosen to indicate phytoplankton biomass, chlorophyll concentration has been a preferred one, because of the central role it plays in the photosynthetic processes, and because of the relative ease with which it can be measured. It also happens to be the biological variable that is most easily monitored from space. The light available at the sea surface can be computed from atmospheric transmission models, and satellite data have proved useful in this area as well. Models are also available now that compute light available at depth in the sea, given information on chlorophyll concentration. Thus, current satellite techniques and optical models can provide information on the two most important variables necessary for computation of primary production: biomass and light. However, no current remote-sensing technique provides information on the rate constants that are essential to fix the functional relationship between light and photosynthesis. Fortunately, in nature, these rate constants vary over a much smaller dynamic range than either chlorophyll or light, and so they may be treated as quasi-stable parameters. From these considerations emerges a protocol for the estimation of remote sensing from satellites: use satellite technology and optical models to provide information on the rapidly changing variables (biomass, light), and supplement them with information on the more stable parameters of the photosynthesis–light models from ship-borne observations.

Satellites provide information only on the near-surface layer of the water column. Typically, this layer is about one-fifth of the productive part of the water column. This introduces the additional requirement that the vertical structure of the productive zone (whether it be with regard to biomass distribution or with regard to change in the photosynthetic parameters with depth) be defined based on in situ observations as well. Note that this problem would not be significant in calculations of primary production for the mixed layer, but it cannot be ignored in calculations for the entire water column.

The principles as outlined above suggest a basic methodology that would consist of the following steps:

1. Compute the light available at the sea surface and account for losses at the air-sea interface.
2. Estimate biomass at the surface.
3. Define the biomass profile. This calls for a procedure for extrapolating from the surface to the base of the productive zone (say the photic zone, or the depth within which the light is reduced to 1% of its surface value).
5. Compute parameters of light transmission underwater. The most crucial parameter is K, the diffuse attenuation coefficient for downwelling light.
6. Compute primary production of the water column (or mixed layer) using photosynthesis–light models.

Of these six steps in calculation, remote sensing can provide useful information on steps 1 and 2, while steps 3 and 4 clearly have to come from in situ observations. The distribution of biomass, from steps 2 and 3, is a necessary input to step 5, the computation of underwater light transmission. Obviously, the accuracy of the computed primary production (step 6) would depend on the accuracy of the first five steps, in addition to the validity or suitability of the model itself that is selected for computing primary production. While recent years have seen considerable progress in all of the six steps outlined above, the quest for the best solution is by no means over. In the following sections, we examine the progress so far, point out the pitfalls, and explore possible avenues for further improvement. Since the inputs required from steps 1 to 5 would depend to some extent on the choice of model in step 6, we examine the photosynthesis–light models first.

Light dependence of photosynthesis

In the remote-sensing context, we recognize that the need is to arrive at estimates over large scales, in both space and time; and therefore the emphasis here is on arriving at estimates of daily primary production integrated over the water column (or the upper, dynamically mixed layer).

The production $P(z,t)$ at depth $z$ and time $t$ may be expressed as:

$$P(z,t) = P^B(z,t)B(z)$$

(1)

where $B(z)$ is the biomass and $P^B(z,t)$ is the rate of primary production per unit biomass. Light is the driving force for photosynthesis, and so specific productivity
PB(z, t) may be expressed as a function p of available light I(z, t):

\[ PB(z, t) = p(I(z, t)) \] (2)

To obtain daily, water-column primary production \( P_{Z,T} \), we have to integrate \( P(z, t) \) over all depths and over all daylight hours:

\[ P_{Z,T} = \int_{b(z,p(I(z,t))} dt. \] (3)

Note that we have assumed here that B is independent of time for the period of one day over which the computations are to be carried out – a constraint which can easily be relaxed if required.

Photosynthesis models take various forms depending on how the function p and the underwater light field \( I(z, t) \) are specified. The function \( p \), which describes the photosynthetic response of phytoplankton to light, is generally referred to as the photosynthesis–light curve, or the P–I curve.

It is well known that at low light levels, photosynthesis increases linearly with available light (linear response phase), while at high light levels, photosynthetic rate becomes independent of the light level (light saturation phase), such that there is no increase in production with increase in light. There may be yet a third phase at extremely high light levels, when photosynthesis begins to decrease with increase in light level (photo inhibition phase).

