Remote Sensing of Environment 112 (2008) 3366–3375

Contents lists available at ScienceDirect

Remote Sensing of Environment

journal homepage: www.elsevier.com/locate/rse

Remote sensing of phytoplankton functional types

Anitha Nair [a], Shubha Sathyendranath [b], Trevor Platt [c], Jesus Morales [d], Venetia Stuart [e], Marie-Hélène Forget [a,*], Emmanuel Devred [e], Heather Bouman [f]

[a] Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1
[b] Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth PL1 3DH, United Kingdom
[c] Bedford Institute of Oceanography, Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2
[d] IFAPA Centro "Agua del Pino", P. O. Box 104, 21071 Huelva, Spain
[e] Department of Oceanography, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1
[f] Department of Earth Sciences, Oxford University, Parks Road, Oxford OX1 3PR, United Kingdom

ARTICLE INFO

Article history:
Received 30 March 2007
Received in revised form 28 November 2007
Accepted 19 January 2008

Keywords:
Ocean colour
Phytoplankton
HPLC
Remote sensing
Phytoplankton pigments
Phytoplankton functional types
Phytoplankton size

ABSTRACT

The principal goal in early missions of satellite-borne visible spectral radiometry (ocean colour) was to create synoptic fields of phytoplankton biomass indexed as concentration of chlorophyll-a. In the context of climate change, a major application of the results has been in the modelling of primary production and the ocean carbon cycle. It is now recognised that a partition of the marine autotrophic pool into a suite of phytoplankton functional types, each type having a characteristic role in the biogeochemical cycle of the ocean, would increase our understanding of the role of phytoplankton in the global carbon cycle. At the same time, new methods have been emerging that use visible spectral radiometry to map some of the phytoplankton functional types. Here, we assess the state of the art, and suggest paths for future work.

© 2008 Elsevier Inc. All rights reserved.

1. Introduction

Carbon dioxide released to the atmosphere by burning fossil fuels, or deforestation, has three possible fates: it may be absorbed by the terrestrial ecosystem, it may be absorbed by the ocean or it may continue to reside in the atmosphere. According to House et al. (2002) 26% is absorbed in the ocean and 40% on land. The ocean, therefore, plays a major role in the planetary carbon cycle. In the face of acute concern about the accelerating greenhouse effect, oceanographers are required to develop models of the ocean carbon cycle, and to predict how it might be affected by climate change.

Phytoplankton functional type (PFT)-based models are the most recent in a series of coupled ocean-ecosystem models developed to achieve a deeper understanding of ocean biogeochemistry. The concept of PFT evolved out of the growing realization, from a biogeochemical perspective, that all phytoplankton are not the same: they differ greatly in their biogeochemical functions. In this concept, the marine autotrophic pool is partitioned such that phytoplankton with common biogeochemical functions (for example calcification, silicification, DMS production or nitrogen fixation), but not necessarily having a common phylogeny, are grouped in the same compartment. Another option for partition is according to cell size, which achieves some of the same goals.

Terms such as guilds, functional traits and functional groups have also been used in the recent literature to describe marine phytoplankton communities and analyse their roles in regional or global processes. These concepts are closely related to those of functional types.

A guild (Root, 1967) is defined as a group of species that exploit the same class of environmental resource in a similar way (Simberloff & Dayan, 1991). The term is applied usually in discussions of competition, and is invoked more generally in animal ecology than in plant studies (Blondel, 2002). However, some recent papers have re-introduced this concept in the analysis of marine phytoplankton populations (Hood et al., 2006; Sabetta et al., 2004, 2005; Vadrucci et al., 2003, 2004), thus linking the concepts of functional groups and types.

A functional trait is "a well-defined, measurable property of organisms, usually measured at the individual level, and used comparatively across species" (McGill et al., 2006). Functional traits can be used to identify phytoplankton functional types (Aiken et al., 2007; Le Quéré et al., 2005). In this context a phytoplankton functional type should be a group of species that, irrespective of phylogeny, share similar traits. The concept of functional traits has recently provided an underpinning for studies in community ecology (Kearney & Porter, 2006; McGill et al., 2006). The interaction between species and environmental changes has provided the ecological concept of functional diversity, defined by

* Corresponding author.
E-mail address: mforget@dal.ca (M.-H. Forget).

0034-4257/$ – see front matter © 2008 Elsevier Inc. All rights reserved.
doi:10.1016/j.rse.2008.01.021

Steele (1991) as "the variety of different responses to environmental changes, especially the diverse space and time scales at which organisms react to each other and to the environment". It is thus easy to see that there are similarities between the concepts of traits and types.

The functional group concept was used in an ecological approach by Fauchald and Jumars (1979) and a freshwater phytoplankton classification into functional groups has been proposed by Reynolds et al. (2002). For marine phytoplankton some attempts have been made to organise species within certain classes of phytoplankton according to their function; thus, dinoflagellates have been analyzed from a habitat distribution perspective (Smayda & Reynolds, 2003) and from a statistical perspective (Vila & Masó, 2005). Iglesias-Rodríguez et al. (2002) have described the functional role of coccolithophorids within the carbon cycle. The functional group concept has also been applied for grouping marine phytoplankton according to their roles in biogeochemical processes or cycles (Hood et al., 2006; Le Quéré et al., 2005), thus linking the concepts of groups and types.

This paper reviews the current status of the PFT concept, its advantages and limitations, and explores the potential for monitoring their distribution globally using remote sensing of visible spectral radiometry.

2. Classification of phytoplankton functional types

2.1. Size and function

An early approach to partitioning of the autotrophic pool was that based on cell size (Sieburth et al., 1978). In this approach, the phytoplankton are separated into the following size classes: picophytoplankton (0.2–2 μm), nanophytoplankton (2–20 μm), and microphytoplankton (>20 μm). The influence of size on the physiology of the phytoplankton is well-established (Chisholm, 1992; Platt & Jassby, 1976; Raven, 1998). Variability in some biogeochemical functions can be addressed by this approach. For example, picophytoplankton, owing to their high surface-area-to-volume ratio, can absorb nutrients with high efficiency under nutrient-limited conditions, and therefore dominate oligotrophic waters. They sink more slowly than larger cells. Microphytoplankton, represented chiefly by diatoms and dinoflagellates, dominate nutrient-rich waters and are the principal agents of the export of carbon to deeper waters. However, a size-based approach would fail to separate some biogeochemical functions, if phytoplankton characterised by different functions fell under the same size class. Both the dimethyl sulphide (DMS) producers and calcifiers are often grouped under the size class of nanophytoplankton (see Table 1 and in Le Quéré et al., 2005), but the two groups have different effects on atmospheric carbon dioxide. DMS producers, with their ability to form cloud-condensation nuclei cause a negative feedback on temperature under increasing atmospheric carbon dioxide, whereas change in alkalinity associated with calcification favour increased release of carbon dioxide to the atmosphere, causing a change in the opposite direction. Further, picoplanktonic nitrogen-fixers, important for new production, are grouped with non-nitrogen-fixing picoautotrophs.

Thus, a size-based approach to functionality in phytoplankton is not fully satisfactory, from a biogeochemical perspective. However, size does have a significant role in marine food webs. For example, the role of pico- and nanophytoplankton in the food web leading to gelatinous zooplankton (e.g. jellyfish) has been described by Parsons and Lalli (2002). Community structure indicated by the size spectrum has been correlated with areas of high fish production (e.g., Caddy et al., 1995; Ryther, 1969) and blooms of microphytoplankton have been correlated with the success of early larval stages of fish: see Cushing (1975) for the background on the match–mismatch theory, and Platt et al. (2003) and Fuentes-Yaco et al. (2007) for application of the theory in a remote-sensing context. The links between size, weight, abundance, growth and metabolic rate, long recognised as the basis for the size spectra of pelagic organisms (Platt & Denman, 1977, 1978), are now known as the metabolic theory of ecology.

Based on their distinct biogeochemical roles, phytoplankton can be classified functionally into nitrogen-fixers, calcifiers, silicifiers and DMS producers. A brief description of each group is given below.

2.2. Nitrogen-fixers

The ability of diazotrophs to utilize atmospheric nitrogen as a raw material for growth has a direct impact on the nitrogen cycle and on other factors that influence climate change. *Trichodesmium* is the dominant nitrogen-fixing organism in oligotrophic oceans. Nitrogen-fixing phytoplankton other than *Trichodesmium* have also been identified. For example, *Katagnymene* sp., which occurs in open-ocean waters, is known to be diazotrophic (Zehr et al., 2000). Cyanobacterial symbionts of certain open-ocean diatoms such as *Chaetoceros*, *Bacteriastrum*, and *Rhizosolenia* are capable of nitrogen fixation. The symbiont of the diatom *Hemiaulus* sp. contributes about 15% of the total nitrogen fixed in the Pacific ocean (Fuhrman & Capone, 2001; Scharek et al., 1999). Molecular techniques have revealed the potential for diazotrophy in a large cyanobacterial population with cell size in the range of 3–10 μm (Zehr et al., 2001).

