Variations in the Absorption Characteristics of Phytoplankton: Implications for Remote Sensing

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Abstract

Over the course of the last ten years, our laboratory has acquired a data base of about 800 absorption spectra of natural phytoplankton samples collected from several oceanic regions. These data have been analysed, along with concurrent information on pigment composition estimated using High Performance Liquid Chromatography (HPLC) techniques. The analysis highlights some general trends in the absorption characteristics and in pigment composition with changes in the phytoplankton biomass, as indexed by the concentration of the main pigment, chlorophyll-a. An empirical, three-parameter model can be used to estimate the absorption coefficient of phytoplankton at a given wavelength as a function of chlorophyll-a concentration. But such models fail to account for deviations in the absorption characteristics from the main trend. The implications for the estimation of both phytoplankton biomass and primary production from remotely-sensed data are examined.

Introduction

In the bi-partite optical classification scheme formulated by Morel and Prieur (Morel and Prieur 1977; Morel 1980; Sathyendranath and Morel 1983), oceanic waters are classified as Case 1 waters, if phytoplankton can be considered to be the major, independent variable responsible for changes in the optical properties of the water. If this condition does not hold, then the waters are classified as Case 2 waters. In Case 1 waters, a suite of parameterisations have been developed, for computing phytoplankton absorption and scattering properties as functions of a single variable, the concentration of chlorophyll-a (Prieur and Sathyendranath 1981; Morel 1988; Sathyendranath and Platt 1988; Sathyendranath et al. 1999). It would, however, be wrong to assume from these developments that chlorophyll-a concentration is the only property that is modified when there is a change in the concentration of phytoplankton. The factors that cause variations in the optical properties of phytoplankton merit more attention, particularly in the context of developing biomass algorithms for quantitative interpretation of ocean-colour data in Case 1 waters. This is the topic of our paper.

What causes variations in ocean colour in Case 1 waters? As shown schematically in Figure 1, the optical properties of phytoplankton, and hence of the waters, will of course depend on the concentration of chlorophyll-a, which is present in all phytoplankton, either in its regular form, or as the variant divinyl chlorophyll-a. However, it must not be overlooked that changes in chlorophyll-a concentration are typically accompanied by variations in the relative concentrations of auxiliary pigments, and in the size structure of the phytoplankton population, both of which can affect the optical properties of phytoplankton. Pigment composition and size structure vary with the species composition of the phytoplankton population. Therefore, one may expect the optical properties to differ depending on whether the population is dominated by a single species or class, or by many species belonging to many classes. In the case of multi-species populations, the optical properties would depend on the species composition, whereas in the case of mono-specific blooms, they would depend on the dominant species present.

If indeed so many changes accompany variations in phytoplankton concentration, how is it that we have been able to develop successful models that employ a single variable, chlorophyll-a, to parameterise the optical properties of phytoplankton in Case 1 waters? The success of these models implies that many of the changes listed above follow certain predictable trends, which follow changes in chlorophyll-a. In this paper we analyse a data base of phytoplankton absorption spectra and pigment composition, to highlight general trends in species succession that accompany changes in phytoplankton concentration (as indexed by chlorophyll-a concentration), and the implications for modelling. We also examine the modifications in pigment composition that occur along with changes in chlorophyll-a concentration, and the possibilities for deriving pigment composition from absorption data.

A certain amount of yellow substance or coloured dissolved organic matter is also expected to be present in Case 1 waters, and to modify ocean colour by its presence (Fig. 1). But in this paper, we focus our attention exclusively on the absorption characteristics of phytoplankton, their variability in oceanic waters, and their implications for remote sensing.

Data and Methods

The absorption data were collected over the course of the last ten years or so, using the filter technique (Yentsch 1962) as modified by Kishino et al. (1985). The measured absorption values were corrected for pathlength amplification on the filters, using the results of Hoepffner and Sathyendranath (1992) and Moore et al. (1995), as outlined in Kyewalyanga et al. (1998) and Stuart et al. (1998). Pigment composition was measured using High Performance Liquid Chromatography (HPLC) technique, following the protocol of Head and Horne (1993). All the data were collected using consistent techniques, during 13 cruises, with the total number of samples numbering about 750.

Results

Species-related Variations in Absorption Spectra: Analysis of diagnostic pigments measured by HPLC technique suggested that prochlorophytes often tended to dominate in very oligotrophic waters, cyanophytes increasing in importance with increase in the chlorophyll-a concentration. Diatoms tended to be the dominant group in high-chlorophyll environments, with prymnesiophytes being present in high concentrations in a diversity of environments. The specific absorption coefficient at 440 nm was very high for the smallcelled prochlorophytes, dropping off to a minimum for the relatively large-celled diatom populations.

The corresponding variations in pigment composition introduced changes in the shapes of the absorption spectra. These changes were found to have non-negligible effects on light absorption by phytoplankton at the base of the euphotic zone (the depth of the 1% light level), in computations that employed a spectral model of light penetration to estimate the spectral quality of light at the 1% light level. At this optical depth, prochlorophytes appear to be most efficient at light absorption in oligotrophic waters, and diatoms in eutrophic waters.

