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Ocean Color Remote Sensing of Phytoplankton Functional Types

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1. Introduction

Interest in phytoplankton diversity has increased in recent years due to its possible role in regulating climate by production and consumption of greenhouse gases. For example, gases can diffuse across the air-sea interface, many of which are synthesized and emitted by certain phytoplankton species or groups. It has been suggested that these variations play an important role in moderating our climate through backscattering of solar radiation and within cloud formation. Climate will ultimately control fundamental environmental conditions that regulate algal growth, including water temperature, nutrients, and light and thus can be expected to result in changes in the species composition, trophic structure and function of marine ecosystems. In the past several decades, the scientific community has witnessed changes in phytoplankton distribution.

The marine phytoplankton community is diverse and includes on the order of tens of thousands of phytoplankton species (Jeffrey & Vesk 1997). On regional scales, phytoplankton biogeography is controlled by the physical, chemical, and meteorological characteristics that force ecosystem dynamics. There is a renewed impetus for new technologies to provide information about the phytoplankton community composition over global scales. Real-time, large-scale taxonomic information, if available, could open up new possibilities and approaches geared toward monitoring highly-dynamic oceanic processes and phenomena such as algal blooms (including harmful algal blooms), frontal structures, eddies, and episodic events (storms, river outflow, and wind mixing). Phytoplankton diversity information provides a valuable quantitative database for structuring sophisticated predictive models that includes taxonomic phytoplankton community information such as size spectra, probability distribution of taxa, and upper trophic level estimations including fisheries productivity (Cheson & Case 1986, De Angelis & Waterhouse 1987). There have been several reviews and books written on phytoplankton community structure, dynamics, and biogeochemistry as measured by ocean color (Mitchell 1994, Martin 2004, Mueller et al. 2004, Miller et al. 2005, Richardson and LeDrew 2006, Longhurst 2007, Robinson 2010).

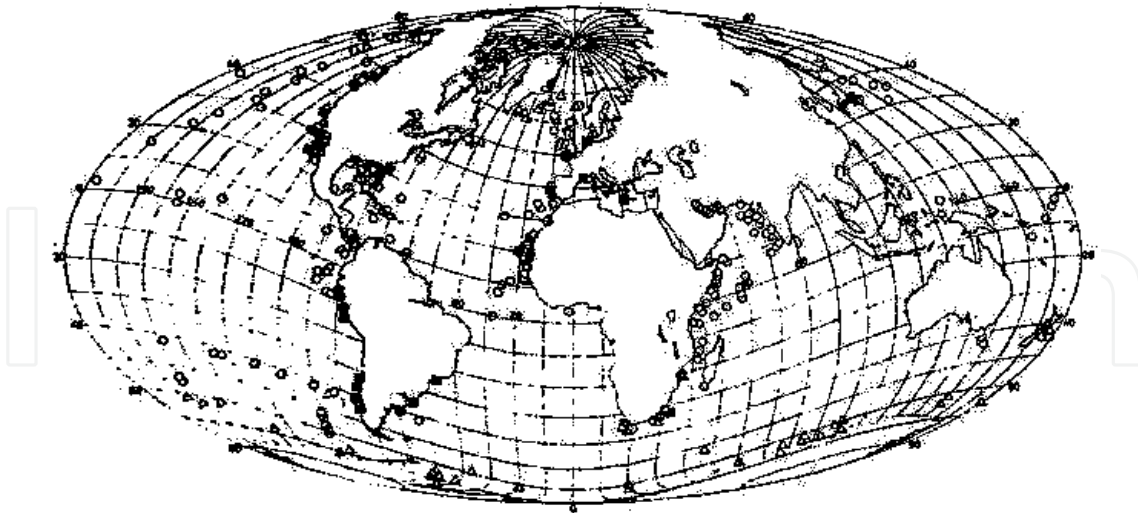


Fig. 1. Distribution of *Nitzschia americana* (solid square), *Nitzschia bicaudata* (open circle) and *Nitzschia pseudonana* (open triangle) from shipboard observations. Modified from Hasle (1976). These data were compiled over several years in order to understand their global distribution.

Approaches have been proposed for remote sensing detection of phytoplankton functional types (PFTs) and may be classified as direct (defined as they exploit optical signatures of phytoplankton that may be detected by sensors on satellite platforms) or indirect (e.g. exploit relationships between chlorophyll-a concentration and functional types). Both approaches have their advantages and limitations. Direct methods are limited to few phytoplankton groups that possess optical signatures distinct from other constituents in seawater. Indirect methods exploit well-established algorithms for retrieval of chlorophyll-a concentrations from ocean color satellite products in combination with phytoplankton community structure, which is validated by *in situ* observations. Optical sensors have ushered in a new capability of remotely sensing the ocean synoptically compared with *in situ* data collected on board ships, which may take years to compile but is capable of exploring ancillary properties inaccessible to remote sensing (Hasle 1976, Figure 1). Early shipboard studies have demonstrated the complexity of the marine ecosystem and how distribution, function, and physiology are linked closely to the biochemistry of carbon, nitrogen, sulfur, and other elements in the sea. This chapter discusses how information on PFTs may be derived from a combination of satellite data and *in situ* observations. It is anticipated that developing an understanding of the large-scale distributions and variability in PFTs will contribute to various ecological problems of the day of paramount economic importance, such as providing an ecological basis for fisheries fluctuations and occurrence of harmful algal blooms. Future satellite sensors with improved spectral resolution or temporal resolution holds promise for improving the accuracy of retrieval of PFTs and understanding their role in the ecology of the ocean.

Global patterns of diversity for the majority of marine organisms are virtually uncharacterized (Worm et al. 2005). For planktonic organisms, which form the base of the marine food web, global ocean geographic distribution of diversity has only been characterized for planktonic foraminifera (Rutherford et al. 1999). Marine biodiversity patterns show a worldwide consistency despite differences in environmental conditions of

various oceanographic regions (Irigolen et al. 2004). Marine phytoplankton diversity, similar to terrestrial vegetation, is described as a uni-modal function of phytoplankton biomass with an occurrence of maximum diversity at intermediate levels of phytoplankton biomass (sub-bloom concentrations) and low diversity during massive blooms (Irigolen et al. 2004). Similar to terrestrial vegetation, phytoplankton diversity is a unimodal function of phytoplankton biomass, with maximal diversity at intermediate levels of phytoplankton biomass and minimum diversity during massive blooms.

