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Spectral fluorescence: an ataxonomic tool for studying the structure of phytoplankton populations*

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Abstract. Although early studies in plankton biology feature detailed analyses of numbers of species, modern studies tend to emphasize bulk changes in biomass associated with rate processes. We argue that the penalty for this approach will eventually be an incomplete understanding of seasonal and spatial changes in the pattern of primary production of ocean waters. The ability of natural populations to respond to changes in the marine environment is due to adaptability at the cellular level (phenotypic) and changes in whole species groups (genotypic). The inability to test the relative importance of these two strategies is due to the incompatiblity of traditional taxonomic approaches and field experimentation where rate processes are being measured. To counteract this difficulty we propose an ataxonomic technique which utilizes the differences in light absorption by phytoplankton for photosynthetic processes. In this report we review how changes in the fluorescence spectral signatures reflect other biochemical features in natural populations. This is examined in concert with physical and chemical changes associated with the characteristics of ocean water masses with specific reference as to how these hydrographic features influence the relative growth of phytoplankton populations.

Introduction

The early studies of phytoplankton biology featured detailed studies of species and individual counts of species. Such studies were valuable in demonstrating the variety and composition of populations and in showing that changes occur in the population diversity associated with environmental factors. As interest shifted more toward primary production and physiological interactions, researchers focused more on the measurement of bulk substances such as chlorophyll pigment, primarily in an effort to establish the size of the population and its productive potential. Coherent with this approach was the attempt to establish rates associated with growth processes. Today such studies dominate research in this field.

The thrust has all but by-passed the important questions associated with the diversity of populations – questions originally proposed by the early workers in this field. Traditional planktonologists argue that much is lost in the interpretation of seasonal and spatial changes if only bulk population size is considered or overall rates measured. The skeptic, however, might ask what is actually lost.

Those of us interested in environmental physiology of phytoplankton are conscious of a functional redundancy in natural populations. By this we mean that the processes of photosynthesis, respiration and nutrient uptake behave as though the total population of phytoplankton with all its species is reacting as a superspecies. Moreover, to support functional redundancies we would argue that much of the observed change in functional responses is due to variations of the degree to which the physiology can respond to environmental changes such as variations in temperature or nutrient avail-

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ability. To support these arguments we assigned to a population the capability to accommodate environmental stress – a term that we call adaptability. The assumption is that much of this accommodation or adaptability occurs at a cellular level.

By judicious use of experimental field and laboratory techniques, we have been able to assemble enough data to place some limits on adaptability for specific functional responses such as photosynthesis, respiration and nutrient uptake. Some of this information has been applied to ecosystem modeling techniques and has been useful in attempts to improve the predictive capabilities of our models. However, we know from studies where detailed accounting has been made of species and their numbers that the composition of populations (diversity) changes in response to factors such as light, temperature and nutrient availability. Therefore, it would appear that the ability of phytoplankton populations to remain as productive units appears to depend on: (i) adaptive measures at the cellular level of single species; and (ii) changes involving whole groups of species. The question we ask is which are the most important – changes in diversity or changes in cellular adaptation. Methodology is of importance in answering this question for, at the present time, it is impossible to measure the functional physiology coherently with species diversity. To overcome this, we believe that one must look for a technique that is ataxonomic in nature, but still provides vital information on the characteristics of the composition of phytoplankton populations.

The taxonomic:functional dilemma has stimulated the development of techniques that would provide information on 'species characteristics' in natural populations. These techniques have emphasized the ease of sample handling, continuous measurement and acquisition of data in near real time. A most important development has been the Coulter particle counter (Sheldon and Parsons, 1967; Parsons, 1967). This unit met all of the criteria stated above, providing information on numbers of individuals and classification of sizes; the major drawback of the system is the inability to separate the particles in terms of biogenic and non-biogenic substances.

In this report, we are concerned with the development of another ataxonomic technique. The technique we are proposing utilizes the excitation and emission characteristics associated with chloroplastic pigment fluorescence. We believe that this technique could provide information on the characteristics of the population both in terms of biochemical differences and more standard allometric discrimination.

Methods and Results

Background on measurement of fluorescence signatures

Our previous research has shown that there are three ways by which light is absorbed and converted to photochemistry in marine planktonic autotrophs (Yentsch and Yentsch, 1979). These can be distinguished by accessory pigments for chlorophyll *a* fluorescence and/or other accessory chlorophylls, carotenoid protein pigments and phycobilins. In all of our observations (Yentsch and Phinney, 1985), we observed two emission bands, one caused by chlorophyll *a* fluorescence centered at 685 nm and the other between 570 and 590 nm, identified as phycoerythrin. We observed considerable difference in the intensity of the two emissions and these are reflected to some extent in changes in the excitation spectrum.

Figure 1 shows the spectra that we believe comprise the majority of the population

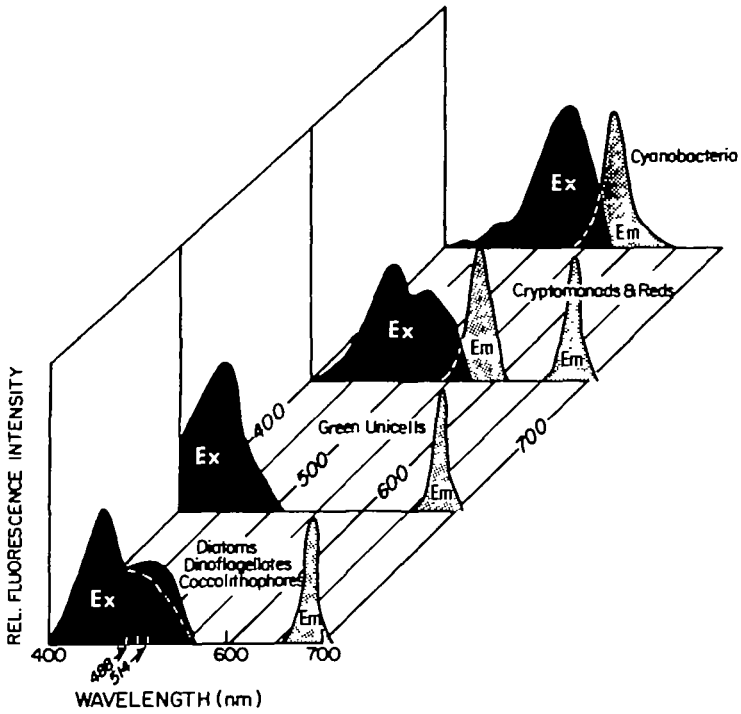

Fig. 1. Spectral fluorescence signatures of major ocean phytoplankton color groups.

