Pico- and ultraplankton Sargasso Sea communities: variability and comparative distributions of Synechococcus spp. and algae*

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ABSTRACT: Ultraplankton (0.2 to 5 μm) provided >88% of euphotic layer chlorophyll (Chl) at 2 Sargasso Sea stations in July/August 1986. Communities were further characterized to quantify the separate abundances of phycocerythrin-fluorescing cyanobacteria Synechococcus spp. and Chl-fluorescing algae in 0.2 to 0.6, 0.6 to 1, and 1 to 5 μm size fractions. Throughout the water-column at both stations, the majority of Synechococcus cells were consistently found in the 0.6 to 1 μm fraction; the Sargasso Sea WH7803 serogroup was not a dominant component of Synechococcus populations at any depth. Highest numbers of Synechococcus cells were always in the surface isothermal layer, where they accounted for >95% of all ultraphytoplankton cells. At the base of the euphotic layer total numbers of photoautotrophs were low, but numbers of algae increased. The varying distribution of the 2 ultraphytoplankton components with depth was also reflected in their separate contributions to Chl concentrations, and algae were the main contributors to Chl maxima at 1 to 3 % L. Above this depth, a pigment maximum in phycocerythrin (PE) occurred at the nitractine, coincident with a peak in primary productivity. PE maxima were due to an increase in PE content of Synechococcus cells and not to an increase in their abundance. The 2 stations did however exhibit significant differences. High surface productivity at Stn 1 was supported by nanomolar changes in nitrate concentrations, which selectively and rapidly induced a Synechococcus bloom. In contrast, the water-column characteristics of Stn 2 were relatively stable, Synechococcus spp. were less abundant throughout the water-column, while algae were twice as abundant at the Chl maximum and 0.5% light level, where most were of picoplankton size (>79% of algae were in <1 μm fractions). Data suggest that there is a considerable degree of variability in the abundance, composition, and productivity of stratified oceanic ultraphytoplankton communities.

INTRODUCTION

During the last decade, increasing efforts in biological oceanography have been focused on defining and quantifying the microbial components of oceanic rate processes, particularly as they affect the cycling of carbon and nitrogen. Renewed interest in oceanic phytoplankton and primary productivity estimates has been largely stimulated by new information on the predominance and activity of ultra- (<3 μm) and picophytoplankters (<1 μm). The ecological success of these in oceanic regions has been partly attributed to the increased efficiency of light-harvesting and nutrient uptake conferred by their small cell size (cf. Fogg 1986, Kirk 1986, Raven 1986) and their negligible sinking rates (Takahashi & Bienfang 1983). Revised higher estimates of oceanic primary productivity (e.g. Laws et al. 1987, Marra & Heinemann 1987) have a direct impact upon developing models of biogeochemical cycling of carbon and nitrogen in the upper ocean, where dynamics are driven by synergistic interactions between ultraplankton-size photoautotrophs, chemooautotrophs, methanotrophs, heterotrophic bacteria and their protozooplankton grazers (cf. reviews by Fogg 1986, Platt & Li 1986, Stockner & Antia 1986).
More recently, it has become apparent that ultraphytoplankton contains both cyanobacteria and algae. These 2 photosynthetic components can be distinguished in mixed communities and enumerated by direct count epifluorescence microscopy, since red-pigmented cyanobacterial cells have a dominant phycoerythrin (PE) fluorescence emission, while all algal species have a predominant Chl fluorescence emission (Glover 1985). While the contribution of marine cyanobacterial populations of *Synechococcus* spp. to primary production has received considerable attention (see reviews by Glover 1985, Waterbury et al. 1986), direct estimates of both the biomass and photosynthetic activity of similarly-sized algae within the same water mass had never been attempted.

During a cruise to the Sargasso Sea in summer 1986, we used 2 recently developed field techniques to measure nanomolar nitrate concentrations in surface waters and *Synechococcus* PE concentrations throughout the water-column. We also compared the abundance of *Synechococcus* spp. to that of algae in different size-fractions and estimated the separate contributions of these 2 phytoplankton components to the total standing crop of Chl and primary productivity at several depths. Measurements and experiments were also designed to define possible differences in adaptive responses employed by *Synechococcus* spp. and algal ultraplankters (<5 μm) to cope with variations in light and nutrient flux that might explain any distributional differences. This manuscript describes the temporal and spatial variations that we observed in PE and Chl concentrations and the numerical abundance of *Synechococcus* spp. and algae in ultra- (<5 μm) and pico- (<1 μm) phytoplankton communities.

