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OVERVIEW

This final report covers research performed over a period of 10 years from 1982 to 1992. During this time, Grant #NAGW410 was funded under three titles through a series of Supplements. The original proposal was entitled 'Photoecology, optical properties and remote sensing of warm core rings'; the second and major portion was entitled ' Continuation of studies of biooptical properties of phytoplankton and the study of mesoscale and submesoscale features using fluorescence and colorimetry'; with the final portion named 'Studies of biooptical properties of phytoplankton, with reference to identification of spectral types associated with meso- and submesoscale features in the ocean'. The focus of these projects was to try to expand our knowledge of the biooptical properties of marine phytoplankton as they apply to satellite remote sensing. We used a variety of techniques, new and old, to better measure these optical properties at appropriate scales, in some cases at the level of individual cells. We also exploited the specialized oceanic conditions that occur within certain regions and features of the ocean around the world in order to explain the tremendous variability one sees in a single remote sensing image. This document strives to provide as complete a summary as possible for this large body of work, including the pertinent publications supported by this funding.

INTRODUCTION

Prior to the advent of satellite remote sensing, the inability to visualize large areas of the ocean impeded our understanding of how the physics of ocean circulation is translated into biological growth. The introduction of ocean color (CZCS) and temperature (AVHRR) sensors and airborne LIDAR systems were the first steps toward filling this void. These tools have provided the oceanographer with a means of comparing planetary fluid dynamics with global patterns of primary production as phytoplankton growth through the visualization of established concepts and validation of the imagery with measurements of the surface and interior of the sea. Our research has sought to measure the optical properties of phytoplankton in the laboratory and in the sea in an attempt to validate and improve remote sensors and their algorithms. We have also attempted to introduce new parameters for identifying optical characteristics of algae, namely light absorption and fluorescence. These properties provide the possibility to "type" particles and to infer information on growth kinetics in the case of phytoplankton.

These methods are non-destructive and have the ability to be made in at least a semi-continuous fashion aboard ship at spatial and temporal scales similar to physical and chemical measurements. Patterns of phytoplankton production are closely coupled to the subsurface distribution of density. At the scale of ocean basins and currents, geostrophic flow and the degree of baroclinicty determine the availability of nutrients to the mixed layer in these highly stratified, oligotrophic waters. Western boundary currents at the continental shelf break advect large volumes of water both horizontally and vertically creating tremendous variability in physical/chemical/biological properties as the energy of the current acts to break down the stability of the central gyres. On the shelf, the effect of winds and tidal energy further erode the depth and stability of the mixed layer to create regions of moderate productivity and, in some areas, competely overwhelm the system resulting in highly productive tidally mixed/upwelling regions. In each case, the transition from one state to the next occurs across a well defined boundary where the optical characteristics and concentrations of the phytoplankton found on either side are markedly different.

The signals that are available to active or passive remote sensors are controlled by the presence of substances in the water which act to either selectively remove wavelengths of light by absorption or contribute light at certain wavelengths by fluorescence. In greater than 95% of the deep ocean, so-called 'case 1' waters, these substances are associated with procaryotic and eucaryotic phytoplankton and their photosynthetic pigments. Using either absorption or fluorescence techniques, the presence of accessory pigments in addition to chlorophyll *a* allows us to differentiate phytoplankton by 'color groups' based on their ability to utilize blue and green wavelengths. In nearshore so-called 'case 2' waters, other dissolved chromophoric substances and particles of terrigenous origin contribute to the removal of blue wavelengths of visible light. This confounds a passive sensor's ability to separate signals which are strictly of a biological nature based solely on absorption . An active sensor such as a LIDAR system can capitalize on the fluorescence excitation and emission characteritics of many of these substances in order to simultaneously map their distributions without interference. The number of naturally occurring fluorescent compounds which can be used to qualitatively and quantitatively discriminate phytoplankton populations and dissolved substances is large when compared to our ability to design systems which can measure them.

Critics of remote sensing often question the science associated with this field, while advocates tend to promote remote sensing as a science. Our present knowledge of oceanic biogeography relies on analytical and numerical models as well as laboratory and field measurements of the environmental physiology of phytoplankton. Satellite ocean color sensors give us the ability to stand back from the natural system and visualize it at global scales. We would argue that remote sensing is primarily a tool for earth sciences which, in the case of oceanography, has advanced the science to a level that would never have been possible from shipboard measurements alone.

SCIENTIFIC APPROACH

Four major research areas were pursued with the intent of improving our capabilities to utilize remote sensing techniques for the study of oceanic processes:

1) Spectral attenuation of marine particulate and dissolved substances

2) Fluorescence spectral signatures of marine phytoplankton

3) Quantitative measurements of chlorophyll and optically active materials

4) Passive remote sensing imagery for ocean color and temperature

5) Aircraft mounted active sensors measuring laser induced fluorescence.