spectra we have observed in different ocean areas. Specifically, there are four major groups which can be fitted with distinguishing spectra. The first is the diatoms and dinoflagellates, all of which have characteristically broader excitation spectra than the green unicells in the population. The cryptomonads and cyanobacteria have similar emission due to phycoerythrin; the major distinction being that the latter has a very reduced chlorophyll *a* emission (Yentsch and Phinney, 1985). From our visual inspections of the fluorescence excitation/emission spectra, there is a strong feeling that there is much to be learned from these signatures that cannot be adequately expressed at this time. There are, however, certain specific features of these signatures that are useful, such as the relationships between wavelengths.

The wavelengths (Table I) designate the three pathways of light absorption and energy transfer. For example, at 450 nm, chlorophyll *a* fluorescence at 685 nm is strongly excited. There is also some fluorescence emission from phycoerythrin, the result of excitation at this wavelength. By exciting at 530 nm, chlorophyll *a* fluorescence at 685 nm can also be stimulated. The degree to which it is stimulated depends upon the number of eukaryote organisms with carotenoid protein, such as fucoxanthin or peridinin and/or phycoerythrin. To specify certain characteristics of the action spectra we utilize the ratio of 530:450 nm, where $F(\lambda_e,\lambda_f)$ is equal to fluorescence excited at λ_e and measured at λ_f and is expressed as:

$$\frac{F(530,685)}{F(450,685)} \quad (1)$$

Table I. Principal accessory pigments and CAP ratios for some common marine phytoplankton.

Components	Principal accessory pigments	CAP ratio	685_{Em}[e]	$570-590_{Em}$
Diatoms	Chl *c*, fucoxanthin	0.8–0.9	Yes	No
Dinoflagellates	Chl *c*, peridinin	0.7–0.8	Yes	No
Coccolithophores	Chl *c*, UC-P[c]	0.3–0.4	Yes	No
Gold-brown unicells[a]	Chl *c*, UC-P	0.3–0.4	Yes	No
Green unicells[b]	Chl *b*, –	0.1–0.2	Yes	No
Cryptomonads	Chl *c*, PE, PC[d]	0.7–0.8	Yes	Yes
Cyanobacteria	– , PE, PC	–	No[f]	Yes

[a]Examples are prymnesiophytes, chrysophytes.
[b]Examples are chlorophytes, prasinophytes.
[c]Unidentified carotenoid protein complex.
[d]PE - phycoerythrin; PC - phycocyanin.
[e]Chlorophyll fluorescence at 685 nm when excited by light at 450 and 530 nm independently.
[f]Chlorophyll fluorescence at 685 nm appears to be undetectable in young marine cultures; some emission at this wavelength can be detected in old cultures.

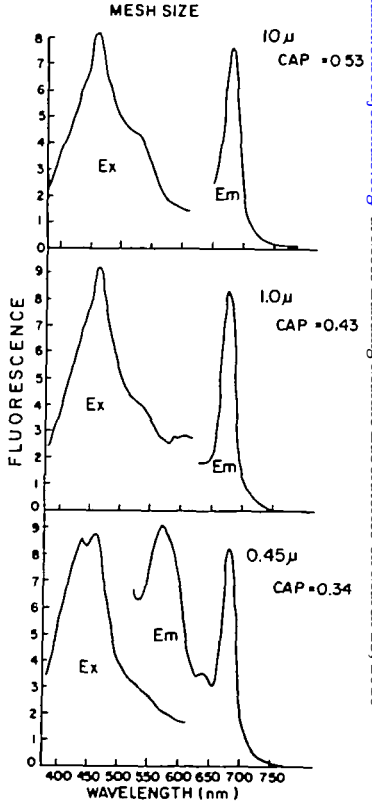

Fig. 2. Spectral fluorescence signatures of phytoplankton retained by different mesh sizes (from Yentsch and Phinney, 1985).

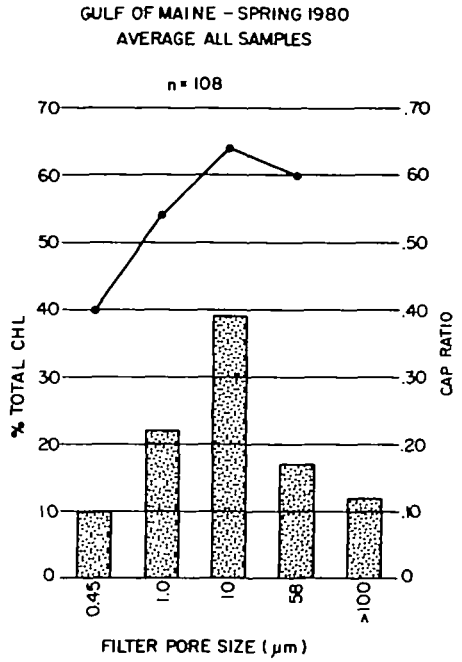

Fig. 3. Percent chlorophyll (bars) and CAP ratio (solid line) for different size fractions of phytoplankton in the Gulf of Maine.