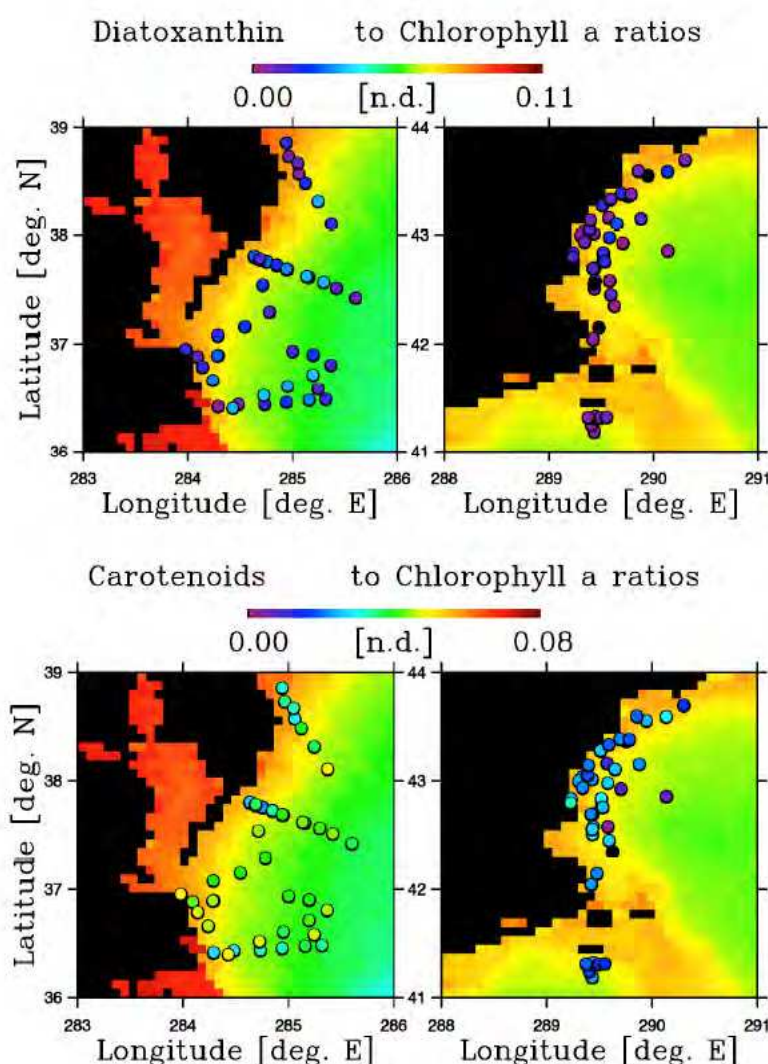


Fig. 2. Ratios of diatoxanthin and carotenoids (to chlorophyll-a) near the Delmarva Peninsula against the SeaWiFS 10 year average. Differences between the values and the SeaWiFS average emphasize that the phytoplankton community is structured differently from the bulk community (e.g. chlorophyll-a).

Moreover, the diversity-productivity relationship of oceanic plankton is similar to the classical relationship observed in early shipboard collections of phytoplankton. The results of PFT distribution return a significantly different pattern compared with the 10-year SeaWiFS average, underscoring that underlying biological processes produce a complex ecological food web matrix in the ocean (Figure 2).

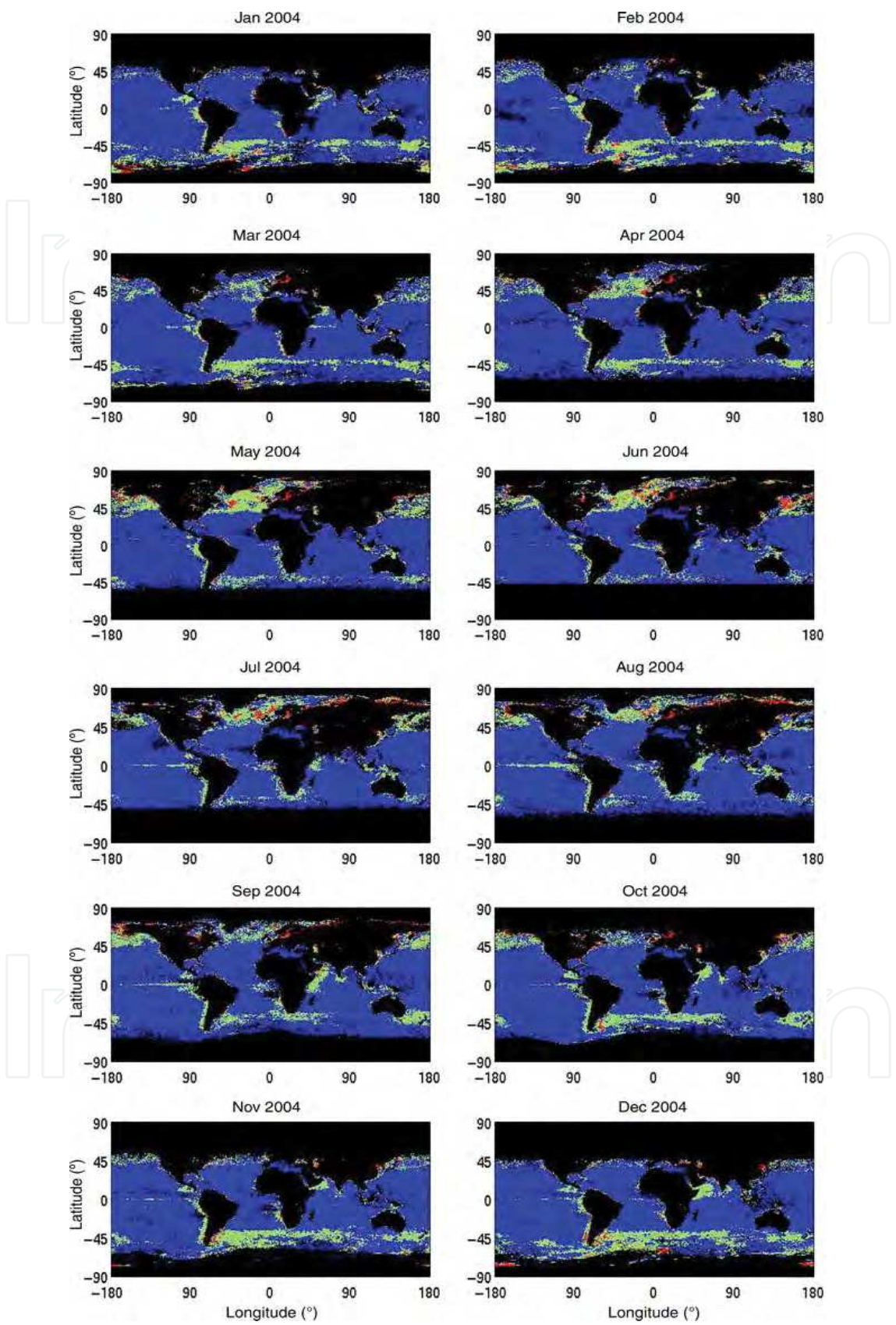


Fig. 3. Monthly SeaWiFS data for 2004 interpreted for phytoplankton, size classes: pico (blue); nano (green); micro (red, Aiken et al. 2009).

Our limited understanding of marine ecosystem responses to various physico-chemical climate drivers, which include genetic and phenotypic adaptation to the unprecedented pace of climate change call for novel methods to study the problem, and remote sensing is one of the potential avenues (Falkowski et al. 2004, Chavez et al. 1999). Understanding the cyclical relationship of phytoplankton groups and how the production of greenhouse gases relates to temperature and productivity provides a better understanding of their coupling to climate (Falkowski et al. 2004). Changes in phytoplankton community structure could potentially provide an early warning for climate-driven perturbations in marine ecosystems (Hallegraeff 2010). Establishing the biogeography of several morphologically and genetically distinct marine species is a complex target for which remote sensing may provide at best, a partial solution.

Historically, satellite sensors have provided oceanographers with bulk phytoplankton pigment concentrations (e.g. chlorophyll-*a*) over global scales with synoptic resolution (McClain, 2009). Coastal Zone Color Scanner (CZCS) was the beginning of the era of satellite remote sensing of ocean color. It was a relatively simple sensor and was successful at the retrieval of chlorophyll-*a* concentrations in open-ocean waters. Models were then developed that utilized satellite-derived chlorophyll-*a* data along with information on photosynthetically available radiation and temperature at the sea surface to compute water column primary production by remote sensing. However, CZCS performed poorly in coastal waters. SeaWiFS and MODIS, the successor to the CZCS, had better radiometric precision and more wavebands and was designed to address the limitations of CZCS, in particular for applications in coastal waters. Satellites with even higher spectral resolution followed (e.g. MERIS). Though the newer generations of satellites were designed for improving performance in coastal waters, there has been increasing recognition of their value in the detection of phytoplankton functional types as well. These satellite missions have provided knowledge and understanding of a variety of events including frontal features and episodic blooms on a global basis. The scientific community has now moved onto predicting ecologically significant characteristics of the food web such as size structure as interpreted for phytoplankton size classes including picoplankton to microplankton (Aiken et al. 2008). Ocean Color has been recognized as an essential climate variable by the Global Climate Observation System (GCOS). As the global time series of ocean color data grows (CZCS, MODIS, & SeaWiFS), there is an increase in satellite products available to study decadal-scale variations in phytoplankton distribution and primary production.

