Invited paper

Spectral effects in bio-optical control on the ocean system

OCEANOLOGIA, 49 (1), 2007.
pp. 5–39.

KEYWORDS
Bio-optical properties of phytoplankton
Remote sensing of ocean colour
Species succession
Primary production
Phytoplankton functional types
Mixed-layer physics

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Received 18 January 2007, revised 26 February 2007, accepted 27 February 2007.

Abstract

The influence of phytoplankton on the spectral structure of the submarine irradiance field is reviewed. The implications for the ocean system of the spectral response by phytoplankton to the ambient light field are discussed. For example, it provides the basis for retrieval of phytoplankton biomass by visible spectral radiometry (ocean-colour remote sensing). In the computation of primary production, the results of spectral models differ in a known and systematic manner from those of non-spectral ones. The bias can be corrected without risk of incurring additional random errors. The models in use for phytoplankton growth, whether based on available light or absorbed light, whether expressed in terms of chlorophyll or carbon, are shown all to conform to the same basic formalism with the same parameters. Residual uncertainty lies less with the models than with the parameters required for their implementation. The submarine light

field and the spectral characteristics of phytoplankton carry latent information on phytoplankton community structure. Differences in spectral response by different functional types of phytoplankton are small but significant. Optical considerations limit the maximum phytoplankton biomass that can be sustained in a given surface mixed layer. Moreover, the upper bound on the biomass depends on the spectral response of the dominant phytoplankton taxa. As a result, an optical control exists in the mixed layer that tends to resist extreme excursions of the biomass and also to maintain biodiversity in the phytoplankton.

1. Introduction

The spectral structure of the submarine irradiance field varies with position, depth, season and time of day. Over all the water column, except for a very shallow layer at the surface, it is confined to the visible range. But within that narrow range, the spectral structure is rich and carries considerable latent information. Variability in the spectral field according to geographical position depends on the abundance, kinds and size of the phytoplankton present as well as on the non-living material suspended or dissolved in the water. This observation underlies the entire methodology of visible spectral radiometry (ocean colour) for retrieval of chlorophyll concentration in the ocean on synoptic scales. Far away from land, the non-living components (solutes and suspensoids) may be taken to covary with phytoplankton as a simplifying assumption, although this is not an essential step. The absorption spectrum of phytoplankton is highly structured. Recognition of this spectral structure, of its rather conservative form, and of its important effect on the submarine light field, are implicit in, and fundamental to, remote sensing of ocean colour, which proceeds through the calculation of spectral reflectance ratios (Gordon & Morel 1983, Sathyendranath (ed.) 2000). It is so well-established as to be beyond all contention.

In such a context, it is curious that oceanographers have been much more reluctant to accept the importance of spectral effects on phytoplankton growth. In plant physiology, the spectral response of algal photosynthesis (the action spectrum) has been established for a century or more (Hall & Rao 1994). Its spectral shape is similar to that of the absorption spectrum, and for the same reasons. Absorption of photons, the essential first step in the photosynthetic chain, must necessarily follow the spectral dependence of the absorption spectrum of phytoplankton. Here is a universal phenomenon, based in the first principles of plant physiology, that if neglected leads to systematic (non-random) error in the estimation of phytoplankton production. It is a known systematic error whose correction is relatively simple and direct. Yet many marine scientists have preferred

to ignore it, to deny its importance or even to claim that, by allowing for it in models of phytoplankton production, the models might be degraded.

In fact, the implications of the phytoplankton response to the enormous spectral richness of the submarine light field, temporally and in three spatial dimensions, and the latent information contained therein, are far reaching. Here, we illustrate this contention with oceanographic examples, including phytoplankton production, biodiversity, species succession and mixed-layer stability. In the course of making these illustrations, we seek to clarify various related issues.

2. Status of models for the ocean ecosystem

For understanding and prediction of climate change, there is an imperative to improve existing models of the ocean carbon cycle. Typically, these coupled circulation-ecosystem models treat the biological components of the problem in very simple terms, usually with a single compartment for plants in the surface ocean. Such an approach can give only a very broad impression of the pelagic ecosystem.

A movement has therefore developed to refine pelagic ecosystem models by partitioning the autotrophic pool into functional types; in this way, particular biogeochemical functions and characteristics of a phytoplankton type can be modelled with more accuracy. An example of a functional type would be the coccolithophorid group, distinguished by a requirement to construct calcite plates, and therefore having a requirement for inorganic carbon beyond that needed for photosynthesis. In the context of climate change, it is important to model the response of coccolithophores to the more acidic conditions that will be present in a high-CO_2 world (Raven et al. 2005). Another important category are the diatoms, characterised by their requirement for silicon, which dominate the spring bloom in temperate waters and which provide an important resource for zooplankton and ultimately for fisheries sustainability. A third important group are the cyanobacteria which dominate in the oligotrophic conditions that apply to much of the tropical oceans: some of them, for example *Trichodesmium*, are able to fix nitrogen.

The recognition of functional diversity has led to the development of a suite of so-called Dynamic Green-Ocean Models, where the qualifier green signifies an improved representation of the photosynthetic components in the models (Anderson 2005, Flynn 2005, Le Quéré et al. 2005). The new generation of models has created demands for information on the eco-physiological characteristics of each group. To make progress in the application of the concept of functional groups requires that we model their growth on a group-by-group basis. Given a photosynthesis response we

need to compile parameter sets appropriate to each group. The differences between the parameter sets for the various groups may lie in the spectral details. We begin by reviewing some relevant aspects of the spectral structure of the submarine light field.

3. Spectral structure of the underwater light field

Given an incident light field at the sea surface, the spectral quality and amplitude of the light flux at any given depth in the ocean are determined by the diffuse attenuation coefficient $K(\lambda)$ for downwelling irradiance (flux per unit area and per unit wavelength λ), which is defined as the rate of decrease of downwelling irradiance at λ, per unit vertical distance, and per unit incident flux:

$$K(\lambda, z) = \frac{1}{E(\lambda, z)} \frac{\mathrm{d}E(\lambda, z)}{\mathrm{d}z}, \tag{1}$$

where $E(\lambda)$ is the downwelling irradiance and z the depth. Since phytoplankton absorption is largely confined to the visible part of the spectrum, the wavelength range of interest in this work is the photosynthetically-active domain, roughly from 400 to 700 nm.

The attenuation coefficient $K(\lambda)$ is influenced by the absorption and scattering properties of seawater and its constituents. One of the simplest representations of the attenuation coefficient is the quasi-single-scattering approximation (Gordon et al. 1975, Sathyendranath & Platt 1988), in which $K(\lambda)$ is expressed as a function of absorption and back-scattering coefficients:

$$K(\lambda) = \frac{a(\lambda) + b_b(\lambda)}{\mu_d(\lambda)}, \tag{2}$$

where a is the absorption coefficient, b_b is the back-scattering coefficient and μ_d is the mean cosine for downwelling light, defined as:

$$\mu_d(\lambda) = \frac{\int_{\phi=0}^{2\pi} \int_{\theta=0}^{\pi/2} L(\theta, \phi, \lambda) \cos\theta \sin\theta \, \mathrm{d}\theta \, \mathrm{d}\phi}{\int_{\phi=0}^{2\pi} \int_{\theta=0}^{\pi/2} L(\theta, \phi, \lambda) \sin\theta \, \mathrm{d}\theta \, \mathrm{d}\phi}. \tag{3}$$

Here $L(\theta, \phi, \lambda)$ is the radiance (flux per unit surface area and per unit solid angle) at wavelength λ from zenith angle θ and azimuth angle ϕ. Note that $\mu_d(\lambda)$ is a weighted mean of the cosine of the zenith angle of the underwater light field, the weighting function being the radiance L.

Eq. (2) illustrates well the roles that the inherent optical properties (absorption coefficient and back-scattering coefficient) and the apparent

optical property (mean cosine) have on the value of K. As defined by Preisendorfer (1976), the inherent optical properties are strictly properties of the medium, unaffected by the ambient light conditions, whereas apparent optical properties are affected by changes in the incident light field. The diffuse attenuation coefficient, since it is influenced by the mean cosine, which in turn is determined by the angular structure of the light field, is an apparent property.

The mean cosine is readily computed if we know the sun zenith angle in water, and the partition of the total light field into direct sun light and diffuse sky light (Sathyendranath & Platt 1988, Sathyendranath & Platt 1989). In this paper, we focus on the impact of the inherent optical properties on the apparent properties, such as $K(\lambda)$. To this end, we first express the inherent optical properties $a(\lambda)$ and $b_b(\lambda)$ as sums of the contributions of the various components of the medium:

$$a(\lambda) = a_W(\lambda) + a_B(\lambda) + a_Y(\lambda) + a_S(\lambda), \tag{4}$$

where the total absorption coefficient is split into its separate components, and the subscripts W, B, Y and S stand for water, phytoplankton, yellow substances (also referred to as chromophoric dissolved organic matter or gelbstoff) and suspended material other than phytoplankton (such as suspended sediments or detritus) respectively. Similarly, we can split the back-scattering coefficient into its components:

$$b_b(\lambda) = b_{bW}(\lambda) + b_{bB}(\lambda) + b_{bS}(\lambda), \tag{5}$$

where the subscripts are as before. For open-ocean waters (commonly called Case 1 waters, following Morel & Prieur 1977), it is generally assumed that phytoplankton absorption is the single independent variable responsible for changes in the total absorption coefficient. Chlorophyll a, the major phytoplankton pigment, is the conventional measure of phytoplankton biomass in the optical oceanographic literature. The contribution from water is a constant background absorption, and the other substances, when present, are assumed to covary with phytoplankton, and hence, with chlorophyll a. Similarly, it is common practice to model back-scattering in open-ocean waters as a function of chlorophyll a.

Because the components of absorption and back-scattering due to phytoplankton vary as their biomass in the water varies, it is convenient to express these components as a product of biomass-specific coefficients, multiplied by the biomass B of phytoplankton, measured in chlorophyll units. This leads to:

$$a_B(\lambda) = a_B^*(\lambda)B, \tag{6}$$

and

$$b_{bB}(\lambda) = b_{bB}^*(\lambda)B. \tag{7}$$

In a_B^* and b_{bB}^*, the asterisks indicate normalisation to chlorophyll concentration. Eqs. (6) and (7) allow us to evaluate the influence of the phytoplankton species composition on the optical properties (which, potentially, may modify the chlorophyll-specific coefficients) as well as the effect of its changing biomass B.

