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Abundance and cellular characteristics of marine *Synechococcus* spp. in the dilution zone of the Changjiang (Yangtze River, China)

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Abstract—Concentrations of the marine cyanobacterium *Synechococcus* were estimated in the dilution zone of the Changjiang (Yangtze River, China) using epifluorescence microscopy while cell size and photosynthetic pigment content were measured with flow cytometry. Cyanobacteria concentrations (10^2–10^3 cell ml^{-1} in winter and 10^2–10^5 cell ml^{-1} in summer) increased in the offshore direction and reached their maximum at the most marine stations in winter and at stations of intermediate salinities (25–30 g l^{-1}) in summer. In the latter season, concentrations in excess of 10^4 cell ml^{-1} developed in the surface layer when the euphotic depth increased beyond 10 m as a result of suspended matter sedimentation. Cell concentrations fell by an order of magnitude below the thermocline in comparison to the surface layer and the highest values were associated with the saline waters of the Taiwan Current. In summer *Synechococcus* cell size (as measured by light scattered at 90° angle) was the smallest in the region of maximum cell concentration, probably in relation to the high population growth rate there. Cell phycoerythrin content (measured by fluorescence) was related to light availability and to a lesser extent to inorganic nitrogen concentration.

INTRODUCTION

UNTIL recently, phytoplankton was thought to be numerically dominated by large cells such as diatoms or dinoflagellates. In the past 10 years however, the importance of the smaller size fractions has been progressively recognized (STOCKNER and ANTIA, 1986). In particular the marine cyanobacterium *Synechococcus* has been shown to be a dominant component of the fraction below 2 μm (WATERBURY *et al.*, 1979; JOHNSON and SIEBURTH 1979). These small coccoid cells, 0.5–2 μm is size, are easily identified by the fluorescence of their main pigment, phycoerythrin (WOOD *et al.*, 1985). They are ubiquitous in oceanic waters, with the exception of the polar seas. Their distribution is affected by temperature and light availability (WATERBURY *et al.*, 1986). Most of the field observations to-date, however, have been made in the oligotrophic regions of the oceans, rather than in nutrient-rich coastal areas. In this respect, dilution zones of major rivers offer an excellent opportunity to study the distribution and characteristics of these cells along a salinity gradient in a variety of environments, ranging from low light, high nutrient conditions inshore to high light, low nutrient ones offshore.

In this paper, we examine marine *Synechococcus* in the dilution zone of one of the major world rivers, the Changjiang (Yangtze River), at periods of low and high runoff (winter and summer, respectively), and attempt to relate cell abundances and characteristics to the observed physical and chemical features of the zone.

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METHODS

Sampling

The region under study spreads roughly between 121° and 124°E in longitude and 31° and 32°N in latitude (Fig. 1), extending about 200 km on the shelf off the mouth of the Changjiang. Water depths range from 10 m at the mouth of the river to 40–50 m offshore. The major topographical feature on the shelf is a submarine canyon, which prolongs the river in the southeast direction (Fig. 1).

Two cruises were conducted aboard the Chinese research vessel *Xiang Yang Hong* 09 in January and July 1986 (Fig. 1). Four "long" stations (C1–C4: Fig. 1) were sampled every 2 h during 26 h at one depth (5 m) in January and at two depths (surface and below the thermocline) in July. From 20 (in January) to 23 (in July) "short" stations (1–23: Fig. 1) were sampled at several depths over a restricted period of 3 days to provide a quasi-synopic view of the zone. River stations (R1–R5: Fig. 1) were sampled with a smaller vessel and processed aboard the main vessel.

Samples were usually taken with a rosette of Niskin bottles attached to a CTD probe. When the current was too strong to allow rosette sampling, surface water was taken with a clean bucket.

Physical and chemical parameters

Whenever possible sample depth, salinity and temperature were measured *in situ* with the CTD probe. For the winter cruise, salinities were also measured with a chlorinometer (CMT 10, Radiometer, Copenhagen Denmark) on preserved samples. Total suspended matter and nutrient concentrations were measured on board by standard oceanographic methods (STRICKLAND and PARSONS, 1972).