We recognize the need for at least one parameter to describe each one of these three phases. The following three are commonly used: the initial slope \( \alpha^B \) of the P–I curve at very low light levels, the asymptotic maximum \( P_m^B \), attained at high light levels, and \( \beta^B \), the negative slope of the P–I curve when photo inhibition occurs. While photo inhibition is known to occur sometimes near the surface, especially in tropical waters, it has not yet been shown that it influences significantly the computations of water-column production. On the other hand, there is some evidence that the opposite may be true (Platt et al., 1990). Therefore, the photo inhibition phase is not discussed further in this paper. But this again is a restriction that is easily removed if necessary (Platt et al., 1990). The requirement from step 4 would therefore be information on \( \alpha^B \) and \( P_m^B \).

The equation for the P–I curve (Equation (2)) may then be rewritten as:

\[ PB(z, t) = p(I(z, t); \alpha^B(z), P_m^B(z)) \] (4)

Many equations have been proposed to represent the function \( p \), with varying degrees of analytical explanations to support them. However, from a practical point of view, it has been shown by Platt et al. (1977) that most of these equations yield similar results for water-column integrals of primary production, which would suggest that the choice of equation for \( p(I) \) is not a crucial one: there are many good ones to choose from, and one may be guided here entirely by convenience.

Non-spectral, uniform-biomass models

All P–I equations have the common feature that I and \( \alpha^B \) always appear as products. The initial slope \( \alpha^B \) and the light transmission under water (and therefore I) are both wavelength selective. If such wavelength dependencies are ignored, we can define a new quantity \( \Pi(z, t) \), given by:

\[ \Pi(z, t) = I(z, t)\alpha^B. \] (5)

Note that \( \Pi \) has the same dimensions as \( PB \), and Equation (4) becomes:

\[ PB(z, t) = p(\Pi(z, t), P_m^B) \] (6)

For the non-spectral case, Platt et al. (1990) have shown that Equation (3) has an analytical solution, for a uniform water column (biomass is independent of depth; \( B(z) = \) constant), provided that the light at the sea surface varies as a sine function with time [(\( I(0, t) = I_m^\sin(\pi t/D) \), where \( I_m^\) is the maximum irradiance at local noon and D is the daylength). They further showed that the solution may be expressed using a simple polynomial approximation:

\[ P_{Z,T} = \Lambda \sum_{i=1}^{n} \Omega_i(I_m^\sin)^i \] (7)

where \( \Lambda = BP_m^B D/(\pi K) \), and \( I_m^\) = \( I_m^\sin/\)K, with \( I_k = P_m^B/\alpha^B \). Note that \( I_m^\) is dimensionless, and so all the dimensions of the result are carried by the scale factor \( \Lambda \). Platt et al. (1990) also showed that their analytical solution is very close to the semi-analytical solution proposed by Talling (1957), when \( I_m^\approx 4 \). Evans and Parslow (1985) have also given an analytical solution to daily water-column production, assuming a triangular function to describe the time dependence of light at the sea surface. We are not aware of any other solution to Equation (3) that does not require additional simplifying assumptions (e.g. that of Rodhe (1966), which is derived from Talling's solution, with the assumption that \( I_m^\) is a constant equal to 5; that of Ryther (1956), which assumes a constant value for \( I_k \); or that of Platt (1986), which is a linear approximation to the curvilinear function represented by Equation (7)).

Given the simplicity of Equation (7), it appears needless to impose additional approximations, unless it is due to insufficient knowledge of the parameters \( \alpha^B \) and \( P_m^B \).
Note that the equation of Rodhe (1966) can be implemented without knowledge of \( \alpha^b \), while the approach of Platt (1986) can be implemented without knowledge of either \( \alpha^b \) or \( P_m^b \), provided that the empirical linear relationship between \( P_{Z,T} \) and \( I(0) \) has been established for the region. Both, however, should be recognized for the approximations that they are, and the results interpreted accordingly.