Some authors have preferred to use an empirical approach to partition the diffuse attenuation coefficient into two components: a fixed background contribution attributed to water, and a variable component associated with changing concentrations of phytoplankton. In this case, we have:

$$K(\lambda) = K_W(\lambda) + k_B(\lambda)B, \tag{8}$$

where $k_B(\lambda)$ is the biomass-specific diffuse attenuation coefficient, and $K_W(\lambda)$ is the attenuation attributed to water. Note that, in such models, $k_B(\lambda)$ does not represent a true phytoplankton-specific attenuation, since it includes also the influence of other material present in the water and covarying with the phytoplankton biomass.

Along a gradient from oligotrophic to eutrophic waters, the phytoplankton community is known to change from small-celled pico-phytoplankton (dominated by *Prochlorococcus* and *Synechococcus*) to micro-phytoplankton (typically dominated by diatoms). The changes in population are also accompanied by modifications in the composition and concentrations of auxiliary pigments that, together with chlorophyll *a*, are always present in phytoplankton (Jeffrey et al. 1997). Such changes in cell-size and species composition may lead to non-linear relationships when absorption and backscattering coefficients (or the diffuse attenuation coefficient) measured in the field are plotted against chlorophyll *a* concentration. Therefore, non-linear forms of eqs. (6), (7) and (8) have also been proposed (e.g., Prieur & Sathyendranath 1981, Morel 1988, Bricaud et al. 1995, Cleveland 1995, Lutz et al. 1996, Loisel & Morel 1998, Ciotti et al. 1999, Sathyendranath et al. 2005, Devred et al. 2006) for estimating the optical properties, given phytoplankton biomass B in the field. Regardless of the formalism used, it is admitted that K is a strong function of phytoplankton biomass B, especially in open-ocean waters.

Empirical models of the diffuse attenuation coefficient for downwelling light, such as represented by eq. (8), have the advantage of simplicity

(only one equation and two parameters per wavelength), compared with the theoretical approach (in which one has to specify the contributions of each of the components). Such empirical models find immediate application in models of light penetration in the ocean. But the theoretical approach is to be preferred in cases where insight is sought into the causes of variability in $K(\lambda)$. The increased understanding would help us to make intelligent assumptions about how $K(\lambda)$ would behave under conditions for which measurements of $K(\lambda)$ are sparse, or lacking. For example, $K(\lambda)$ measurements are usually made close to local noon. Thus, empirical models would be biased towards high sun-zenith angles, relatively high values of $\mu_d(\lambda)$, and hence minimal values of $K(\lambda)$. An analytical model would be able to allow $\mu_d(\lambda)$, and hence the computed $K(\lambda)$ values, to vary according to incident light conditions.

Referring back to eqs. (2), (4) and (5), we see that the total absorption and back-scattering coefficients, and hence K, will vary with wavelength to the extent that the optical properties of the components are wavelength-dependent. In fact, water has a very strong absorption coefficient in the red, accompanied by a very weak absorption in the blue (Pope & Fry 1997). Phytoplankton typically have a primary absorption maximum in the blue and a secondary absorption maximum in the red. A consequence of these spectral characteristics is that clear water is much more transparent to blue light than red, such that the light field in the ocean becomes increasingly blue with increasing depth. As the waters become more eutrophic, the increased absorption by phytoplankton in the blue shifts the wavelength of maximum penetration from blue to green, and the water at depth becomes more green as a consequence.

This strong dependence of $K(\lambda)$ on phytoplankton biomass allows us to model light penetration in the water as a function of phytoplankton biomass B (Morel 1988, Sathyendranath & Platt 1988). Non-spectral models of light penetration are also available (Kyewalyanga et al. 1992) that compute K for the entire photosynthetically-active radiation. For such non-spectral models, we have:

$$K(z) = \frac{1}{E}\,\frac{\mathrm{d}E(z)}{\mathrm{d}z}, \tag{9}$$

where E without the argument λ represents total downwelling irradiance integrated over the photosynthetically active range. With such models it is not easy to account for depth-dependent variations in K that might arise, for example, from the rapid attenuation of red light in the surface waters by pure water. Such problems may be overcome by splitting photosynthetically-active radiation into at least two components (Woods

et al. 1984), or by defining K for very small depth intervals, especially close to the surface (Platt & Satheyendranath 1991). Even if one has a non-spectral model of light that faithfully represents E at every depth in the ocean, such a model would, by its very nature, be incapable of describing changes in the spectral quality of light underwater. This could have important implications for primary production models, as we shall see in detail in the next section.

The strong dependence of optical properties of water on phytoplankton concentration forms the basis of remote sensing of ocean colour. Algorithms for retrieval of phytoplankton biomass from satellite-derived data on ocean colour rely on changes in reflectance R at the sea surface, with changes in phytoplankton biomass. Reflectance at the sea surface $R(\lambda)$ is defined as:

$$R(\lambda) = \frac{E_u(\lambda, 0)}{E(\lambda, 0)}, \tag{10}$$

where $E_u(\lambda)$ is the upwelling irradiance at the sea surface (depth = 0). Empirical algorithms relate changes in spectral values of R directly to biomass B (Gordon & Morel 1983), but analytic or semi-analytic algorithms are also available that make use of models relating R to the inherent optical properties (Gordon et al. 1975, Sathyendranath & Platt 1997):

$$R(\lambda) = r\ \frac{b_b(\lambda)}{a(\lambda) + b_b(\lambda)}, \tag{11}$$

where r is a proportionality factor. A similar expression is given by Prieur (1976) and Morel & Prieur (1977):

$$R(\lambda) = r\ \frac{b_b(\lambda)}{a(\lambda)}. \tag{12}$$

Since b_b is often small compared with a, eqs. (11) and (12) often give comparable results.

Analytic algorithms rely on mathematical or statistical tools to extract $a(\lambda)$ from remotely-sensed values of $R(\lambda)$, which is then decomposed into its basic components (Lee (ed.) 2006). From $a_B(\lambda)$ so-derived, the phytoplankton biomass B can be retrieved if we know $a^*_B(\lambda)$. However, as we noted earlier, the specific absorption spectrum of phytoplankton changes when there is a change in the community structure. Small celled-phytoplankton usually have a higher specific absorption, since their small size diminishes the flattening effect. This effect is observed on absorption spectra of material packaged into discrete particles, when compared with

the absorption by the same material in solution (Duysens 1956, Kirk 1975a,b, Morel & Bricaud 1981, Sathyendranath et al. 1987). Large-celled phytoplankton, such as diatoms, on the other hand, have a flatter spectrum with a lower specific absorption coefficient.

Fig. 1a shows five specific absorption spectra, each representing samples dominated by one of five major groups of phytoplankton: *Prochlorococcus*, *Synechococcus*, prymnesiophytes, green algae and diatoms. These spectra were selected from our field data, and the dominant type was determined on the basis of the concentrations of diagnostic pigments relative to chlorophyll *a*, as separated by HPLC (High Performance Liquid Chromatography) techniques (Gieskes & Kraay 1989, Jeffrey et al. 1997, Stuart & Head 2005). The absorption coefficient of phytoplankton per unit concentration of the

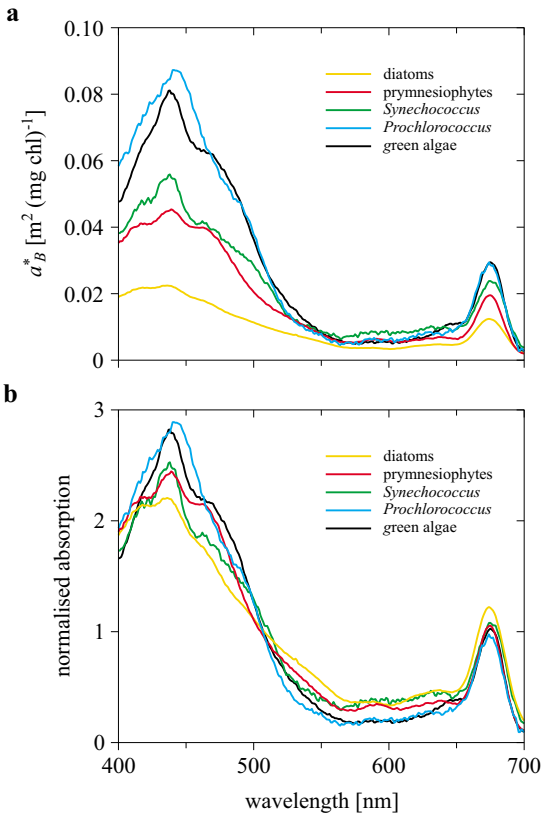

Fig. 1. Phytoplankton absorption spectra of field samples dominated by one of five major groups: green algae, diatoms, prymnesiophytes, *Synechococcus* and *Prochorococcus*. Each spectrum is normalised to the chlorophyll *a* concentration (B) in the sample (a). Same spectra as in (a), but after normalisation to the mean absorption in the 400–700 nm range (b)

main pigment chlorophyll a is known to vary by a factor of five or more in the ocean (Prieur & Sathyendranath 1981, Sathyendranath et al. 1987, Devred et al. 2006), a consequence of changes in phytoplankton taxa, and associated variations in cell size as well as intracellular pigment concentration and composition (Duysens 1956, Kirk 1975a,b, Platt & Jassby 1976, Morel & Bricaud 1981, Sathyendranath et al. 1987). But variability in the spectral shape of the absorption coefficient of phytoplankton is relatively small (Fig. 1b, see also Prieur & Sathyendranath 1981, Devred et al. 2006) and is often ignored in spectral models of light penetration and photosynthesis in the ocean (Sathyendranath & Platt 1988).

General models of light absorption by phytoplankton, and hence ocean-colour models, allow for common trends in the variations in specific absorption as biomass B changes; however, variabilities around the norm introduce uncertainties in retrieval accuracy. Such variability appears as noise in the model and in the biomass-retrieval algorithms for use in remote sensing.

But, since we know the source of the non-linear relationship between B and various optical properties, we could ask ourselves whether the very nature of the relationship (and the noise around it) carries any useful information on the types of phytoplankton present in the water. For example, Devred et al. (2006) have shown that phytoplankton absorption spectra are indicators not only of the biomass of phytoplankton, but also of the size class of the phytoplankton population. We have also shown that field data on phytoplankton absorption and chlorophyll concentration can be used in a model (Sathyendranath et al. 2001) to derive the specific absorption spectra of two component populations of phytoplankton in the samples. Ciotti et al. (2002) have related the shape of the phytoplankton absorption spectra to the dominant size class. Sathyendranath et al. (2004) have demonstrated that ocean-colour algorithms can be devised to map the distribution of diatoms in the North West Atlantic, using satellite data. Algorithms for identification of cyanobacteria from ocean-colour data have also been proposed (Jupp et al. 1994, Subramaniam et al. 2002). More generally, Alvain et al. (2005) have used an empirical method to retrieve the distribution of several phytoplankton types. As our knowledge of optical properties of sea-water constituents grows, as ocean-colour technology moves towards improved instruments with higher spectral resolution and lower noise, and as our interest in phytoplankton functional types increases, we may anticipate that the next generation of optical models will develop further in the direction of extracting additional information from optical data, whether it be from absorption spectra or from ocean-colour data.