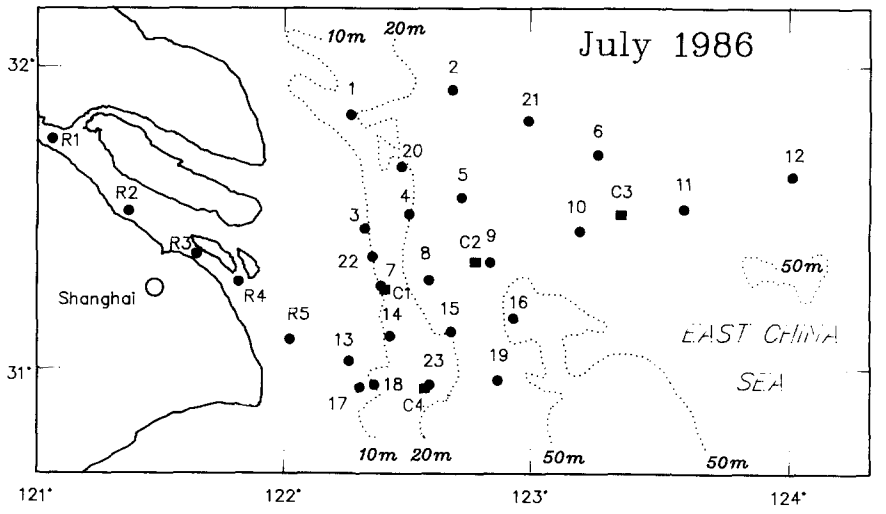

Fig. 1. Map of the sampling stations in the dilution zone of the Changjiang (Yangtze River) for the July 1986 cruise. Bottom topography is indicated by the dotted lines with depths in meters. Stations C1–C4 were sampled every 2 h over 26 h, Stas 1–23 and R1–R5 were sampled only once at several depths. In January 1986, only Stas 1–20 were sampled and Stas C1–C4 were located closer to shore.

Sample preservation

Samples were kept in the dark at 4°C until processing, which took place in general within 24 h of collection, except for the river stations for which the maximum delay was of 5 days. For flow cytometry analyses (July cruise only) 1 ml of water was quickly frozen in liquid nitrogen. Frozen samples were stored at –20°C.

Epifluorescence microscopy

All epifluorescence determinations of *Synechococcus* were made on board. For each sample, from 10 to 40 ml were filtered on a 25 mm diameter, 0.2 μm pore size, black Nuclepore filter. Vacuum was produced with a hand-held pump and did not exceed 200 mm Hg. The Nuclepore filter was immediately placed on a glass slide with a 20 μl drop of sample water and covered with a coverslip. The edges of the cover slip were sealed with nail polish to minimize filter drying.

Slides were counted under an Olympus BH-2 epifluorescence microscope. Green excitation was obtained with an Olympus G filter set supplemented by an additional EO 530 excitation filter resulting in narrow-band green excitation around 530 nm. Two types of phycobiliproteins were distinguished according to their excitation and emission fluorescence characteristics (Wood *et al.*, 1985): (1) Phycoerythrin (PE) fluoresced brightly orange–yellow. Its emission was only slightly decreased by adding a short pass 670 emission filter, indicating that emission occurred below 670 nm. (2) Phycocyanin (PC) fluoresced red–orange. In contrast to PE, its emission was significantly reduced by a short pass 670 nm, indicating that part of it occurred above this wavelength.

Two methods were used for cell counting:

(1) Immediate counting. Slides were counted on board the ship using a ×40 objective. Usually two transects were counted on each filter with 200–300 cells per transet. If cells were too dense to allow the counting of a whole transect, a fraction of the field was delimited on an eye-piece grid and counted.

(2) Delayed counting on photographs. Five pictures of randomly chosen fields containing about 100 cells each were taken with either a ×10 or a ×16 objective, using Kodacolor VR400 film (400 ASA). Exposure times were around 1 min. Cells were enumerated on 9 × 13 cm color prints. This method was only used during the winter cruise. It resulted in a slight overestimate (about 10%) of cell concentrations in comparison to direct eye counts. The distinction between the fluorescences of phycoerythrin (orange–yellow) and of chlorophyll (brick-red) was less easy to make on the pictures than by eye; therefore some small eukaryote cells containing chlorophyll were mistaken for *Synechococcus*. The overestimate had however very little effect on our conclusions.

Flow cytometric analysis

Analyses were performed 6 months after sample collection. Frozen samples were allowed to thaw at room temperature and were maintained thereafter at 0°C. They were analysed on an EPICS 541 (Coulter, Hialeah Florida) flow cytometer equipped with a 5 W laser. Excitation light was produced by the 488 nm line at a power of 1.3 W, focused through a confocal lens which delivers a higher light output than a standard lens. Light scatter at 90° angle (LS90) was collected after reflection on a 488 nm dichroic filter and orange fluorescence was collected between 530 and 590 nm. Both signals were amplified on a three-decades logarithmic scale. The LS90 signal is dependent on both cell size and

cell optical properties (KERKER, 1983), but appears to be a good sizing parameter for phytoplankton (VAULOT, unpublished results). *Synechococcus* orange fluorescence has been shown to be proportional to phycoerythrin content (GLIBERT *et al.*, 1986).