**MATERIALS AND METHODS**

This study was conducted in the Sargasso Sea (Fig. 1) during the summer of 1986 from the RV 'Endeavor' (Cruise EN-146). Stn 1 was 140 km east of Bermuda (32°42′ N, 63°01′ W) and was occupied from 20 to 28 July. Stn 2 was 165 km NNW of Bermuda (33°42′ N, 65°22′ W) and was occupied from 2 to 9 August.

**Physical/chemical measurements and sample collection.** The research vessel received daily charts of sea surface temperature derived from NOAA satellite images (AVHRR) and the position of the Gulf Stream and cold-core eddies in Fig. 1 were taken from NOAA/National Weather Service analysis on 18 July. Subsequent thermal maps indicated that these features did not change significantly throughout the cruise.

A submersible pumping system (180 m) was constructed to collect discrete samples, while providing simultaneous continuous vertical profiles of temperature, in vivo Chl fluorescence and quantum irradiance (Biospherical design) as a function of depth. One modification over the prior system (Prézelin et al. 1987) was the use of an internal hose diameter of 5 cm, intentionally enlarged to minimize shear effects on phytoplankton populations, and pumping was demonstrated to have no effect on either phytoplankton biomass or photosynthetic activity, when compared to replicate samples collected with GOFLO bottles. The flow rate was ca 113 l·m⁻¹·min⁻¹, with a 3 min transit time from intake to outlet. Pump effluent was directed through an adapted Turner fluorometer to measure in vivo Chl fluorescence. Analog data from the fluorometer, temperature and depth probes, in situ irradiance and daily incident irradiance, (quantum sensor, Biospherical Instruments) were recorded on strip charts.

Samples from discrete depths were collected from the fluorometer outflow into 125 ml polyethylene bottles and frozen for subsequent onshore analysis of nitrate concentrations. Nitrate in the upper 60 m was measured using a chemiluminescent technique (precision of ±2 nM; Garside 1982), and at greater depths by the standard colorimetric method (precision of ±80 nM; Strickland & Parsons 1972). Discrete samples were collected directly from the pump effluent into darkened 201 polypropylene carboys, that were immediately transported into the shipboard laboratory for analysis. All apparatus used for the collection and incubation of water samples was cleaned by the procedure of Fitzwater et al. (1982). To recycle, the vessels were rinsed with 0.25 N HCl followed by deionized water.

**Cell enumeration of photoautotrophs.** Numbers of

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**Fig. 1.** Locations of 2 stations in the Sargasso Sea during RV 'Endeavor' Cruise EN-146, 17 July to 11 August 1986. Position of Gulf Stream (GS) and cold-core eddies (CE) were taken from NOAA/National Weather Service analyses on 18 July.
Chl-fluorescing algae and PE-fluorescing Synechococcus cells were determined by epifluorescence microscopy in 3 size-fractions of unpreserved samples separated by differential filtration (Glover et al. 1986). A minimum of 100 cells were counted and standard deviations were 10 to 25% of the mean count of several microscope fields for 1 to 5 μm and 0.6 to 1 μm assemblages. Standard deviations were however routinely >25% for 0.2 to 0.6 μm assemblages, principally due to the very low cell counts in this size range. The percentage of total phytoplankton cells represented by Synechococcus spp. in each size range is shown in Table 1. Duplicate samples were preserved in buffered formalin and stored in the dark at 4°C for onshore enumeration of 2 Synechococcus serogroups by immunofluorescence labelling (Campbell & Carpenter 1987). Antiserum produced against the Sargasso Sea isolate WH7803 was cross-absorbed with cells of the coastal isolate WH8016, and vice versa, before use.

**Cell enumeration of bacteria.** Numbers of bacteria were also determined in preserved samples, using the acridine orange direct counting method of Hobbie et al. (1977). A minimum of 100 cells were counted and standard deviations were 3 to 21% of the mean count of several microscope fields.