In the following sections we examine biological and physical implications of variations in the magnitude and spectral distribution of light in the sea, and in the specific absorption spectra of phytoplankton. We consider first the estimation of primary production.

4. Existing models of phytoplankton production

Many models are available for estimating primary production by phytoplankton in the ocean: choosing between them can be sometimes difficult. A systematic analysis, comparison and classification of the models can be very helpful in identifying the differences if any, between models, and in selecting the right model for a particular application. The various models could be grouped into a few classes, as described below. We shall show that they can all be written in terms of the same parameter set – an important consideration when designing a programme to derive parameters from existing data sets.

Available-light or photosynthesis-irradiance models. Models of primary production that are formulated as functions of available light make use of equations such as the following (Platt et al. 1980):

$$P = BP_m^B \left(1 - \exp\left(-\frac{\langle\, \alpha^B \,\rangle}{P_m^B} E\right)\right), \tag{13}$$

where production P is computed using $\langle\, \alpha^B \,\rangle$, the initial slope measured for a flat incident spectral light field covering the entire photosynthetically-active wavelength domain, and P_m^B, the assimilation number of the light-saturation curve, both normalised to B, the concentration of chlorophyll a, which is taken as an index of the phytoplankton biomass. In the above equation, E is the total available irradiance in the photosynthetically-active range (about 400 to 700 nm). Note that all quantities in eq. (13) are depth-dependent, but to simplify the notations the depth dependence is not stated explicitly. Given that $P_m^B / \langle\, \alpha^B \,\rangle = E_k$, the photoadaptation parameter (which has dimensions of irradiance), we can substitute $E_* = E/E_k$ in eq. (13):

$$P = BP_m^B(1 - \exp(-E_*)), \tag{14}$$

where E_* is dimensionless light.

Absorbed-light models. With $\langle\, \alpha^B \,\rangle = \phi_m \langle\, a_B^* \,\rangle$ (see Platt & Jassby 1976), where ϕ_m is the realised maximum quantum yield and $\langle\, a_B^* \,\rangle$ is the the spectral average of the biomass-normalised absorption coefficient of

phytoplankton, it is easy to transform eq. (14) into an absorbed-light model (Kiefer & Mitchell 1983, Platt et al. 1988):

$$P = B\langle a_B^* \rangle \phi_m E_k (1 - \exp(-E_*)). \tag{15}$$

In the implementation of eq. (15), E_k would be calculated using the identity $E_k = P_m^B / (\langle a_B^* \rangle \phi_m)$, thereby avoiding the explicit invocation of $\langle \alpha^B \rangle$, which is a parameter characteristic of available-light models rather than of absorbed-light models.

Biomass-independent, or inherent-optical-property models. Noting that $B\langle a_B^* \rangle = \langle a_B \rangle$, where $\langle a_B \rangle$ is the spectral average of the absolute absorption coefficient by phytoplankton, eq. (15) can be expressed as:

$$P = \langle a_B \rangle \phi_m E_k (1 - \exp(-E_*)), \tag{16}$$

in which the biomass does not appear explicitly, and where one of the independent variables, the absorption coefficient of phytoplankton, is an inherent optical property. It could be argued that a biomass-independent model (Morel et al. 1996, Smyth et al. 2005) would be advantageous in circumstances where estimates of B would be subject to greater error than estimates of $\langle a_B \rangle$.

Growth models or carbon-based models. Growth models of phytoplankton (expressed in carbon units) use the growth parameter g, which is defined as the rate of change of carbon per unit time, normalised to the initial concentration of phytoplankton carbon:

$$g = \frac{1}{C} \frac{\mathrm{d}C}{\mathrm{d}t}, \tag{17}$$

where C is the initial pool of phytoplankton carbon and t is time. In fact, production estimated from any of the models discussed above is a measure of rate of change of phytoplankton carbon, so we have $P = \mathrm{d}C/\mathrm{d}t$. Also, initial phytoplankton carbon biomass is given by $C = \chi B$, where χ is the carbon-to-chlorophyll ratio ($\chi = C/B$). This leads to the result:

$$g = \frac{1}{\chi B} P. \tag{18}$$

Thus, it is in principle a trivial matter to transform production models into growth models (which are also called carbon-based models), if we know the carbon-to-chlorophyll ratio χ in addition to other variables and parameters in photosynthesis-irradiance models.

Spectral models. All the models described above deal with total light in the photosynthetically-active range without taking into account the spectral selectivity in absorption and utilisation of light available for photosynthesis. They may be categorised as non-spectral models. To account for spectral effects in photosynthesis we recognise that the coupling between light and phytoplankton photosynthesis depends on the product $\langle \alpha^B \rangle E$ (or its analogue $\phi_m \langle a_B^* \rangle E$ in absorbed-light models). Thus, to transform non-spectral models into spectral models, all that is required (Sathyendranath & Platt 1993) is to replace the product $\langle \alpha^B \rangle E$ with its spectral equivalent $\int \alpha^B(\lambda) E(\lambda)\, \mathrm{d}\lambda$. In this case, eq. (13) and eq. (16) transform into (Platt & Sathyendranath 1988, Sathyendranath & Platt 1989, Sathyendranath & Platt 1993):

$$P = BP_m^B \left(1 - \exp\left(-\int \alpha^B(\lambda) E(\lambda) \mathrm{d}\lambda / P_m^B\right)\right). \tag{19}$$

The spectral equivalent of $\phi_m \langle a_B^* \rangle E$ is $\int E(\lambda) \alpha^B(\lambda) \mathrm{d}\lambda$. Note that the spectral versions of eqs. (13) and (16) will be identical to each other, and that the chlorophyll concentration reappears in the solution for the inherent-optical property model. The perceived advantage of inherent-property models then disappears. Note that the spectral model of Morel (1991) employs another set of parameters from the ones used here, and at a first glance, appears to be very different from those presented above. But the parameters of the Morel model, such as $KPUR$, are defined in terms of the parameters of the photosynthesis-irradiance curve (see Morel et al. 1996), and after appropriate substitutions, it can be shown that the Morel model also reduces to eq. (19), as demonstrated in the Appendix. A further point of interest is the ease with which growth g can be expressed in terms of a spectrally-resolved production model. Explicitly,

$$g = \frac{1}{\chi B} P = \frac{1}{\chi} P_m^B \Big(1 - \exp\Big(-\int \alpha^B(\lambda) E(\lambda) \mathrm{d}\lambda / P_m^B\Big)\Big). \tag{20}$$

Such models are extremely useful for the elucidation of spectral effects on phytoplankton growth, and we shall use them later in this paper.

Whereas there has been animated discussion in the recent literature on the choice of models to compute primary production (e.g., Behrenfeld et al. 2005), the above summary shows that it is easy to transform one type of model into another without loss of generality. There is no fundamental difference between them. We may use any of them according to convenience, provided we have a basic set of model parameters. Moreover, we may reasonably expect that the results recovered from the various types of non-spectral models should be identical to each other, provided that equivalent

parameters are used in the appropriate models. These remarks apply to production at a particular depth at a given time. Similar conclusions were reached by Platt & Sathyendranath (1993) after comparing models of daily-integrated water-column primary production with uniform biomass distribution: many apparently different models can be shown to be very similar to each other, and it is reassuring that they should be so. Apparent discrepancies in implementation can usually be traced to differences in parameter assignment, or even to errors in computation.

The most important difference revealed by comparison of models is that between spectral and non-spectral models: the wavelength integral $\int \alpha^B(\lambda)E(\lambda)\mathrm{d}\lambda$ differs from the term $\langle\, \alpha^B \,\rangle E$ in non-spectral models, to the extent of the covariance between $\alpha^B(\lambda)$ and $E(\lambda)$. To see this, we can express both $\alpha^B(\lambda)$ and $E(\lambda)$ as sums of a spectral average and a wavelength-dependent departure Δ from the average. That is, $\alpha^B(\lambda) = \langle\, \alpha^B \,\rangle + \Delta_\alpha(\lambda)$ and $E(\lambda) = \langle\, E \,\rangle + \Delta_E(\lambda)$. Now the spectral product integral can be written as

$$\int \alpha^B(\lambda)E(\lambda)\ \mathrm{d}\lambda = \int (\langle\, \alpha^B \,\rangle + \Delta_\alpha(\lambda))(\langle\, E \,\rangle + \Delta_E(\lambda))\,\mathrm{d}\lambda. \tag{21}$$

Expanding the terms under the integral sign, we find

$$\begin{aligned}\int \alpha^B(\lambda)E(\lambda)\ \mathrm{d}\lambda &= \int \langle\, \alpha^B \,\rangle\langle\, E \,\rangle\ \mathrm{d}\lambda \\ &+ \int \langle\, \alpha^B \,\rangle\Delta_E(\lambda)\,\mathrm{d}\lambda + \int \langle\, E \,\rangle\Delta_\alpha(\lambda)\,\mathrm{d}\lambda + \int \Delta_\alpha(\lambda)\Delta_E(\lambda)\,\mathrm{d}\lambda.\end{aligned} \tag{22}$$

Note that the averages can be taken outside the integration sign and that in the middle two integrals on the right-hand side the integrals of the fluctuations Δ over the spectrum go identically to zero. Then,

$$\int \alpha^B(\lambda)E(\lambda)\ \mathrm{d}\lambda = \langle\, \alpha^B \,\rangle\langle\, E \,\rangle \int \mathrm{d}\lambda + \int \Delta_\alpha(\lambda)\Delta_E(\lambda)\,\mathrm{d}\lambda. \tag{23}$$

Now the quantity $\langle\, E \,\rangle \int \mathrm{d}\lambda$ in the first term on the right-hand side of eq. (23) is just the total incident energy E summed over all wavelengths. Therefore

$$\int \alpha^B(\lambda)E(\lambda)\ \mathrm{d}\lambda = \langle\, \alpha^B \,\rangle E + \int \Delta_\alpha(\lambda)\Delta_E(\lambda)\,\mathrm{d}\lambda. \tag{24}$$

The first term on the right now corresponds to the non-spectral product, and we can see that it differs from the spectral integral by the covariance integral $\int \Delta_\alpha(\lambda)\Delta_E(\lambda)\,\mathrm{d}\lambda$. Because the spectral structure of the submarine light field itself is so strongly modified by the absorption of phytoplankton,

we cannot expect this covariance to vanish. In fact, it can be shown that, for any depth horizon in a vertically-homogeneous water column, the spectral and non-spectral terms will be equal for one and only one value of the pigment biomass. Moreover, the difference between the two types will vary according to the functional groups of phytoplankton present, each with its distinctive spectral signature. Such subtleties are completely lost in a non-spectral model.