Two replicates of 0.2 ml, to which green fluorescing beads (diameter 1 μm: Polysciences, Warrington, PA) were added as internal standards, were analysed for each collected sample. Two-parameter distributions of LS90 and PE fluorescence were recorded and analysed on the EPICS MDADS system (Fig. 2). Preserved *Synechococcus* cells appeared in the left part of the two-parameter distributions, as confirmed by analysis of pure *Synechococcus* cultures, while the 1 μm beads appeared in the upper right quadrant (Fig. 2). A second population of degraded *Synechococcus* cells appeared in the lower left corner (see below). For samples where suspended matter was too high, such as those taken in the river itself, it was not possible to discriminate *Synechococcus* from non-living fluorescing particles. On each distribution the average LS90 and PE fluorescence (both on logarithmic scales) of the preserved *Synechococcus* population were computed as well as those of the standard beads. Variation in the position of the standard beads was taken into account and the logarithmic scale was transformed to a linear scale for the expression of the final results.

Effect of sample freezing on flow cytometry measurements

Freezing modifies both scatter and fluorescence characteristics of cyanobacteria. In order to assess these effects, we subjected five cultures of a local strain of *Synechococcus* (ROSCOFF03), grown at different light intensities between 2 and 200 μE m^{-2} s^{-1} in f/2 medium (GUILLARD, 1975), and one natural sample from the English Channel to a treatment similar to that of the field samples (Fig. 3). The population-averaged 90° light scatter decreased by 10% after freezing (Fig. 3a), while phycoerythrin fluorescence increased by 50% (Fig. 3b). For both parameters the values after freezing were, however,

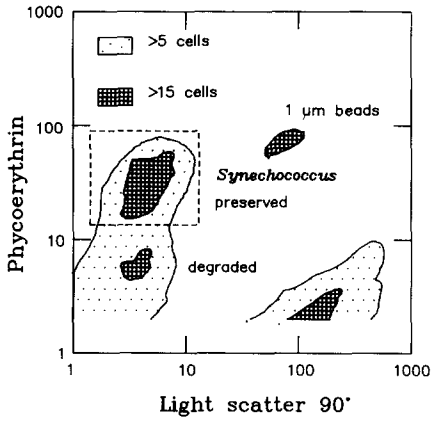

Fig. 2. Distribution of *Synechococcus* cell size (as measured by light scatter at 90° angle—LS90) and phycoerythrin (PE) fluorescence obtained by flow cytometry for a 0.2 ml sample collected at Sta. 5 (5 m) in July 1986. Both axes are graduated in relative units on a 3-decade logarithmic scale. Contoured regions correspond to specific particle or cell populations: dotted regions contain more than five particles per channel and hatched ones more than 15. The populations in the upper right quadrant correspond to 1 μm fluorescent beads added to the sample as internal standard. The preserved *Synechococcus* population appears in the dashed window, while the degraded cells appear in the lower left corner (see Fig. 4).

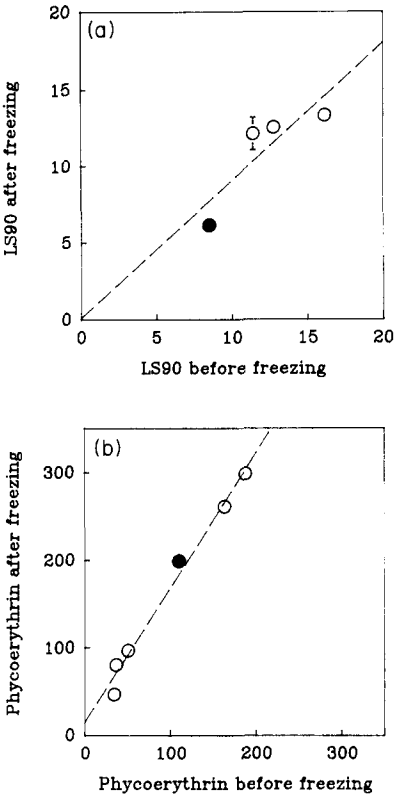

Fig. 3. Effect of sample freezing on flow cytometric measurements of 90° light scatter (a) and phycoerythrin fluorescence (b). Six *Synechococcus* populations (five grown in the laboratory, open circles; and one sampled from the English Channel, closed circle) were analysed fresh and after freezing in liquid nitrogen followed by thawing at room temperature. Symbols correspond to population averages. Error bars correspond to standard error of duplicate samples and are omitted when smaller than the symbols. Dashed lines correspond to linear regression lines. For LS90 the relation was $y = 0.9\,x + 0.09$ ($r^2 = 0.86$) and for phycoerythrin $y = 1.53\,x + 14.8$ ($r^2 = 0.99$), where x and y correspond to fresh and frozen populations, respectively.

linearly related to that of fresh samples. The increase in phycoerythrin fluorescence is in fact related to cell death, and not to freezing, since the same increase was observed when cells were killed with glutaraldehyde (data not shown).