2.3. Silicifiers

Four taxonomic groups of phytoplanktonic silicifiers are recognised, namely chrysophyta, silicoflagellates, xanthophyta and bacillariophyta (Brownlee & Taylor, 2002). Diatoms (bacillariophyta) are the dominant silicifiers in the marine ecosystem and contribute about 40% of the total marine primary production (Sarthou et al., 2005). They are usually found in nutrient-rich waters and are known to be the major organisms in the spring bloom occurring in temperate and polar regions (Sarthou et al., 2005). Diatoms use silica to form their cell walls, known as frustules. The siliceous cell wall increases the density of the cells which causes them to sink faster thus contributing to the carbon export. Further, the cell wall protects them against grazing by zooplankton (Smetacek, 2001).

2.4. Calcifiers

Phytoplankton calcifiers (coccolithophores) are characterised by the presence of external plates, called coccoliths, made of calcium carbonate. The formation of calcium carbonate lowers the surface ocean carbonate concentration, reduces sea water alkalinity, and produces carbon dioxide. The release of carbon dioxide during calcification causes an increase in the partial pressure of carbon dioxide in surface waters and therefore serves as a potential source of carbon dioxide to the atmosphere (Robertson et al., 1994; Rost & Riebesell, 2004). The increasing concentration of atmospheric carbon dioxide in turn lowers the carbonate concentration of the surface ocean and affects calcification. The calcium carbonate produced constitutes a potential sink for

Table 1
Summary of the properties of different phytoplankton functional groups

Trait	Pico-autotrophs	Nitrogen-fixers	Calcifiers	Silicifiers	DMS producers
Cell size (μm)	0.7–2.0	Variable	5–10	20–200	5
Light	High	High	Low	Low	High–Low
Nutrient required		N_2 gas	Calcium	Silica	
Iron	Low	High	High	High	High
Loss	Grazing	Viral lysis	Sinking	Sinking	Lysis, grazing
Bio-optical properties	High a^*_β	a^*_B high in UV High $b^*_{b\beta}$	High $b^*_{b\beta}$	Low, flat a^*_β	?
Remote sensing	Yes	Yes	Yes	Yes	No

Nominal size ranges for different functional types are taken from Le Quéré et al. (2005).

particulate inorganic carbon. Further, calcium carbonate also serves as a ballast for the efficient transport of particulate organic carbon to deep sea (Armstrong et al., 2002). The distribution of coccolithophores ranges from oligotrophic subtropical gyres to temperate and high-latitude semi-eutrophic waters (Brown & Yoder, 1994).

2.5. DMS producers

Marine dimethyl sulphide (DMS) emission is the main natural source of reduced sulphur to the atmosphere and contributes about 15×10^{12} to 33×10^{12} g S per year to the total atmospheric sulphur budget (Simó, 2001). DMS influences the Earth's climate through the formation of sulphate aerosols. The sulphate aerosols maintain the global radiation balance by serving as cloud-condensation nuclei that can back-scatter the radiation from the sun and help in cooling the earth. The acidic oxidation products of DMS react with rain droplets to produce acid rain (Liss et al., 1997). In the ocean, DMS is produced by the enzymatic cleavage of dimethylsulfoniopropionate (DMSP), a low molecular-mass sulphur compound found in phytoplankton belonging to the classes dinophyceae, haptophyceae, chrysophyceae, pelagophyceae and prasinophyceae. The intracellular concentration of DMSP is highest in dinoflagellates and haptophytes (Sunda et al., 2002). Haptophytes such as *Emiliania huxleyi* and *Phaeocystis* sp. are known to form extensive blooms in several coastal and oceanic waters (Tyrell & Merico, 2004). Since *E. huxleyi* is a coccolithophore as well, it is both a calcifier and a DMS producer. *Phaeocystis* blooms may represent extremely high values of carbon biomass: up to 10 mg C L^{-1} (Schoemann et al. 2005).

Thus, classification of phytoplankton into functional types is not straightforward: the same taxonomic size class may contain phytoplankton of different functional types, and the same taxonomic class of phytoplankton may include phytoplankton with diverse biogeochemical functions, and straddle a wide range of size classes. Furthermore, as we see below, no single *in situ* technique for identification of phytoplankton types is completely satisfactory.

3. Identification of phytoplankton functional types in the field

The earliest method for identifying phytoplankton was by using a light microscope. Microscopes (including light and electron microscope) are unsurpassed in the information they can provide on the phytoplankton composition up to the species level. Nevertheless, there are limitations to this method. It relies on the taxonomic skills of the observer. Species identification using the light microscope relies entirely on morphological characteristics. Thus, it is very difficult to identify picoplankton such as *Prochlorococcus* and *Synechococcus*, which contribute significantly to the total marine primary production, due to the lack of distinct morphological features. Furthermore, many species do not survive the sample preservation technique used for routine analysis. The development of epifluoroscence microscopy and electron microscopy (scanning and transmission) enabled the identification of picophytoplankton. Epifluorescence microscopy exploits the autofluorescence properties of chlorophyll and biliproteins to differentiate between *Synechococcus* and picoeukaryotic phytoplankton (Putland & Rivkin, 1999). With electron microscopy, fine details of taxonomic importance can be studied. However, the time requirement of these methods renders them unsuitable for analysis of large numbers of samples.

The limitations in microscopy can be resolved to a certain extent by the use of flow cytometry. In this method, cells in liquid suspension are allowed to pass one by one through a light field. As each cell passes, its fluorescence and light-scatter properties are measured. Scattering depends on the size, shape and refractive index of the cells. Phytoplankton possess fluorescing pigments such as chlorophyll-a and biliproteins. Chlorophyll-a (or its divinyl derivatives) is present in all phytoplankton and produces a red fluorescence signal (~685 nm). Biliproteins (phycoerythrin and phycocyanin) present in *Synechococcus* and some cryptophytes and rhodophytes, give an orange fluorescence signal (550–590 nm). The scattering and autofluorescence properties are exploited to identify different phytoplankton. The pico (0.2–2 μm) and nano (2–20 μm) eukaryotes produce a greater light-scatter signal and brighter red fluorescence than the prokaryotic picoplankton and can be distinguished from them (Dubelaar & Jonker, 2000). Prokaryotic picoplankton of similar sizes, such as *Synechococcus* and *Prochlorococcus*, can be distinguished based on the orange fluorescence signal produced by the phycoerythrin pigments present in large concentrations in *Synechococcus*, though they may be present in trace amounts in *Prochlorococcus* (Veldhuis & Kraay, 2004). Cells with special properties such as the long thin shape of pennate diatoms, the calcareous cell walls of coccolithophores, and the gas vacuoles in cyanobacteria produce specific scattering signals which can be used to distinguish them (Collier, 2000). New developments in flow cytometry include automated submersible instruments that allow long-term measurements (Olson et al., 2003; Olson & Sosik, 2007) and cell-imaging capabilities that extend the use of flow cytometer to enumerate and characterise microplankton (Sieracki et al., 1998) in addition to smaller phytoplankton.

Although the ability of flow cytometers to make rapid measurements of cells (10^5 cells per second) and to identify picoplankton confers an advantage over microscopy, there are some drawbacks. Standard flow cytometers have a limited particle size range (with an upper limit of only 15–20 μm in some instruments), which results in a selectivity against larger and colony-forming phytoplankton. Further, the carotenoids in phytoplankton do not fluoresce directly. Therefore, eukaryotes can be identified only on the basis of their size and are often classified as small or large phytoplankton. We cannot know to which algal class they belong (Collier, 2000).

Alternatively, chromatographic analysis of pigments using High Performance Liquid Chromatography (HPLC) will facilitate the separation of phytoplankton on the basis of their marker pigments (Jeffrey et al., 1997). Pigments in phytoplankton can be divided into three groups: chlorophylls (a,b,c), carotenoids (carotenes and their oxygenated derivatives known as xanthophylls) and biliproteins (phycoerythrin, phycocyanin and allophycocyanin). Apart from chlorophyll-a, which is ubiquitous and present in all phytoplankton groups (in *Prochlorococcus* as divinyl chlorophyll-a), the distribution of all the other pigments varies in different taxa of phytoplankton. Several pigments are restricted to one or two taxa and can be used as marker pigments (also called pigment fingerprints) to identify those taxa (Jeffrey et al., 1997). Phytoplankton that cannot be separated by microscopic or flow-cytometric analyses (for the reasons mentioned under the respective methods) can be classified with HPLC on the basis of their marker pigments. Automated HPLC facilitates rapid analysis of pigments to determine the phytoplankton groups from field samples. Some marker pigments are unique to certain phytoplankton taxa (unambiguous markers; see Table 2). For example, divinyl chlorophyll-a and b are unique to *Prochlorococcus* and alloxanthin to cryptophytes. However, many marker pigments are not restricted to one group. Rather, they are present in more than one phytoplankton group, which makes the identification of groups difficult (Fig. 1). The pigment composition within a particular phytoplankton class is further influenced by factors

Table 2
Unambiguous pigments in phytoplankton

Pigment	Algal-class	Reference
Divinyl chl-a and Divinyl chl-b	*Prochlorococcus*	Wright (2005)
Alloxanthin	Crytophyta	Wright (2005)
Perdinin	Type-I Dinoflagellata	Ornótfsdóttir et al. (2003)
Gyroxanthin diester	Type-2 Dinoflagellata	Ornótfsdóttir et al. (2003)
Prasinoxanthin	Type-3 Prasinophyta	Egeland et al. (1997)