Understanding the spatial and temporal distribution of PFTs will allow us to improve our knowledge of biologically-mediated fluxes of elements between the upper ocean and the ocean interior (Falkowski & Raven, 1997). The performance of biogeochemical models in the ocean has improved substantially as a result of incorporating PFTs into ecosystem models. The spatial variability and concentration of various PFTs are critical to improving primary-productivity estimates, and understanding the feedbacks of climate change. The ability to observe PFTs on a global scale that relate to key biogeochemical processes such as nitrogen fixation, silicification, and calcification is valuable to studies of marine elemental cycles. Despite the paucity of data on functional groups, our understanding of ecosystem linkages is improving as we accrue larger amounts of data. Major divisions of phytoplankton taxonomic groups such as diatoms, coccolithophores, dinoflagellates, chlorophytes, and cyanobacteria are often separated into distinct functional groups, as these taxonomic groups have unique biogeochemical signatures

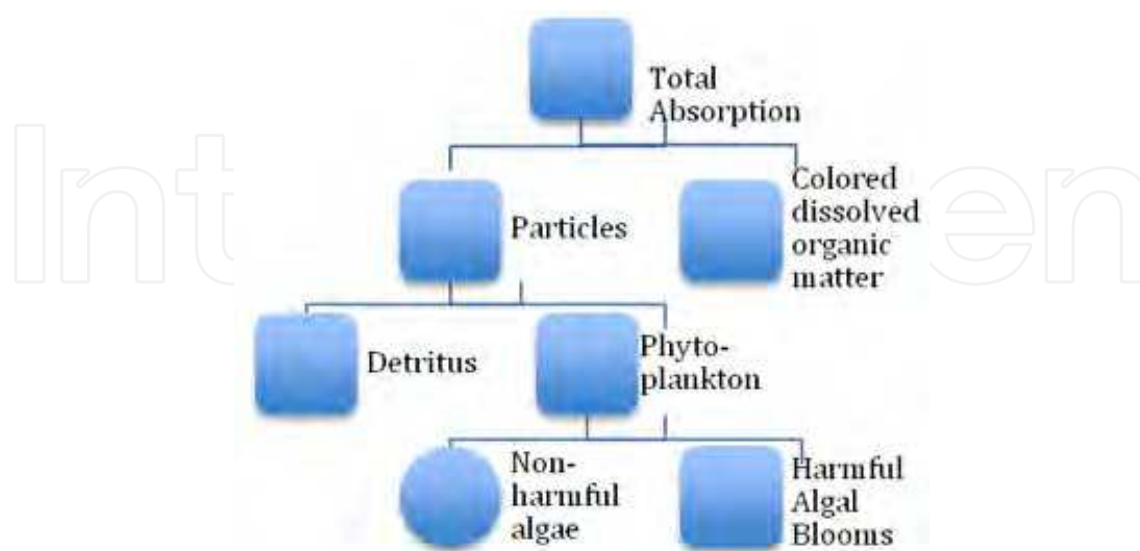


Fig. 4. Schematic diagram showing sources of variation in optical characteristics which influence ocean color. (Keller et al. 1989)

Aiken et al. (2009) shows how different size classes of phytoplankton are distributed globally, and size is often related to function (Nair et al. 2008). Nonetheless, there are limitations to discriminating phytoplankton taxonomic composition or even functional groups by remote sensing, due to our inability to discriminate various phytoplankton types optically. Remote-sensing reflectance ($R_{rs}(\lambda)$) is influenced by absorption and backscattering by seawater, phytoplankton, colored dissolved organic matter, detrital matter and other suspended material (Garver & Siegel 1997). We show the various optical pools that contribute to absorption, which contributes to the spectral variability of $R_{rs}(\lambda)$, Figure 4). Remote sensing of particular types of phytoplankton is only possible if optical characteristics are identified for those types that can be used to distinguish them from all other types of material in the water.

New technological developments and improved scientific knowledge have allowed for the development of several approaches for detecting phytoplankton biomass and some functional groups of phytoplankton including coccolithophores (Balch et al. 1991, Balch et al. 1996) and *Trichodesmium* (Subramanian et al. 1994, 1999 a,b, Hu et al. 2010). More recently, algorithms have been developed to distinguish additional phytoplankton groups and size classes (Sathyendranath et al. 2004, Alvain et al. 2005, Moisan et al. 2011ab). High Performance Liquid Chromatography (HPLC) is the *in situ* method of choice to serve as ground truth for satellite products due to its accuracy and rapid processing. A relatively new analysis tool called CHEMical TAXonomy (CHEMTAX) has been developed that is designed to yield information on the phytoplankton composition using HPLC data (Mackey et al. 1996), but it has to be recognized that HPLC models have their limitations (e.g. Latasa 2007).

2. “History of terminology for phytoplankton functional types”: Ecological, biogeochemical, and optical definitions

The Ocean Color community has utilized a reductionist approach to describe phytoplankton taxonomic composition and refers to optical signatures of certain phytoplankton groups/species or PFTs. In this chapter, we will refer to Phytoplankton Functional Types (PFTs) in order to utilize current terminology. Please take into account that we may be defining groups within different levels of complexity that relate to phylogeny or bio-optically similarities etc. Taxonomic characterization has utilized different terminology over the years and we delve into the history of its classification because it may define many different levels of complexity.

Present studies on diversity are not too far removed from the original ideas invoked by G.E. Hutchinson’s “Paradox of the Plankton” (Hutchinson, 1961) and J. H. Connell’s “Intermediate Disturbance Hypothesis” (Connell, 1978). Ocean variability, through eddies, storms, seasonal cycles, and El Niño, have been documented to play a role in controlling diversity. How this level of stochastic variability manifests itself spatially and temporally due to climate change is unknown. Falkowski & Oliver (2007) suggest that resource competition theory is adequate to describe global distribution of marine eukaryotic phytoplankton taxa during equator-to-pole and continent-to-land thermal gradients. These results are supportive in light of describing phytoplankton beyond a bulk approach of utilizing only chlorophyll *a*.

A functional group is used as an ecological term to define a group of organisms that have similar biogeochemical processes e.g. nitrogen fixation, silicifiers, and calcifiers (Fauchald & Jumars 1979, Reynolds et al. 2002, Nair et al. 2008). Functional groups in phytoplankton are defined as groups of organisms related through common biogeochemical processes but are not necessarily phylogenetically related (Iglesias-Rodríguez et al. 2002). Homologously similar sets of organisms are referred to as “functional groups” or “biogeochemical guilds” following Totterdell et al. (1993). For marine phytoplankton, some attempts have been made to organize species within certain classes of phytoplankton according to their ecological and biogeochemical function or habitat distribution perspective (Iglesias-Rodríguez et al. 2002, Smayda & Reynolds, 2003, Vila & Masó, 2005). Thus, terminology has finally evolved to the usage of Phytoplankton Functional Type (PFT) or Phytoplankton Functional group but these classifications are not necessarily straightforward and include a wide range of different taxonomic classification approaches such as size, biogeochemistry, or traditional taxonomic hierarchies (see discussion by Nair et al. 2008).

3. On the road to predicting remote sensing reflectance: Fundamental basis between pigments and *in vivo* absorption

Algorithm development for remote sensing is focused on estimating the quantities of various optically-active constituents in the ocean. Various pigments present in phytoplankton play a role in determining the total absorption coefficient of phytoplankton, which is a key determinant of the spectral variability in remote-sensing reflectance. We utilize a reconstruction model to demonstrate the spectral variability of photoprotective and photosynthetic pigments (Sathyendranath et al. 1987, Bidigare 1990). There are differences in the weight-specific absorption spectra of various *in vitro* (extracted) phytoplankton pigments (Figure 5). The comparison of maximal peaks of mass-specific absorption spectra

and center wavelengths on ocean color satellite platforms proves that coupling taxonomic and optical properties is quite challenging (Table 1). Future sensors with increased temporal and spectral resolution will provide more spectral information for development of algorithms. Future development of hyperspectral sensors would cover pigment-specific peaks at relatively high spatial and temporal resolution, which would allow retrieval of photosynthetic and photo-protective pigments.