Measurements of spectral absorption and fluorescence were made in the field within the context of companion measurements of physical, chemical and optical properties of the water column and aircraft overflights provided through program support such as Warm Core Rings, Nantucket Shoals, etc. Many diverse oceanographic regions were sampled over this time period with simultaneous CZCS coverage provided through 1987. Resulting datasets were analyzed with the following goals:

1) to provide ground truth data of concentrations of optically active substances for validation of active and passive sensors

2) to evaluate patterns in the spatial and temporal distributions of spectral absorption and fluorescence in terms of the physical control of nutrients and light within the euphotic zone including the mixed layer and subsurface chlorophyll maximum

3) to use CZCS and AVHRR imagery to explain spatial and temporal distributions of phytoplankton at meso- and submesoscales in the North Atlantic and other areas

4) to examine the contribution of oceanic processes and optically active substances to errors in the CZCS pigment estimates and to develop improved algorithms and sensor designs which minimize these errors

5) to uncover additional optically active substances and to develop new methods and instruments which will improve our ability to assess variability in ocean color

6) to use the information gained from the above activities to model phytoplankton primary production and ocean color in the North Atlantic.

RESULTS OF SPECTRAL ABSORPTION STUDIES

The presence of phytoplankton causes a shift in the color of coastal water from blue to green in proportion to their concentration and spectral diffuse attenuation characteristics. The total diffuse attenuation coefficient can be partitioned as the sum of attenuation due to water, phytoplankton and dissolved colored substances. We have found that the ratio of the absorbance at 530nm due to carotenoids (primarily fucoxanthin) to the absorbance at 450nm due to chlorophyll as measured by the filter pad technique between 350 and 750nm in a spectrophotometer is indicative of the type of phytoplankton present in a sample. Diatoms and dinoflagellates exhibit a high 530:450 ratio (>0.4) while chlorophytes and green unicells display a lower value (<0.2). Since diatoms are predominant in coastal waters where ocean color is shifted to the green, the 530:450 ratio can be linked to changes in the diffuse attenuation coefficient of phytoplankton for different water types.

Following Beer's Law, the diffuse attenuation coefficient for phytoplankton should be linearly related to chlorophyll concentration, however, the observed relationship is non-linear at low chlorophyll concentrations characteristic of oligotrophic waters. This is caused by the presence of non-pigmented detrital particles included in the filter pad measurement and the manner in which pigment is distributed in large versus small cells, the so-called 'packaging effect'. The smaller cell sizes found in oligotrophic regions exhibit a higher effective absorption coefficient since pigments are distributed throughout the cell and the surface area to volume ratio is high. Photosynthetic pigments in larger diatoms and dinoflagellates are located in chloroplasts which occupy only a small portion of the cell volume. The combination of differences in the 530:450 ratio and the packaging effect led us to believe that mean phytoplankton cell size can be predicted from the shape of the spectral absorption curve, once corrected for detritus.

To test this hypothesis, we began measuring the size distribution and determining the concentrations of total and chlorophyll containing particles by flow cytometry in conjunction with spectral absorption measurements by the filter pad technique. Flow cytometry is a powerful technique which utilizes Coulter impedance volume to size individual particles which can be differentiated by the fluorescence of photosynthetic pigments. The ratio of chlorophyll containing to total particles can be used to estimate the proportion of dertital particles present on the absorption sample filter. This research is a central part of our continuing studies.

We have also extended the wavelength range of our spectral absorption measurement into the ultraviolet to 200nm as a means to investigate the role of UV photoprotective pigments contained in phytoplankton and colored dissolved organic material (CDOM or gelbstoff) abundant in coastal waters due to riverine discharge. Mycosporine-like UV photoprotective pigments with peak absorption at 320nm are found in many algal species, especially in natural populations from the clearest ocean waters at low latitudes. In the North Atlantic, the presence of phytoplankton containing these pigments is highly variable. CDOM can be measured on 0.2μm filtered seawater in a 10cm spectrophotometer cell, with peak absorbance occurring at 265nm. The slope of the curve increases exponentially with decreasing wavelength with s = -0.014, similar to values determined by other workers. The distribution closely follows salinity in coastal waters with the detection limit of this method exceeded in waters of salinity >30psu. Qualitative differences in the spectra were also found for different sources of the material.