As noted earlier, computations of diffuse attenuation coefficient also differ between spectral and non-spectral models, which can lead to differences in computed values of available light at particular depths in the ocean, which in turn would lead to differences in modelled production at those depths. Hence, where possible, one should account for spectral effects in calculating production by phytoplankton. The differences between the results of spectral and non-spectral models are systematic, not random. In comparisons between the two model types, if the differences are found to be random, one should suspect either computational errors or difficulties with the parameter assignments.

An issue at present unresolved is access to appropriate model parameters. Any of the model types discussed here could be used with the same small set of fundamental parameters. This set would consist of: the initial slope $\langle \alpha^B \rangle$, the assimilation number P_m^B, the biomass-normalised absorption coefficient of phytoplankton $\langle a_B^* \rangle$, and the carbon-to-chlorophyll ratio χ. Other parameters in use, such as the quantum yield ϕ_m, the photoadaptation parameter E_k or $KPUR$ (see Appendix), can all be derived from this basic set. To implement spectral models, one would need spectrally-resolved values of $a_B^*(\lambda)$, and also of $\alpha^B(\lambda)$, if it could not be assumed that their spectral shapes were similar (for example, in waters with high concentrations of non-photosynthetic pigments, we may anticipate that the spectral shapes of $a_B^*(\lambda)$ and $\alpha^B(\lambda)$ would differ). But biological rate parameters are notoriously undersampled in the world ocean (Longhurst et al. 1995), and it is not a trivial problem to assign parameter values when implementing models, especially at large scales (Banse & Postel 2003).

Furthermore, Dynamic Green Ocean Models (Anderson 2005, Flynn 2005, Le Quéré et al. 2005) require that we understand how different functional groups respond to changes in environmental conditions. In other words, the number of parameters needed to model photosynthesis increases linearly with the number of separate phytoplankton compartments in the model. Clearly, such information is essential, if one is to understand the present distribution of phytoplankton functional types globally, and its potential response to climate change.

More work is therefore needed, not so much on models as on model parameters. What causes the photosynthesis model parameters to vary? One school of thinking (Morel 1991, Behrenfeld & Falkowski 1997) has advocated the use of empirically-fitted parameters to model primary production at the global scale. Others (Sathyendranath et al. 1995, Behrenfeld et al. 2006) have advocated the use of parameters that are assigned on the basis of ecological partitions in the ocean. Some results have emphasised the importance of environmental factors such as temperature on photosynthetic parameters (Eppley 1972, Morel et al. 1996, Behrenfeld & Falkowski 1997, Woźniak et al. 2002, Bouman et al. 2005) whereas others have highlighted the role of phytoplankton community structure (Bouman et al. 2005). But each one of these approaches has its drawbacks: the province-based approach provides only limited insight into the causes of variability; global approaches do not perform equally well in different regions of the world oceans. It would be fair to say that the key to variability in parameters of photosynthesis models has eluded us so far. The recent growing interest in modelling phytoplankton functional types has prompted a series of reviews on bio-optical characteristics and rate parameters of a number of phytoplankton types (LaRoche & Breitbarth 2005, Sarthou et al. 2005, Schoemann et al. 2005, Veldhuis et al. 2005), which have also brought into focus another issue: most of what we know about the physiological properties of phytoplankton functional types is derived from laboratory experiments. We do not yet know whether these results are representative of values attained in the real ocean.

So far we have considered only photosynthesis and phytoplankton growth. Observed changes of phytoplankton biomass in the surface layer of the ocean, and the initiation of blooms, depend on the balance between growth and loss terms in the layer, and this is the topic we treat next.

5. Mixed-layer physics and phytoplankton blooms

Consider a system containing water and phytoplankton. Photons passing through this layer may be absorbed by the water or the phytoplankton, and the partition will depend on the relative sizes of the absorption coefficients. When the water absorbs a photon, the energy it carries will heat the water. The same is true for most of the photons absorbed by phytoplankton: the energy of only a small proportion of them is converted to chemical energy by photosynthesis. By virtue of the thermal dissipation of most of the visible electromagnetic energy absorbed by phytoplankton, this microflora plays an important role in the heat budget of the surface layer of the ocean. Even the energy transformed in photosynthesis is destined to be lost as heat, a consequence of respiration.

Thermodynamically, the ocean ecosystem is open and dissipative, creating entropy through respiration. It is sustained only by the constant input of energy from the sun. The interface by which the trophic chain is coupled to this energy supply is provided by the pigments contained in phytoplankton. Thus, the phytoplankton have an important dual role in the dynamics of the upper ocean. On the one hand they control the way the ocean is heated: the presence of phytoplankton increases K, and hence the heating of the water by the penetrating component of solar energy is confined more towards the surface, favouring a shallower mixed layer, than would be the case in the absence of phytoplankton (see Fig. 2). On the other hand, phytoplankton represent the essential transducer through which the ecosystem can exploit solar energy as a basis for life: a more shallow mixed layer favours higher growth per unit volume than does a deeper one. This dual role of phytoplankton ensures that the physics and biology of the upper ocean will be coupled. In particular, the physical and biological dynamics will be coupled through the pigment biomass B, explicitly through the effect of B on the diffuse vertical attenuation coefficient K (eq. (8) and its broad-spectrum analogue, $K = K_W + k_B B$, in which K_W and k_B are computed for total irradiance underwater).

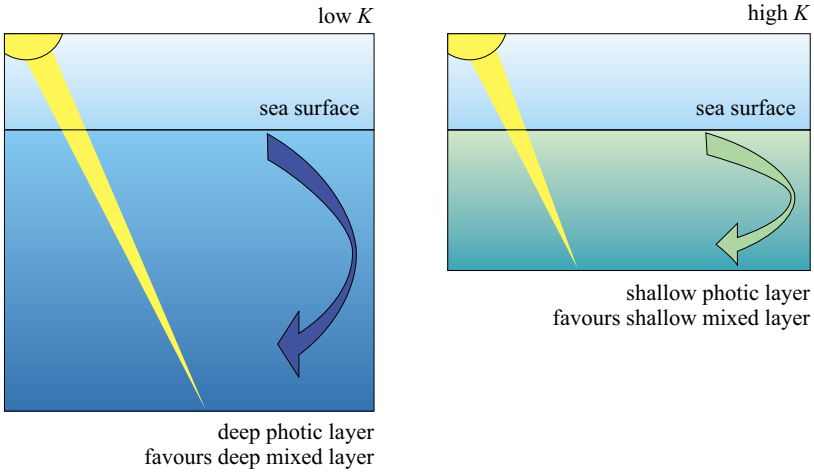

Fig. 2. Schematic diagram showing the relationship between K (the diffuse attenuation coefficient for downwelling irradiance) and mixed-layer dynamics

Consider a vertically-uniform surface layer in which the net production is greater than zero, such that B increases. The increment in B leads directly to an increase in K, modifying the heating term in the energy budget for the mixed layer, such that the mixed-layer depth is adjusted to be shallower.

Of course, the effect of a change in K is not confined just to the physical system. It has profound consequences for the biological system as well. The growth rate of phytoplankton in the mixed layer depends on the dimensionless product (optical thickness of the mixed layer) KZ_m where Z_m is the mixed-layer depth (Platt et al. 1991). Lower values of KZ_m favour higher growth rates and *vice versa*. Shallowing of the mixed layer increases phytoplankton growth rate, such that (provided nutrients are non-limiting) a positive feedback loop might be established between the physical and biological dynamics, tending to increase B indefinitely (Fig. 3).

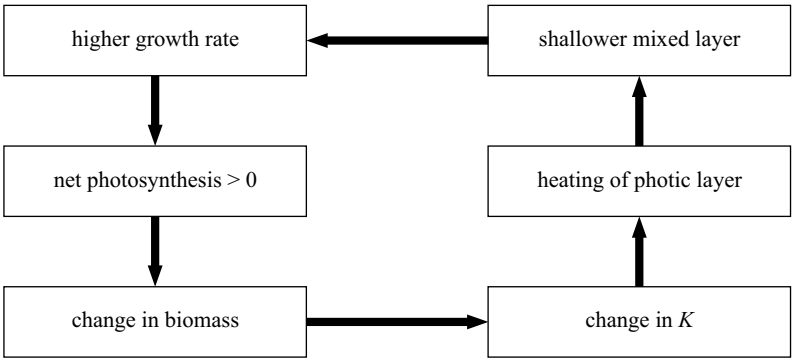

Fig. 3. Schematic diagram showing the biofeedback in the mixed layer, linking phytoplankton growth and mixed-layer dynamics

If this simple model represented reality, one would expect a much higher incidence of uncontrolled phytoplankton blooms than is in fact observed. What processes intervene to prevent this from happening? To answer the question we need to reconsider the earlier assumption of positive net growth in the mixed layer. We need to recognise two important depth horizons. One is Z_m itself, determined by the balance between stratification through solar heating and destratification due to wind-driven turbulence. The other is Sverdrup's (1953) critical depth Z_{cr}, determined by the null balance between growth and loss of phytoplankton integrated over depth (see Fig. 4). Both of these horizons are strongly influenced by the magnitude of K (Platt et al. 1991). Severdrup (1953) gives a general expression for Z_{cr}. See also Platt et al. (1991):

$$Z_{cr} = \frac{E(0)}{E_c} \, \frac{[1 - \exp(-KZ_c)]}{K}. \tag{25}$$

In eq. (25), E_c is the compensation depth (see Fig. 4), at which production is exactly balanced by growth. Provided that $Z_{cr} > Z_m$, net phytoplankton growth integrated over the mixed layer will be positive (see Fig. 5).