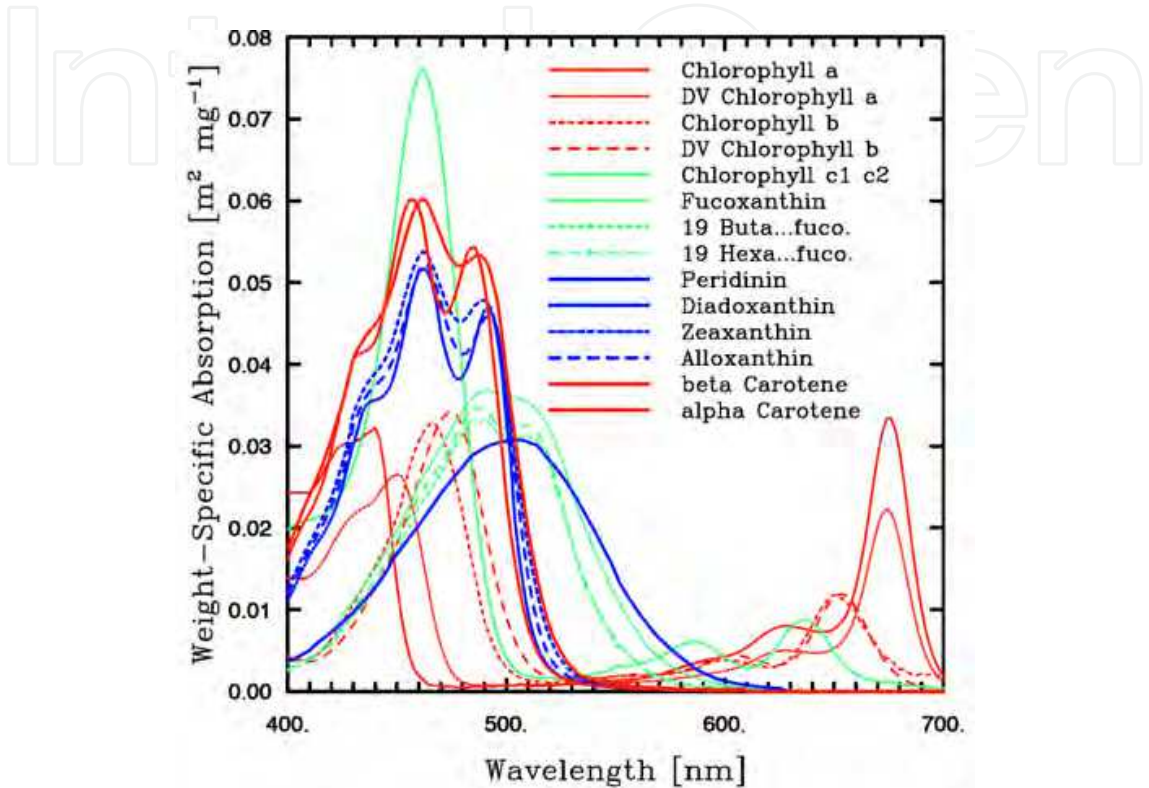


Fig. 5. Weight-specific in vitro absorption spectra of various pigments, $a_i^*(\lambda)$, derived from measuring the absorption spectra of individual pigments in solvent and shifting the maxima of the spectra according to Bidigare et al. (1990). Data obtained courtesy of A. Bricaud (Bricaud et al. 2004).

| SeaWiFS | MODIS | MERIS | OCM2 | OCTS | CZCS |
|---------|-------|-------|------|------|------|
| 412 | 412 | 413 | 415 | 412 | 443 |
| 443 | 443 | 443 | 442 | 443 | 520 |
| 490 | 469 | 490 | 491 | 490 | 550 |
| 510 | 488 | 510 | 512 | 516 | 670 |
| 555 | 531 | 560 | 557 | 565 | |
| 670 | 547 | 620 | 620 | 667 | |
| | 555 | 665 | | | |
| | 645 | 681 | | | |
| | 667 | 709 | | | |
| | 678 | | | | |

Table 1. Past and present Ocean Color Sensors and their respective center wavelengths (nm).

The multi-spectral radiance measurements from the satellite sensor can be corrected for the influence of the atmosphere to yield remote-sensing reflectance. It has been demonstrated using various types of models (e.g. Morel & Prieur 1977; Sathyendranath & Platt 1988) that remote sensing reflectance, $R_{rs}(\lambda)$, at a particular wavelength (λ) increases with the backscattering coefficient of light at a wavelength, and decreases with the absorption coefficient:

$$R_{rs}(\lambda) \text{ is proportional to } b_b(\lambda) / [a(\lambda) + b_b(\lambda)]$$

where $b_b(\lambda)$ is backscattering coefficient and $a(\lambda)$ is the total absorption coefficient. The total absorption coefficient can be partitioned into its components:

$$a(\lambda) = a_w(\lambda) + a_{ph}(\lambda) + a_g(\lambda) + a_d(\lambda)$$

where the subscripts w , ph , g , and d relate to seawater, phytoplankton, gelbstoff and detritus, respectively. A similar equation can be written for backscatter. The absorption coefficient of phytoplankton can be further broken down into contributions from various pigments to the total phytoplankton absorption.

$$a(\lambda) = \sum_{i=1}^n C_i a_{ci}^*(\lambda)$$

where c_i is the concentration of the individual pigments derived from HPLC analysis and $a_i^*(\lambda)$ is the absorption coefficient for the phytoplankton pigment.

As the pigment composition of phytoplankton changes with changes in community structure, the absorption spectra will be modified accordingly. Furthermore, it has been well demonstrated that the absorption spectra of phytoplankton are also modified by changes in the size structure of the community (Duysens 1956; Morel and Bricaud 1981; Sathyendranath et al. 1987; Moisan and Mitchell 1999). Therefore, pigment packaging significantly affect $a_{ph}^*(\lambda)$, Figure 6). To the extent that size and function are related, size-dependent changes may also be related to changes in functional types. Remote sensing of PFTs must rely on such deviations in the spectral signatures of phytoplankton associated with changes in the phytoplankton community structure. Note that such approaches can be adapted to account for the contribution of mycosporine-like amino acids to absorption in the UV regions, which have some but limited taxonomic value (Moisan et al. 2011a, b).

4. Algorithm development of ocean color phytoplankton functional types

PFT algorithms have been developed to map the distribution of numerically- and ecologically-important organisms that demonstrate an anomalous relationship to a satellite-derived reflectance product, such as chlorophyll-a. Generally, algorithm development has capitalized on the backscattering or absorption characteristics of a particular phytoplankton group, or utilized sophisticated modeling efforts. In earlier years, a particular species/group was targeted, whereas more recently mathematically sophisticated algorithms have produced multiple products relating to phytoplankton community structure. Both approaches provide valuable data products, which enhance our understanding of the spatial and temporal variability in ecological structure and function. We present a generalized description of present algorithms for *in situ* data and satellite-derived data that describe phytoplankton taxonomic composition.