Cell concentrations measured by flow cytometry on frozen Changjiang samples were 50–80% lower than those recorded by immediate on-board epifluorescence counting. This was most likely due to the degradation of a fraction of the cells as a consequence of partial thawing during sample transportation. Cell fluorescence degradation after thawing is, however, not a continuous but a discrete phenomenon: cells either degrade or do not degrade. This has been observed in the laboratory on *Synechococcus* cultures (Fig. 4a). Immediately after thawing, the phycoerythrin histogram presents a single peak. Five hours later, a second peak appears to the left of the first one, corresponding to cells which have about 10 times less fluorescence; the position of the first peak remains unchanged and is representative of the preserved cells. The same phenomenon is clearly

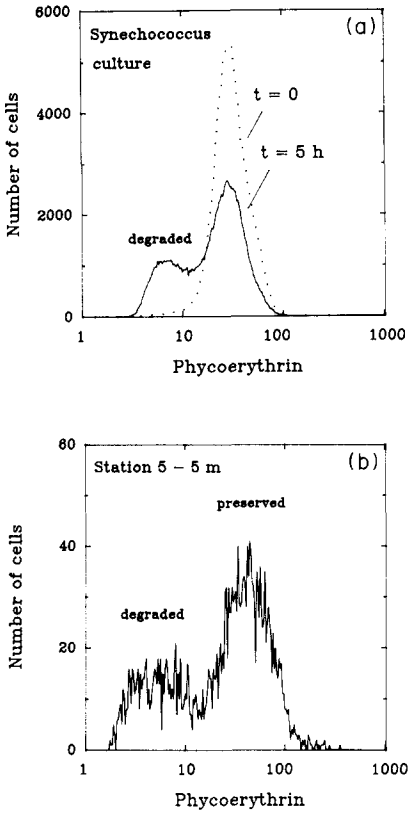

Fig. 4. Cell degradation after thawing at room temperature of liquid nitrogen frozen samples. A *Synechococcus* laboratory culture was frozen and then allowed to thaw at room temperature. A flow cytometric analysis of PE fluorescence was done immediately after thawing (t = 0) and then 5 h later (a). The initial fluorescence histogram presents a single peak, while a second peak appears after 5 h, corresponding to degraded cells with 10 times less fluorescence. However, the initial peak has not moved. The same type of double-peaked histogram is clearly seen in samples from the Changjiang dilution zone (b), in which some of cells have been degraded following partial thawing during sample transportation.

seen in the Changjiang samples where phycoerythrin histograms of the *Synechococcus* population exhibit two peaks corresponding, respectively, to degraded and preserved cells (Fig. 4b).

RESULTS

Hydrographic features

Although a detailed description of the physical dynamics of the region under study will be presented elsewhere (LAZUR *et al.*, in preparation), we provide here a brief overview of the main physical features of the zone as they are relevant to the observed distribution of *Synechococcus*.

In winter during low river flow, no thermal stratification occurred offshore and haline stratification was only present close to the river mouth. According to the surface salinity field (Fig. 5a), fresh and cold (5°C) Changjiang water flowed southward along the