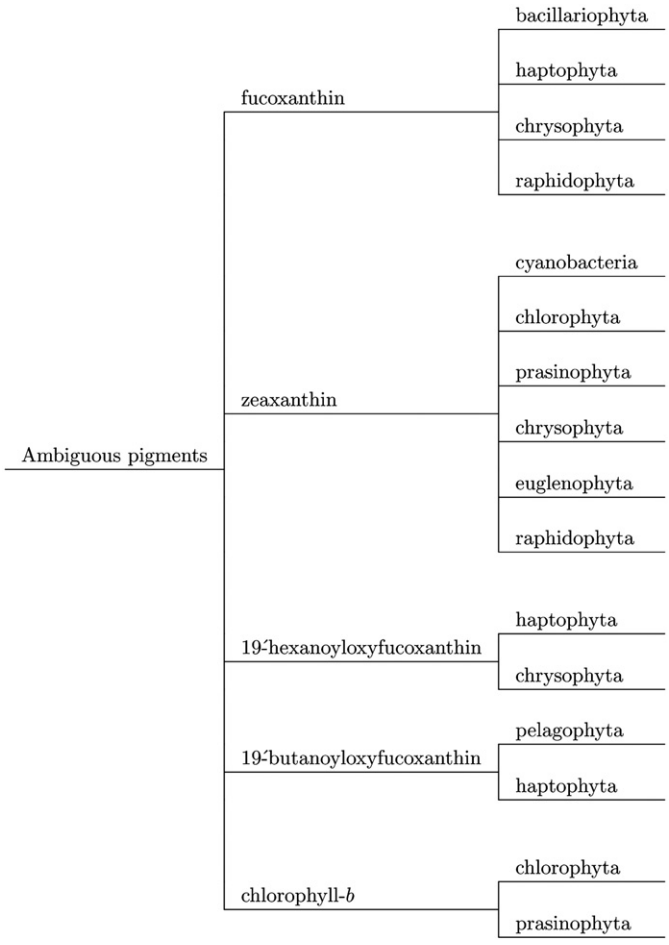

Fig. 1. Ambiguous markers for phytoplankton (summarised from Wright, 2005).

such as light (Goericke & Montoya, 1998), nitrogen (Henriksen et al., 2002; Sosik & Mitchell, 1998) and iron (Kosakowska et al., 2004), and varies with strain (Zapata et al., 2004). Separation of phytoplankton into classes with HPLC is further complicated by the presence of endosymbionts in some phytoplankton classes such as cyanobacteria in diatoms, which will give a mixed pigment signature (Hallegraeff & Jeffrey, 1984).

Molecular methods provide a solution to the limitations encountered with HPLC. These methods exploit genetic variations to distinguish between phytoplankton. DNA sequencing and probing techniques have opened avenues to distinguish organisms at all taxonomic levels, from the level of classes to ecotypes. For example, using oligonucleotide probes targeting 10 algal classes, Fuller et al. (2006) were able to survey the community structure of eukaryotic picophytoplankton in the Arabian Sea. To examine the large-scale distribution of cyanobacterial lineages a variety of methods have been employed, including dot-blot hybridization (Bouman et al., 2006; Zwirglmaier et al., 2007), fluorescence *in situ* hybridization (Zwirglmaier et al., 2008) and quantitative polymerase chain reaction (Johnson et al., 2006). In the case of *Prochlorococcus*, genetic variability is intimately linked with biogeochemical function, since different ecotypes are known to utilise different forms of nitrogen (Moore et al., 2002; Rocap et al., 2003). However, probes are not available for all possible phytoplankton functional types and specificity of probes remains an area of ongoing research.

The advantages and limitations of the methods discussed above lead to the conclusion that the use of any one of the methods in isolation would imply identification of phytoplankton that may not be entirely dependable. Hence incorporating different types of knowledge provided by the various methodologies leads to a more accurate and complete diagnosis of the phytoplankton groups. Remote sensing, which is yet another method to probe the distribution of phytoplankton types, is discussed next in more detail.

4. Remote sensing of phytoplankton functional types

Recognition of the important biogeochemical roles played by different phytoplankton groups has stimulated scientists to find ways to identify the groups using remote sensing. This is one of the major problems of the day in ocean optics (Platt et al., 2006).

Ocean-colour sensors mounted on satellites measure upwelling radiation at the top of the atmosphere in different spectral bands of the visible spectrum, which can then be processed to reveal information on water-leaving radiance and reflectance at the sea surface. Reflectance is, in turn, influenced by the absorption and scattering properties of the water column. An expression relating the reflectance $R(\lambda)$ at the sea surface, at wavelength λ, to the absorption and back-scattering coefficients is (Sathyendranath & Platt, 1997a):

$$R(\lambda) \propto \frac{b_b(\lambda)}{a(\lambda) + b_b(\lambda)}, \tag{1}$$

where $b_b(\lambda)$ and $a(\lambda)$ are the back-scattering and absorption coefficients at wavelength λ.

Similar equations with higher-order terms have also been proposed (Gordon et al., 1975; Sathyendranath & Platt, 1997b). Prieur (1976) and Morel and Prieur (1977) suggested an expression of the form:

$$R(\lambda) \propto \frac{b_b(\lambda)}{a(\lambda)}. \tag{2}$$

Under the assumption that $b_b(\lambda) \ll a(\lambda)$, which often holds for open-ocean waters, the above two equations are equivalent.

Absorption coefficient can be expressed as the sum of contributions from pure water and the dissolved and particulate substances present in it:

$$a(\lambda) = a_W(\lambda) + a_B(\lambda) + a_Y(\lambda) + a_S(\lambda), \tag{3}$$

where the subscripts W, B, Y and S represent water, phytoplankton, yellow substances (also known as coloured dissolved organic material or gelbstoff) and other suspended material (sediments, detritus, or other particulate matter) respectively. Similarly, back-scattering coefficient can be expressed as:

$$b_b(\lambda) = b_{bW}(\lambda) + b_{bB}(\lambda) + b_{bS}(\lambda), \tag{4}$$

where b_{bW}, b_{bB} and b_{bS} are contributions to back-scattering from water, phytoplankton and other particulate matter, respectively. For open-ocean waters (commonly called case 1 waters, following Morel, 1980), it is generally assumed that phytoplankton absorption is the single independent variable responsible for variations in the total absorption coefficient. Chlorophyll-a, the major phytoplankton pigment, is the conventional measure of phytoplankton abundance in the optical oceanographic literature (note, however, that other indices of abundance may also be selected according to convenience, such as the concentration of carbon associated with phytoplankton, or the magnitude of the phytoplankton absorption coefficient at a particular wavelength, as in Prieur & Sathyendranath 1981). 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, in case 1 waters. Similarly, it is common practice to model back-scattering in open-ocean waters as a function of chlorophyll-a. It has however, been argued that phytoplankton are not directly responsible for the detected back-scatter, and that the observed relationship between chlorophyll and back-scattering relies

on links between abundance of phytoplankton and other smaller scattering organisms such as bacteria and viruses (see for example Ulloa et al., 1994).

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

$$a_B(\lambda) = a_B^*(\lambda)B, \quad (5)$$

and

$$b_{bB}(\lambda) = b_{bB}^*(\lambda)B. \quad (6)$$

In a_B^* and b_{bB}^*, the asterisks indicate normalisation to chlorophyll concentration. Changes in phytoplankton species composition have the potential to modify the chlorophyll-specific coefficients, and hence b_{bB} and a_B, and the spectral reflectance. It is the differences in the spectral optical properties of different phytoplankton types that can be exploited (at least in some cases) to derive information on their presence from ocean-colour, or spectral reflectance data. As examples, some specific absorption spectra of field samples dominated by different types of phytoplankton are shown in Fig. 2. Additional examples can be found in an IOCCG report (IOCCG, 2000). It is well-known that the specific absorption characteristics of a particular phytoplankton species can vary with growth conditions (Fig. 3), introducing uncertainties into algorithms designed for PFT retrievals from space. Another problem is that we know little about potential variations in the back-scattering properties of various phytoplankton functional types in the field. Many of the issues related to modelling back-scattering have been discussed by Morel and Maritorena (2001). This is clearly an area where more work is needed, if only to establish the limits of applicability of methods designed for remote sensing of PFTs.

To identify phytoplankton types from space, one has to rely on particular optical characteristics of each type that may be used to distinguish that type from all others. Since the major changes in the remotely-sensed signal from the ocean arise from changes in abundance (the concentration B varies over four orders of magnitude in the ocean), identification of types is a second-order problem which has to rely on very small signals (changes in the shape of spectral optical characteristics) (IOCCG, 1998). Otherwise, it has to rely on phytoplankton abundance (expressed for example as chlorophyll concentration or absorption coefficient) as an indicator for phytoplankton type, since it is well-known that the phytoplankton community structure changes with the trophic status of the waters.