We call this the chlorophyll accessory pigment ratio (CAP).

Because of the variation in the accessory pigmentation of different groups of algae, the CAP ratio (Table I) changes. Organisms with chlorophyll *c*, having the highest CAP ratio (0.8), are diatoms and dinoflagellates. Coccolithophores, which also contain chlorophyll *c*, have an intermediate CAP ratio of 0.3 – 0.4. Golden-brown unicells are also in this same range. The lowest CAP ratios occur in green unicells, which contain chlorophyll *b*. Among the organisms containing phycoerythrin, cryptomonads have a relatively high CAP ratio, as opposed to the cyanobacteria which have very little emission at 685 nm and hence have a lower CAP value.

By using large volumes of seawater collected from waters around Boothbay Harbor, Maine, we selectively sized the spectral signatures of natural populations. Figure 2 shows an example of a suite of sizes ranging between 10 and 0.45 μm. The spectra for excitation and emission are shown as a function of wavelength. An important feature of this is that at the 10 μm size, one can see a strong shoulder between 500 and 550 nm which is due to the presence of carotenoid proteins. As one examines the organisms of 1 μm size one can see that they no longer contain proportionately as much of the shoulder caused by carotenoid protein. The organisms that pass the 1 μm net have very little or none of that material. All size fractions show chlorophyll *a* emission, but strong phycoerythrin emission does not show up in sizes other than the smaller size fractions. Figure 3 shows chlorophyll and CAP as a function of size. These data confirm the concepts that the smaller size fractions have lower CAP ratios.

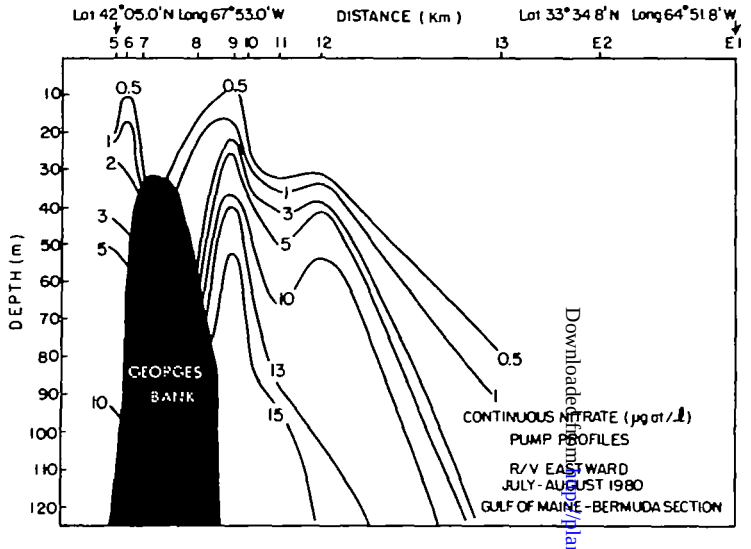

Fig. 4. Nitrate concentration, Georges Bank to sea.

The relationship between changes in fluorescent spectral signatures and specific features of water masses

In the course of our measurements (Yentsch and Yentsch, 1979; Yentsch and Phinney, 1985), we were aware that the observed changes in spectral signatures appeared to be associated with certain oceanographic features, specifically features known to be important in the regulation of phytoplankton growth. This awareness is summarized as follows: (i) high CAP ratios are generally observed in areas high in phytoplankton; (ii) low CAP ratios generally predominate in the sparse populations of oligotrophic water masses; and (iii) we observed high CAP ratios in coastal waters (consistent with the dominance of diatoms and dinoflagellates in these regions). The species are rich in carotenoid proteins and generally have a mean cell size larger than species in oligotrophic offshore waters.

To expand our observations, we concentrated on two specific ocean regimes where changes in the biological and physical charcteristics of water masses are marked. The first compared fluorescence parameters in an area dominated by tidal activity, which forms a strong thermal front separating mixed and stabilized water masses, and hence nutrient-rich from nutrient-poor waters (Figure 4). This front is a persistent feature of the southern flank of Georges Bank formed by tidal friction, and separates warm slope waters frequently intruded on by filaments from the Gulf Stream from cool, tidally stirred water over the Bank. At the seaward edge of the Bank (Figure 5), the isotherms are nearly vertical, reflecting the intensity of tidal stirring in this region. The breakdown in the thermal stability of the slope water mixes the nutrients (nitrate-nitrogen) throughout the entire water column. This enrichment is reflected in the abundance of phytoplankton chlorophyll which is observed adjacent to and on top of the Bank. The major transition from chlorophyll-rich to chlorophyll-poor waters occurs approximately at the 60 m isobath.

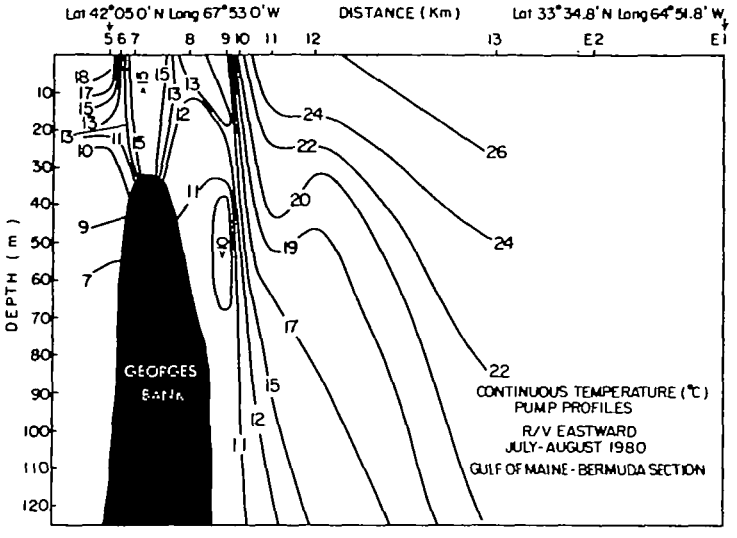

Fig. 5. Temperature, Georges Bank to sea.