General Trends in the Concentrations of Some Major Auxiliary Pigments Relative to Chlorophyll-a: The concentration of chlorophyll-b relative to chlorophyll-a dropped off with increasing concentrations of phytoplankton, whereas the relative concentration of chlorophyll-c tended to increase with phytoplankton concentration. We also examined the trends in non-photosynthetic carotenoids (diadinoxanthin, diatoxanthin, zeaxanthin, alloxanthin, β-carotene) and in photosynthetic carotenoids (fucoxanthin, 19'-hexanoyloxyfucoxanthin, 19'-butanoyloxyfucoxanthin, peridinin, prasinoxanthin, α-carotene). The concentrations of non-photosynthetic carotenoids relative to chlorophyll-a tended to fall off with depth, and with latitude, with highest values (predominantly zeaxanthin) appearing in surface waters of oligotrophic tropical oceans. On the other hand, the relative concentrations of photosynthetic carotenoids (mostly fucoxanthin) showed a tendency to increase with increase in phytoplankton concentration. Some of these trends were weak, and there was a certain amount of variability around them. A consequence of the variations in the size structure and in the pigment composition of phytoplankton with change in concentration was that the relationship between phytoplankton absorption at 440 nm and the chlorophyll-a concentration was non-linear, requiring empirical fits that involved two or three parameters. The variability around these trends was reflected in the fact that chlorophyll-a was able to explain only about 72% of the variance in the data, even with a non-linear fit.

Relationships between Pigments and Phytoplankton Absorption: If one used linear relationships, then chlorophyll-a by itself was able to explain only 68% of the variance in phytoplankton absorption at 440 nm. The explained variance increased to 79% if the concentrations of chlorophylls-b and -c and photosynthetic and non-photosynthetic carotenoids were included in a multiple linear regression.

From the perspective of remote sensing, it is also interesting to pose the question from the opposite angle, and examine whether information on phytoplankton absorption at multiple wavelengths can be used to derive any information on pigment composition, over and above information on chlorophyll-a concentration. In fact, multiple linear regression of various pigments on SeaWiFS wavelengths in the visible showed that these absorption values could be used to derive some information on pigments other than chlorophyll-a (Table 1). Of all the major pigments examined, the results were poorest for chlorophyll-b. But, as mentioned earlier, the relative concentration of chlorophyll-b tended to decrease with increase in chlorophyll-a concentration, and it is possible that the methods would work better in waters where chlorophyll-b was present in significant amounts. To examine this idea further, the data set were split into two groups, based on the relative concentration of chlorophyll-c to chlorophyll-a. Table 2 shows the results for analyses on the sub-set of data for which the chlorophyll-c:chlorophyll-a ratio was less than 0.2. In fact, for this subset, the variances explained are higher, not just for chlorophyll-b, but for all pigments.

Discussion and Conclusion

Models of phytoplankton absorption in Case 1 waters rely on a suite of changes in phytoplankton cell size and pigment composition that typically accompany variations in chlorophyll-a concentration. Fluctuations around these general trends can introduce significant effects on the performance of algorithms for interpretation of ocean-colour data, as demonstrated by Sathyendranath et al. (1999), using data on the absorption characteristics of diatom and prymnesiophyte blooms from the Labrador Sea. The results reported here, preliminary as they are, suggest that it may be possible to overcome some of the limitations of present-day algorithms by making use of multiple wavelengths to distinguish between some of the major pigments. Partitioning the data based on an index of pigment composition (say the ratio of chlorophyll-c to chlorophyll-a) appears to improve the results, suggesting that branching algorithms may perform better than universal algorithms, and that the criteria for branching might be based on remotely-detectable signals.

The analysis presented here is based on absorption data, and has not broached the additional problems associated with the non-linearity in the relationships between absorption and ocean colour or those problems associated with the influence of substances such as yellow substances on ocean colour. In this sense, the results presented here must be considered to be preliminary, from the point of view of interpretation of remotely-sensed data on ocean colour.