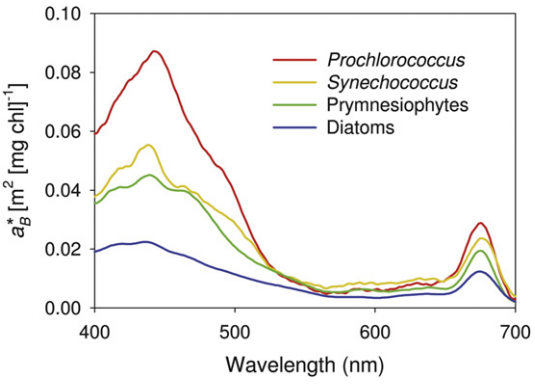

Fig. 2. Specific absorption spectra of field samples of phytoplankton dominated by different phytoplankton types to illustrate variations in optical properties of phytoplankton related to changes in type. The curves have been smoothed to minimise spikes due to noise in the signal (see also Sathyendranath & Platt, 2007).

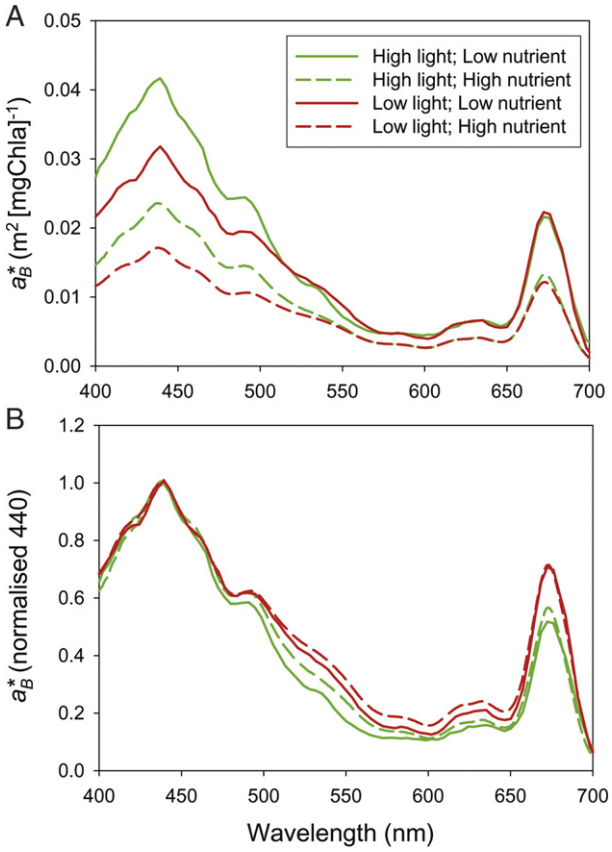

Fig. 3. Absorption spectra of laboratory cultures of a species of diatom, *Thalassiosira pseudonana*, grown under different light and nutrient regimes. (A) Spectra are normalised to the concentration of chlorophyll-a in the culture. (B) Spectra are normalised to the value of absorption coefficient at 440 nm.

We next examine algorithms that are now available for identifying some phytoplankton types from space.

4.1. Coccolithophores

Algorithms are already in use to identify coccolithophores from space (Ackleson et al., 1994; Brown & Podestá, 1997; Brown & Yoder, 1994; Gordon et al., 2001; Smyth et al., 2002; Tyrell et al., 1999). The calcite plates, or coccoliths produced by coccolithophores are highly reflective (they have high back-scattering), and under bloom conditions, impart a milky-turquoise colour to the water which is visible in satellite images (Fig. 4). Only *E. huxleyi* and *Gephyrocapsa oceanica* are known to form such large blooms detectable by satellites (Iglesias-Rodríguez et al., 2002). It is important to note that this qualitative method identifies the presence of calcites and not the presence of the live phytoplankton themselves. Conditions arising from other causes that mimic the reflectance of coccolithophore blooms also exist, with potential to introduce errors in the coccolith algorithms. For example, accumulation of hydrogen sulphide is found to impart a milky-turquoise colour to the waters off the coast of Namibia (Weeks et al., 2002). Furthermore, Broerse et al. (2003) found that SeaWiFS images of the Bering sea in winter showed pale turquoise-coloured water patches resembling coccolithophore blooms. *In situ* sampling in the area, however, showed no indication of a bloom. Instead it revealed the presence of a large number of empty diatom frustules assumed to be the remnants of the spring bloom that were resuspended from the seafloor as a result of storms. The bright patches observed in the satellite image were attributed to the back-scattering by opal material of which diatom frustules are made. Suspended sediments having a calcareous composition can also mimic coccolithophore blooms

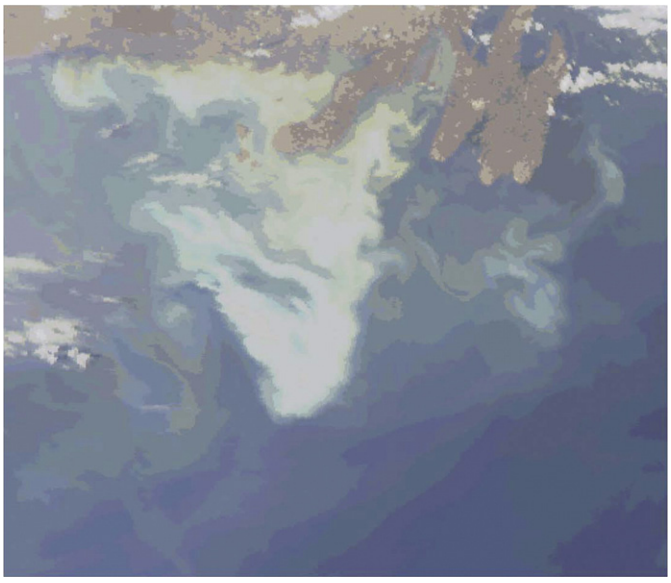

Fig. 4. Image of a coccolithophore bloom off Newfoundland from a pseudo-true-colour SeaWiFS image of 26 August, 2005 (Credit: SeaWiFS Project, NASA/GSFC and Orbimage).

(Brown & Podestá 1997). Such difficulties indicate that remote sensing of coccoliths will not be straight forward. Further, the ratio of coccolith numbers to cell numbers is variable with the physiological state of the population, which complicates the quantitative estimation of coccolithophores from the coccolith algorithms.

4.2. Cyanobacteria

Trichodesmium is a cyanobacterium that can be identified from remotely-sensed data (Subramaniam et al., 1999). The features associated with *Trichodesmium* blooms that can be detected by ocean-colour sensors include the characteristic golden yellow colour of *Trichodesmium* blooms on the surface waters, and associated exudation of CDOM (coloured dissolved organic matter) which increases the absorption in the near UV and blue portion of the spectrum (Steinberg et al., 2004); the increased absorption in the UV region by water-soluble pigments known as mycosporine-like amino acids; the high back-scattering of light attributed to the gas vesicles present in the *Trichodesmium* cells; and the distinctive absorption and fluorescence spectra of their major accessory pigment phycoerythrin (Subramaniam et al., 2002). Algorithms have been developed to identify *Trichodesmium* from other phytoplankton under very low chlorophyll-a conditions (Subramaniam et al., 2002). Westberry et al. (2005) have used a reflectance model that exploits the differences between the optical properties of *Trichodesmium* and those of other "typical" phytoplankton to identify this PFT from space, and have shown that the algorithm has a high rate of correct identification, using an independent *in situ* data set.

The nitrogen-fixing cyanobacterium *Nodularia* is known to form extensive blooms in the Baltic Sea. Since they are known to float on the surface waters and have optical properties similar to *Trichodesmium*, information supplemented from *in situ* observations would be required, if one wished to distinguish between the two species, even though functionally they are both classified as nitrogen-fixers. For example, according to existing *in situ* observations, *Trichodesmium* and *Nodularia* do not coexist anywhere, facilitating their identification based on biogeographical region. Jupp et al. (1994) have also suggested a method to identify and map cyanobacteria in turbid coastal waters by remote sensing, which is based on the fluorescence signal of biliproteins in the cyanobacteria. This method, which was successfully applied to turbid coastal waters around Australia, has not, to our knowledge, been tested elsewhere.

4.3. Diatoms

Algorithms have also been proposed to identify diatoms from space. Sathyendranath et al. (2004) proposed an algorithm to discriminate diatoms from other types of phytoplankton in the North West Atlantic. The variations in the specific absorption coefficient of phytoplankton with taxa and cell size (Sathyendranath et al., 2001) are used as the basis for the algorithm, which was used to generate regional maps of distribution of diatoms. They pointed out that errors in atmospheric correction, and resultant errors in the estimated spectral reflectance, were a limiting factor. Comparisons with available *in situ* data gave good results. An example of a diatom distribution map generated using this algorithm is shown in Fig. 5. Further testing with data from other regions is necessary before implementing the algorithm on a global scale.