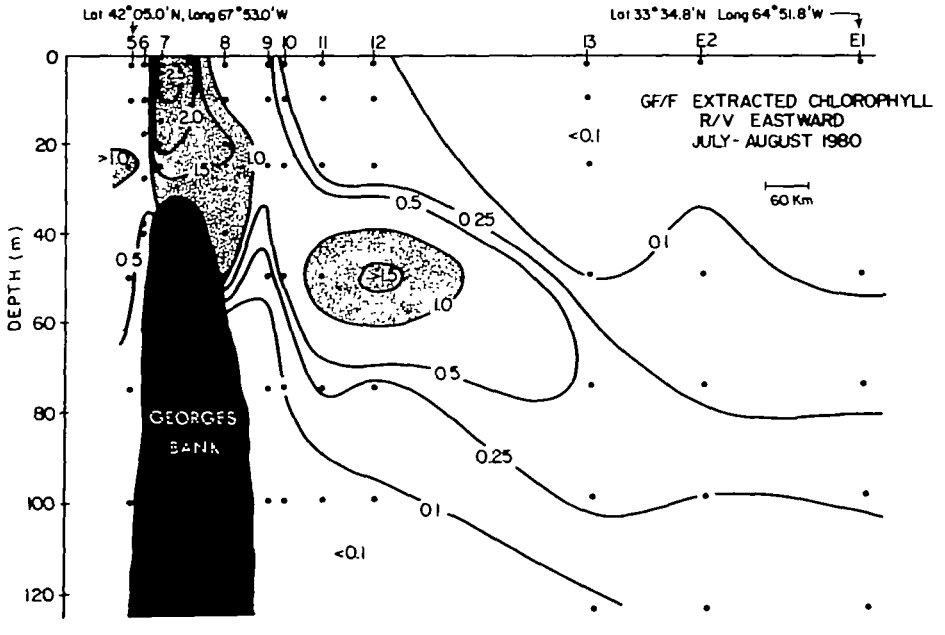

Fig. 6. Chlorophyll concentration, Georges Bank to sea.

Moving seaward from the Bank, a chlorophyll maximum (Figure 6) is seen in the water column at 50 m depth extending seaward at least 60 km. This maximum has continuity with the Bank proper which we interpret to mean that phytoplankton populations over the Bank are transported off the Bank by a subsurface density flow, a

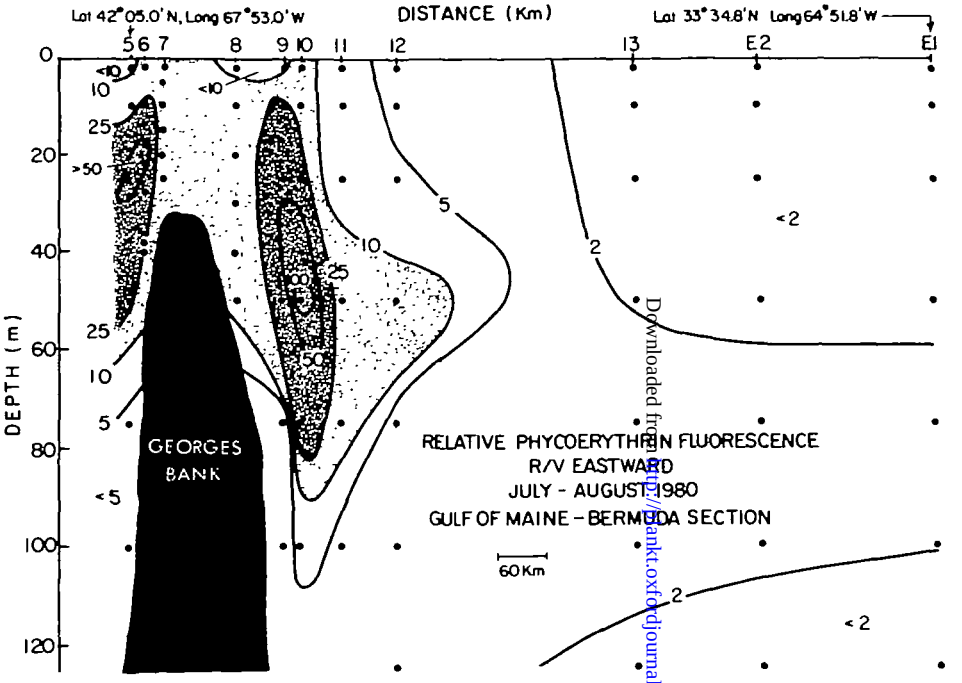

Fig. 7. Phycoerythrin fluorescence, Georges Bank to sea.