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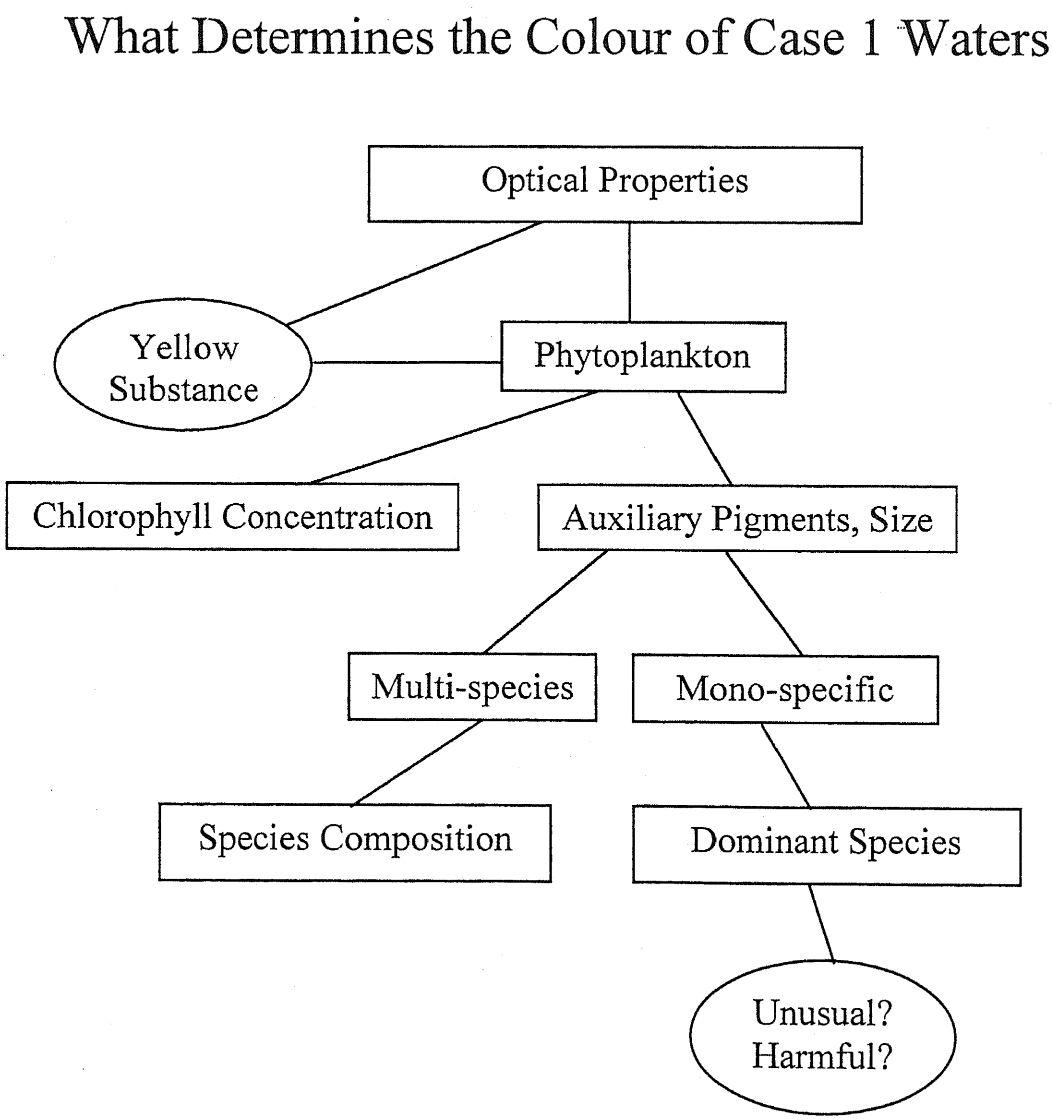

Figure 1: Schematic diagram showing sources of variations in phytoplankton absorption characteristics in the aquatic environment. These in turn influence ocean colour.

Table 1. Results of multiple linear regression analysis of HPLC-derived pigment concentration on phytoplankton absorption at SeaWiFS wavelengths in the visible region of the spectrum, using the entire database ($n = 757$). Wavelengths used in the multiple regression are indicated by tick marks. All the coefficients associated with these wavelengths were significant ($p = 0.0000$). Extending the multiple regression to include all six SeaWiFS wavelengths in the visible did not result in any marked increase in the reported r^2 values. 19-Hex = 19'-Hexanoyloxyfucoxanthin; PC = photosynthetic carotenoids; NPC = non-photosynthetic carotenoids (see text for list of carotenoids in each group).

	SeaWiFS wavelengths used						
Pigment	**412 nm**	**443 nm**	**490 nm**	**510 nm**	**555 nm**	**670 nm**	r^2
Chl-*a*			✓	✓		✓	0.86
Chl-*b*	✓		✓	✓	✓		0.47
Chl-*c*	✓					✓	0.74
Fucoxanthin			✓	✓		✓	0.87
19-Hex	✓	✓	✓			✓	0.53
PC			✓	✓	✓		0.86
NPC		✓	✓	✓	✓		0.72

Table 2. Results of multiple linear regression analysis of HPLC-derived pigment concentration on phytoplankton absorption at SeaWiFS wavelengths in the visible region of the spectrum, similar to the analyses presented in Table 1 in all respects, except that only samples with chlorophyll-a:chlorophyll-c ratios < 0.2 ($n = 450$) are used here.

	SeaWiFS wavelengths used						
Pigment	**412 nm**	**443 nm**	**490 nm**	**510 nm**	**555 nm**	**670 nm**	r^2
Chl-*a*	✓	✓			✓	✓	0.91
Chl-*b*		✓	✓	✓		✓	0.66
Chl-*c*	✓	✓	✓		✓	✓	0.94
Fucoxanthin	✓	✓			✓	✓	0.93
19-Hex	✓		✓			✓	0.65
PC	✓	✓			✓	✓	0.92
NPC	✓	✓		✓	✓	✓	0.75