4.4. Multiple types

Alvain et al. (2005) identified dominant phytoplankton groups using an empirical approach based on their spectral effects on ocean colour. Four phytoplankton groups, namely haptophytes, *Prochlorococcus*, *Synechococcus*-like cyanobacteria and diatoms were identified by their method. Gege (1998) applied absorption spectra derived from reflectance spectra using an inverse-reflectance model to identify five taxonomic groups of phytoplankton. Aiken et al. (2007) compiled a list of diagnostic bio-optical traits for various types of phytoplankton, and used that for mapping the distribution of those types in the southern

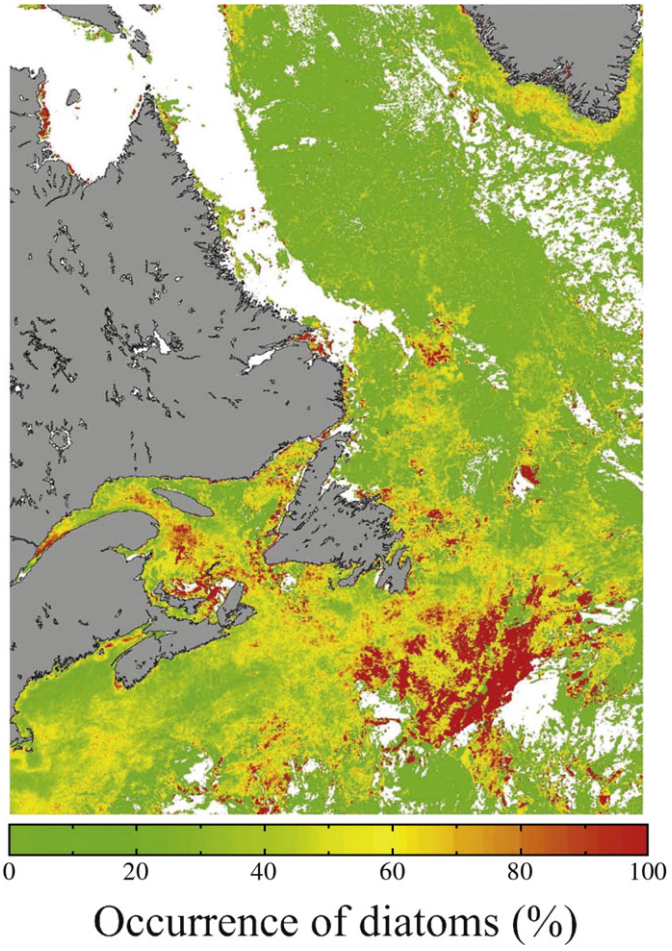

Fig. 5. Image showing the probability of occurrence of diatoms in the North-West Atlantic, for the bi-weekly period of 1–15 April, 2005, generated using the algorithm of Sathyendranath et al. (2004).

Benguela ecosystem using MERIS (MEdium Resolution Imaging Spectrometer) data.

The possibility of retrieval of spectral inherent optical properties, especially the absorption coefficient, from ocean-colour data (IOCCG, 2006) increases the potential for elucidating the chemo-taxonomic (or pigmental) composition of phytoplankton based on absorption spectra (Bricaud et al., 2007; Devred et al., 2006; Sathyendranath et al., 2005). Clearly, the number of independent variables retrieved cannot be greater than the number of independent wavebands available for retrieval algorithms. Furthermore, when working with data that are not error-free, a built-in redundancy of wavebands is recommended. Some of these and related problems associated with retrieval of multiple variables from remote sensing of ocean colour has been discussed by IOCCG (1998).

The remote-sensing methods described above have to rely on small deviations in the spectral signatures of phytoplankton (either absorption or back-scattering) associated with changes in the phytoplankton community structure. Another approach is to relate phytoplankton type to the total phytoplankton abundance in the water, or related optical properties.

4.5. Phytoplankton size from space

Uitz et al. (2006) analysed a large HPLC pigment database of samples collected from open-ocean waters. They used the method of Vidussi et al. (2001) to partition the phytoplankton into different size classes (micro-, nano- and picophytoplankton) using pigment markers. They then combined their results with those of Morel and Berthon (1989) to calculate the contribution of the three size classes of phytoplankton to total chlorophyll-a integrated over the euphotic depth and to create vertical profiles of size-fractionated chlorophyll-a. Since surface chlorophyll-a is measurable from satellites, and since empirical relationships are established linking surface chlorophyll-a to size structure and vertical structure, the authors were able to map the distribution of the three size classes of phytoplankton at the global scale. The method of Uitz et al. (2006) exploits typically-observed relationships between phytoplankton types and chlorophyll concentrations: in low-chlorophyll, oligotrophic conditions, small-celled organisms such as *Prochlorococcus* and *Synechococcus* dominate, and in higher-chlorophyll, eutrophic waters, large-celled phytoplankton such as diatoms tend to dominate (Sathyendranath et al., 2005).

Several procedures are now available to extract phytoplankton absorption spectra from remotely-sensed data (IOCCG, 2006). Rather than simple wavelength-ratios of reflectances that are used in many chlorophyll-retrieval algorithms, these algorithms rely on more sophisticated mathematical tools, including neural networks and non-linear optimisation techniques. Spectral characteristics of absorption so-retrieved can then be used to infer the size of phytoplankton present: (Ciotti et al., 2002; Ciotti & Bricaud 2006; Devred et al., 2006). These methods rely on the decrease in the specific absorption of phytoplankton and an increased flattening of the absorption spectrum, with increase in cell size of phytoplankton.

5. Discussion

It may be said that there are two types of approaches to deriving PFTs from ocean-colour data. In one type, which we might call the abundance-based approach, the eutrophic status of the waters, as indicated by chlorophyll concentration (Uitz et al., 2006) or related variables such as the magnitude of the absorption coefficient of phytoplankton, is related to community structure. Aiken et al. (2007) used bio-optical ranges to classify phytoplankton into three size classes, and then used back-scattering characteristics to subdivide size classes into functional types. In the other type, which we might call the spectral-characteristics approach, small differences in the optical traits of PFTs (for example, change in the shape of the absorption spectrum of phytoplankton) are used to distinguish one type of phytoplankton from another. Both types have their advantages and disadvantages. In the abundance-based approach, PFT algorithms build on existing, well-established algorithms for retrieval of total phytoplankton abundance or the inherent optical properties of phytoplankton. On the other hand, this type of algorithm will not be able to distinguish between blooms of different PFTs that might have the same abundance. For example, blooms of *Phaeocystis* and diatoms are known to co-occur in the Labrador Sea (Sathyendranath et al., 2001). An abundance-based approach would not be able to distinguish between these two types of blooms, if both blooms had similar abundances. The spectral-characteristics approach does not have this particular limitation; on the other hand, efforts to exploit small differences in the spectral characteristics of phytoplankton may not be always successful. Clearly, the spectral-characteristics approach will not be able to distinguish between different PFTs with the same optical features. Another issue to tackle with this approach is within-species or within-functional-type variability in optical properties. For example, diatoms are typically large-celled organisms and show flattened absorption spectra that are characteristic of large cells (Sathyendranath et al., 2004; Sathyendranath & Platt, 2007). But not all diatoms are large, and the absorption spectrum of small diatoms will likely look different from that of their large counterparts, and would probably be misclassified with the spectral-characteristics approach. As seen in Fig. 3, the absorption characteristics of the same species can change with growth conditions.

Our information base on both the absorption and scattering characteristics of various types of phytoplankton has to be improved to understand better the potential and limitations of ocean colour as a tool for mapping phytoplankton functional types from space. This will require both controlled experiments in the laboratory on key functional types as well as *in situ* measurements of these properties in the field under different environmental conditions. As we understand better how the optical traits of PFTs vary with environmental conditions, it may become possible to constrain better the assignment of optical properties of functional types in particular cases.

As we have seen, there are size-based approaches to classifying functional types, and pigment-based approaches. Both cell size and pigment composition affect spectral characteristics of phytoplankton absorption (Sathyendranth et al., 1987): the larger the cells, the flatter the phytoplankton absorption spectra. The pigment composition of the cells imposes further modifications on the absorption spectra as does the intracellular concentration of pigments. Thus, at present, the remote-sensing approach is more compatible with size-based classification and chemo-taxonomic classification than with flow-cytometric methods or microscopic enumeration. In some instances, it may even be argued that remote sensing provides advantages over some of the *in situ* methods. In particular, both *Phaeocystis* and coccolithophores, which are functionally quite distinct, are both in the same class (haptophytes); they belong to the same size class, and they have similar pigments. But when the coccolithophores are in a different functional mode, producing large numbers of coccoliths, they are easily detectable from space (subject to some caution, as noted earlier). In fact, remote sensing may be credited with the discovery of the widespread nature of coccolithophore blooms.

Although blooms of phytoplankton such as coccolithophores, diatoms and *Trichodesmium* can be detected successfully from space, the real challenge of ocean-colour remote sensing lies in the identification of different groups of phytoplankton under non-bloom conditions. When multiple types of phytoplankton are present in the water, we have to rewrite Eq. (5) as:

$$a_{\mathrm{B}}(\lambda) = \sum_{i=1}^{n} a^{*}_{\mathrm{B}i} B_i, \tag{7}$$

where B_i is the chlorophyll concentration of the ith phytoplankton type, $a^{*}_{\mathrm{B}i}(\lambda)$ is the specific absorption of that type at λ, and n is the number of phytoplankton types present. Gege (1998) has used

spectral decomposition of phytoplankton absorption spectra retrieved from reflectance data to obtain information on the major phytoplankton types present in Lake Constance. Hoepffner and Sathyendranath (1993) and Stuart et al. (1998) for example, have used spectral decomposition of phytoplankton absorption data to derive information on phytoplankton types present (see also Sathyendranath et al., 2005). Such methods have great potential for remote sensing when hyperspectral remote-sensing data become available. At present, the limited wavelength resolution of satellite data available, combined with errors introduced by atmospheric correction procedures, inhibits further developments in this direction: since the system is non-linear, small errors in atmospheric correction can introduce large errors in retrieved absorption, and hence in the PFTs identified. Realistically, these errors and the non-linearities will set an upper limit on the number of functional types that can be retrieved from space, and on the circumstances in which the methods can be applied successfully. However, these limitations are yet to be established: there is certainly scope for further improvements in the area as hyperspectral remote sensing from space becomes a reality.