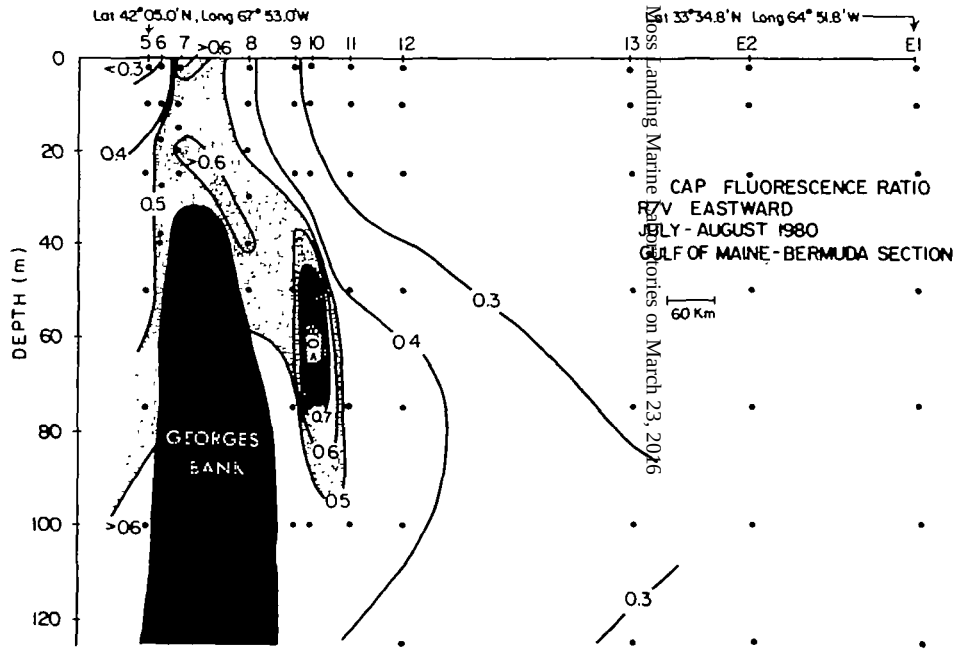

Fig. 8. CAP ratio, Georges Bank to sea.

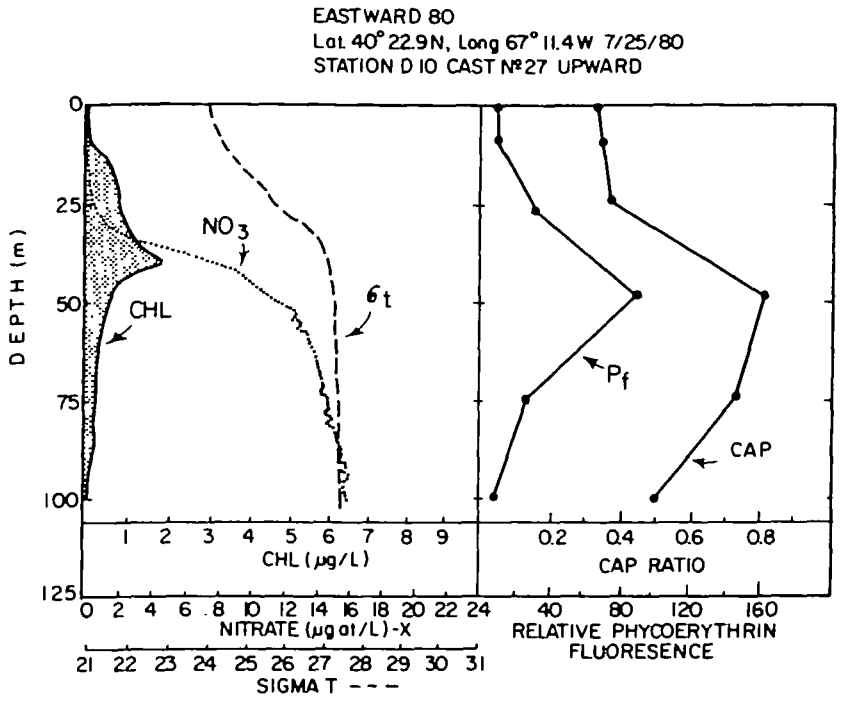

Fig. 9. Vertical profile of chlorophyll, phycoerythrin fluorescence and CAP ratio in a stratified water column.

mechanism similar to that described by Simpson *et al.* (1982).

The fluorescence of phycoerythrin shown in this section (Figure 7) is similar in pattern to that observed for chlorophyll. Note that the major concentration appears to be located in the seaward edge of the front and not over the Bank, which is the case for chlorophyll. The pattern of CAP ratios closely resembles the pattern for phycoerythrin (Figure 8). The ratio is high all around and over the bank (>0.5) with the highest values (>0.8) occurring at 40 m in the front. The CAP ratios in the slope waters are <0.4 at all depths sampled in the water column.

In the course of making the Georges Bank/Bermuda section, we made fluorescent microscopic counts of organisms in surface waters. By concentrating populations on 0.2 μm Nuclepore filters, we made a visual estimate of size and a distinction between orange phycoerythrin fluorescing species (procaryotes) and red chlorophyll fluorescing species (eucaryotes). We found that over Georges Bank and in the immediately adjacent waters, the procaryotes exceeded the eucaryotes by only ten times in cell number, which is in agreement with the findings of Glover *et al.* (1985). For the most part, the eucaryotes were assemblages of large celled diatoms and dinoflagellates. In contrast, the populations in the surface waters of the slope region comprised small cell sizes and procaryotes exceeded the numbers of eucaryotes by more than one hundred times.

We concluded from observations made in this section that the tidal-thermal front which marks a transition in biomass, also marks a transition in abundance of phycoerythrin