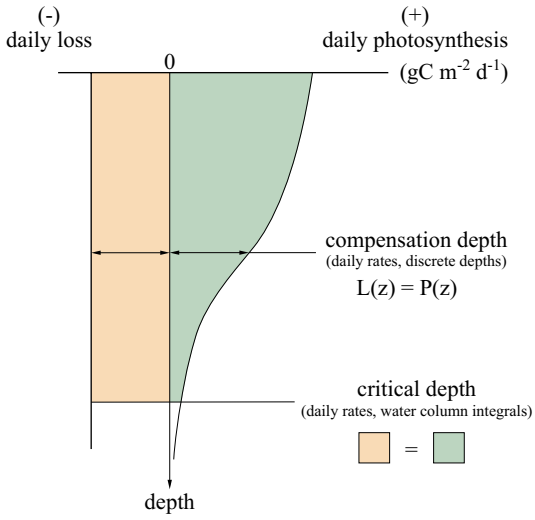

Fig. 4. Schematic diagram showing critical depth and compensation depth

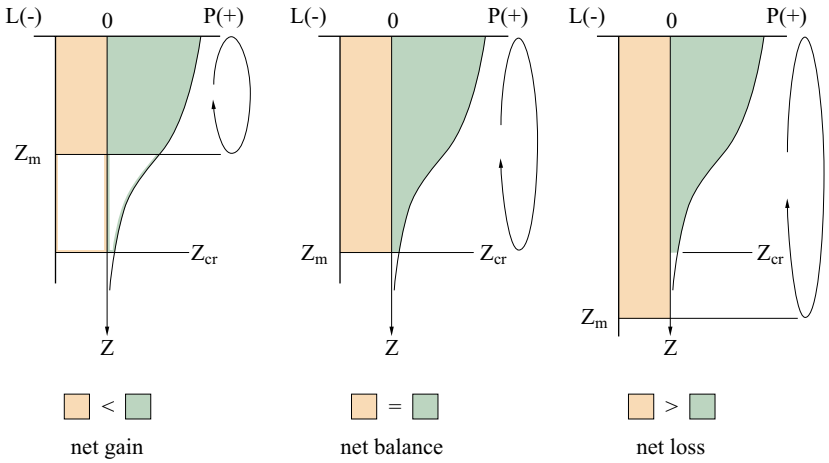

Fig. 5. Schematic diagram showing the influence of mixed-layer depth and critical depth on phytoplankton growth

We can now re-examine the simple feedback-model outlined earlier. At the point where Z_m becomes just shallower than Z_{cr}, net growth becomes positive and K increases, thereby reducing Z_{cr}. Unless there were a simultaneous change in Z_m, the Sverdrup criterion for net growth would no longer be met, such that phytoplankton accumulation in the mixed layer would be self-regulating. But there is a concomitant reduction in Z_m caused by the increase in K as phytoplankton accumulate. Is the change in

mixed-layer depth sufficient to maintain the Sverdrup condition $Z_{cr} > Z_m$? Sathyendranath & Platt (2000) have shown that the relative changes in Z_{cr} and Z_m when K is increased (beginning at $Z_{cr} = Z_m$) are such that $Z_{cr} < Z_m$, the Sverdrup condition is not met, and growth is self-regulated.

We can also show (Platt et al. 2003a) that in the mixed layer, the biomass will converge towards a fixed-point value B_*. This value is attracting in the mathematical sense, and it is mathematically bounded. The fixed-point biomass is a limit on the maximum B possible in the layer. Moreover, B_* is under bio-optical control:

$$B_* = \frac{\theta_*}{k_B Z_m} - \frac{K_W}{k_B}, \tag{26}$$

where θ_* is the optical thickness of the mixed layer when biomass is B_*. That is, $\theta_* = Z_m(K_W + k_B B_*)$. We have shown (Platt et al. 2003a) that B_* is always positive, implying a resistance to the extinction of phytoplankton under adverse conditions (during periods of net loss of phytoplankton, the biomass will decrease only until a new and lower value of B_* is reached; it is unlikely to go to zero).

We can now relate Z_{cr} to Z_m in a way that includes explicitly the fixed-point biomass:

$$Z_{cr}(t) = Z_m \left(\frac{K_W + k_B B_*}{K_W + k_B B(t)} \right), \tag{27}$$

showing that because the fixed point is attracting (that is to say $B(t)$, biomass at time t, will tend toward B_*), the critical depth will be attracted to the mixed-layer depth (Platt et al. 2003a). If this balance is reached for low values of the fixed-point biomass B_*, then further development of a bloom will be arrested, regardless of whether there is residual nitrogen in the mixed-layer or not. Here could be an explanation for the presence of the so-called High-Nitrogen-Low-Biomass (HNLC) regimes in the world oceans, where stereotypic blooms that draw-down all available nutrients are not typically in evidence (Platt et al. 2003b).

This argument may apparently contradict evidence from iron enrichment experiments where significant increases in biomass have been reported in HNLC regions following addition of iron (Boyd et al. 2000). To reconcile the two results, let us recall that, generally, iron enrichment experiments have led to a change in the phytoplankton population from small-cell-dominated to large-cell-dominated populations (Lindley & Barber 1998). Such a change would decrease the specific absorption coefficient of phytoplankton, and hence k_B. This decrease in k_B would in turn lead to a higher fixed-point biomass B_* (see eq. (26)). One might argue on the basis of the Platt et al.

(2003a) model that adding more and more iron to HNLC regions would not guarantee complete draw-down of excess nitrogen: if the new fixed-point biomass were reached before all available nitrogen is exhausted, further draw-down would be arrested at this point (Platt et al. 2003b). In fact, it is remarkable that iron-enrichment simulations coupled to a detailed General Circulation Model (Aumont & Bopp 2006) have yielded results that are entirely consistent with the theoretical results of Platt et al. (2003a,b).

Thus, we see that much can be gained by studying the biological and physical processes in the ocean as a coupled system, the coupling being provided by the light field and the phytoplankton pigments. So far, we have not considered the importance of the spectral quality of the light field in this context, a subject we treat in the next section.

6. Spectral quality of underwater light and species succession

Elucidation of the controls on distribution of phytoplankton functional types (PFT) is central to understanding the structural and functional significance of biodiversity in the marine microflora for the dynamics of the Earth system. The seasonal cycle of phytoplankton biomass is associated with a succession of taxa belonging to different PFTs (Smayda 1963). As we have seen earlier, phytoplankton regulate the intensity and spectral quality of the submarine light field, which changes continuously as the abundance and community structure of phytoplankton change. We have also seen that the specific absorption coefficient of phytoplankton is highly variable, depending on the type of phytoplankton present. In the section on primary production in the ocean, we saw that the spectral light field and the absorption coefficient are coupled in the process of light utilisation for photosynthesis. Here we examine the potential role of the spectral quality of the underwater light in modulating species succession in the ocean.

As we saw earlier, the specific absorption spectra of different types of phytoplankton are often distinctly different (Fig. 1a). But the differences in their shapes (Fig. 1b) are more subtle, and hence often ignored in models. However, although they are subtle, these differences are real and they are systematic rather than random: they reflect, at least partially, evolutionary diversification in the pigment complement of phytoplankton groups in the ocean. What is their significance?

The spectral composition of underwater light changes continuously with depth as it penetrates downwards from the surface. At the base of the photic zone (where irradiance is 1% of the surface value), the spectral composition of the residual irradiance E computed using an underwater light transmission model (Sathyendranath & Platt 1988) varies with the

concentration of phytoplankton in the layer above. Under light-limited conditions, phytoplankton production is determined by $\phi_m \int a_B(\lambda)E(\lambda)\,\mathrm{d}\lambda$, where ϕ_m is the realised maximum quantum yield of photosynthesis (usually taken to be spectrally neutral), $a_B(\lambda)$ is the phytoplankton absorption coefficient and λ is the wavelength, so that phytoplankton with photosynthetic pigments matching the spectral quality of the light available would be able to absorb more light, and hence photosynthesise at a higher rate than others whose pigments were chromatically less well-suited.

We have plotted the integral $\int a_B(\lambda)E(\lambda)\,\mathrm{d}\lambda$ over the photosynthetically-active range of 400–700 nm, for the five phytoplankton types represented in Fig. 1, and for phytoplankton pigment concentrations in the water column ranging from 0.01 to 25 mg m^{-3} (Fig. 6). The computation is for the base of the photic zone under a common surface irradiance, such that, for all pigment concentrations, $\int E(\lambda)\,\mathrm{d}\lambda$ is always the same, and equal to 1% of the incident light: the spectral shape may change, but the integral is conserved, and we set it to unity. Also, the absorption coefficients of each of the phytoplankton types at the photic depth are normalised such that their spectral mean over the wavelength range from 400 to 700 nm,

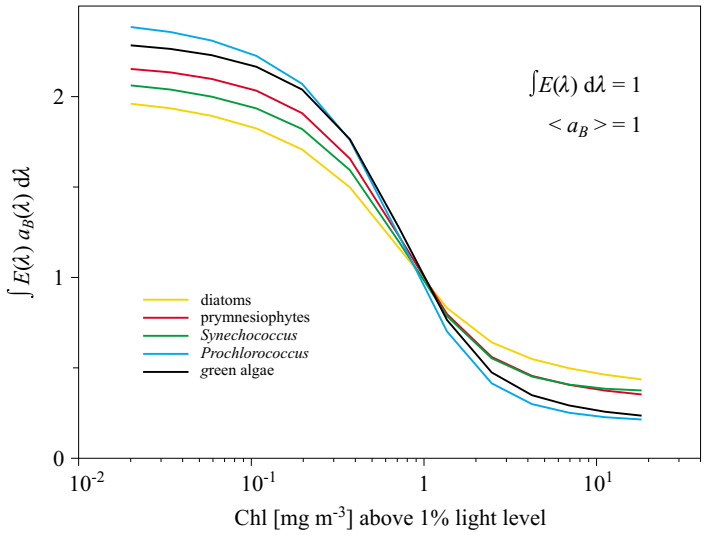

Fig. 6. The spectral integral of irradiance E and phytoplankton absorption a_B at the base of the photic zone for the five different types of phytoplankton considered. The irradiance and the absorption are normalised such that their non-spectral product would be one. The results are shown for different chlorophyll concentrations in the water. Note that the only factor causing changes in the integral for a given phytoplankton type is the changing spectral quality of light at the photic depth, as the phytoplankton concentration in the water changes

$\langle a_B \rangle = \int a_B(\lambda)\,\mathrm{d}\lambda / \int \mathrm{d}\lambda$, is unity for each of the phytoplankton types (see Fig. 1b). The product of total irradiance and mean absorption is then equal to one for all groups. Thus, the computation isolates the impact of spectral variations in the available light and the phytoplankton absorption coefficient: the spectral integral of the product $a_B(\lambda)E(\lambda)$, and therefore the growth, would be greater when the pigments and light were chromatically well-matched, than when they were not.