### Spectral models

The models discussed so far are non-spectral; i.e. they ignore the spectral effects in light transmission, and the spectral dependence of \( \alpha^b \). However, such effects are a reality, and spectral models are to be preferred over non-spectral ones. The incorporation of spectral effects requires the function \( \Pi \) (Equation (5)) to be redefined as:

\[
\Pi(z,t) = \int I(\lambda,z,t) \alpha^b(\lambda) d\lambda
\]  

(8)

where \( \lambda \) is the wavelength, and the integration is carried out over the photosynthetically active region (about 400–700 nm). Equation (8) can also be modified to include effect of angular distribution of light under water (Sathyendranath and Platt, 1989a). Once \( \Pi \) has been redefined, then \( P_{Z,T} \) can be computed, for the spectral case, using the same formulation of the \( P-I \) curve as for the non-spectral case (Equation (6)). No analytical solutions are available for the spectral models of daily water-column primary production (Equation (3)), and so the solutions have to be obtained by numerical integration (Platt and Sathyendranath, 1988; Sathyendranath and Platt, 1989a; Platt et al., 1991). This can be time-consuming, even with modern computers, if the computations are to be repeated for every pixel in a satellite image. It is therefore worthwhile to examine means of achieving economy of computation. One approach, proposed by Platt and Sathyendranath (1991), is to apply a correction factor to results from the non-spectral model. The correction factors would be established based on a systematic comparison of results of the spectral and non-spectral models, for the range of parameters and variables of interest. Another possibility, suggested by Platt et al. (1991), is to adjust the value of \( K \) in the non-spectral model, such that the answers from spectral and non-spectral models give similar results (see also Kyewalyanga et al., 1992).

Note that implementation of the spectral model also requires additional information from step (4). It would no longer be sufficient to have an estimate of \( \alpha^b \) for white light as in the case of non-spectral models; we would now require the action spectrum (a description of \( \alpha^b \) as a function of wavelength). It is only since the last decade that it has become possible to measure the action spectrum routinely at sea (Lewis et al., 1985), and we probably have much to learn yet about its variability in the natural environment. Values of \( \alpha^b \) from white-light experiments can be used in spectral models if we assume that the variations in the shape of the action spectrum are unimportant, compared to the possible variations in the magnitude at each wavelength. We find this to be a useful approximation (Sathyendranath et al., 1989).

### Non-uniform biomass

Yet another problem, not accounted for in the models discussed above, is the effect of non-uniformity in the vertical structure of biomass. A first step in developing models that will account for the effect of this non-uniformity on daily, water-column primary production is to parameterize the vertical pigment profile (step 3). One would require a minimum of four parameters to define a chlorophyll profile characterized by a surface, or subsurface peak: one parameter to fix the depth of occurrence of chlorophyll maximum; one to define the width of the peak, one to define the relative importance of the peak with respect to the background, and yet another to fix the absolute magnitude. Platt et al. (1988) proposed a Gaussian curve, superimposed on a constant background, to parameterize \( B(z) \):

\[
B(z) = B_0 + \left( h/(\sigma \sqrt{2\pi}) \right) \exp \left[ -((z - z_m)^2)/2\sigma^2 \right]
\]  

(9)

where \( B_0 \) is the background biomass, \( z_m \) is the depth of the chlorophyll maximum, \( h/(\sigma \sqrt{1\pi}) \) is the height of the peak, and the width of the peak is determined by \( \sigma \). They showed that this parameterization is able to reproduce faithfully many types of observed profiles. This parameterization has also been adopted by Morel and Berthon (1989). Mueller and Lange (1989), on the other hand, have proposed a triangular parameterization of the subsurface peak, and shown it to be very successful in representing data from the Pacific. Neither the Gaussian nor the triangular parameterization allows for asymmetry in the vertical distribution. To describe such distributions, one would have to use functions with more parameters, like the five-parameter function used by Li and Wood (1988). No analytical solutions have yet been proposed for computing water-column primary production for cases of non-uniform biomass, either for the triangular or the Gaussian parameterization. Therefore, in the case of non-uniform profiles also the solution to Equation (3) has to be obtained by numerical integration, whether the model used is spectral or non-spectral. In a series of papers, we have shown (Platt et al., 1988; Sathyendranath et al., 1989; Platt et al., 1991) that ignoring the deep chlorophyll maximum in computations of primary production can often lead to significant errors. Non-uniformity in vertical structure is
therefore well worth accounting for, whenever the necessary information is available.