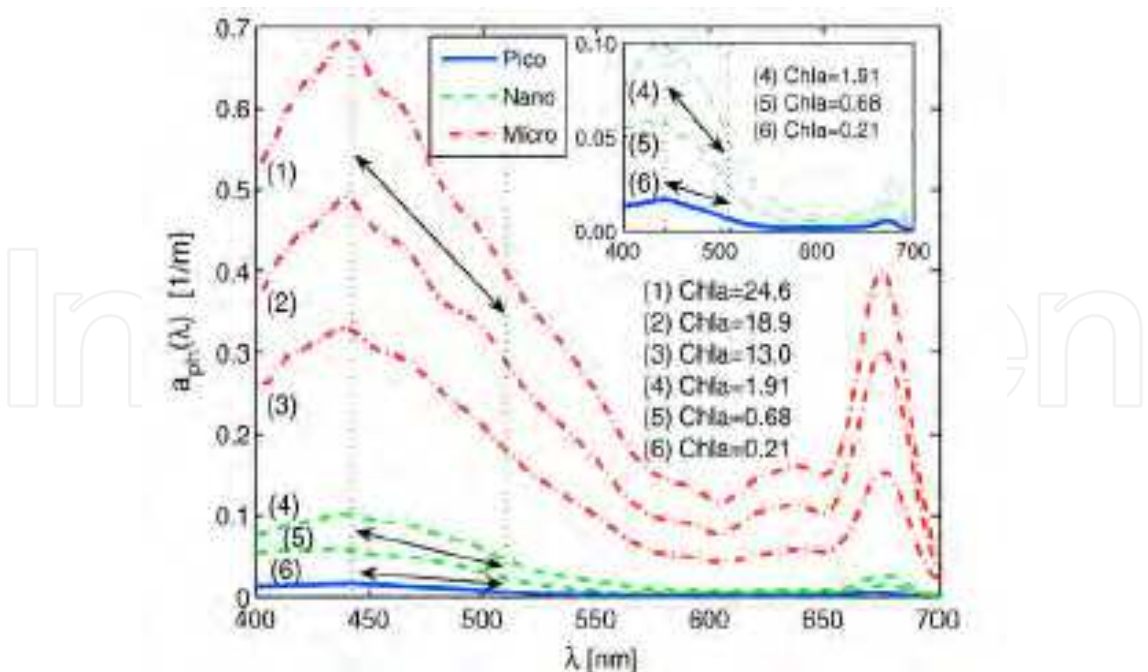


Fig. 6. Phytoplankton absorption spectra for a range of Chl a (24.6, 18.9, 13.0, 1.91, 0.68, 0.21 mg m⁻³) and taxonomic size classes (pico, nano and micro) with decreasing slope from high to low aph (λ) and Chl a; inset spectra of pico and nanoplankton at expanded range (Hirata et al 2008).

| | Chlorophylls | | | | | | | Carotenes | | Xanthophylls | | | | | | | | | | | |
|-----------------|--------------|-------|---------|---------|--------|--------|--------|-----------|---------|--------------|--------|---------|------|------|--------|-----|-----|-----|------|-------|-----|
| | Chl-a | Chl-b | DVChl-a | DVChl-b | Chl-c1 | Chl-c2 | Chl-c3 | β,ε-car | β,β-car | Allo | 19-But | Diadino | Dino | Fuco | 19-Hex | Lut | Neo | Per | Pras | Viola | Zea |
| Prokaryota | | | | | | | | | | | | | | | | | | | | | |
| Synechococcus | - | | | | | | | - | - | | | | | | | | | | | | - |
| Prochlorococcus | | | - | - | | | | - | - | | | | | | | | | | | | - |
| Eukaryota | | | | | | | | | | | | | | | | | | | | | |
| Rhodophyta | - | | | | | | | - | - | | | | | | | | | | | | - |
| Cryptophyta | - | | | | | - | | - | - | - | | | | | | | | | | | |
| Chlorophyceae | - | - | | | | | | • | - | | | | | | | | | | | | - |
| Prasinophyceae | - | - | | | | | | • | - | | | | | | | • | | | | | - |
| Eulgenophyta | - | - | | | | | | | - | | | | | | | | • | | | | |
| Eustigmatophyta | - | | | | | | | | - | | | | | | | | | | | | • |
| Bacillariophyta | - | | | | | | | | • | | | | | | | | | | | | |
| Dinophyta | - | | | | - | - | | | • | | | | • | | | | | | | | |
| Prymnesiophyta | - | | | | - | - | - | • | • | | | | | | | | | - | | | |
| Chrysophyceae | - | | | | - | - | - | | • | | | | | | | | | | | | |
| Raphidophyceae | - | | | | - | - | | | - | | | | | | | | | | | | |

Table 2. Distribution of pigments across the divisions and classes of the algae that are conventionally measured by high performance liquid chromatography. • = major pigment (>10%); • =minor pigment (≤10%) of the total chorophylls or carotenoids. (Modified from Jeffrey & Vesk 1997)

5. Pigments as a diagnostic tool for identifying phytoplankton functional types

Because conventional light microscopy is labor-intensive and biased towards the larger phytoplankton, biological oceanographers have sought alternative approaches to derive information on community structure of the entire phytoplankton population. The most common method to achieve this is by measuring the phytoplankton pigment composition. Algal pigments have been routinely used as chemotaxonomic markers in studies of phytoplankton ecology and biogeochemistry. Chlorophyll-*a*, in its monovinyl and divinyl forms, is found within all photosynthetic microalgae and cyanobacteria, and is used as a universal proxy of autotrophic biomass. However, there also exist other chlorophylls and carotenoids that are routinely measured by High Performance Liquid Chromatography (HPLC) and may serve as class-specific markers.

It should be noted that most algal pigments are found in more than one class, while some are not necessarily present in every member of the same class. Given the complexity of the distribution of pigments between and within various phytoplankton taxa, a number of statistical and mathematical methods have been developed to partition the bulk pigment biomass into the various phytoplankton groups. In addition to using pigments as class-specific markers, pigments indices of phytoplankton classes have been developed based on certain diagnostic pigments that tend to dominate in a particular size class. In this section we briefly describe these approaches. For a more detailed review of the use of pigments as taxonomic markers see Wright & Jeffrey (2005).

Pigments in relation to taxa

The increased use of HPLC pigment analyses in ecological, remote sensing and biogeochemical studies of marine systems has created an impetus to try to extract from pigment data not only the bulk chlorophyll-*a* biomass of the entire population, but also the distribution of phytoplankton groups from the class to the genus level. The quantitative use of pigment markers to assess the relative contribution of taxa to chlorophyll-*a* biomass is still a relatively new and developing area of research. The task of estimating the contribution of various taxa to the pigment signature of natural samples is complex, given that many pigments are found in more than one algal class. The distribution of phytoplankton pigments across the various phytoplankton classes is illustrated in Table 1.

There are three basic approaches used to extract information on algal taxonomic composition based on pigments: multiple linear regression (Gieskes & Kraay 1983, 1986), inverse methods (Bidigare & Ondrusek 1996, Everitt et al. 1990, Letelier et al. 1993, Vidussi et al 2001) and matrix factorization analysis (Mackey et al. 1996, Wright & Jeffrey 2006).

Multiple linear regression analysis

The principal motivation behind the use of multiple linear regression studies of phytoplankton pigments was to establish a relationship between diagnostic pigments & the ubiquitous light harvesting pigment, chlorophyll-*a*, a universal proxy of phytoplankton biomass. One of the aims of the approach was to account for the fraction of phytoplankton cell biomass that may not be detected by conventional microscopy counts. Using multiple linear regression of diagnostic pigments against chlorophyll-*a* concentration, Gieskes & Kraay (1983) revealed that cryptophytes accounted for about half of the chlorophyll-*a* standing stock during a spring bloom study of the central North Sea, although these cells were not detected by microscope counts. The evidence was compelling, given that cryptophytes have a unique 'pigment

fingerprint' (alloxanthin), and this carotenoid was the most abundant accessory pigment in the field samples. The explanation for the discrepancy between the pigment data and the cell counts was that small flagellates and photosynthetic ciliates that harbour alloxanthin are poorly preserved in Lugol's solution, resulting in underestimated cell abundances whereas the larger microphytoplankton (diatoms and dinoflagellates) are better preserved and more easily to identified. The authors also commented on the difficulty in assigning other pigments, such as fucoxanthin, to a particular class, given it is also found in other algal classes, such as prymnesiophytes and chrysophytes.