The integrals shown in Fig. 6 for the five phytoplankton types are always greater in blue waters (lower biomass) than in green waters (higher biomass), but subtle differences are present that could hold the key to species succession. The integral is greater for *Prochlorococcus* than for the others in blue waters, suggesting that, other factors being equal, *Prochlorococcus* would out-perform all other phytoplankton types in clear, blue, oligotrophic waters, at least under light-limited conditions. On the contrary, the integral is greater for diatoms than the other phytoplankton types in green, eutrophic waters. Thus, comparison of the spectral quality of the underwater light field with the absorption spectra of the five groups of phytoplankton indicates that the spectral form of absorption confers Darwinian fitness on phytoplankton taxa according to the trophic status of the environment. These results explain, for example, the dominance of *Prochlorococcus* in deep chlorophyll maxima in oligotrophic waters. And in general, we expect that phytoplankton types would be stratified in the vertical according to the compatibility between the absorption spectra of their pigment complements and the chromatic quality of the ambient light field. These results are consistent with the conclusion (Ting et al. 2002) that the pigment complements of *Prochlorococcus* and *Synechococcus* contribute to differentiating their ecological niches in the ocean.

On an aside, let us note that the integral in Fig. 6 takes the value of one, when the biomass is approximately 1 mg m^{-3}. The exact biomass at which this occurs is different for the different phytoplankton types studied here. Since we have taken $\langle a_B \rangle$ and E to be unity in this computation, non-spectral models of production would also have yielded $\langle a_B \rangle E = 1$. Comparing with eq. (24) we see that the covariance term must be zero when the spectral and the non-spectral computations yield the same values for light-limited production. For all other cases, the spectral model would yield a primary production that is greater than, or less than, the non-spectral analogue.

To see these results in their broader oceanographic context, recall first that the attenuation coefficient for visible light is a key property in the heat budget of the surface ocean and therefore an important determinant of mixed-layer depth and temperature. It has also been shown that

there is a stable (fixed-point) solution for the biomass in the mixed layer, whose magnitude is set by the depth of the mixed layer and bio-optical properties therein. As a result of bio-optical coupling, the mixed-layer depth is a mathematical attractor for the critical depth, or in other words, the critical depth will adjust until the fixed-point biomass is reached, so that mixed-layer depth and critical depth become equal (Platt et al. 2003a). Perturbations in critical depth will tend to be damped out by this mechanism, which is therefore a stabilising one. It is also relevant, but hitherto not analysed, that as the fixed-point biomass adjusts to a new mixed-layer depth, the spectrum of the ambient light at depth will also change. A given biomass will lead to a given light spectrum, and so to a preference for growth of the autotrophs chromatically enabled to use it. Such a condition will persist until the mixed-layer depth is perturbed, for example by a storm, when a new fixed-point biomass and thus a new submarine light spectrum will be established. Bio-optical coupling thus emerges as a conservative mechanism in that it restricts uncontrolled phytoplankton growth (or loss) and because, by continuously changing the spectral distribution of underwater light, it ensures that growth conditions do not always favour the same taxa: maintenance of biodiversity in phytoplankton (Hutchinson 1961) is assured.

Since the spectral quality of the submarine light field changes continuously with depth, we may expect a vertical stratification of taxa below the mixed layer, for which there is ample evidence from the field (Hoepffner & Sathyendranath 1992). Moreover, phytoplankton have a certain plasticity with respect to pigment complement (Subramaniam et al. 1999a,b, MacIntyre et al. 2002, Rodriguez et al. 2006), which may vary to a certain extent according to growth conditions. These variations may acquire reinforcement at the molecular level, leading to the emergence of ecotypes (Moore et al. 1998, Bouman et al. 2006), thereby adding to biodiversity. The mechanisms presented above modulate the positive feedback loop (Fig. 3), providing instead a bio-optical homeostasis in which biodiversity is maintained or enhanced and autotrophic biomass is constrained to particular values according to conditions (Fig. 7).

7. Concluding remarks

The development of ocean-colour remote sensing has been an outstanding success with an undoubtedly beneficial impact on all branches of oceanography. Its technical foundation lies in the spectral character of phytoplankton optical properties, in particular the shape of the absorption spectrum. This spectrum is generally conservative in nature. Its shape may be considered constant to a first approximation (as in the operational

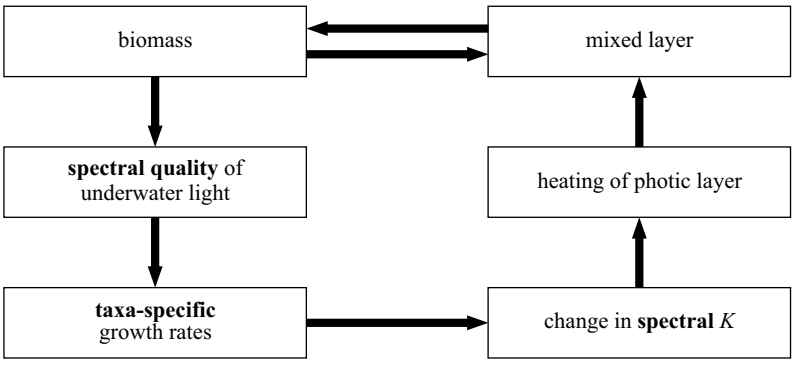

Fig. 7. Modified schematic diagram showing how the same feedback loop illustrated in Fig. 3, when coupled with the spectral effects shown here, can lead to species succession and biodiversity in the ocean. There is now a constraint on the positive feedback between biomass and mixed-layer depth (the opposing arrow). When the biomass in the mixed layer reaches the fixed-point biomass for the species composition optimised to the spectral quality of the submarine light field, the system will stabilise. This is an optical homeostasis that tends to resist extremes of biomass or of single-species dominance under all conditions

retrieval of chlorophyll concentration), although subtle differences are known to exist between phytoplankton functional types. Precisely the same spectrum, with the same generally conservative shape, governs the spectral response of phytoplankton in photosynthesis. The response may differ in magnitude according to environmental conditions, but not, to first order, in shape. But even though scientists have been willing to accept the premise for chlorophyll retrieval, they have been more reluctant to invoke it for calculation of phytoplankton production and growth. This is all the more surprising given that the underlying phenomenon is well established in plant physiology and that the potential error is systematic with a well-understood correction. The notion that a spectral treatment of phytoplankton production, because it is more complex than a non-spectral one, may lead to additional random errors is spurious because the variable property (magnitude of action spectrum) is required for both treatments whereas the additional input required for a spectral treatment (shape of spectrum) is conservative.

With a second-order treatment, the known variablity in these spectra has significant consequences. In particular, it favours niche proliferation in phytoplankton. The direct effect of an increase in biomass by one taxon is to modify the spectral character of the ambient light field, such that its own response to that light field is modified. Such a mechanism, by which an organism's growth (at a rate dependent on the spectral properties of

the light environment) alters the environmental conditions to which it will now have to respond, acts against the dominance of one phytoplankton type to the exclusion of others. In other words, it promotes biodiversity. More generally, optical effects, modulated by the spectral details, provide restraint on extreme fluctuations in biomass of phytoplankton. They ensure that, in the mixed layer, seasonal changes in physical and biological conditions unfold in a coherent manner.

The spectral structure of the submarine light field also contains information that the oceanic microflora might use to direct life-history processes. All green plants are now known to possess signal-transducing photoreceptors called phytochromes (Smith 2000, Kehoe & Gutu 2006). This group of proteins converts between active and inactive forms according to the spectral structure of the ambient light field, thus providing the basis for a switching mechanism. They are believed to have originated in the photosynthetic prokaryotes and are present in algae, including cyanobacteria. Their role in marine systems is as yet uncertain. Ragni & D'Alcalà (2004) point out that the submarine light field carries information on time of day, depth and presence of immediate neighbours: but the strong attenuation of red light in the sea would seem to limit the utility of a transducing system sensitive to red light, except close to the sea surface, unless the red light were generated at depth by trans-spectral processes.

Acknowledgements

Part of this work was carried out at the University of Bristol, where SS and TP were Benjamin Meaker Visiting Professors in 2005. Funding support from the Natural Sciences and Engineering Research Council of Canada and from the Canadian Space Agency is also gratefully acknowledged. Help from Carla Caverhill, George White, Marie-Hélène Forget and Venetia Stuart is gratefully acknowledged. The authors, who have long admired the outstanding contributions to marine optics made by Polish scientists, thank the Editors for the invitation to write in this journal.

References

Alvain S., Moulin C., Dandonneau Y., Bréon F. M., 2005, *Remote sensing of phytoplankton groups in case 1 waters from global SeaWiFS imagery*, Deep-Sea Res. Pt. I, 52 (11), 1989–2004.

Anderson T. R., 2005, *Plankton functional type modelling: running before we can walk?*, J. Plankton Res., 27 (11), 1073–1081.

Aumont O., Bopp L., 2006, *Globalizing results from ocean in situ iron fertilization studies*, Global Biogeochem. Cy., 20 (2), doi: 10.1029/2005GB002591.

Banse K., Postel J. R., 2003, *On using pigment-normalized, light-saturated carbon uptake with satellite-derived pigment for estimating column photosynthesis*, Global Biogeochem. Cy., 17 (3), 1079, doi: 10.1029/2002GB002021.

Behrenfeld M., Boss E., Siegel D., Shea D. M., 2005, *Carbon-based ocean productivity and phytoplankton physiology from space*, Global Biogeochem. Cy., 19, GB1006, doi: 10.1029/2004GB002299.

Behrenfeld M. J., Falkowski P. G., 1997, *Photosynthetic rates derived from satellite-based chlorophyll concentration*, Limnol. Oceanogr., 42 (1), 1–20.

Behrenfeld M. J., Worthington K., Sherrell R. M., Chavez F. P., Strutton, P., McPhaden M., Shea D. M., 2006, *Controls on tropical Pacific Ocean productivity revealed through nutrient stress diagnostics*, Nature, 442 (7106), 1025–1028, doi: 10.1038/nature05083.

Bouman H., Platt T., Sathyendranath S., Stuart V., 2005, *Dependence of light-saturated photosynthesis on temperature and community structure*, Deep-Sea Res. Pt. I, 52 (7), 1284–1299.

Bouman H., Ulloa O., Scanlan D., Zwirglmaier K., Li W. K. W., Platt T., Stuart V., Barlow R., Leth O., Clementson L., Lutz V., Fukasawa M., Watanabe S., Sathyendranath S., 2006, *Oceanographic basis of the global surface distribution of Prochlorococcus ecotypes*, Science, 312 (5775), 918–921.

Boyd P. W., Watson A. J., Law C. S., Abraham E. R., Trull T., Murdoch R., Bakker D. C. E., Bowie A. R., Buesseler K. O., Chang H., Charette M., Croot P., Downing K., Frew R., Gall M., Hadfield M., Hall J., Harvey M., Jameson G., LaRoche J., Liddicoat M., Ling R., Maldonado M. T., McKay R. M., Nodder S., Pickmere S., Pridmore R., Rintoul S., Safi K., Sutton P., Strzepek R., Tanneberger K., Turner S., Waite A., Zeldis J., 2000, *A mesoscale phytoplankton bloom in the polar Southern Ocean stimulated by iron fertilization*, Nature, 407 (6805), 695–702.