Recently, considerable attention is being given to the use of PFTs as a tool to enhance prediction of the response of the ecosystem to anthropogenic changes in the global environment. It has been recognized that ecosystem models, incorporating multiple phytoplankton groups, might help to overcome some of the limitations of conventional models that treat phytoplankton as a single pool (Doney, 1999). Attempts to formulate such PFT-based ecosystem models and to couple them with general circulation models have met with some success (e.g., Gregg et al., 2003; Le Quéré et al., 2005; Moore et al., 2004). The PFT-based biogeochemical models are a recent development and some problems are apparent. Some authors (Anderson, 2005; Flynn, 2005) have challenged the predictive capability of such models, arguing that the increase in complexity of models is accompanied by an increase in the number of parameters and that the available observations are inadequate either to constrain the parameter values or to evaluate the performance of the models. More information, therefore, is required on the distribution of PFTs, as well as on their responses to different factors, both abiotic and biotic, to improve such models and to test them. Remote sensing constitutes an important source of data on the distributions of some PFTs.

Though this paper has emphasised the biogeochemical functions of different types, and how remote sensing could contribute to mapping the distribution of these types from space, it must also be recognised that these recent developments also serve as a contribution from remote sensing to the mapping of biodiversity in marine phytoplankton at the global scale: an achievement that was unimaginable only a few years ago.

6. Conclusion

Remote sensing is the only means to obtain concurrent global distribution of PFTs, and scientists rely heavily on satellite information for comparison with outputs from models. One necessary requisite for facilitating such applications of satellite-derived PFTs is improved understanding of the errors associated with the satellite-derived fields: when comparing model outputs with remotely-sensed fields of PFTs, modellers should be able to use confidence limits on the data. Such information is at present mostly lacking, given the status of development of PFT algorithms, and given the paucity of suitable *in situ* data for evaluating remotely-sensed fields.

Comparison of satellite data with *in situ* data also has to address the difficult issue of differences in the scales of the two types of measurements: *in situ* measurements are typically made on volumes of the order of 1 L of sea water, whereas satellite measurements are applicable to areas of the order of 1 km^2. It is also extremely difficult to obtain match-ups of the two types of data streams that are concurrent in both time and space. When the goal is to obtain values that are representative of large areas, one might even ask whether *in situ* observations constitute the "truth" for validation of satellite data. One possible approach to address the issue of scale would be to design experiments in which standard *in situ* sea truth measurements are made along with local ocean-colour measurements at sea level, to validate the algorithm at compatible time and space scales. The errors so established would then have to be combined with error estimates for atmospheric correction and errors in the performance of the sensors themselves to establish overall errors in remote sensing from space. These considerations highlight the importance of field experiments that combine biological and optical measurements as a tool for testing and validating remote-sensing algorithms.

Attempts to identify PFTs from space represent a new development, and no doubt have potential for further improvement: as our understanding of the optical properties of phytoplankton grows; as spectral and radiometric resolution of satellite sensors improves; and as our ability to tease out information from the highly-complex and non-linear system represented by ocean colour increases, we anticipate further advances in extracting information on PFTs from space. But it is just as important to realise that remote sensing cannot provide all the answers. What is needed is a judicious combination of *in situ* and remote-sensing techniques, to help extract maximum information on the distribution of PFTs at the global scale.

Acknowledgements

This work is supported by the Canadian Space Agency (GRIP Programme) and by Discovery Grants to TP and SS from the Natural Sciences and Engineering Research Council of Canada. This work is also a contribution to NCEO and Oceans 2005 programmes of NERC (UK). Satellite data courtesy of NASA and Orbimage. The manuscript benefitted from helpful and detailed comments from Heidi Sosik and two other reviewers and the editors of the special issue.

References

Aiken, J., Fishwick, J. R., Lavender, S. J., Barlow, R., Moore, G., Sessions, H., et al. (2007). Validation of MERIS reflectance and chlorophyll during the BENCAL cruise October, 2002: Preliminary validation of new products for phytoplankton functional types and photosynthetic parameters. *International Journal of Remote Sensing*, *28*, 497–516.

Ackleson, S. G., Balch, W. M., & Holligan, P. M. (1994). Response of water-leaving radiance to particulate calcite and chlorophyll a concentrations: A model for Gulf of Maine coccolithophore blooms. *Journal of Geophysical Research*, *99*, 7483–7499.

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 Research I*, *52*, 1989–2004.

Anderson, T. R. (2005). Plankton functional type modelling: Running before we can walk? *Journal of Plankton Research*, *27*, 1073–1081.

Armstrong, R. A., Lee, C., Hedges, J. I., Honjo, S., & Wakeham, S. G. (2002). A new, mechanistic model for organic carbon fluxes in the ocean based on the quantitative association of POC with ballast minerals. *Deep-Sea Research*, *49*, 219–236.

Blondel, J. (2002). Guilds or functional groups: Does it matter? *Oikos*, *100*, 223–231.

Bouman, H. A., Ulloa, O., Scanlan, D. J., Zwirglmaier, K., Li, W. K. W., Platt, T., et al. (2006). Oceanographic basis of the global surface distribution of *Prochlorococcus* ecotypes. *Science*, *312*, 918–921.

Bricaud, A., Mejia, C., Blondeau-Patissier, D., Claustre, H., Crepon, M., & Thiria, S. (2007). Retrieval of pigment concentrations and size structure of algal populations from their absorption spectra using multilayered perceptrons. *Applied Optics*, *46*, 1251–1260.

Broerse, A. T. C., Tyrrell, T., Young, J. R., Poulton, A. J., Merico, A., Balch, W. M., et al. (2003). The cause of bright waters in the Bering Sea in winter. *Continental Shelf Research*, *23*, 1579–1596.

Brown, C. W., & Yoder, J. A. (1994). Coccolithophorid blooms in the global ocean. *Journal of Geophysical Research*, *99*, 7467–7482.

Brown, C. W., & Podestá, G. P. (1997). Remote sensing of coccolithophore blooms in the Western South Atlantic Ocean. *Remote Sensing of Environment*, *60*, 83–91.

Brownlee, C., and Taylor, A.R. (2002) Algal calcification and silification. In: Encyclopedia of life sciences. Macmillan Publishers Ltd, Nature Publishing Group. 1-6.

Caddy, J. F., Fefk, R., & Do-Chi, T. (1995). Productivity estimates for the Mediterranean: Evidence of accelerating ecological change. *Effects of riverine inputs on coastal ecosystems and fisheries resources. FAO Tech. Rep.* (Vol. 249, pp. 1–17). Rome: FAO.

Chisholm, S. W. (1992). Phytoplankton size. In P. G. Falkowski & A. D. Woodhead (Eds.), *Primary productivity and biogeochemical cycles in the sea* (pp. 213–237). Plenum press.

Ciotti, A. M., & Bricaud, A. (2006). Retrievals of a size parameter for phytoplankton and spectral light absorption by colored detrital matter from water leaving radiances at SeaWiFS channels in a continental shelf region off Brazil. *Limnology and Oceanography Methods*, *4*, 237–253.

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

Collier, J. L. (2000). Flow cytometry and the single cell in phycology. *Journal of Phycology*, *36*, 628–644.

Cushing, D. H. (1975). *Marine ecology and fisheries.*: Cambridge University Press 292 pp.

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. *Journal of Geophysical Research*, *III*, C03011, doi:10.1029/2005JC002880.

Doney, S. C. (1999). Major challenges confronting marine biogeochemical modelling. *Global Biogeochemistry Cycles*, *13*, 705–714.

Dubelaar, G. B. J., & Jonker, R. R. (2000). Flow cytometry as a tool for the study of phytoplankton. *Scientia Marina*, *64*, 135–156.

Egeland, E. S., Guillard, R. R. L., & Liaaen-Jensen, S. (1997). Additional carotenoid prototype representatives and a general chemosystematic evaluation of carotenoids in Prasinophyceae (Chorophyta). *Phytochemistry*, *44*, 1087–1097.

Fauchald, K., & Jumars, P. A. (1979). The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biology Annual Review*, *17*, 193–284.

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

Fuentes-Yaco, C., Koeller, P. A., Sathyendranath, S., & Platt, T. (2007). Shrimp (*Pandalus borealis*) growth and timing of the spring phytoplankton bloom on the Newfoundland-Labrador Shelf. *Fishery and Oceanography*, *16*, 116–129.

Fuhrman, J. A., & Capone, D. G. (2001). Nifty nanoplankton. *Nature*, *412*, 593–594.

Fuller, N. J., Tarran, G. A., Cummings, D. G., Woodward, E. M. S., Orcutt, K. M., Yallop, M., et al. (2006). Molecular analysis of photosynthetic picoeukaryote community structure along an Arabian Sea transect. *Limnology and Oceanography*, *51*, 2502–2514.