**Phytoplankton pigment concentrations.** Duplicate samples were filtered to determine particulate Chl concentrations, the volume (50 ml to 1 l) depending on the in vivo Chl fluorescence signal from the pump profile and the filter pore size. Each sample was divided into 4 portions, which were filtered through separate Nuclepore filters of 5, 1, 0.6 and 0.2 μm pore sizes and filtrates were discarded. Methods for filtration and extraction are described in Glover et al. (1986). Chl concentrations were determined directly for >5 μm communities and by mathematical subtraction for 1 to 5, 0.6 to 1 and 0.2 to 0.6 μm fractions. Standard errors were routinely <10% of the mean. Cell-specific Chl concentrations in pure 0.6 to 1 μm Synechococcus populations (92 to 100% of all autofluorescent cells; Table 1), were used in conjunction with cell numbers in the 1 to 5 and 0.2 to 0.6 μm fractions, to estimate Synechococcus Chl in these other size ranges. The quantity of algal Chl in 1 to 5 and 0.2 to 0.6 μm fractions could then be calculated by subtracting the amount of Synechococcus Chl from the total concentration in each size category. It was only at the Chl max and the 0.5% light depth that the 0.6 to 1 μm fraction could not be considered a pure population of Synechococcus, as they routinely represented <50% of all the autofluorescing cells in this size range (Table 1). At these depths, we could only estimate cellular Chl concentrations of Synechococcus spp. by proportion, using relative numbers of Synechococcus:algal cells within the 0.6 to 1 μm assemblages.

Synechococcus Chl may therefore have been overestimated at the base of the euphotic layer, as algae in this size fraction would probably contain more Chl per cell than Synechococcus spp. (see Table II of Glover et al. 1987), since the former were probably larger and Chl is one of their primary light-harvesting pigments.

PE concentrations were determined at sea, using the in vivo fluorescence method of Wyman & Carr (1988), which is based on the ability of glycerol to uncouple energy transfer between PE and phycocyanin (Wyman et al. 1985). Samples (1 l) were filtered through Nuclepore filters of 0.6 μm pore size to collect Synechococcus cells. Cells were resuspended in 5 ml of 50% glycerol, excited at 520 nm and PE fluorescence emission was determined at 570 nm in an adapted Turner fluorometer.

**Table 1.** Percentage of autofluorescing phytoplankton cells represented by PE-rich Synechococcus spp. within 3 size fractions at various depths in the euphotic zone. Mean value (x), and range (in brackets) is provided for samples collected from different pump casts over 5 d.
ter, calibrated with both whole cells and isolated phycobilisomes from the Sargasso Sea *Synechococcus* clone, WH7803. Since the washing procedure did not remove all the cells from the filter, cell numbers were determined in the glycerol suspension and data were corrected accordingly.

**Photosynthesis measurements.** Diurnal measurements of photosynthesis-irradiance (P-I) relations were conducted on whole communities collected from 8 depths at dawn, midday and dusk. Values reported here are for midday values only. Procedures for filtration, washing and determining rates of 14C fixation are described by Prézelin et al. (1986). Photosynthetic parameters were derived from non-linear curve fits for the P-I data (Prézelin et al. 1986). Independent measurements of P$_{\text{max}}$ indicated that one standard deviation was routinely $<15\%$ of the mean value.

In situ rates of daily primary production were determined for whole communities from 8 depths. 14C-bicarbonate was added to duplicate 230 ml samples in polycarbonate bottles (1.3 to 1.5 μCi ml$^{-1}$ final concentration). At dawn, bottles were suspended at each depth using an in situ line and float. Bottles were retrieved at dusk (12 h incubation) and 50 ml portions were filtered through Nuclepore filters of 0.2 μm pore size. Additional samples from each depth were also filtered immediately after the addition of 14C-bicarbonate, for zero time controls. One standard deviation ranged from 2 to 16 $\%$ of the mean value (with one exception of 30 $\%$). Procedures for filtration, washing, and determining photosynthetic rates are provided in Glover et al. (1986).

**RESULTS**

Both stations were stratified with pigment maxima below the thermocline and more than 88 $\%$ of the integrated standing crop of Chl was found in ultra-plankton (0.2 to 5 μm). Vertical profiles of light availability as well as the abundance and composition of ultraphytoplankton assemblages were different at the 2 stations (Figs. 2 to 5). In addition, the water-column characteristics at Stn 2 were relatively stable over the monitoring period, while temporal changes occurred in the surface isothermal layer at Stn 1.