Bricaud A., Babin M., Morel A., Claustre H., 1995, *Variability in the chlorophyll-specific absorption coefficients of natural phytoplankton: analysis and parameterization*, J. Geophys. Res., 100 (C7), 13321–13332.

Ciotti Á. M., Cullen J. J., Lewis M. R., 1999, *A semi-analytical model of the influence of phytoplankton community structure on the relationship between light attenuation and ocean color*, J. Geophys. Res., 104 (C1), 1559–1578.

Ciotti Á. M., Lewis M. R., Cullen J. J., 2002, *Assessment of the relationships between dominant cell size in natural phytoplankton communities and the spectral shape of the absorption coefficient*, Limnol. Oceanogr., 47 (2), 404 –417.

Cleveland J. S., 1995, *Regional models for phytoplankton absorption as a function of chlorophyll a concentration*, J. Geophys. Res., 100 (C7), 13333–13344.

Devred E., Sathyendranath S., Stuart V., Maass H., Ulloa O., Platt T., 2006, *A two-component model of phytoplankton absorption in the open ocean: Theory and applications*, J. Geophys. Res., 111, C03011, doi: 10.1029/2005JC002880.

Duysens L. N. M., 1956, *The flattening of the absorption spectrum of suspensions, as compared to that of solutions*, Biochim. Biophys. Acta, 19, 1–12.

Eppley R. W., 1972, *Temperature and phytoplankton growth in the sea*, Fish. Bull., 70 (4), 1063–1085.

Flynn K. J., 2005, *Castles built on sand: dysfunctionality in plankton models and the inadequacy of dialogue between biologists and modellers*, J. Plankton Res., 27 (12), 1205–1210.

Gieskes W. W. C., Kraay G. W., 1989, *Estimating the carbon-specific growth rates of the major algal species groups in eastern Indonesian waters by ^{14}C labeling of taxon-specific carotenoids*, Deep-Sea Res., 36 (8), 1127–1139.

Gordon H. R., Brown O. B., Jacobs M. M., 1975, *Computed relationships between the inherent and apparent optical properties of a flat, homogeneous ocean*, Appl. Opt., 14, 417–427.

Gordon H. R., Morel A., 1983, *Remote assessment of ocean color for interpretation of satellite visible imagery. A review*, Lect. Notes Coast. Estuar. Stud. No 4, Springer-Verlag, New York, 114 pp.

Hall D. O., Rao K. K., 1994, *Photosynthesis*, 5th edn., Cambridge Univ. Press, Cambridge, 211 pp.

Hoepffner N., Sathyendranath S., 1992, *Bio-optical characteristics of coastal waters: Absorption spectra of phytoplankton and pigment distribution in the western North Atlantic*, Limnol. Oceanogr., 37 (8), 1660–1679.

Hutchinson G. E., 1961, *The paradox of plankton*, Am. Nat., 95, 137–147.

Jeffrey S. W., Mantoura R. F. C., Wright S. W., 1997, *Phytoplankton pigments in oceanography*, UNESCO Publ., Paris, 661 pp.

Jupp D. L. B., Kirk J. T. O., Harris G. P., 1994, *Detection, identification and mapping of cyanobacteria – using remote sensing to measure the optical quality of turbid inland waters*, Aust. J. Mar. Fresh. Res., 45, 801–828.

Kehoe D., Gutu A., 2006, *Responding to color: the regulation of complementary chromatic adaptation*, Annu. Rev. Plant Biol., 57, 127–150.

Kiefer D. A., Mitchell B. G., 1983, *A simple, steady state description of phytoplankton growth based on absorption cross section and quantum efficiency*, Limnol. Oceanogr., 28 (4), 770–776.

Kirk J. T. O., 1975a, *A theoretical analysis of the contribution of algal cells to the attenuation of light within natural waters. I. General treatment of suspensions of pigmented cells*, New Phytol., 75, 11–20.

Kirk J. T. O., 1975b, *A theoretical analysis of the contributions of algal cells to the attenuation of light within natural waters. II. Spherical cells*, New Phytol., 75, 21–36.

Kyewalyanga M., Platt T., Sathyendranath S., 1992, *Ocean primary production calculated by spectral and broad-band models*, Mar. Ecol. Prog. Ser., 85, 171 –185.

LaRoche J., Breitbarth E., 2005, *Importance of the diazotrophs as a source of new nitrogen in the ocean*, J. Sea Res., 53 (1–2), 67–91.

Le Quéré C., Harrison S. P., Prentice I. C., Buitenhuis E. T., Aumont O., Bopp L., Claustre H., da Cunha L. C., Geider R., Giraud X., Klaas C., Kohfeld K. E.,

Legendre L., Manizza M., Platt T., Rivkin R. B., Sathyendranath S., Uitz J., Watson A. J., Wolf-Gladrow D., 2005, *Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models*, Glob. Change Biol., 11, 2016–2040.

Lee Z.-P. (ed.), 2006, *Remote sensing of inherent optical properties: fundamentals, tests of algorithms, and applications*, IOCCG, Rep. No 5, Dartmouth, (Canada), 126 pp.

Lindley S. T., Barber R. T., 1998, *Phytoplankton response to natural and experimental iron addition*, Deep-Sea Res. Pt. II, 45 (6), 1135–1150.

Loisel H., Morel A., 1998, *Light scattering and chlorophyll concentration in case 1 waters: A reexamination*, Limnol. Oceanogr., 43 (5), 847–858.

Longhurst A., Sathyendranath S., Platt T., Caverhill C., 1995, *An estimate of global primary production in the ocean from satellite radiometer data*, J. Plankton Res., 17 (6), 1245–1271.

Lutz V. A., Sathyendranath S., Head E. J. H., 1996, *Absorption coefficient of phytoplankton: Regional variations in the North Atlantic*, Mar. Ecol. Prog. Ser., 135, 197–213.

MacIntyre H. L., Kana T. M., Anning T., Geider R. J., 2002, *Photoacclimation of photosynthesis irradiance response curves and photosynthetic pigments in microalgae and cyanobacteria*, J. Phycol., 38, 17–38.

Moore L. R., Rocap G., Chisholm S. W., 1998, *Physiology and molecular phylogeny of coexisting Prochlorococcus ecotypes*, Nature, 393 (6684), 464–467.

Morel A., 1988, *Optical modeling of the upper ocean in relation to its biogenous matter content (Case I waters)*, J. Geophys. Res., 93 (C9), 10749–10768.

Morel A., 1991, *Light and marine photosynthesis: a spectral model with geochemical and climatological implications*, Prog. Oceanogr., 26, 263–306.

Morel A., Antoine D., Babin M., Dandonneau Y., 1996, *Measured and modeled primary production in the northeast Atlantic (EUMELI JGOFS program): the impact of natural variations in photosynthetic parameters on model predictive skill*, Deep-Sea Res. Pt. I, 43 (8), 1273–1304.

Morel A., Bricaud A., 1981, *Theoretical results concerning light absorption in a discrete medium, and application to specific absorption of phytoplankton*, Deep-Sea Res. Pt. I, 28 (A11), 1375–1393.

Morel A., Prieur L., 1977, *Analysis of variations in ocean color*, Limnol. Oceanogr., 22, 709–722.

Platt T., Bird D. F., Sathyendranath S., 1991, *Critical depth and marine primary production*, Proc. Roy. Soc. Lond. B-Biol. Sci., 246, 205–217.

Platt T., Broomhead D. S., Sathyendranath S., Edwards A. M., Murphy E. J., 2003a, *Phytoplankton biomass and residual nitrate in the pelagic ecosystem*, Proc. Roy. Soc. Lond. A-Math. Phys., 459, 1063–1073.

Platt T., Denman K. L., Jassby A. D., 1977, *Modeling the productivity of phytoplankton*, [in:] *The Sea. Vol. 6. Ideas and observations on progress in the study of the seas*, E. D. Goldberg (ed.), John Wiley, New York, 807–856.

Platt T., Gallegos C. L., Harrison W. G., 1980, *Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton*, J. Mar. Res., 38 (4), 687–701.

Platt T., Jassby A. D., 1976, *The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton*, J. Phycol., 12 (4), 421–430.

Platt T., Sathyendranath S., 1988, *Oceanic primary production: Estimation by remote sensing at local and regional scales*, Science, 241, 1613–1620.

Platt T., Sathyendranath S., 1991, *Biological production models as elements of coupled, atmosphere-ocean models for climate research*, J. Geophys. Res., 96 (C2), 2585–2592.

Platt T., Sathyendranath S., 1993, *Estimators of primary production for interpretation of remotely sensed data on ocean color*, J. Geophys. Res., 98 (C8), 14561–14576.

Platt T., Sathyendranath S., Caverhill C. M., Lewis M. R., 1988, *Ocean primary production and available light: Further algorithms for remote sensing*, Deep-Sea Res. Pt. I, 35 (6), 855–879.

Platt T., Sathyendranath S., Edwards A. M., Broomhead D. S., Ulloa O., 2003b, *Nitrate supply and demand in the mixed layer of the ocean*, Mar. Ecol. Prog. Ser., 254, 3–9.

Pope R. M., Fry E. S., 1997, *Absorption spectrum (380–700 nm) of pure water: II. Integrating cavity measurements*, Appl. Opt., 36, 8710–8723.

Preisendorfer R. W., 1976, *Hydrologic optics. Vol. I. Introduction*, U. S. Dept. Comm., Nat. Ocean. Atmos. Adm., Environ. Res. Lab., Honolulu.

Prieur L., 1976, *Transfert radiatif dans les eaux de la mer. Application à la détermination des paramètres optiques caractérisant leur teneur en substances dissoutes et leur contenu en particules*, Dissertation, Univ. Pierre et Marie Curie, Paris, 326 pp.

Prieur L., Sathyendranath S., 1981, *An optical classification of coastal and oceanic waters based on the specific spectral absorption curves of phytoplankton pigments, dissolved organic matter, and other particulate materials*, Limnol. Oceanogr., 26, 671–689.

Ragni M., D'Alcalà M. R., 2004, *Light as an information carrier underwater*, J. Plankton Res., 26 (4), 433–443.

Raven J., Caldeira K., Elderfield H., Hough-Guldberg O., Liss P., Riebesell U., Shepherd J., Turley C. M., Watson A., 2005, *Ocean acidification due to increasing atmospheric carbon dioxide*, Roy. Soc. Lond. Policy Doc. 12/05, 68 pp.