There are caveats to using the multiple linear regression approach to examine shifts in phytoplankton community structure (Gieskes et al. 1988). In the study by Gieskes et al. (1988), a clear influence of light adaptation on pigment composition was apparent in surface and deep populations, which were characterized by different ratios and intracellular concentrations of diagnostic pigments. As a result, poor taxon specificity of pigment markers such as fucoxanthin may mislead authors to conclude that microscopic counts provide superior quantitative estimates of taxon-specific biomass compared to pigment data.

Inverse methods

In order to estimate the contribution of various algal taxa to chlorophyll-a, inverse methods have been adopted to studies of phytoplankton pigments. The inversion method uses ratios of chlorophyll-a to accessory pigments based on literature values for representative taxa, (Everitt et al. 1990, Letelier et al. 1993, Bidigare et al. 1996). From these data a series of simultaneous equations for each algal group is derived to determine their contribution to total chlorophyll-a biomass. The method also addresses the problem of shared pigments between classes by subtracting out the contribution by other taxonomic groups for a particular pigment marker. The culture-based pigment: chlorophyll-a seed values are then modified by matrix inversion to the field data to find the least squares best solution. Constraints are also applied to the pigment ratios to avoid negative contributions by taxa.

The inverse method was used by Everitt et al. (1990) to demonstrate that nanophytoplankton species dominated the waters of the western Equatorial Pacific, and showed significant variation in community structure. Seasonal changes in the composition of phytoplankton groups (*Prochlorococcus*, other cyanobacteria, prymnesiophytes and chrysophytes) that comprise the deep chlorophyll maximum were examined for the Station ALOHA time series (Letelier et al. 1993). This approach has also been adopted by Vidussi et al. (2001) to assess the shift in community structure during a spring bloom in the northwestern Mediterranean Sea.

Matrix factorization of HPLC pigments (CHEMTAX)

CHEMTAX (CHEMical TAXonomy) is a MATLAB program that estimates the relative contributions of different phytoplankton taxa to the bulk chlorophyll-a concentration of a given sample (Mackey et al. 1996, Wright et al. 2000). Over the years this method has been used to separate out the phytoplankton community into taxonomic groups to at least the class, and in some cases, the genus or species level. To implement this algorithm an input pigment matrix is constructed based on knowledge of the kinds of taxa likely to be present in the study area and information on the cell-specific pigment composition and concentrations of these groups from culture studies. Unlike the multiple linear regression or inversion methods, which use only one or two diagnostic pigment markers for each taxa in

the analyses, the CHEMTAX pigment matrixes make use of a wider range of accessory pigments. However, some criticisms within the community have occurred regarding its application because it assumes constant pigment ratios (Latasa 2007).

Given that the growth conditions of microalgae are known to influence the pigment composition of phytoplankton. The principal factors that led to chromatic adaptation of microalgae include the quality and spectral quantity of irradiance and nutrient status. In addition to the effect of taxa, growth conditions of microalgae are known to influence the pigment composition of phytoplankton. The principal factors that lead to chromatic adaptation of microalgae include the quality and spectral quantity of irradiance and nutrient status. Variability in pigment composition caused by these factors is seen both in the change in the intracellular concentration of the cells as well as the ratios of accessory pigments (such as the relative concentrations of photosynthetic or photoprotective pigments). Therefore, similar to inversion methods, it is recommended that sample be divided according to light regime before running the matrix factorization.

Other inverse methods focus on the absorption term related to phytoplankton as has been estimated using a wide range of algorithms. An alternative approach proposed by Bidigare et al. (1989 & 1990) utilizes the absorption signatures of the various pigments to reconstruct the unpackaged absorption spectra of marine phytoplankton. Using the pigment outputs for various algal groups from CHEMTAX, an unpackaged absorption spectra for a particular phytoplankton group can be constructed when regarding the absorption spectra solely as a function of the chlorophyll-a concentration and the chlorophyll-a specific absorption spectra. Several inverse modeling capabilities are available that can make use of these absorption formulations for other pigments. Moisan et al. (2011ab) have developed a matrix inverse modeling technique that produces photoprotective and photosynthetic pigments with relatively accurate results ($r^2 > 0.80$) using HPLC pigments as validation (Figure 7).

Modeling pigments in relation to cell size fractions

Fortuitously, the major taxa of marine phytoplankton tend to fall within the three size classes originally proposed by Sieburth (1979), the micro- ($>20\mu\text{m}$), nano- ($2\text{-}20\mu\text{m}$) and picophytoplankton ($<2\mu\text{m}$). Thus pigment markers of particular taxonomic groups can provide insight into the relative contribution of a particular size class to the pigment biomass. The use of pigment markers to derive a size index of phytoplankton populations was proposed by Claustre (1994). The approach used seven diagnostic pigments to obtain an index of the relative contribution of microphytoplankton to pigment biomass integrated over the watercolumn. The two marker pigments ascribed to the microphytoplankton size class are fucoxanthin, associated with the diatom fraction, and peridinin, representing the dinoflagellate fraction. The index also used markers pigments that tend be dominant accessory pigments in natural populations: 19'-hex, 19'-but, alloxanthin, zeaxanthin and chlorophyll-b. Thus by summing the watercolumn-integrated concentration of diagnostic pigments associated with the microphytoplankton fraction, and dividing by the sum of all water-column integrated accessory pigments, an index of the relative contribution of microphytoplankton to total integrated pigment biomass can be calculated according to the equation:

$$F_p = \frac{(\sum fuco + \sum perid)}{\sum fuco + \sum perid + \sum 19'hex + \sum 19'but + \sum allox + \sum zeax + \sum chl b}.$$