**Similarities between stations**

Both stations exhibited a number of similar features: An in vivo PE glycerol-uncoupled fluorescence maximum occurred on the 21.5°C isotherm at 3.7 to 6.5 $\%$ Chl, in the upper part of the nitracline (Figs. 2 and 3) and coincident with a maximum in midday photosynthetic capacity (Table 2). Below the PE maximum there was an in vivo Chl fluorescence maximum, which followed the 21°C isotherm (Fig. 2) at the base of the nitracline (>10 μM NO$_3$). Extracted Chl concentrations showed similar depth distributions (Fig. 3), such that the Chl fluorescence:biomass ratio was constant. One excep-

![Fig. 2. Depth profiles of temperature and irradiance at the 2 stations. Temperature structure and position of in vivo Chl fluorescence maximum were derived from continuous vertical pump profiles taken at various times ( ). Attenuation coefficients (Kd) for each station are mean values obtained from several profiles of downwelling irradiance taken over similar time frames. Position of PE maximum was derived from discrete analyses of samples from the pump outflow. Arrows (1a, 1b and 2) indicate the times of pump casts for collection of data presented in Figs. 3, 5, 6, 7 and 9](image-url)
Fig. 3. Concentrations of nitrate (left graphs), phycoerythrin (middle graphs) and chlorophyll (right graphs) in water samples from different depths in the euphotic zones of the 2 stations. Temporal changes at Stn 1 are seen by the differences in depth profiles between 20 July (solid symbols) and 25 July (open symbols). Data for Stn 2 are from 2 August.

Table 2. Photosynthetic rates and characteristics of whole phytoplankton communities (>0.2 μm)

<table>
<thead>
<tr>
<th>Light depth (% I₀)</th>
<th>20 July</th>
<th>20 July</th>
<th>21 July</th>
<th>21 July</th>
<th>20 July</th>
<th>20 July</th>
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</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Iₘₐₓ</td>
<td>Pₘₐₓ</td>
<td>In situ</td>
<td>production</td>
<td>Iₘₐₓ</td>
<td>Pₘₐₓ</td>
<td>In situ</td>
<td>production</td>
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<tr>
<td></td>
<td>(µE m⁻² s⁻¹)</td>
<td>(µg C l⁻¹ h⁻¹)</td>
<td>(µg C l⁻¹ d⁻¹)</td>
<td>(µg C l⁻¹ h⁻¹)</td>
<td>(µg C l⁻¹ d⁻¹)</td>
<td>(µg C l⁻¹ h⁻¹)</td>
<td>(µg C l⁻¹ d⁻¹)</td>
<td>(µg C l⁻¹ d⁻¹)</td>
</tr>
<tr>
<td>PEₘₐₓ</td>
<td>379</td>
<td>0.45</td>
<td>3.20</td>
<td>40</td>
<td>103</td>
<td>0.05</td>
<td>1.55</td>
<td></td>
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<tr>
<td>90</td>
<td>172</td>
<td>0.86</td>
<td>3.77</td>
<td>19</td>
<td>262</td>
<td>0.25</td>
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<td>64</td>
<td>138</td>
<td>0.26</td>
<td>2.40</td>
<td>26</td>
<td>257</td>
<td>0.14</td>
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</tr>
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<td>42</td>
<td>0.16</td>
<td>2.45</td>
<td>4</td>
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</tr>
<tr>
<td>5</td>
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<td>0.5</td>
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<td>0.03</td>
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<td>0.17</td>
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<td>0.5</td>
<td>22</td>
<td>0.03</td>
<td>0.38</td>
<td></td>
</tr>
</tbody>
</table>

* I₀ = surface irradiance
* Iₘₐₓ = Pₘₐₓ/minimum amount of light required to saturate photosynthesis
* Midday rates of light-saturated photosynthesis, from P-I curves
* Dawn to dusk rates of photosynthesis at in situ irradiances

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tion occurred on 2 August at Stn 2, when maximum concentrations of PE and Chl per liter were coincident.