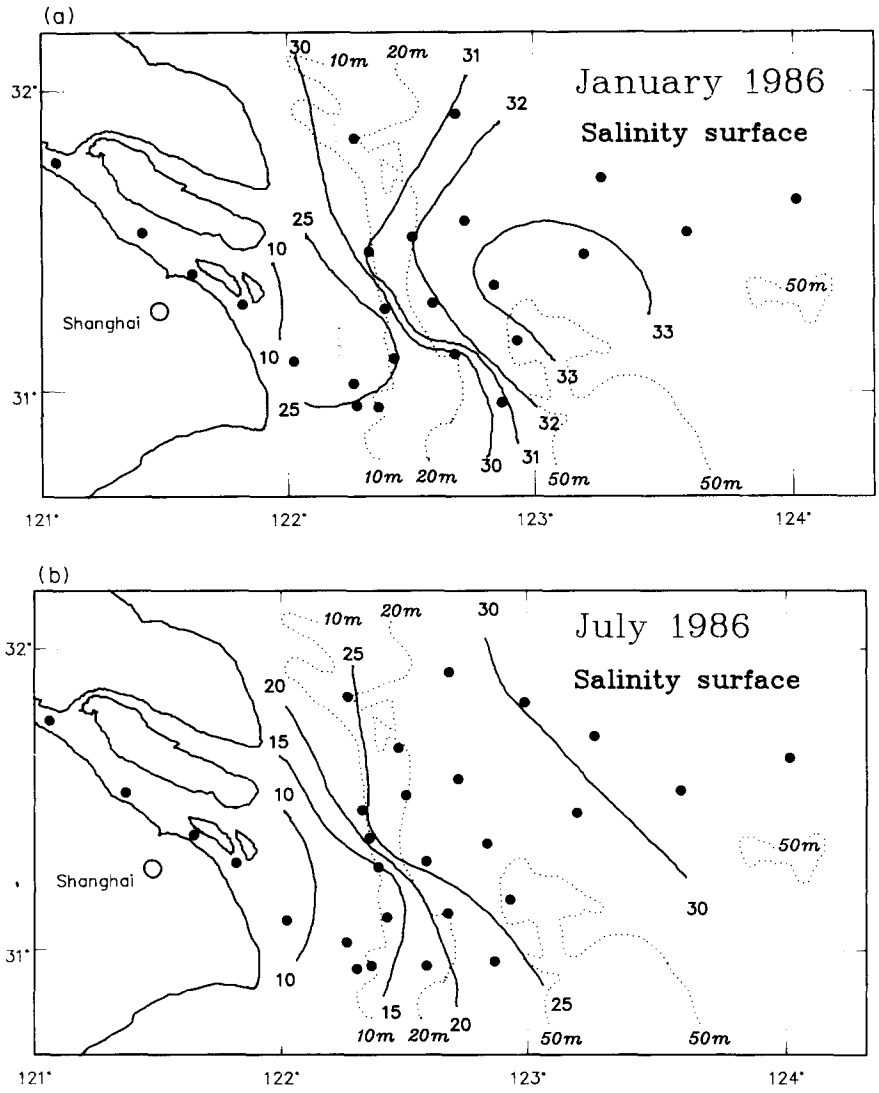

Fig. 5. Surface salinity (g l^{-1}) distribution in January 1986 (a) and in July 1986 (b).

Zhejiang coast. Saline (33 g l^{-1}) and warm (13°C) water from the Taiwan Current (an onshore branch of the Kuroshio) intruded the zone from the southeast following the submarine river relic located off the river mouth (Fig. 5a), as noted previously by BEARDSLEY *et al.* (1985). The Yellow Sea Current carried from the north less saline (30 g l^{-1}), cold (5°C) and particle-loaded water along the coast.

In summer, the water column was thermally stratified offshore, besides the salinity-induced stratification onshore. The surface and bottom layers had very distinct features. The fresh and warm (27°C) Changjiang water flowed at the surface southward along the coast (Fig. 5b) as observed in winter, but fresh water influence extended much farther offshore as a result of higher runoff (YANG *et al.*, 1983). A tongue of relatively

warm surface water (25°C) spread offshore in the northeast direction. In the bottom layer, river water influence was limited to the coast and Taiwan Current water, colder and more saline than the surrounding waters, intruded from the southeast along the submarine valley as in winter.

Suspended matter and nutrients

The Changjiang brings into the East China Sea large loads of suspended matter, which spread in a complex spatial pattern made of numerous plumes under the combined influence of tides and winds with a net southward transport (YUN and WAN, 1982; MILLIMAN *et al.*, 1985b). During the present study, suspended matter concentrations in the river were higher in winter (150 mg l^{-1}) than in summer (85 mg l^{-1}) although runoff is usually larger in the latter season (YANG *et al.*, 1983). Maximum concentrations were encountered south of the river mouth (Stas 13, 14 and 17; Fig. 1). A plume of surface turbid water extended in summer in the northeast direction coinciding with the temperature plume described above. In winter, but not in summer, the Yellow Sea Coastal Current brought particles originating from the Huang He (Yellow River) and from the Gulf of Bohai located north of the study zone as observed by MILLIMAN *et al.* (1985a).

Along with its suspended load, the Changjiang also carries large quantities of dissolved nutrients (EDMOND *et al.*, 1985). Nitrate concentrations were higher in summer than in winter. In contrast to previous measurements (EDMOND *et al.*, 1985), the highest values (20 μM in winter and 70 μM in summer) were not encountered in the river itself but immediately southeast of its mouth close to the turbidity maximum. Maximum phosphate concentrations were below 2 μM in winter and 1 μM in summer.

Abundance of Synechococcus

In the vast majority of the samples we only found cells containing PE. In a few samples collected in summer, we also found cells containing PC. Their concentration was always low (10^3 cell ml^{-1}) and they were restricted to salinities below 10 g l^{-1} corroborating the observations of WATERBURY *et al.* (1986) that these cells are usually associated with fresh and coastal waters. In the following, we will only deal with the first type of cells, i.e. those containing PE, which were ubiquitous and for which we have the most comprehensive data set.

In winter, *Synechococcus* cells were associated with marine waters (Fig. 6a). Both the horizontal and vertical distributions were very uniform with cell densities oscillating between 10^3 and 2.10^3 cell ml^{-1}.