As noted earlier, the satellite signal does not penetrate very deep (the depth of penetration of the satellite signal is estimated to be about 20% of the photic zone, according to Gordon and McCluney, 1975). The satellite data will therefore have to be combined with in situ information on vertical structure. Morel and Berthon (1989) have suggested that the shape of the pigment profile is related to the surface biomass, and so the complete vertical profile can be recovered from the satellite-derived biomass. Sathyendranath and Platt (1989b) have suggested that, since vertical structure in biomass is a slowly varying property, both in space and time, information on the shape of the biomass can be built into regional biomass algorithms. They use a semi-analytical biomass algorithm to demonstrate the approach. They have also pointed out some of the problems that exist with such approaches, which arise from mismatch between theoretical predictions of ocean colour and the empirical algorithms currently in use. We hope that the planned launch of the next satellite for ocean colour measurements (the SeaWiFS, scheduled to be launched in August 1993) will give a new impetus to research on ocean colour, and that we will soon see improvements in our understanding of factors that influence ocean colour, and consequently, in biomass algorithms.

Underwater light field

In the remote-sensing context, primary production models cannot rely on in situ measurements of the light field; so one has to rely on models to estimate the light available at the sea surface (step 1). The light reaching the surface can be computed, for clear-sky conditions, given latitude, day number, and local time. Information on aerosol optical thickness and ozone concentration, required in these calculations, could come from satellite data. A choice of spectral, clear-sky models has appeared in the last decade (Bird, 1984; Bird and Roridan, 1986; Tanré et al., 1979), and Gregg and Carder (1990) have adapted the model of Bird (1984) for application in oceanography. Correction for clouds is considerably more difficult, not just from the increased computational load, but also because of the difficulty of meeting the additional data requirements. Remote-sensing techniques, which use cloud information from geostationary satellites (Gautier et al., 1980; Bishop and Rossow, 1991), hold the best potential for obtaining operational estimates of surface short-wave radiation in the presence of clouds. Most of the efforts to date in estimating surface radiation from satellite data have focused on total short-wave radiation, while, from the point of view of primary production studies, it is the photosynthetically active radiation (PAR, from about 400 to 700 nm) that is of interest. For application of spectral models, one would require spectral decomposition within that range as well. Some recent papers have begun to address this problem (Pinker and Laszlo, 1990). Once we have information on the light reaching the sea surface, it is a relatively easy matter to correct for losses due to reflection at the air–sea interface using Fresnel’s Law. For low solar elevations, this correction should include wind effect on sea-surface roughness (Gregg and Carder, 1990).

Given the surface light field, the flux at any depth z in the ocean can be computed, given the attenuation coefficient for downwelling light, K (step 5). Phytoplankton biomass is considered the most important factor responsible for changes in the optical properties of sea water, at least in the open ocean, and, therefore, satellite data contain information on the parameters of light transmission also. The parameter K can be computed either directly from satellite data (Austin and Petzold, 1981) or indirectly, using the biomass data (Smith and Baker, 1978a, b; Sathyendranath and Platt, 1988; Morel, 1988). Note that, when using spectral models of primary production, K also has to be established as a function of wavelength; and when using non-uniform biomass profiles, the K values will vary with depth as well. It must be pointed out that, for computation of light transmission, knowledge of the vertical distribution of biomass (from steps 2 and 3) is a minimum requirement. To account for what might be considered second-order effects, any additional information on the optical properties of substances present in the water column would be useful. Such information would include the pigment composition and concentrations of yellow substances and particulate material other than phytoplankton. The CZCS does not provide such information, but this situation should improve with the next generation of ocean-colour satellites, like the SeaWiFS.

Bio-geochemical provinces

A given model of primary production, and its applicability in a given situation, can (and should) be tested using local measurements of the P–I parameters and pigment-profile parameters. But, application of the model to large scales, using remotely-sensed data, imposes an additional requirement: a method has to be devised for extrapolating these parameters to those pixels where no direct measurements exist. This is a very important aspect of the problem of remote sensing of primary production. The in situ and satellite data are acquired at very different spatial and temporal scales, and all available oceanographic knowledge and intuition
have to be used to make the match between these different data sets. The methods proposed so far to achieve this goal are very simple; to some extent, this is imposed by our limited knowledge on the global distribution of the parameters.