At both stations, *Synechococcus* spp. were most abundant in the surface isothermal layer (Fig. 4), but they represented less than 8% of the total number of prokaryotes, as bacterial abundance was 198 to $283 \times 10^6$ cells l$^{-1}$ above the thermocline at both stations (Fig. 5). Depth distribution studies indicated that high cell numbers of *Synechococcus* occurred in the mid to upper portion of the euphotic zone ($>10\% I_o$) above pigment maxima and the maximum abundance of algal ultraplankters (Fig. 5). Since *Synechococcus* cell numbers were lower at the PE maximum than those in the surface isothermal layer.
(Figs. 4 and 5), the relatively higher PE concentrations at the nitracline maximum (Fig. 3) were due to an increase in cellular PE content. Fig. 6 shows the increase in Synechococcus PE cell$^{-1}$ below the 10% isolume at both stations. Synechococcus spp. accounted for >95% of all ultraphytoplankton cells in surface waters and they were also numerically dominant at the nitracline PE maximum (Figs. 4 and 5). At the base of the euphotic layer total numbers of phototrophs were low, but numbers of algae increased (Fig. 5) and they became a significant component of deepest ultraphytoplankton assemblages (Fig. 4). In contrast, bacterial abundance remained relatively high throughout the euphotic layer (note abscissa scales on Fig. 5).

The distribution of the 2 ultraphytoplankton components with light depth (Fig. 5) was also reflected in their relative contributions to Chl concentrations (Fig. 7). That is, Synechococcus spp. were generally the major contributors to the standing crop of Chl in the surface isothermal layer, while ultraplankton algae provided most at the Chl maximum and 0.5% light level (Fig. 7). At both stations, ultraplankton algae made a significantly greater contribution to integrated water-column Chl than Synechococcus spp., while >5 μm algae provided only a minimal part of the total concentration (Fig. 7).

We further characterized the Synechococcus components of the ultraplankton by examining their relative abundance in 3 size classes and by using immunofluorescence assays to enumerate 2 different Synechococcus serogroups in 0.6 to 1 and 1 to 5 μm fractions. At both stations, the majority of Synechococcus cells were consistently found in the 0.6 to 1 μm fraction, while the minority were in the smallest 0.2 to 0.6 μm fraction (Fig. 8). However, the mean size of the population increased with increasing depth (Fig. 8). Immunofluorescent labelling of populations by antiserum directed against the Sargasso Sea isolate WH7803 showed that there was no apparent difference in the labelling patterns of Synechococcus cells in either 0.6 to 1 μm or 1 to 5 μm size-fractions (Fig. 9). Similar results were obtained with antiserum directed against the coastal Synechococcus isolate WH8016 at Stn 2 (data not shown). Furthermore, very weak reactions and low percentage labelling at most depths suggests that the oceanic WH7803 serogroup was not a dominant component of populations at either station (Fig. 9) and 75 to 93% of all Synechococcus cells at any depth were not labelled by either antiserum at Stn 2.

**Temporal changes at Stn 1**

In addition to the PE maximum located at the nitracline, an additional PE maximum was also found within the isothermal layer at 10 m on 20 July at Stn 1 (Fig. 3). It was evident that both PE maxima represented depths of relatively high total primary productivity (Table 2) and cellular photosynthesis (data not shown), with phytoplankton assemblages dominated by Synechococcus spp. (89 to 97% of all <5 μm cells) that were highly enriched in PE (28 and 40 fg PE cell$^{-1}$ at 64 and 6% I,$_o$, respectively; Fig. 6). The 10 m PE maximum did not persist. Indeed, the water-column at Stn 1 was in transition throughout our 5 d monitoring period: there was a 1°C warming above the thermocline between 20 and 26 July (Fig. 2). Adveective forces did not appear to be involved, since the surface warming could be solely accounted for by local heating (incident solar radiation was $13 \times 10^7$ J m$^{-2}$ during the period in which $5.3 \times 10^7$ J m$^{-2}$ of heating occurred). During the same period,
there was a 4-fold reduction in nitrate concentrations in the upper 25 m of the water-column (417 μmol NO₃ m⁻²) and a Synechococcus bloom occurred. Elevated surface nitrate concentrations on 20 July (Fig. 3) were accompanied by high rates of primary production (Table 2), and were followed 48 h later by a 50% net increase in Synechococcus cell numbers (Fig. 4). In contrast, numbers of ultraplankton algae remained the same (Fig. 4). Numbers of Synechococcus spp. subsequently declined from a maximum of 17 × 10⁶ cells l⁻¹ in surface waters (2 to 5 m) to 8 × 10⁶ cells l⁻¹ by 25 July. Between 20 and 25 July, the 4-fold reduction in nitrate concentrations in the upper 25 m of the water-column was accompanied by a 5-fold decrease in PE concentrations, but only a 2-fold decrease in Chl concentrations (Fig. 3). The reduction in PE concentrations in surface waters was not solely due to the decrease in Synechococcus cell numbers, since the mean cellular PE content also declined from 24 to 6 fg PE cell⁻¹ during the same period.