In summer, *Synechococcus* were also characteristic of marine waters and were only encountered at very low densities inside the estuary. A marked difference was registered between the two layers separated by the thermocline. In the surface layer (Fig. 6b), cell concentrations increased gradually in the first 60 km offshore, from 10^2 cell ml^{-1} in the estuary to 10^4 cell ml^{-1}. Then cell densities climbed rapidly to peak values of 2.10^5 cell ml^{-1}, to finally decrease gradually to values of 3.10^4 cell ml^{-1} at the most marine station (Sta. 12). Their horizontal distribution closely resembled that of salinity (Fig. 5b). In the bottom layer, cell densities were usually lower than above the thermocline. Their horizontal distribution still reflected that of salinity. In particular, the intruding marine waters from the Taiwan Current were clearly associated with cell densities in excess of 10^4 cell ml^{-1}. Vertical distributions of *Synechococcus* (Fig. 7) indicated that cell density stratification followed closely thermal stratification. In the region of maximum cell

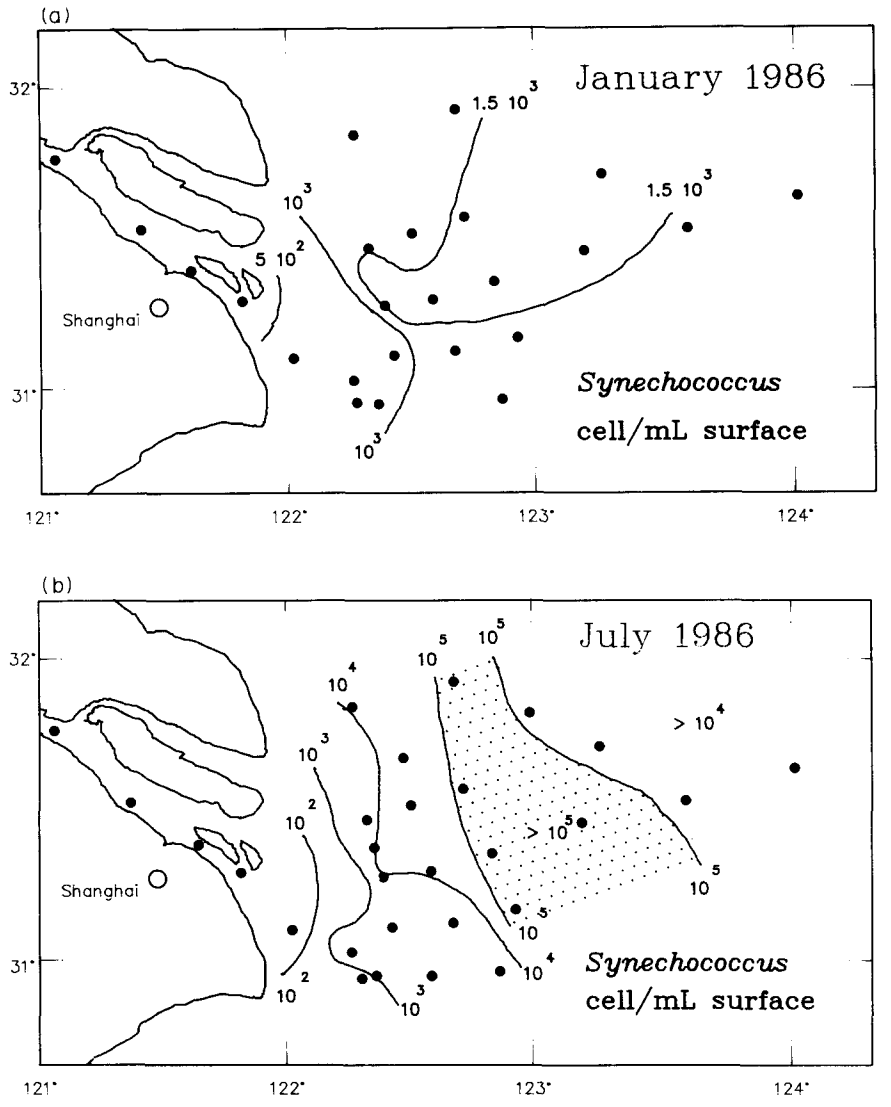

Fig. 6. Surface abundance of *Synechococcus* (cell ml^{-1}) in January 1986 (a) and in July 1986 (b).

densities (10^5 cell ml^{-1}), the ratio of cell densities in the two layers exceeded 20 and was much larger than at the stations with pronounced marine influence, where it dropped to about 5 (Fig. 7a). Near the river mouth (Fig. 7b), where the physics are fairly complicated (BEARDSLEY *et al.*, 1985), we observed a mid-depth cell concentration maximum, probably due to the overlapping of a saline layer rich in *Synechococcus* by a layer of fresh water poor in *Synechococcus*.