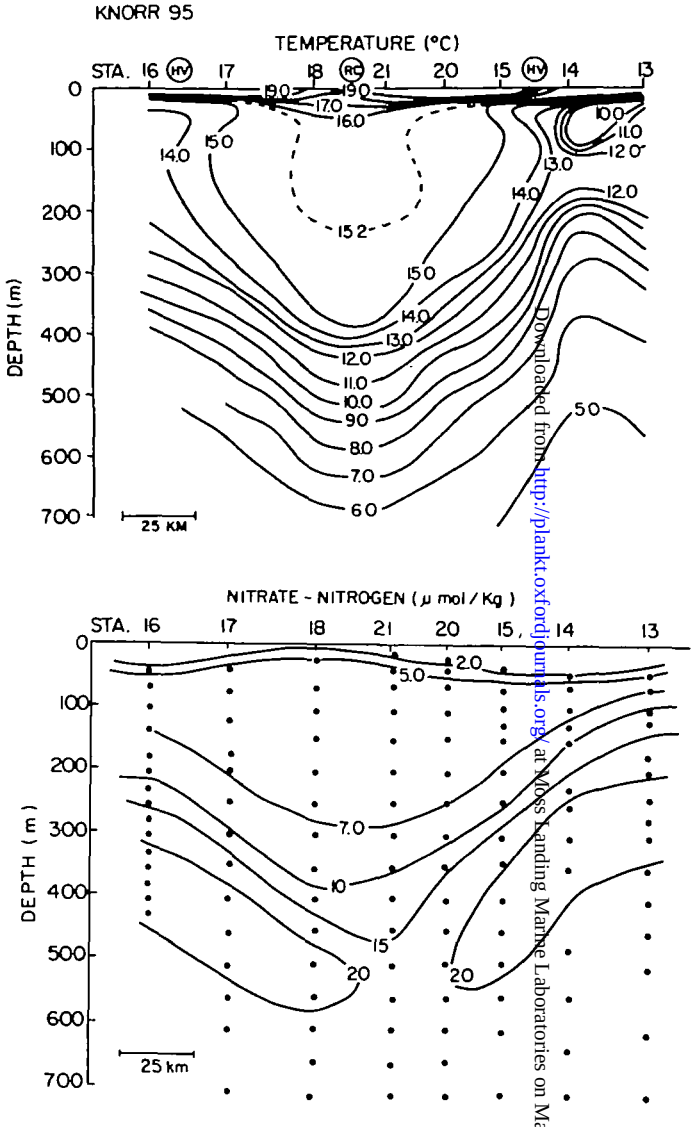

Fig. 10. Temperature and nutrient concentrations in a warm core ring 82B, Knorr 95, June 1982.

and change in CAP ratios. The microscopic examinations suggest that the fluorescent parameters reflect a shift in the diversity of the population.

In thermally stratified water masses, we observed marked changes in spectral signatures that coincided with changes in the vertical profile of nitrate and density (Figure 9). In these cases, the chlorophyll maximum occurs at depths where the nitrate/nutricline is steep. It is also in this region that the highest amount of phycoerythrin and the highest CAP ratio occur. Both are lower above and below the chlorophyll maximum. We interpret this to mean that the chlorophyll maximum comprises species, such as diatoms and dinoflagellates, that have a large mean cell size and relatively high sinking rate,

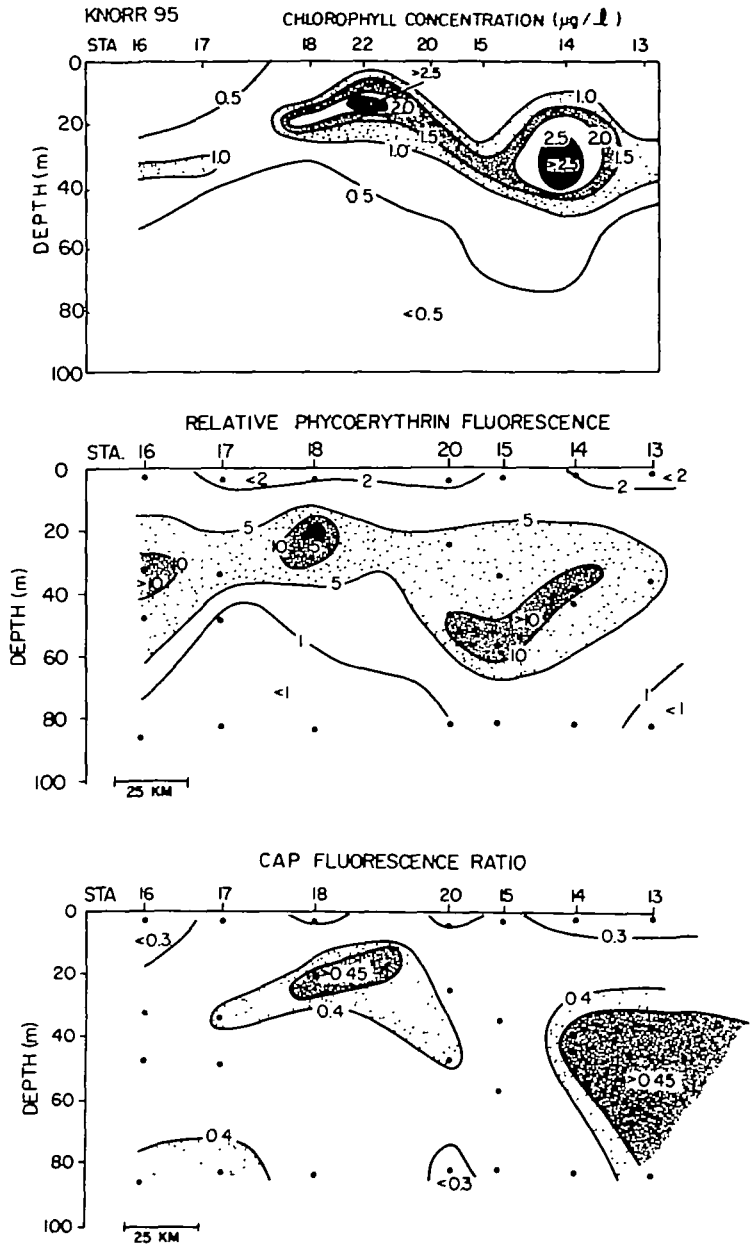

Fig. 11. Chlorophyll, phycoerythrin fluorescence and CAP ratio in a warm core ring 82B, Knorr 95, June 1982.

and that low phycoerythrin and a low CAP ratio in the water column above the chlorophyll maximum are caused by species of small cell size and low sinking rates .