The method proposed by Platt and Sathyendranath (1988) consists of partitioning the ocean into a number of bio-geochemical provinces and of classifying these provinces according to their P-I properties and vertical biomass structure (very much like the use of temperature and salinity to classify water masses in classical physical oceanography). The rationale for this approach is that the distribution of P-I parameters shows some distinct regional trends. For estimating the average production within that region (or province) using satellite data, it would be safe to use the average parameters for that region rather than, say, a global average. Admittedly, such a classification would have to allow for seasonal variations in the parameters and in their vertical structure (Platt et al., 1992), and for possible seasonal variations in the boundaries of the province. Platt et al. (1992) have shown that the P-I parameters for the Sargasso Sea during spring bloom are significantly higher than those typical of other seasons. Since spring blooms are associated with high biomass, there is a covariance between biomass and P-I parameters; therefore, if primary production is computed from satellite data at the annual scale without accounting for seasonal trends in the parameters, the results would be biased. If the boundaries between provinces are demarcated by fronts, then satellite data could prove useful for identifying these boundaries.

The large-scale estimates of primary production from remotely-sensed data would obviously be sensitive to the parameter values assigned to provinces. The limited information currently available on these parameters is inadequate for arriving at a global classification of bio-geochemical provinces. This is one area where much in situ work is still required to complement satellite data. The advent of new methods such as the active laser technique (Falkowski and Kolber, this volume), which provide quick estimates of P-I parameters, should go a long way towards addressing the problem of undersampling in these parameters.

Concluding remarks

The biggest source of error in remote sensing of primary production is the error associated with biomass retrieval from satellite. With the CZCS data, the accuracy in biomass retrieval is estimated to be about ±35% at best. This may appear to be disappointingly poor at a first glance, but when one considers that pigment concentrations in the oceans vary over four orders of magnitude, then it is easy to appreciate that, at large scales, such information is indeed valuable. The performance of the CZCS admittedly deteriorates in coastal waters. However, one should not forget that the CZCS represents our first foray into remote sensing of phytoplankton biomass from satellites. The next generations of ocean colour sensors will have higher spectral and radiometric resolution, and we believe that we can look forward to better performances from these satellites.

Remote sensing has neither generated nor requires new models of photosynthesis. What is required of such models is the same, whatever the application: we look for models capable of describing the photosynthetic response of phytoplankton to changes in the quality and quantity of light available. Therefore, the discussion of the models undertaken in this paper is by no means limited to remote-sensing applications. However, in the remote-sensing field, the picture has been clouded by the fact that models are sometimes tested with parameters that are guessed rather than directly measured (Balch et al., 1992), and poor results due to bad parameter estimates might then be interpreted as poor performance of the model itself. This is a dangerous tendency, and problems with estimating parameters have to be clearly separated from problems with the model itself if we are not to reject useful models for the wrong reasons. The right way to test a model against observations is with the best parameters available, and any uncertainties in the parameter estimates have to be borne in mind when interpreting the model results.

It is also important, in the remote-sensing context, to avoid comparing results at scales that are mismatched. For example, consider the case where average parameters have been proposed for a biogeochemical province. The only use of those parameters should be for estimating the average productivity of that province. The use of average parameters can lead to significant errors at the pixel level (for example, see Babin et al., 1993); but that would not automatically invalidate the usefulness of the average parameter at large scale. At this scale, the average parameters would yield wrong results only if (i) the estimated average for the province is not the true average, or (ii) the non-linear effects (which are ignored when averaging the parameters) introduce a bias in the computed primary production. Such a bias can, in principle, be estimated and corrected for.

The accuracy of satellite-based estimates of chlorophyll concentration does not approach that attainable from in situ observations. Clearly, therefore, satellite data are no substitute for in situ measurements. Their usefulness is in providing synoptic information on variability in surface biomass that is impossible to come by from in situ measurements. In other words, in situ and satellite observations are complementary and, together,
they provide a more complete picture of the distribution of biomass and primary production in the ocean than would otherwise be possible.

The approach as outlined here has some obvious advantages: the remote-sensing methodology for primary production can be built soundly on the existing edifice of plant physiology; no information acquired by methods other than remote sensing is thrown away; instead, remote sensing provides additional information on large-scale variability in space and time. When posed with the problem of estimating oceanic primary productivity at the basin or the global scale, this would clearly be the preferred method over any method that chooses to ignore the wealth of information in the satellite data.

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