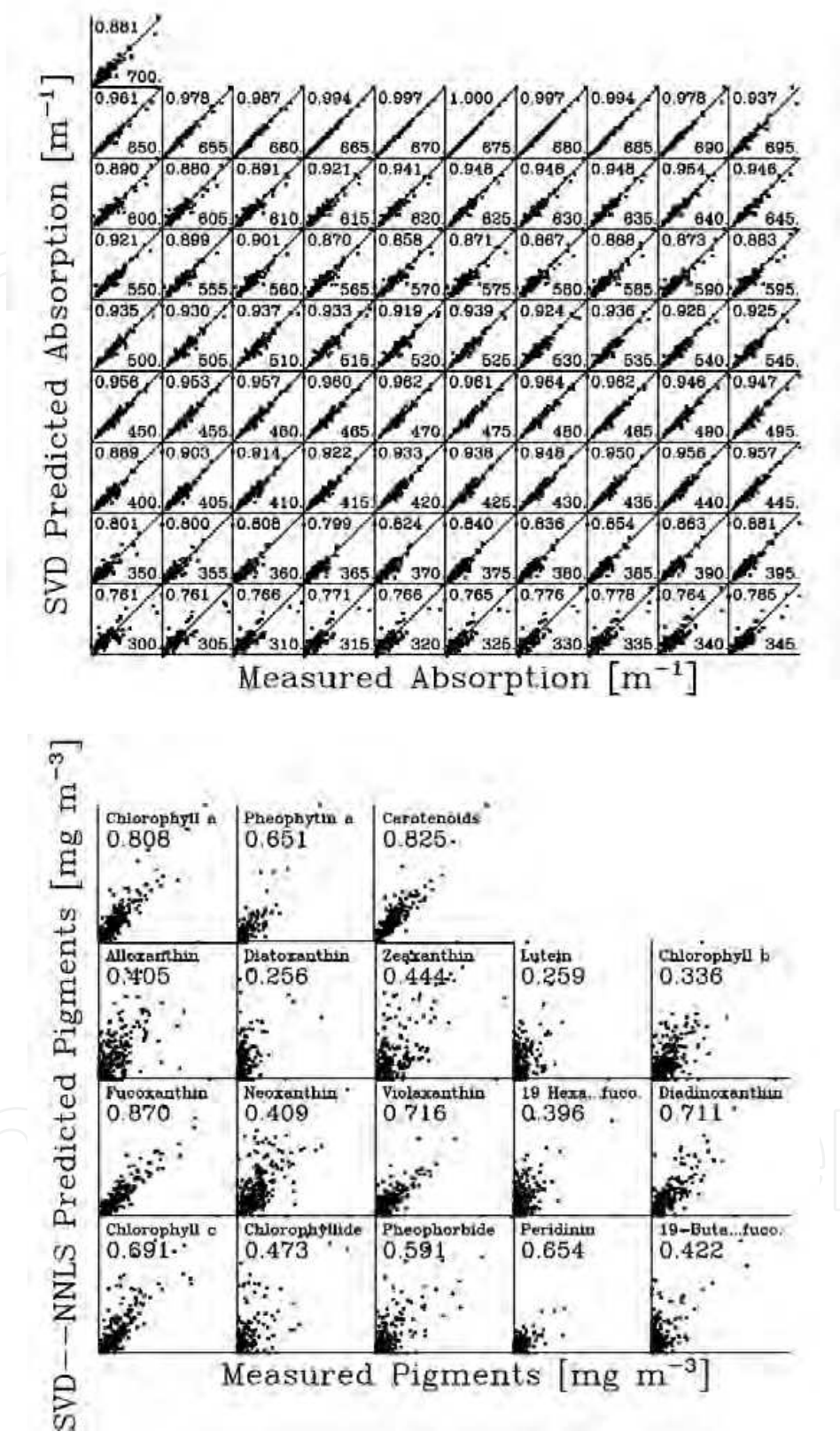


Fig. 7. (top) Predicted absorption versus measured absorption (Algorithm II) for values every 10 nm ranging from 300 nm to 700 nm using matrix inversion methods using a single value decomposition. (bottom) Predicted pigments versus measured HPLC pigments for use in photosynthesis and photoprotection pigments. See Moisan et al. (2011 ab for more details).

A F_p value equal to one means that fucoxanthin and peridinin made up the entire integrated diagnostic pigment concentration, whereas a value of zero means that neither indicator pigment of microphytoplankton were found in the water column.

The size-based approach was refined by Vidussi et al. (2001) to obtain a pigment-derived indices of the contribution of the three size classes of phytoplankton (micro- (>20mm), nano- (2-20mm) and picophytoplankton (<2mm) to integrate pigment biomass. To determine the relative contribution of the three size classes to chlorophyll-a biomass, Uitz et al. (2006) combined the multiple linear regression analysis of Gieskes et al. (1983, 1988) with the size-specific index of Vidussi et al. (2001) to derive estimates of all three size fractions and used not only to derive an index of the presence of the three size classes, but also to estimate their relative contribution to total chlorophyll concentration, similar to the inversion methods and CHEMTAX. It is important to note that in this approach integrated rather than discrete pigment concentrations are used. The approach to using size as a description of the phytoplankton community is becoming a well-accepted PFT, which provides an important link between the fields of remote sensing and marine ecology.

6. Modeling trophic structure through correspondence between taxa, size and function

The relationship between phytoplankton size and biogeochemical function has been well established. Diatoms (silicifiers) tend to be large, and their negative buoyancy leads to their significant contribution to export production (Sarmiento & Gruber 2004). Picophytoplankton, on the other hand, are more important in microbial food webs where rapid recycling of organic matter in the surface ocean leads to a reduction in biogenic export to the deep ocean. Recent molecular studies on the picocyanobacterium *Prochlorococcus*, which dominates the chlorophyll-a biomass in the oligotrophic gyres, have revealed that many strains are unable to utilize nitrate as a nutrient source, and consequently can be considered obligate participants in regenerative production.

The use of pigment markers to provide insight on the trophic structure of marine ecosystems was examined by Claustre (1994). He proposes that the contribution of microphytoplankton (in particular diatoms) to the integrated concentration of diagnostic pigments, which can be considered to be an indicator of the f -ratio and hence new production. In addition, information on the contribution of various phytoplankton taxa to chlorophyll-a standing stock has led to the generation of taxon-specific maps of primary production using global relationships on the relationship between surface chlorophyll-a concentration and the ratio of integrated diagnostic pigments to integrated chlorophyll-a concentration (Uitz et al. 2006). Although the simple pigment indices invoked by Claustre (1994) and Uitz et al. (2006) cannot resolve instances where other taxa contribute to the diagnostic pigment markers used in their analysis, it provides a useful first attempt at obtaining information on the global distribution of phytoplankton size classes (Uitz et al. 2006), the environmental factors that control their biogeography (Bouman et al. 2003) and their relative contribution to marine productivity (Bouman et al. 2005, Uitz et al. 2006).

7. Societal benefits of ocean color approaches to algorithm development for key phytoplankton functional types: Fisheries and habitat applications

A fundamental goal of phytoplankton biogeography is to describe how PFTs are distributed spatially and temporally and how these patterns relate to processes that control primary

production/new production. Several theories have been postulated about what governs biological diversity, which stabilizes community dynamics. Future satellites with increased spectral resolution will allow for algorithms of different proxies for diversity whether the products are pigments, size spectra, or biogeochemical indicators. Such phytoplankton diversity indicators will lead to a better understanding of the response of marine ecosystems to climate and human activities (Platt et al. 2008, 2009). To date, the scientific community has been able to describe phytoplankton community structure based on broad size classes, pigmentation, probability of occurrence, or some other index of presence or absence. We have focused on two successful applications including fisheries management and harmful algal blooms.

a. Fisheries applications

Satellite ocean color application on broad scales allow for PFTs, namely diatoms, to be put into an ecological context regarding El Niño events in the Humboldt ecosystem (Jackson et al. 2011, Figure 8). A locally tuned algorithm for detecting diatom distribution allowed for critical observations in shifts in the size structure of the phytoplankton community, which provide a food source for anchovies. Changes in carbon structure will affect food stress on the fish populations and appears to influence landings in the following year. Mapping the distribution and abundance of phytoplankton using remotely sensed data assists in the creation of targeted and quantitative fishing strategies. Satellites can provide strategies and tools together with modeling and other satellite. Both ocean color and other satellite data, coupled with models, can provide resource managers the information of food web components (other than the chlorophyll-a product), which may be used to direct shipboard sampling on regional scales.

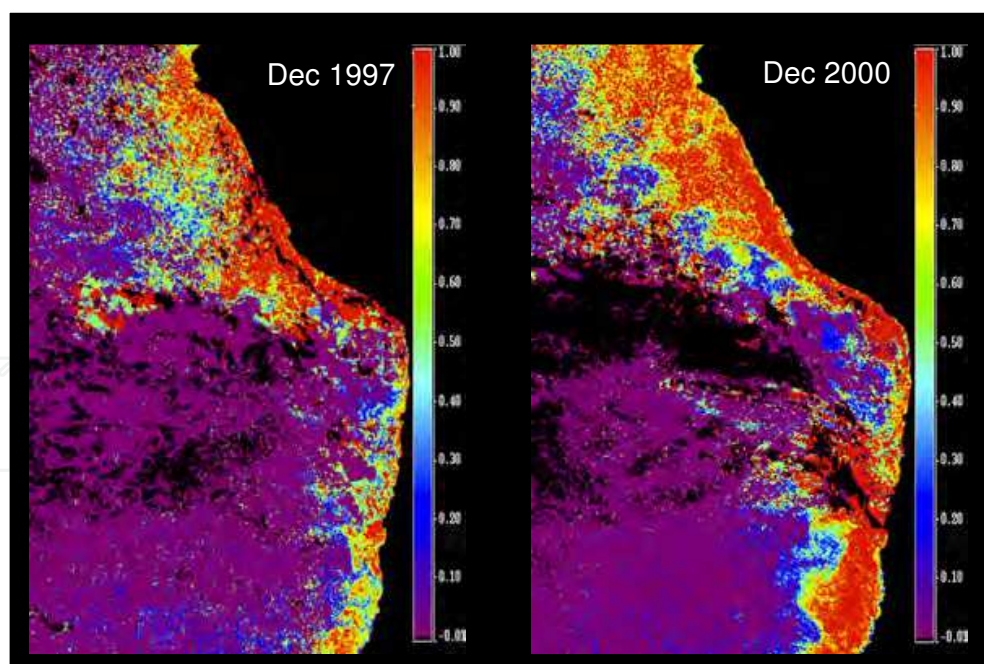


Fig. 8. Climate-induced changes in the spatial distribution of diatoms in the Humboldt system. The figure shows a marked reduction in the presence of diatoms during the 1997 El Niño event compared with the control period (December 2000), which represents typical oceanic conditions for the study region. The color bar represents the fraction of pixels identified as diatoms. Modified from Jackson et al. (2011).