We also measured intensively spectral signatures in the mesoscale warm core eddies spawned by the Gulf Stream. These areas were chosen primarily because the eddies

are composed of distinctly different water masses. Within these eddies, change in biomass and species diversity appear to be closely related to the fluid dynamics of the eddy (Ortner *et al.*, 1979; Yentsch and Phinney, 1984). Because of a clockwise rotation of the eddy, the isotherms and lines of equal nitrate-nitrogen (Figure 10) bow upward from a ring center to the extremes of the eddy as shown in a radial section. We believe that the pattern of growth and phytoplankton abundance in this radial section reflects the baroclinicity. In essence, the ring is a circular front with a ridge of phytoplankton abundance concentration at or near the peripheral region of the eddy. In newly formed eddies, this ridge of abundance encircles a core of oligotrophic, phytoplankton-poor water. However, the distribution of phytoplankton throughout is complicated by the fact that the eddy undergoes deep convective mixing during winter residence in the slope waters. When convection is arrested due to increased solar heating, thereby stabilizing the water masses, a bloom of phytoplankton occurs that dominates the pattern of abundance within the eddy. Figure 11 illustrates the seasonal situation where a spring bloom of phytoplankton has occurred in the central region of the eddy. Note that across the radial section there are three regions of relatively high phytoplankton chlorophyll: the bloom at the ring center and midwater maxima at the two extremes of the radial section. The patterns of chlorophyll, phycoerythrin and CAP ratios tend to mirror one another. We also found that eucaryote cell numbers follow the chlorophyll distribution and the procaryote cell numbers follow the phycoerythrin fluorescence. The spring bloom at the ring center consisted largely of diatoms and dinoflagellates (G.A.Fryxell, personal communication). Their presence accounts for the fact that the CAP ratio is high in this section of the radial. In contrast, high CAP ratios (>0.4) occurring in the populations at the extremes of the radial were dominated by coccolithophores.

We believe that the observations on fluorescent signatures within an oceanographic feature such as an eddy can be explained by shifts in population diversity due to differences in the growth conditions throughout the eddy. The spring bloom condition gives rise to spectral signatures characteristic of organisms with large amounts of carotenoid proteins such as diatoms and dinoflagellates. The large populations occurring in the intense baroclinic regions also have spectral signatures indicative of actively growing populations, but the species composition is different.

Proposed strategies for changes in fluorescence spectral signatures

In this section, we will analyze the causes of change in spectral signature and propose a general scheme to account for the distribution observed in ocean water masses.

There are two major reasons why fluorescence spectral signatures change in natural populations. The first would be in cellular response to external environmental factors, such as change in light intensity or quality, or change in nutrient supply. In the language of evolutionary biologists, this response would be phenotypic. A second reason for this change would require that species having different spectral fluorescent signatures would be added to or subtracted from the population in response to environmental change. This process would be genotypic.

In considering the meaning of change in fluorescence signatures, we emphasize that a single measurement reflects a genotypic mean that can be modified by phenotypic

processes. For example, the CAP ratio from equation (1) is:

$$\mathrm{CAP} = \frac{\mathrm{F}(530,685)}{\mathrm{F}(450,685)} = \frac{\sum_a n^a \, \mathrm{F}(530,685)}{\sum_a n^a \, \mathrm{F}(450,685)} + n^b + n^c \qquad (2)$$

where n is the number of individuals of species a, b or c depending on the species composition of the population. A phenotypic response requires that for a single species, for example, species a

$$\Delta \mathrm{F}\,(450,685) \sum_a n^a \cong (\mathrm{f})\ \Delta,\mathrm{I},\mathrm{N} \qquad (3)$$

We emphasize that there is no single means to determine which process [equation (2) or (3)] is influencing the CAP ratio. Both strategies for adaptation undoubtedly operate to some degree but, from our observations, we feel that in terms of importance, spectral signature changes reflect changes in the species composition of natural populations. This is supported by the studies of Murphy and Haugen (1985) which show that the dominant species in the open Atlantic Ocean are not diatoms or dinoflagellates, but small unicells of procaryotes and eucaryotes. These workers, together with R.R.L.Guillard, have cultured these species and assembled data on action spectra for chlorophyll and phycobilin fluorescence and specific carotenoid identification. As indicated in Table I, the new small chlorophyll *c* eucaryotes do not have carotenoid proteins identical to fucoxanthin. The new pigments have yet to be identified. It is apparent from their absorption spectra that they are not as effective as fucoxanthin in the absorption of green light. These small chlorophyll *c*-containing eucaryotes, as well as some chlorophyll *b*-containing unicells, give rise to the low CAP ratios of the surface waters of the oligotrophic oceans. From the curves shown in Figure 1, the procaryote cyanobacteria do not effectively utilize absorbed blue light for fluorescence hence their contribution to chlorophyll *a* fluorescence is low. Consequently, their presence in the population does not measurably influence the CAP ratio. The presence of procaryote cyanobacteria, however, greatly changes the ratio of phycoerythrin to chlorophyll fluorescence. As we measure fluorescence, phycoerythrin fluorescence has been observed to be greater than chlorophyll fluorescence in oligotrophic waters. The reverse is true in eutrophic waters.

In nutrient-rich waters, such as the coastal oceans, the dominance of diatoms and dinoflagellates causes CAP ratios to exceed 0.4 and, at times, they are >0.7. The question we pose is that if physical-chemical processes are involved in regulating spectral signatures, to what specific physical processes do we refer? We believe the answer is in the amount of vertical turbulence in the water mass.