Cellular characteristics of Synechococcus

With flow cytometry we determined the average size (measured by light scatter at 90° angle: LS90) and PE content (measured by PE fluorescence) of *Synechococcus* cells for

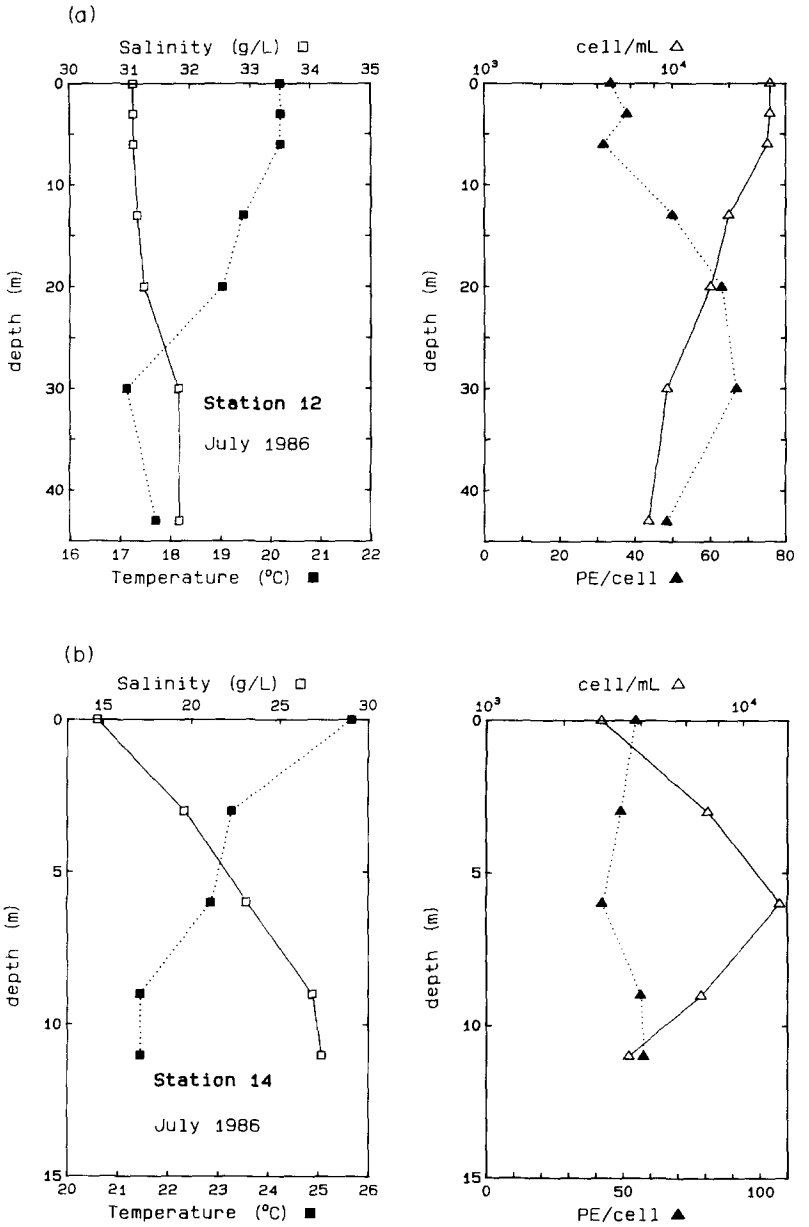

Fig. 7. Depth distributions of temperature, salinity, *Synechococcus* cell concentration and PE/cell in July 1986 at Stas 12 (a) and 14 (b).

samples taken at the "short" stations during the July 1986 cruise (Fig. 8). Two population types were clearly distinct. For the vast majority of the samples, the average LS90 was larger than 3.8 (relative units), while for a small group of samples it was one third smaller. The smaller *Synechococcus* cells (Fig. 9) were recorded at the surface and at stations where cell densities exceeded 10^5 cell ml^{-1} (Fig. 6b). Cell PE content varied by

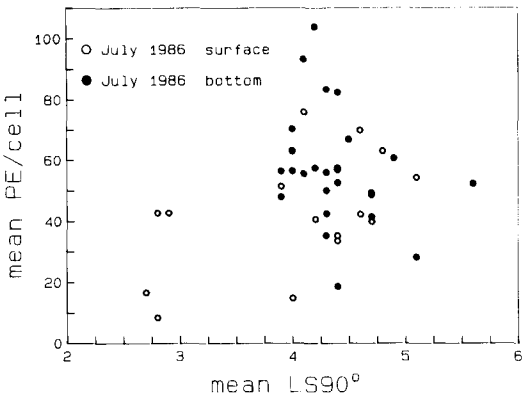

Fig. 8. Relationship between the average *Synechococcus* cell LS90 (size) and PE (relative units) measured by flow cytometry in July 1986 at Stas 1–23.