Temporal changes in Synechococcus abundance were not confined to the surface isothermal layer, since cell numbers doubled between 20 and 22 July at the Chl maximum (Fig. 4). After 22 July, Synechococcus cell numbers declined and the Chl maximum became deeper and more sharply defined. By 25 July, PE concentrations below the 7% light level were also 2 to 4 times lower than those at a corresponding depth 5 d earlier (Fig. 3).

**Depth-dependent differences between stations**

Despite the temporal variability at Stn 1, differences were still evident in phytoplankton distributions between the 2 stations. Comparing time course data sets obtained over 5 d at each station, we found that Synechococcus spp. were consistently more abundant within the surface isothermal layer, the PE/nitracline maximum and the Chl maximum at Stn 1 (Fig. 4). The higher phytoplankton abundance presumably explains why the attenuation coefficient for the water-column was higher at Stn 1 (Fig. 2). While numbers of ultraplankton algae increased below the nitracline at both stations, they were nearly twice as abundant at the Chl maximum and 0.5% light level of Stn 2, where they represented 54 to 75% of all autofluorescent ultraplankton (<5 μm) cells (Fig. 4). Station differences in the relative abundance of the 2 ultraphytoplankton components were also reflected in estimates of their separate contributions to the standing crop of Chl. Fig. 7 shows that Synechococcus spp. made a greater contribution to integrated water-column Chl at Stn 1, compared with that at Stn 2, while the converse was true for ultraplankton algae.
Fig. 8. Distribution of *Synechococcus* spp. in 3 size fractions (black: 0.2 to 0.6 μm; hatched: 0.6 to 1 μm; stippled: 1 to 5 μm), at 4 locations in the water-column over the course of the monitoring periods at Stn 1 (left graph) and Stn 2 (right graph).

Fig. 9. Percentage of *Synechococcus* cells labelled by antiserum directed against the Sargasso Sea isolate WH7803 in 2 size fractions at different light depths on 20 July at Stn 1 (left graph) and on 2 August at Stn 2 (right graph).

Not only were uliplankton algae more abundant below the 10% light level at Stn 2 (Fig. 5), but there were proportionately more smaller cells (Fig. 10). There was a reduction in mean cell size below the nitricline, and 79 to 89% of the algae at the base of the photic layer at Stn 2 were in the picoplankton fraction (passing through 1 μm Nuclepore filters).

**DISCUSSION**

Open ocean regions constitute three-quarters of the world's oceans, yet the rates of oceanic carbon and nitrogen cycling are uncertain by one order of magnitude (e.g. Eppley 1960, Jenkins & Goldman 1985). Some of the discrepancies between data sets may be
due to the time scales over which observations were made (Kerr 1986). It has been suggested that in nitrogen-limited ocean systems, episodic increases in nitrate concentrations may support a significant fraction of the total annual primary production (Platt & Harrison 1985). Nitrate pulses could be easily missed by occasional sampling strategies. Results from Stn 1 show that transient nanomolar increases in surface nitrate concentrations do indeed occur in stratified oceanic waters over a few days (Fig. 3), and can rapidly enhance phytoplankton production over similar time scales (Fig. 4). The temporal sequence of phytoplankton properties describing the nitrate-dependent Synechococcus bloom in the surface isothermal layer at Stn 1 is provided in more detail in a note by Glover et al. (1988). The change in nitrate concentrations between 20 and 25 July was stoichiometrically consistent with the subsequent cellular production of Synechococcus carbon and measured grazing rates (Glover et al. 1988). Data suggested that Synechococcus spp. alone responded to the enhanced supply of nitrate, which may have been due to faster uptake kinetics conferred by their high surface area/volume ratio (Raven 1986), but may also reflect a capacity to rapidly translate increased cellular nitrogen into growth and cell division (Collos 1986).