Goericke, R., & Montoya, J. P. (1998). Estimating the contribution of microalgal taxa to chlorophyll-*a* in the field-variations of pigment ratios under nutrient and light-limited growth. *Marine Ecology. Progress Series*, *169*, 97–112.

Gordon, H. R., Boynton, G. C., Balch, W. M., Groom, S. B., Harbour, D. S., & Smyth, T. J. (2001). Retrieval of coccolithophore calcite concentration from SeaWiFS imagery. *Geophysical Research Letters*, *28*(8), 1587–1590.

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

Gege, P. (1998). Characterization of the phytoplankton in Lake Constance for classification by remote sensing. *Archivos Hydrobiology*, *53*, 179–193.

Gregg, W. W., Ginoux, P., Schopf, P. S., & Casey, N. W. (2003). Phytoplankton and iron: Validation of a global three-dimensional ocean biogeochemical model. *Deep-Sea Research II*, *50*, 3143–3169.

Hallegraeff, G. M., & Jeffrey, S. W. (1984). Tropical phytoplankton species and pigments of continental shelf waters of north and north-west Australia. *Marine Ecology. Progress Series*, *20*, 59–74.

Henriksen, P., Riemann, B., Kaas, H., Sorensen, H. M., & Sorensen, H. L. (2002). Effects of nutrient-limitation and irradiance on marine phytoplankton pigments. *Journal of Plankton Research*, *24*, 835–858.

Hoepffner, N., & Sathyendranath, S. (1993). Determination of the major groups of phytoplankton pigments from the absorption spectra of total particulate matter. *Journal of Geophysical Research*, *98*, 722789–722803.

Hood, R. R., Laws, E. A., Armstrong, R. A., Bates, N. R., Brown, C. W., Carlson, C. A., et al. (2006). Pelagic functional group modeling: Progress, challenges and prospects. *Deep-Sea Research II*, *53*, 459–512.

House, J. I., Prentice, I. C., & Le Quéré, C. (2002). Maximum impacts of future reforestation or deforestation on atmospheric CO_2. *Global Change Biology*, *8*, 1047–1052.

Iglesias-Rodríguez, M. D., Brown, C. W., Doney, S. C., Kleypas, J., Kolber, D., Kolber, Z., et al. (2002). Representing key phytoplankton functional groups in ocean carbon cycle models: Coccolithophorids. *Global Biogeochemistry Cycles*, *16*, 1100, doi:10.1029/2001GB001454.

IOCCG. (1998). Minimum requirements for an operational ocean-colour sensor for the open ocean. In A. Morel (Ed.), *Reports of the International Ocean-Colour Coordinating Group, No. 1* Dartmouth, Canada: IOCCG. 46 pp.

IOCCG. (2000). Remote sensing of ocean colour in coastal, and other optically-complex, waters. In S. Sathyendranath (Ed.), *Reports of the International Ocean-Colour Coordinating Group, No. 3.* Dartmouth, Canada: IOCCG. 140 pp.

IOCCG. (2006). Remote sensing of inherent optical properties: Fundamentals, tests of algorithms and applications. In Z. P. Lee (Ed.), *Reports of the International Ocean-Colour Coordinating Group, No. 5.* Dartmouth, Canada: IOCCG. 126 pp.

Jeffrey, S. W., Mantoura, R. F. C., & Wright, S. W. (1997). *Phytoplankton pigments in oceanography: Guidelines to modern methods* (pp. 447). Paris: UNESCO.

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. *Australian Journal of Marine and Freshwater Research*, *45*, 801–828.

Johnson, Z. I., Zinser, E. R., Coe, A., McNulty, N. P., Woodward, E. M. S., & Chisholm, S. W. (2006). Niche partitioning among *Prochlorococcus* ecotypes along ocean-scale environmental gradients. *Science*, *311*, 1737–1740.

Kearney, M., & Porter, W. P. (2006). Ecologists have already started rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, *21*, 481–482.

Kosakowska, A., Lewandowska, J., Stoń, J., & Burkiewicz, K. (2004). Qualitative and quantitative composition of pigments in *Phaeodactylum tricornutum* (Bacillariophyceae) stressed by iron. *BioMetals*, *17*, 45–52.

Le Quéré, C., Harrison, S. P., Prentice, C. I., Buitenhuis, E. T., Aumonts, O., Bopp, L., et al. (2005). Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models. *Global Change Biology*, *11*, 2016–2040.

Liss, P. S., Hatton, A. D., Malin, G., Nightingale, P. D., & Turner, S. M. (1997). Marine sulphur emissions. *Philosophical Transactions of the Royal Society of London. B*, *352*, 159–169.

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends Ecology Evolution*, *21*, 178–185.

Moore, K. J., Doney, S. C., & Lindsay, K. (2004). Upper ocean ecosystem dynamics and iron cycling in a global three-dimensional model. *Global Biogeochemistry Cycles*, *18*, GB4028, doi:10.1029/2004/GB002220.

Moore, L. R., Post, A. F., Rocap, G., & Chisholm, S. W. (2002). Utilization of different nitrogen sources by the marine cyanobacteria *Prochlorococcus* and *Synechococcus*. *Limnology and Oceanography*, *47*, 989–996.

Morel, A. (1980). In-water and remote measurement of ocean color. *Boundary-Layer Meteorology*, *18*, 177–201.

Morel, A., & Prieur, L. (1977). Analysis of variations in ocean color. *Limnology and Oceanography*, *22*, 709–722.

Morel, A., & Berthon, J. F. (1989). Surface pigments, algal biomass profiles, and potential production of the euphotic layer: Relationships reinvestigated in view of remote-sensing applications. *Limnology and Oceanography*, *34*, 1545–1562.

Morel, A., & Maritorena, S. (2001). Bio-optical properties of oceanic waters: A reappraisal. *Journal of Geophysical Research*, *106*, 7163–7180.

Olson, R. J., Shalapyonok, A. A., & Sosik, H. M. (2003). An automated submersible flow cytometer for pico- and nanophytoplankton: FlowCytobot. *Deep-Sea Research I*, *50*, 301–315.

Olson, R. J., & Sosik, H. M. (2007). A submersible imaging-in-flow instrument to analyze nano- and microplankton: Imaging FlowCytobot. *Limnology and Oceanography Methods*, *5*, 195–203.

Ornólfsdóttir, E. B., Pinckney, J. L., & Tester, P. A. (2003). Quantification of the relative abundance of the toxic dinoflagellate, *Karenia brevis* (Dinophyta), using unique photopigments. *Journal of Phycology*, *39*, 449–457.

Parsons, T. R., & Lalli, C. M. (2002). Jellyfish population explosions: Revisiting a hypothesis of possible causes. *La Mer*, *40*, 111–121.

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

Platt, T., & Denman, K. L. (1977). Organisation in the pelagic ecosystem. *HelgolaÉnder Wissenschaftliche Meeresuntersuchungen*, *30*, 575–581.

Platt, T., & Denman, K. L. (1978). The structure of pelagic marine ecosystems. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* (pp. 60–65).

Platt, T., Fuentes-Yaco, C., & Frank, K. T. (2003). Spring algal bloom and larval fish survival. *Nature*, *423*, 398–399.

Platt, T., Sathyendranath, S., & Stuart, V. (2006). Why study biological oceanography? *Aquabiology*, *28*, 542–557.

Prieur, L. (1976) Transfer radiatif dans les eaux de mer. Application à la détermination de paramètres optiques caractérisant leur teneur en substances dissoutes et leur contenu en particules. D.S. thesis, Univ. Pierre et Marie Curie.

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. *Limnology and Oceanography*, *26*, 671–689.

Putland, J. N., & Rivkin, R. B. (1999). Influence of storage mode and duration on the microscopic enumeration of *Synechococcus* from a cold coastal ocean environment. *Marine Ecology. Progress Series*, *17*, 191–199.

Raven, J. A. (1998). Small is beautiful: The picophytoplankton. *Functional Ecology*, *12*, 503–513.

Reynolds, C. S., Huszar, V., Kruk, C., Naselli-Flores, L., & Melo, S. (2002). Towards a functional classification of the freshwater phytoplankton. *Journal of Plankton Research*, *24*, 417–428.

Robertson, J. E., Robinson, C., Turner, D. R., Holligan, P., Watson, A. J., Boyd, P., et al. (1994). The impact of a coccolithophore bloom on oceanic carbon uptake in the Northeast Atlantic during the summer 1991. *Deep-Sea Research I*, *41*, 297–314.

Rocap, G., Larimer, F. W., Lamerdin, J., Malfatti, S., Chain, P., Ahlgren, N. A., et al. (2003). Genome divergence in two *Prochlorococcus* ecotypes reflects oceanic niche differentiation. *Nature*, *424*, 1042–1047.

Root, R. B. (1967). The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs*, *37*, 317–350.

Rost, B., & Riebesell, U. (2004). Coccolithophores and the biological pump: Responses to environmental changes. In H. R. Thierstein & J. R. Young (Eds.), *Coccolithophores, from molecular processes to global impact* (pp. 99–126). Springer.

Ryther, J. H. (1969). Photosynthesis and fish production in the sea. *Science*, *166*, 72–76.