The role of turbulence is to change the amount of light available, to influence nutrient level and to influence sinking rates. For example, in a strongly mixed water column (Figure 12), nutrient enrichment favors the growth of large chlorophyll-rich populations with a large mean cell size and a relatively high sinking rate. The residence time within the euphotic zone is dependent upon the degree of turbulent mixing. As surface waters become buoyant from solar heating, nutrients are depleted and the cells sink

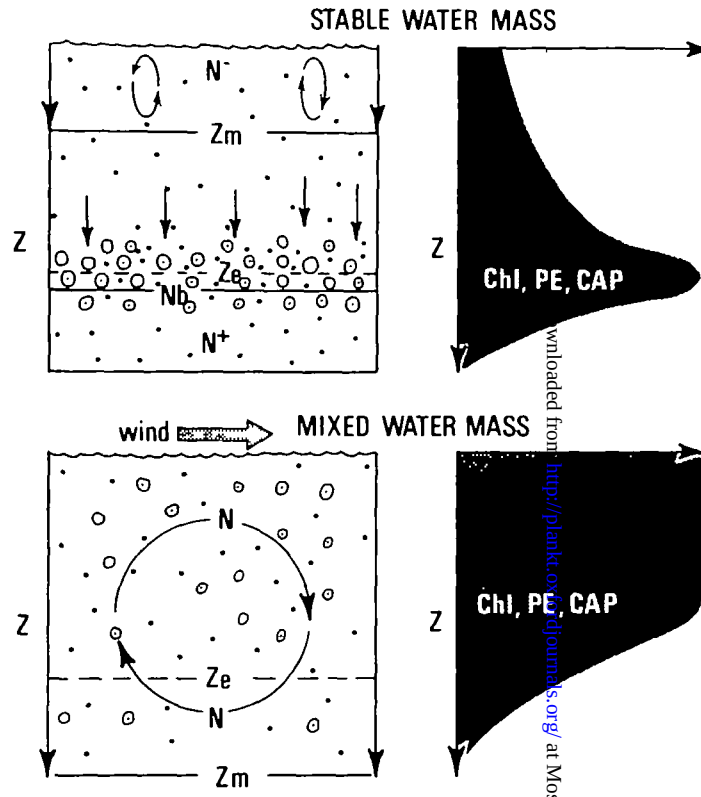

Fig. 12. Conceptual diagram of the role of mixing and sinking on the distribution of pigment-fluorescence parameters in ocean environments. Z_m is the depth of the mixed layer, Z_e is the euphotic zone depth and N_b is the nitrate nutricline. N^- and N^+ are nutrient-poor and nutrient-rich waters, respectively.

to the base of the nutricline allowing the small unicells which do not sink to remain in the entire water column. Differential sinking rate as a function of cell size is consistent with measurement of cell sinking rates in oligotrophic waters (Bienfang, 1980).

The scheme shown in Figure 12 represents a physical separation of large eucaryotes, such as diatoms, from small procaryotes and eucaryote unicells with spectral signatures changing accordingly. Thus, there are low CAP ratios and total pigment fluorescence in surface waters and high CAP ratios and pigment fluorescence at the thermocline. In the chlorophyll maximum, pigment ratios may be accentuated by the growth of specific species capable of utilizing low light conditions. Glover and Morris (1981) demonstrated that small coccoid procaryotes photosynthesize effectively at light intensities lower than large eucaryotes. H.Glover (personal communication) has reported growth of small eucaryotes in the chlorophyll maximum of the open ocean. If this is the case, pigment ratio changes are the result of oceanographic processes (i.e., turbulence of the water column) and not primarily a problem of cellular photoadaptation. We believe that fluorescence responses to environmental factors such as light and nutrients are accommodated by changes in species or groups of species.

Adaptability and ataxonomy —a summary

Our original goals, as stated in the Introduction, were to assess progress in the development of fluorescent spectral analysis primarily as an ataxonomic tool for studying the physiological ecology of natural populations of phytoplankton. We first had to assess the degree to which we could characterize populations by this method (Yentsch and Phinney, 1985). We then attempted to standardize this method based on specific wavelengths of excitation and emission and examine changes in these parameters in the marine environment. This is what is reported in this paper. We feel that indicators such as CAP ratios and the amount of phycoerythrin will become companion measurements to the more routine measurements of chlorophyll and will provide a better means of assessing growth potential in natural phytoplankton populations. This leads into a third area where progress has been slow. If this ataxonomic tool is to be of value, then it must have some basis for classification. Should it be a physiological functional grouping, or perhaps an allometric classification? In either case, this becomes a goal for future study.

We believe our measurements have posed interesting questions concerning the adaptability of natural populations to ocean conditions. The plant physiological and biological oceanographic literature contains considerable information on the degree of functional freedom particular species have to environmental stress. It has become routine for the marine biologist to think of cellular chlorophyll as an example of a labile substance that reflects photoactive changes in concentration as a response to light. Yet since the early comparative physiological studies of Steeman-Nielsen and co-workers (see review by Richardson *et al.*, 1983), we know that some photoadapt in this manner and others do not. More recent studies on single cells (E.Sakshaug and C.M.Yentsch, personal communication) show a wide range of pigment photoadaptability in species, although all species tested appear to have common photoadaptive growth characteristics.

To the ecologist interested in the adaptability of natural populations composed of many species, the comparative photoadaptive information makes phenotypic interpretations extremely difficult and experimental testing almost impossible. Faced with this dilemma, we argue that adaptability in the most general sense, can come about by (i) cellular adjustments to environmental changes; or (ii) changes in the composition of species in the total population. Some would argue that both statments operate, but on different time scales. We would agree with this had we not measured pigment fluorescence parameters in natural populations. We now believe that the aspect of cellular change may have been overestimated and what is important is the degree of photoadaptability among species. Furthermore, these changes (i.e., functional changes in general), which appear to have an 'apparent' photoadaptive interpretation, are in reality reflecting changes in species diversity which, in turn, reflect the conditions for growth of marine phytoplankton.

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