The source of the initially high nitrate concentrations in the surface isothermal layer is a matter of conjecture. A numerical study showed that wind-surface current interactions can affect both the instantaneous nutrient distribution and the mean level of its transport through the thermocline (Klein & Coste 1984), and there were major storms in the Sargasso Sea between 2 and 4 July and between 9 and 11 July (log of RV 'Cape Hatteras' Cruise CH-12-86). These events were apparently sufficient to cause mixing at Stn 1, which resulted in a surface isothermal layer that was 1°C cooler than typical seasonal values, and temperatures of >26°C were observed only after 23 July (Fig. 2). Using the chemiluminescent nitrate method, Eppley & Renger (1988) also reported nanomolar increases in surface layer nitrate concen-

![Fig. 10. Distribution of ultraplankton algae in 3 size fractions (black: 0.2 to 0.6 μm; hatched: 0.6 to 1 μm; stippled: 1 to 5 μm), at 4 locations in the water-column over the course of the monitoring periods at Stn 1 (left graph) and Stn 2 (right graph).]
trations following a small wind event in stratified California waters.

It is well established that oceanic *Synechococcus* spp. use PE as their primary light-harvesting pigment (see review by Glover 1985), but the ability of marine *Synechococcus* spp. to use some of their PE pigment as a nitrogen reserve has recently been debated (Barlow & Alberite 1985, Wyman et al. 1985, Glibert et al. 1986, Yeh et al. 1986 vs Wyman et al. 1986, Kana & Glibert 1987). Data presented here support the additional role of PE in nitrogen storage: first, the 4-fold decline in surface layer nitrate concentrations between 20 and 25 July at Stn 1 (Fig. 3) was accompanied by a 4-fold decrease in PE concentrations within *Synechococcus* cells (24 to 6 fg PE cell⁻¹). Secondly, in the surface isothermal layer there was a 2-fold decline in PE/Chl ratios in the total *Synechococcus* population (>0.6 μm) during this period (Glover et al. 1988). This change in the pigment ratio of *Synechococcus* cells is unlikely to have resulted from photoadaptation, since populations were at light-saturating depths for growth 90 to 34 % I₀ (Glover et al. 1967), with I₀ values (Table 2) and Chl contents (Fig. 6) that are typical of high-light adapted cells (Glibert et al. 1986, Prézelin et al. 1986, Glover et al. 1987). Thus, our data suggest a causal relationship between initially high nitrate concentration and high cellular PE content.

Our data provide the first measurements of maxima in PE concentrations per liter in the Sargasso Sea by looking at glycerol-uncoupled PE fluorescence yield. Without these measurements, we would not have had a sampling rationale for locating sites of PE-rich *Synechococcus* cells with high photosynthetic activity, nor would we have been able to determine how the PE content of *Synechococcus* cells varied with depth-dependent changes in light and nutrient availability. The deep PE maxima we identified were associated with the nitracline (Fig. 3) and resulted from the increased PE content of *Synechococcus* cells and not from an increase in their abundance (compare Figs. 5 and 6). These data substantiate earlier flow cytometry results of an increase in PE fluorescence intensity per cell with increasing depth (Olson et al. 1985). While *Synechococcus* cells had a relatively high PE content at deep PE maxima (Fig. 6), I₀ values attested to the fact that communities would not be limited by the in situ irradiance during most of the day and primary productivity was relatively high (Table 2). Thus, these *Synechococcus* populations appeared to effectively use the increased nitrogen flux at the nitracline for PE synthesis, thereby enhancing absorption of the available blue radiation and resulting in relatively high cellular rates of photosynthesis. Furthermore, these *Synechococcus* populations were not dominated by the WH7803 serotype (Fig. 9), but contained cells whose PE fluorescence emission characteristics were typical of clone WH8103 (Campbell & Iturriaga 1988), whose higher complement of phycoerythrobilin to phycoerythrobilin chromophores enhances absorption at shorter blue wavelengths of 490 nm (Ong et al. 1984). Using flow cytometry single cell analysis, Olson et al. (1988) reported that the high phycoerythrobilin pigment type invariably dominated oceanic *Synechococcus* populations from other regions.

Comparing our results with data sets from several other investigations (Glover et al. 1985, Murphy & Haugen 1985, Waterbury et al. 1986, Campbell & Carpenter 1987, Iturriaga & Marra 1988), it appears that there is considerable temporal and spatial variability in the abundance and composition of Sargasso Sea *Synechococcus* populations: Fig. 3 demonstrates the variability that we observed in PE concentrations per liter above the thermoclines (>30 % I₀) at the 2 stations. These differences were not solely related to *Synechococcus* cellular abundance. The 10 m transient PE maximum at Stn 1 was due to a *Synechococcus* population with increased pigment content (28 fg PE cell⁻¹) and relatively high photosynthetic activity (Table 2). These results suggest that this 10 m community was actively growing and that the isothermal layer was not necessarily a homogenous mixed layer at this time. *Synechococcus* cell numbers at Stn 1 were always higher in surface waters, the PE maximum and the Chl maximum, compared with those at Stn 2 (Fig. 4). This was reflected in their contribution to the standing crop of Chl (Fig. 7) and the different attenuation coefficients of the 2 water-columns (Fig. 2). The significance of *Synechococcus* spp. at the Chl maximum of Stn 1 was shown by their enhanced contribution to the Chl concentration (Fig. 7) and a doubling in their abundance (Fig. 4) over the 3 d in which the temporal changes occurred in the upper 25 m.