Rodriguez F., Garrido J., Crespo B., Arbones B., Figueiras F., 2006, *Size-fractionated phytoplankton pigment groups in the NW Iberian upwelling system: Impact of the Iberian Poleward Current*, Mar. Ecol. Prog. Ser., 323, 59–73.

Sarthou G., Timmermans K. R., Blain S., Tréguer P., 2005, *Growth physiology and fate of diatoms in the ocean: a review*, J. Sea Res., 53 (1–2), 25–42.

Sathyendranath S. (ed.), 2000, *Remote sensing of ocean colour in coastal, and other optically-complex, waters*, IOCCG, Rep. No 3, Dartmouth, (Canada), 145 pp.

Sathyendranath S., Cota G., Stuart V., Maass H., Platt T., 2001, *Remote sensing of phytoplankton pigments: a comparison of empirical and theoretical approaches*, Int. J. Remote Sens., 22 (2–3), 249–273.

Sathyendranath S., Lazzara L., Prieur L., 1987, *Variations in the spectral values of specific absorption of phytoplankton*, Limnol. Oceanogr., 32 (2), 403–415.

Sathyendranath S., Longhurst A., Caverhill C. M., Platt T., 1995, *Regionally and seasonally differentiated primary production in the North Atlantic*, Deep-Sea Res. Pt. I, 42 (10), 1773–1802.

Sathyendranath S., Platt T., 1988, *The spectral irradiance field at the surface and in the interior of the ocean: A model for applications in oceanography and remote sensing*, J. Geophys. Res., 93 (C8), 9270–9280.

Sathyendranath S., Platt T., 1989, *Computation of aquatic primary production: extended formalism to include effect of angular and spectral distribution of light*, Limnol. Oceanogr., 34 (1), 188–198.

Sathyendranath S., Platt T., 1993, *Remote sensing of water-column primary production*, [in:] *Measurement of primary production from the molecular to the global scale*, W. K. W. Li & S. Y. Maestrini (eds.), ICES Mar. Sci. Symp. Vol. 197, 236–243.

Sathyendranath S., Platt T., 1997, *Analytic model of ocean color*, Appl. Opt., 36 (12), 2620–2629.

Sathyendranath S., Platt T., 2000, *Mixed-layer dynamics and primary production in the Arabian Sea*, [in:] *The changing ocean carbon cycle: A midterm synthesis of the Joint Global Ocean Flux Study*, R. B. Hanson, H. W. Ducklow & J. G. Field (eds.), Int. Geosph.-Biosph. Prog. Book Ser., Cambridge Univ. Press, Cambridge, 285–299.

Sathyendranath S., Stuart V., Platt T., Bouman H., Ulloa O., Maass H., 2005, *Remote sensing of ocean colour: Towards algorithms for retrieval of pigment composition*, Indian J. Mar. Sci., 34 (4), 333–340.

Sathyendranath S., Watts L., Devred E., Platt T., Caverhill C., Maass H., 2004, *Discrimination of diatoms from other phytoplankton using ocean-colour data*, Mar. Ecol. Prog. Ser., 272, 59–68.

Schoemann V., Becquevort S., Stefels J., Rousseau W., Lancelot C. 2005, *Phaeocystis blooms in the global ocean and their controlling mechanisms: a review*, J. Sea Res., 53 (1–2), 43–66.

Smayda T. J., 1963, *Succession of phytoplankton, and the ocean as an holocoenotic environment*, [in:] *Symposium on marine microbiology*, C. H. Oppenheimer (ed.), Charles C. Thomas, Springfield, Illinois, 260–274.

Smith H., 2000, *Phytochromes and light signal perception by plants – an emerging synthesis*, Nature, 407 (6804), 585–91.

Smyth T. J., Tilstone G. H., Groom S. B., 2005, *Integration of radiative transfer into satellite models of ocean primary production*, J. Geophys. Res.-Oceans, 110 (C10), C10014, doi: 1029/2004JC002784.

Stuart V., Head E., 2005, *The BIO method*, [in:] *The Second SeaWiFS HPLC Analysis Round-Robin Experiment (SeaHARRE-2)*, S. B. Hooker (ed.), Greenbelt, MD, NASA/TM 2005-212785, 112 pp.

Subramaniam A., Brown C. W., Hood R. R., Carpenter E. J., Capone, D. G., 2002, *Detecting Trichodesmium blooms in SeaWiFS imagery*, Deep-Sea Res. Pt. II, 49 (1–3), 107–121. 29

Subramaniam A., Carpenter E. J., Falkowski P. G., 1999a, *Bio-optical properties of the marine diazotrophic cyanobacteria Trichodesmium spp. II. A reflectance model for remote sensing*, Limnol. Oceanogr., 44 (3), 618–627.

Subramaniam A., Carpenter E. J., Karentz D., Falkowski P. G., 1999b, *Bio-optical properties of the marine diazotrophic cyanobacteria Trichodesmium spp. I. Absorption and photosynthetic action spectra*, Limnol. Oceanogr., 44 (3), 608 –617.

Sverdrup H. U., 1953, *On conditions for the vernal blooming of phytoplankton*, J. Conseil, 18 (3), 287–295.

Ting C. S., Rocap G., King J., Chisholm S. W., 2002, *Cyanobacterial photosynthesis in the oceans: the origins and significance of divergent light-harvesting strategies*, Trends Microbiol., 10 (3), 134–142.

Veldhuis M. J. W., Timmermans K. R., Croot P., van der Wagt B., 2005, *Picophytoplankton; a comparative study of their biochemical composition and photosynthetic properties*, J. Sea Res., 53 (1–2), 7–24.

Woods J. D., Barkmann W., Horch A., 1984, *Solar heating of the oceans – diurnal, seasonal and meridional variation*, Q. J. Roy. Meteorol. Soc., 110, 633–656.

Woźniak B., Dera J., Ficek D., Ostrowska M., Majchrowski R., 2002, *Dependence of the photosynthesis quantum yield in oceans on environmental factors*, Oceanologia, 44 (4), 439–459.

Appendix
The Morel Model

According to Morel (1991), Morel et al. (1996) and Smyth et al. (2005), chlorophyll-specific production P^B at depth z and time t is given by (with notation as in Morel et al. 1996):

$$P^B = 12\phi_\mu \int a^*(\lambda)E(\lambda)\mathrm{d}\lambda \tag{28}$$

where $E(\lambda)$ is the irradiance at depth z and wavelength λ, $a^*(\lambda)$ is the specific absorption by phytoplankton at λ, and ϕ_μ is given by:

$$\phi_\mu = \phi_{\mu\max}\frac{KPUR}{PUR}\left(1 - e^{-PUR/KPUR}\right), \tag{29}$$

if photoinhibition is ignored such that we have:

$$P^B = 12\phi_{\mu\max}\frac{KPUR}{PUR}\left(1 - e^{-PUR/KPUR}\right)\int a^*(\lambda)E(\lambda)\mathrm{d}\lambda. \tag{30}$$

Here, $\phi_{\mu\max}$ is the maximum realised quantum yield of photosynthesis, and the model parameters PUR and $KPUR$ are defined as:

$$PUR = \frac{\int a^*(\lambda)E(\lambda)\mathrm{d}\lambda}{a^*_{\max}} \tag{31}$$

and

$$KPUR = E_k\frac{\overline{a^*}}{a^*_{\max}}. \tag{32}$$

The quantity $\overline{a^*}$ in eq. (32) is a weighted integral, where the weighting function is the irradiance $E(\lambda)$:

$$\overline{a^*} = \frac{\int a^*(\lambda)E(\lambda)\mathrm{d}\lambda}{\int E(\lambda)\mathrm{d}\lambda}, \tag{33}$$

and $E_k = P^B_m/\alpha^B$, where α^B is again a weighted integral, as defined in these models:

$$\alpha^B = 12\phi_{\mu\max}\overline{a^*} = 12\phi_{\mu\max}\frac{\int a^*(\lambda)E(\lambda)\mathrm{d}\lambda}{\int E(\lambda)\mathrm{d}\lambda}. \tag{34}$$

Now, eq. (30) has two parts: a scale factor, say A:

$$A = 12\phi_{\mu\max}\frac{KPUR}{PUR}\int a^*(\lambda)E(\lambda)\mathrm{d}\lambda \tag{35}$$

which multiplies an exponential function with exponent $-PUR/KPUR$. From eqs. (31) and (32), we have:

$$\frac{PUR}{KPUR} = \frac{\int a^*(\lambda)E(\lambda)\mathrm{d}\lambda}{a^*_{\max}}\ \frac{12\overline{a^*}\phi_{\mu\max}a^*_{\max}}{12P^B_m\overline{a^*}} \tag{36}$$

and cancelling terms, we get:

$$\frac{PUR}{KPUR} = \frac{\phi_{\mu\max}}{P^B_m}\int a^*(\lambda)E(\lambda)\mathrm{d}\lambda. \tag{37}$$

The above equation assumes that the maximum realised quantum yield of photosynthesis, $\phi_{\mu\max}$, is wavelength independent. If we dropped that assumption, quantum yield would have to be taken inside the wavelength integral. Since, by definition, we have $\phi_{\mu\max}(\lambda)a^*(\lambda) = \alpha^B(\lambda)$ (see Platt & Jassby 1976), the above equation can be rewritten as:

$$\frac{PUR}{KPUR} = \frac{1}{P^B_m}\int \alpha^B(\lambda)E(\lambda)\mathrm{d}\lambda. \tag{38}$$

Substituting for $KPUR/PUR$ and for $\alpha^B(\lambda)$ in eq. (35) the scale factor A becomes:

$$A = 12\int \alpha^B(\lambda)E(\lambda)\mathrm{d}\lambda\frac{P^B_m}{\int \alpha^B(\lambda)E(\lambda)\mathrm{d}\lambda}, \tag{39}$$

and cancelling like terms, we get:

$$A = 12P^B_m. \tag{40}$$

The equation for chlorophyll-specific production can now be written as:

$$P^B = 12P^B_m\left(1-\exp\left(\frac{\int \alpha^B(\lambda)E(\lambda)\mathrm{d}\lambda}{P^B_m}\right)\right), \tag{41}$$

which has the same formalism as the Platt & Sathyendranath (1988) and Sathyendranath & Platt (1989) model, at least to within a factor of μ, the mean cosine for downwelling irradiance, and the factor of 12, which arises from reporting production in moles instead of by weight. The difference of

μ also disappears if the photosynthetically-active radiation in the model of Morel (1991) is measured in scalar irradiance instead of vector irradiance. Note that Platt & Sathyendranath have sometimes used a different $P-E$ formalism than that of Platt et al. (1980), but it has been shown that the choice of equation for the $P-E$ relationship does not lead to much difference in the answers, if one stays away from a couple of extremes (Platt et al. 1977).