b. Monitoring and tracking through the identification of harmful algal blooms

Ocean Color satellites have had a valuable application for many marine biological processes such as red tides and harmful algal blooms (HABs, reviewed in Stumpf & Tomlinson 2005). HABs are not only harmful to the marine ecosystem but substantive economic losses occur in coastal regions worldwide and the need for remote detection of blooms is critical (Anderson et al. 1997, Schofield et al. 1999, Sellner et al. 2003). HAB events threaten human health, living marine resources, and ecosystem health. Their occurrence has increased in frequency, duration, and severity over the last several decades (Figure 9). Current monitoring efforts of toxic cells and toxin levels in shellfish tissue are relatively slow and lack the synoptic coverage of satellites (Schofield et al. 1999). Nevertheless, HAB monitoring can occur at unprecedented scales with detailed shipboard and drifters to predict arrival, transport time, and possibly toxicity of the bloom (Figure 9, Schofield et al. 1999). Knowledge such as this allows the public to know location, timing of the bloom and close any fisheries that are impacted economically. An excellent example of this type work has been conducted on the mesoscale blooms of *Karenia brevis* in the Gulf of Mexico with ocean color derived chlorophyll a and solar stimulated fluorescence (Stumpf et al. 2003, Hu et al. 2005, Figure 9). Most HAB studies have focused on monitoring with chlorophyll-a as a biomass indicator, however, photo-protective pigments such UV mycosporine-like amino acids and gyroxanthin from other non-toxic organisms (Kahru & Mitchell 1998, Moisan et al. 2011). Several countries all over the world have successfully monitored HABs over broad spatial scales with supplemented satellite imagery and aircraft monitoring in the Gulf of Mexico that allows for tracking of the bloom by satellite and drifters to notify the public.

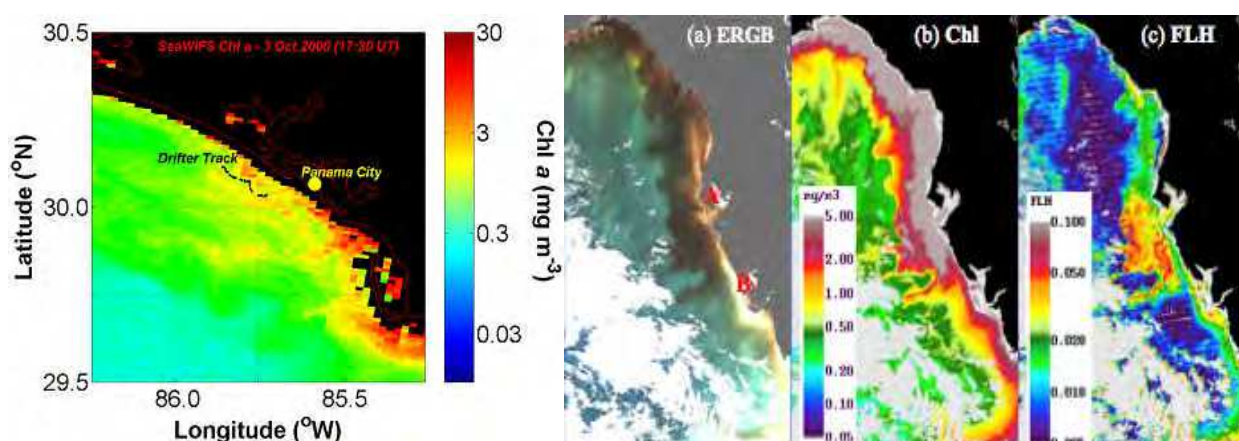


Fig. 9. Left figure: Harmful algal bloom image in the Gulf of Mexico while using drifters and ocean color satellite imagery that allows for tracking for responses to the public (Lohrenz et al., unpub.). Right figure: Fluorescence Line Height is a better indicator than the satellite-based Chl for chlorophyll-a biomass in CDOM-rich waters. This image is for a *Karenia brevis* bloom (modified from Hu et al. 2005, Courtesy of Dr. Chuanmin Hu). Please note that images from different years.

8. Future directions of algorithm development using ocean color

Over the past few decades, the dominant phytoplankton biomass product, chlorophyll-a, has been observed over a long time period on global scales. Recent investigations using ecological provinces have indicated additional regional variability and have provided

information based on marine ecology and biogeochemistry in the broader context of climate change (Falkowski et al. 2004). Although validated satellite data is not a substitute for ship-based sampling, *in situ* information about the physical/biological regimes is still required to produce sound ecological products. Hence, the future lies in the combined utilization of *in situ* data, remote sensing, and modeling. The remote sensing of PFTs in the ocean will bring about a greater understanding of how phytoplankton community structure affects climate with biologically-produced greenhouse gases. In contrast, PFTs will contribute to an overall understanding of global marine biodiversity and that knowledge will provide insight on the relationship between ecosystem stability and ocean biogeochemistry.

9. Acknowledgements

We would like to thank Rich Landa and Rachel Steinhardt for their excellent assistance. Many thanks to Chuanmin Hu, and Steve Lohrenz. We thank our reviewers for their excellent and generous comments on our earlier work. Our work was partially funded by the National Atmospheric and Space Administration's Biodiversity Program 05-TEB/05-0016, the National Oceanic and Atmospheric Administration (NOAA) and the National Environmental Research Council (NERC) UK.

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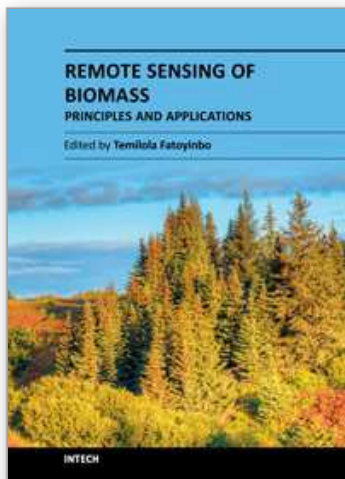
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Remote Sensing of Biomass - Principles and Applications

Edited by Dr. Lola Fatoyinbo

ISBN 978-953-51-0313-4

Hard cover, 322 pages

Publisher InTech

Published online 28, March, 2012

Published in print edition March, 2012

The accurate measurement of ecosystem biomass is of great importance in scientific, resource management and energy sectors. In particular, biomass is a direct measurement of carbon storage within an ecosystem and of great importance for carbon cycle science and carbon emission mitigation. Remote Sensing is the most accurate tool for global biomass measurements because of the ability to measure large areas. Current biomass estimates are derived primarily from ground-based samples, as compiled and reported in inventories and ecosystem samples. By using remote sensing technologies, we are able to scale up the sample values and supply wall to wall mapping of biomass. Three separate remote sensing technologies are available today to measure ecosystem biomass: passive optical, radar, and lidar. There are many measurement methodologies that range from the application driven to the most technologically cutting-edge. The goal of this book is to address the newest developments in biomass measurements, sensor development, field measurements and modeling. The chapters in this book are separated into five main sections.

How to reference

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