Reported abundances of *Synechococcus* spp. in July and August in Sargasso surface waters range from 3 to 17 × 10⁶ cells 1⁻¹ (Glover et al. 1985, Murphy & Haugen 1985, Waterbury et al. 1986) with the maximum value being found on 22 July at Stn 1 (Fig. 4). In stratified oceanic regions, greatest numbers of *Synechococcus* spp. are often in surface waters (Waterbury et al. 1986; Fig. 4), but a maximum has been found at much lower light levels, where the nutrient supply is increased (Glover et al. 1985, Murphy & Haugen 1985, Waterbury et al. 1986, Campbell & Carpenter 1987). In April 1985, Iturriaga & Marra (1988) recorded maximum abundances of *Synechococcus* cells in surface waters north of the Subtropical Atlantic Convergence, while maximum numbers occurred near the bottom of the euphotic zone south of the front (24°N). Variability also occurs in the serogroup composition of *Synechococcus* spp.
populations in the Sargasso Sea (Campbell & Carpenter 1987).

While *Synechococcus* spp. were the dominant component of ultraplankton communities above 10 % Chl, Chl-fluorescing algae became the dominant component of ultraplankton biomass at the bottom of the euphotic zone, particularly at Stn 2 (Figs. 4, 5 and 7). Data from Stn 2 (Figs. 4 and 5) confirm previous light depth distribution patterns in the composition of ultraplankton in stratified oceanic systems (Furuya & Marumo 1983, Takahashi & Bienfang 1983, Takahashi & Hori 1984, Glover et al. 1985, Murphy & Hauga 1985, Gieskes & Kraay 1986, Trees et al. 1986).

At both stations there was a change in the cell size distribution of ultraplankton algal communities with increasing depth (Fig. 10). The majority of algae were in the 1 to 5 μm fraction above the nitracline, while with increasing depth below it, there were proportionately more smaller cells. This was particularly evident at Stn 2, where 79 to 89 % of algal cells at the bottom of the euphotic layer were in the < 1 μm picoplankton fraction (Fig. 10). Since sinking rates of these small forms is negligible (Takahashi & Bienfang 1983), increases in the abundance of picoplankton algae at depth (Fig. 5) may be attributed to in situ growth, and their ecological success at low intensities of blue-violet light may be due, in part, to their complement of blue-violet absorbing accessory pigments (Brown 1985, Wood 1985, Glover et al. 1987) and a relatively high specific absorption coefficient conferred by their small cell volume (Kirk 1986). While the high phycourorubin to phycoerythrobilin chromophore complement in the PE of *Synechococcus* populations would enhance their ability to use the blue light available at the nitracline PE maximum, the pigmentation of oceanic picoplankton algae gives them a competitive advantage deeper in the water-column. It should be noted however, that while the numerical abundance of ultraplankton algae was greatest in the blue-violet light regime found at 0.5 % Chl at both stations (Fig. 5), low I<sub>b</sub> values and photosynthetic rates (Table 2) suggested that even though these communities were shade-adapted, photosynthesis was light-limited.

The numerical dominance of *Synechococcus* spp. in surface waters (Fig. 4) cannot be explained in terms of irradiance, since at saturating intensities of white light and nutrient sufficient conditions, clones of oceanic *Synechococcus* and ultraplankton algae have comparable growth rates (Glover et al. 1987). Consequently, the varying depth distributions of the 2 ultraplankton groups can be partially explained in terms of light intensity and quality, but it seems likely that differences in nutrient uptake kinetics could also be a factor.

In conclusion, comparisons between previous data sets and those presented here for summer Sargasso Sea communities suggest that there is a considerable degree of temporal and geographic variability in the abundance and composition of ultra- and pico-phytoplankton at comparable locations within the water-column.

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LITERATURE CITED


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