Sabetta, L., Fiocca, A., Margheriti, L., Vignes, F., Basset, A., Mangoni, O., et al. (2004). Phytoplankton size structure and environmental forcing within the euphotic zone in the Southern Adriatic-Ionian Coastal Area. *Chemistry and Ecology*, *20*, 303–317.

Sabetta, L., Fiocca, A., Margheriti, L., Vignes, F., Basset, A., Mangoni, O., et al. (2005). Body size-abundance distributions of nano- and micro-phytoplankton guilds in coastal marine ecosystems. *Estuarine Coastal Shelf Science*, *63*, 645–663.

Sarthou, G., Timmermans, K. R., Blain, S., & Tréguer, P. (2005). Growth physiology and fate of diatoms in the ocean: A review. *Journal of Sea Research*, *53*, 25–42.

Sathyendranath, S., Cota, G., Stuart, V., Maass, H., & Platt, T. (2001). Remote sensing of phytoplankton pigments: A comparison of empirical and theoretical approaches. *International Journal of Remote Sensing*, *22*, 249–273.

Sathyendranath, S., & Platt, T. (1997). Analytical model of ocean colour. *Applied Optics*, *37*, 2216–2227.

Sathyendranath, S., & Platt, T. (1997). Angular structure of under-water light field: Importance for ocean-colour models. In S. G. Ackleson & R. Frouin (Eds.), *Proc. SPIE 2963, Bellingham, USA. Ocean Optics* (Vol. XIII, pp. 26–31).

Sathyendranath, S., & Platt, T. (2007). Spectral effects in bio-optical control on the ocean system. *Oceanologia*, *49*, 5–39.

Sathyendranth, S., Prieur, L., & Morel, A. (1987). Variations in the spectral values of specific absorption of phytoplankton. *Limnology and Oceanography*, *32*, 403–415.

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 Journal of Marine Sciences*, *34*, 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. *Marine Ecology. Progress Series*, *272*, 59–68.

Scharek, R., Tupas, L. M., & Karl, D. M. (1999). Diatom fluxes to the deep sea in oligotrophic North Pacific gyre at Station ALOHA. *Marine Ecology. Progress Series*, *182*, 55–67.

Schoemann, V., Becquevort, S., Stefels, J., Rousseau, V., & Lancelot, C. (2005). *Phaeocystis* blooms in the global ocean and their controlling mechanisms: A review. *Journal of Sea Research*, *53*, 43–66.

Sieburth, J. M., Smetacek, V., & Lenz, J. (1978). Pelagic ecosystem structure: Heterotrophic compartments of the plankton and their relationship to plankton size fractions. *Limnology and Oceanography*, *23*, 1256–1263.

Sieracki, C. K., Sieracki, M. E., & Yentsch, C. S. (1998). An imaging-in-flow system for automated analysis of marine microplankton. *Marine Ecology. Progress Series*, *168*, 285–296.

Simberloff, D., & Dayan, T. (1991). The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics*, *22*, 115–143.

Simó, R. (2001). Production of atmospheric sulfur by oceanic plankton: Biogeochemical, ecological and evolutionary links. *Trends in Ecology & Evolution*, *16*, 287–294.

Smayda, T. J., & Reynolds, C. S. (2003). Strategies of marine dinoflagellate survival and some rules of assembly. *Journal of Sea Research*, *49*, 95–106.

Smetacek, V. (2001). A watery arms race. *Nature*, *411*, 745.

Smyth, T. J., Moore, G. F., Groom, S. B., Land, P. E., & Tyrell, T. (2002). Optical modeling and measurements of a coccolithophore bloom. *Applied Optics*, *41*, 7679–7688.

Sosik, H. M., & Mitchell, B. G. (1998). Absorption, fluorescence, and quantum yield for growth in nitrogen-limited *Dunaliella tertiolecta*. *Limnology and Oceanography*, *36*, 910–921.

Steele, J. H. (1991). Marine functional diversity. *BioScience*, *41*, 470–474.

Steinberg, D. K., Nelson, N. B., Carlson, C. A., & Prusak, A. C. (2004). Production of chromophoric dissolved organic matter (CDOM) in the open ocean by zooplankton and the colonial cyanobacterium *Trichodesmium* spp. *Marine Ecology. Progress Series*, *267*, 45–56.

Stuart, V., Sathyendranath, S., Platt, T., Maass, H., & Irwin, B. D. (1998). Pigments and species composition of natural phytoplankton populations: Effect on the absorption spectra. *Journal of Plankton Research*, *20*, 187–217.

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

Subramaniam, A., Carpenter, E. J., Karentz, D., & Falkowski, P. G. (1999). Optical properties of the marine diazotrophic cyanobacteria *Trichodesmium* spp.; I-absorption and spectral photosynthetic characteristics. *Limnology and Oceanography*, *44*, 608–617.

Sunda, W., Kleber, D. J., Klene, R. P., & Huntsman, S. (2002). An antioxidant function for DMSP and DMS in marine algae. *Nature*, *418*, 317–320.

Tyrell, T., Holligan, P. M., & Mobley, C. D. (1999). Optical impacts of oceanic coccolithophore blooms. *Journal of Geophysical Research*, *104*, 3223–3241.

Tyrell, T., & Merico, A. (2004). *Emiliania huxleyi*: Bloom observations and the conditions that induce them. In H. R. Theirstein & J. R. Young (Eds.), *Coccolithophores, from molecular processes to global impact* (pp. 75–97).

Uitz, J., Claustre, H., Morel, A., & Hooker, S. (2006). Vertical distribution of phytoplankton communities in open ocean: An assessment based on surface chlorophyll. *Journal of Geophysical Research*, *111*, CO8005, doi:10.1029/2005JC003207.

Ulloa, O., Sathyendranath, S., & Platt, T. (1994). Effect of the particle–size distribution on the backscattering ratio in seawater. *Applied Optics*, *33*, 7070–7077.

Vadrucci, M. R., Vignes, F., Fiocca, A., Basset, A., Santarpia, I., Carrada, G. C., et al. (2003). Space-time patterns of co-variation of biodiversity and primary production in phytoplankton guilds of coastal marine environments. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *13*, 489–506.

Vadrucci, M. R., Semeraro, A., Zaccarelli, N., & Basset, A. (2004). Nutrient loading and spatial–temporal dynamics of phytoplankton guilds in a Southern Italian coastal lagoon (Lake Alimini Grande, Otranto, Italy). *Chemistry in Ecology*, *20*, S285–S301.

Veldhuis, M. J. W., & Kraay, G. W. (2004). Phytoplankton in the subtropical Atlantic Ocean: Towards a better assessment of biomass and composition. *Deep Sea Research I*, *51*, 507–530.

Vidussi, F., Claustre, H., Manca, B. B., Luchetta, A., & Marty, J. C. (2001). Phytoplankton pigment distribution in relation to the upper thermocline circulation in the Eastern Mediterranean Sea during winter. *Journal of Geophysical Research*, *106*, 19939–19956.

Vila, M., & Masó, M. (2005). Phytoplankton functional groups and harmful algal species in anthropogenically impacted waters of the NW Mediterranean Sea. *Scientia Marina*, *69*, 31–45.

Weeks, S., Currie, B., & Bakun, A. (2002). Massive emissions of toxic gas in the Atlantic. *Nature*, *415*, 493–494.

Westberry, T. K., Siegel, D. A., & Subramaniam, A. (2005). An improved bio-optical model for the remote sensing of *Trichodesmium* spp. blooms. *Journal of Geophysical Research*, *110*, C06012, doi:10.1029/02004JC002517.

Wright, S. W. (2005). Analysis of phytoplankton populations using pigment markers. *Workshop on pigment analysis of Antarctic microorganisms* : University of Malaya June 29-July 1, 2005.

Zapata, M., Jeffrey, S. W., Wright, S. W., Rodríguez, F., Garrido, J. L., & Clementson, L. (2004). Photosynthetic pigments in 37 species (65 strains) of Haptophyta: Implications for oceanography and chemotaxonomy. *Marine Ecology. Progress Series*, *270*, 83–102.

Zehr, J. P., Carpenter, E. J., & Villareal, T. A. (2000). New perspectives on nitrogen-fixing microorganisms in tropical and subtropical oceans. *Trends Microbiology*, *8*, 68–73.

Zehr, J. P., Waterbury, J. B., Turner, P. J., Montoya, J. P., Omoregie, E., Steward, G. F., et al. (2001). Unicellular cyanobacteria fix N_2 in the subtropical North Pacific Ocean. *Nature*, *412*, 635–638.

Zwirglmaier, K., Heywood, J. L., Chamberlain, K., Woodward, E. M. S., Zubkov, M. V., & Scanlan, D. J. (2007). Basin-scale distribution pattern of picocyanobacterial lineages in the Atlantic Ocean. *Environmental Microbiology*, *9*, 1278–1290.

Zwirglmaier, K., Jardillier, L., Ostrowski, M., Mazard, S., Garczarek, L., & Not, F. (2008). Global phylogeography of marine *Synechococcus and Prochlorococcus* reveals a distinct partitioning of lineages amongst oceanic biomes. *Environmental Microbiology*, *10*, 147–161.