RESULTS OF PHYTOPLANKTON SPECTRAL FLUORESCENCE

Spectral fluorescence excitation and emission curves are measured on the same filter pad as the absorption method. The filter is placed upright in a fluorescence spectrophotometer in the manner of a front surface measurement. There is no interference from detritus or sediment particles, only the pigments contained in algae fluoresce. There are three basic ways that light is harvested by photosynthetic autotrophs in the ocean according to phylogenetic color groups differentiated by light absorbing accessory pigments in addition to the main pigment chlorophyll *a*. The groups are indexed with specific types of pigments, namely, the accessory chlorophylls *b* and *c*, carotenoid proteins such as fucoxanthin and peridinin, and the phycobiliproteins: phycoerythrin and phycocyanin.

Observations performed at sea show that two primary emission bands are common to populations throughout the world ocean: one centered at 685nm due to chlorophyll *a* and one centered at 570nm due to phycoerythrin. Considerable variation exists in the excitation spectra for chlorophyll *a* caused by the presence or absence of organisms containing carotenoids. A combination of the fluorescence excitation ratio at 530:450 and the presence of phycoerythrin can be also be used to divide phytoplankton populations according to color groups. The chlorophyll accessory pigment (CAP) ratio offers a larger dynamic range than the absorption ratio; CAP ratios for diatoms and dinoflagellates are >0.8 while chlorophytes are <0.2. Cryptomonads have high CAP ratios, cyanobacteria have low CAP ratios, both have phycoerythrin. By selectively sizing natural populations through a series of filters of decreasing pore size, we confirmed that the size relationship was also true for the CAP ratio, small cell sizes found in oligotrophic waters have low CAP ratios while coastal, eutrophic waters have high CAP ratios and large mean cell size.

Additional variability was observed in the peak wavelength of phycoerythrin with two spectral types occurring in natural phytoplankton populations. Type I phycoerythrin contains two chromophores: phycoerythrobilin (PEB) and phycourobilin (PUB), and exhibits a peak emission wavelength at 560nm. PUB is able to absorb blue-green light at 500nm while PEB absorbs green light at 555nm. Type II phycerythrin lacks PUB and exhibits peak emission at 578nm. Both types of phycoerythrin can be found in either cryptomonads or cyanobacteria. Measurements from over 100 stations in the Northwest Atlantic showed that only Type I phycoerythrin occurs in the oligotrophic waters east of the Gulf Stream where PUB can utilize the predominant blue wavelengths of light. In the slope and coastal waters, Type II phycoerythrin occurs in highly productive green waters while Type I pigment can occur in strongly stratified waters with low chlorophyll concentrations. This distribution pattern based on strong biogeographic selection is an important advance in understanding the variability of active and passive remote sensing signals.

RESULTS OF QUANTITATIVE MEASUREMENTS OF OPTICAL SUBSTANCES

We have primarily been involved with the measurement of chlorophyll as it relates to estimates of phytoplankton specific biomass. The parameter that we traditionally report is a value for total chlorophyll which represents the sum of chlorophyll *a* and it's degradation products, the phaeopigments, as measured by a filter fluorometer. We use this parameter as remote sensors are unable to distinguish the two forms given their similar absorption and fluorescence properties. Many papers in the literature have discussed the problems associated with the fluorometric technique for chlorophyll including interference by chlorophyll *b*, pigment losses caused by partcles passing through large porosity filters and differences among workers due to storage, solvent extraction and instrument setup. We have contributed a number of papers to this body of literature including a novel chlorophyll method that measures pigment without the need for filtration, thus lending itself to automation. All of our chlorophyll measurements have been pulled together to create a North Atlantic database to be used for validation of CZCS scenes.

Studies of the distribution of organisms which contain phycoerythrin have been hampered by the lack of a method for the quantitative measurement of this water soluble pigment. While the fluorescence measurement for the extracted pigment is relatively simple, the major difficulty is obtaining high extraction yields from cyanobacteria, which are the predominant phycoerythrin containing picoplankton. Harsh mechanical methods have been used in the laboratory, but these methods will never become routine at sea. We have tried several enzyme/detergent systems in conjunction with sonication to break down the cell walls and solubilize the pigment protein complex, to date none of these methods have been successful.

RESULTS OF PASSIVE OCEAN COLOR STUDIES

We have taken the two geophysical parameters that can be measured from satellite sensors, ocean color and temperature, to isolate features in the ocean which amplify levels of primary production. Our initial studies concerned warm core Gulf Stream rings which pinch off into the slope waters south of Georges Bank and Cape Cod. The satellite imagery was used to confirm our model of primary production within regions of the ring. The rotary motions cause steady state production in the central region of the ring while geostrophic forces in the outer high velocity region act to deliver nutrients to the euphotic zone which drive enhanced production.

Similar processes act along tidally driven thermal fronts in the Gulf of Maine and along Georges Bank and Nantucket Shoals. Warm surface waters coincide with stratified waters with lower surface chlorophyll concentrations while colder vertically mixed waters exhibit high chlorophyll concentrations. The important factor in determining if the water column is vertically mixed is the strength of the tidal energy compared to the water depth, H/u^3. The tidal model predicts that the water column would be mixed when bottom depths are much shallower than the depths observed from satellite imagery which suggests that other processes are also active in destratification. We have studied these regions in terms of their temperature/chlorophyll patterns, nutrient supply and resulting production.

Another type of ocean front can be found along western boundary currents such as the Gulf Stream or Somali Current. These high energy regions are associated with marked differences in density formed between the ocean currents and adjacent gyres. Strong geostrophic forces and wind forcing create regions of localized divergence and convergence where phytoplankton production can be enhanced or subducted. The satellite imagery shows that the pattern of large-scale plankton patchiness is more complex than would be anticipated from general features of ocean circulation. Therefore, it is possible to study the interaction of global climate and primary production using ocean color imagery at scales similar to those used to look at heat and carbon fluxes. Climatology affects the mixed layer depth, hence, regulating the mean light intensity and nutrient flux to the euphotic zone. A model of new production was developed which traces the sequence of primary production along the central meridian in the North Atlantic as the sun moves from the winter to summer solstice. The annual pattern reflects the cross-sectional distribution of density and nitrate in the baroclinic regions of the mid-ocean gyres and currents in the North Atlantic. The model estimates realistic values of primary production and is useful for explaining the patterns of surface chlorophyll observed by ocean color imagery.

We have also been concerned with determining the causes of errors in the CZCS pigment estimates in order to improve future algorithm and sensor development. Early studies investigated the influence of colored dissolved organic materials in the Amazon outflow where pigment concentrations were grossly overestimated. Saturated areas of the Gulf of Maine where extremely high pigment concentrations were estimated turned out to be blooms of coccolithophores, phytoplankton cells covered with highly scattering calcium carbonate plates which dramatically affected the optical properties of the water without significantly increasing chlorophyll. Color banding on Georges Bank was found to be caused by the tidal current running across the submarine dune fields creating divergent and convergent cells which act to concentrate phytoplankton in bands parallel to the dunes. The North Atlantic chlorophyll database was extended globally and used to validate CZCS composite scenes where satellite estimates were found to be lower than extracted pigment concentrations by a factor of two. In the open ocean, chlorophyll content is expected to be overestimated due to the enhanced attenuation of blue light by the 'packaging effect'. In coastal waters, colored dissolved organic matter and detritus cause similar overestimates.

RESULTS OF ACTIVE REMOTE SENSING STUDIES

The majority of these activities were performed in collaboration with the Airborne Oceanographic Lidar group at Wallops Island, MD, led by Frank Hoge and Bob Swift. During NASA sponsored programs such as Warm Core Rings and the Nantucket Shoals Experiment, we were responsible for collecting surface calibration samples and in-water optical measurements simultaneously with overflights. As biologists, we also assisted the AOL engineers with data interpretation in terms of the biological causes of variability they observed along flight tracks. For example, the presence of phycoerythrin was detected early in the development of their system, we attributed differences in signal strength between offshore and nearshore waters to the changeover from Type I to Type II PE which we had observed in our fluorescence spectral signature studies. We also contributed to laboratory studies at Wallops Island using UV excitation to differentiate between cyanobacteria and cryptomonad phycoerythrin fluorescence using an excimer laser.

These studies led us to develop a laser fluorometer for shipboard measurements. Two pulsed dye lasers and two photomultiplier tubes were used to simultaneously measure three colors of fluorescence in a static or flow through cuvette. The system output analog voltage signals to strip chart recorders via a boxcar averager. While the fluorometer was originally designed to measure the fluorescence CAP ratio and phycoerythrin, during the initial field test in the Gulf of California in 1988 we found it was also useful for measuring CDOM and luciferin, the bioluminescence molecule.

SUMMARY

The research we have conducted over the past ten years has coalesced into a hypothesis which we continue to pursue, namely, that primary production occurs in the ocean according to two major pathways. The first pathway occurs in unstratified regions where nitrate is delivered to the euphotic zone supporting large cells which are grazed by copepods in a traditional food chain. The second pathway occurs in stratified waters where recycled nutrients in the form of ammonium support small cell sizes as the base of a complex food web. Nutrients are the key factor in each pathway, and the density field is what controls their availability. We seek to capitalize on the mean cell size differences found in each regime which affect the way light is absorbed in the water column. Given the fact that spectral absorption and fluorescence are directly related to mean phytoplankton cell size, our hypothesis includes the idea that a measure of this parameter can be gained from satellite ocean color.

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