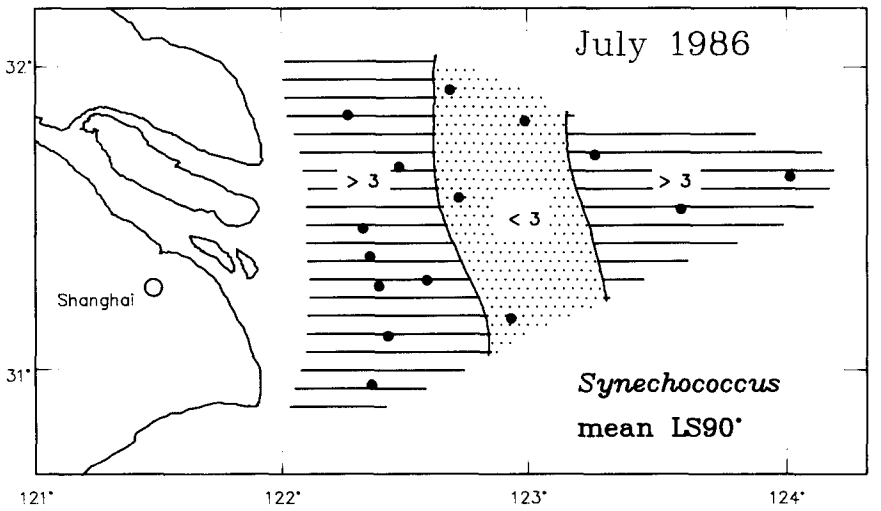

Fig. 9. Distribution of the average *Synechococcus* cell LS90 (size) at the surface in July 1986.

almost an order of magnitude amongst the stations. It increased in the horizontal from the marine to the river stations and in the vertical from the surface to bottom (Fig. 7a).

DISCUSSION

Synechococcus concentrations encountered during this study compared well with those measured elsewhere. Values of 10^3 cell ml^{-1} in winter are typical of most coastal waters such as those of the East Coast of the United States (Waterbury *et al.*, 1986), the Irish Sea (El Hag and Fogg, 1986) or the English Channel (Vaulot, unpublished results). In summer, the values encountered for the most marine stations (10^4–3.10^4 cell ml^{-1}) were rather low for coastal waters (El Hag and Fogg, 1986) and were closer to those encountered in oligotrophic areas such as the Sargasso Sea (Davis *et al.*, 1985; Olson *et*

al., 1985) or the Japan Sea (TAKAHASHI *et al.*, 1985). In contrast the maximum values found in the Changjiang dilution zone (2.10^5 cell ml^{-1}) were among the highest recorded (Celtic Sea: EL HAG and FOGG, 1986; northeast Atlantic: EXTON *et al.*, 1983; GLOVER *et al.*, 1986; WATERBURY *et al.*, 1986).

In winter the highest concentrations (10^3 cell ml^{-1}) were recorded offshore for salinities between 30 and 35 g l^{-1} (Fig. 10). Cell densities uniformly decreased towards low salinities. The absence of a cell concentration maximum in the dilution zone, despite high nutrient concentrations, was most likely a combined consequence of the low temperatures (5–10°C) and of the absence of stratification resulting in a reduction of the average light intensity over the productive part of the water column. Both temperature and light limitations probably reduced growth rates to levels too low (WATERBURY *et al.*, 1986) to compete efficiently with the large diffusion rates existing on the shelf.

In contrast, temperature and stratification conditions allowed in summer the formation of a region of maximum *Synechococcus* cell densities at the surface for salinities ranging from 25 to 30 g l^{-1} (Fig. 10). This region was distinct from the physical front resulting from the mixing of river and marine waters (LAZUR *et al.*, in preparation), and from the turbidity front occurring for suspended matter values of 100 mg l^{-1} (YUN and WAN, 1982), both being much closer to the river mouth. The inverse relationship observed between cell densities and suspended matter for the surface samples (Fig. 11) indicates that light was a critical factor controlling surface *Synechococcus* abundances in the dilution zone. Cell densities exceeded 10^4 cell ml^{-1} only when suspended matter fell below a threshold value of 5 mg l^{-1}, which corresponded to a depth of the euphotic zone in excess of 10 m (NING *et al.*, submitted). Patchy diatom blooms were also observed for the same value of euphotic zone depth (NING *et al.*, submitted). The second factor critical to the proliferation of *Synechococcus* was the high inorganic nutrient load originating from the river. However, nutrients alone were not sufficient to induce high population densities. The highest nitrate and phosphate concentrations (70 and 0.8 μM, respectively) corresponded to very low *Synechococcus* abundances. It was only when suspended matter had sedimented enough that surface *Synechococcus* populations climbed to their

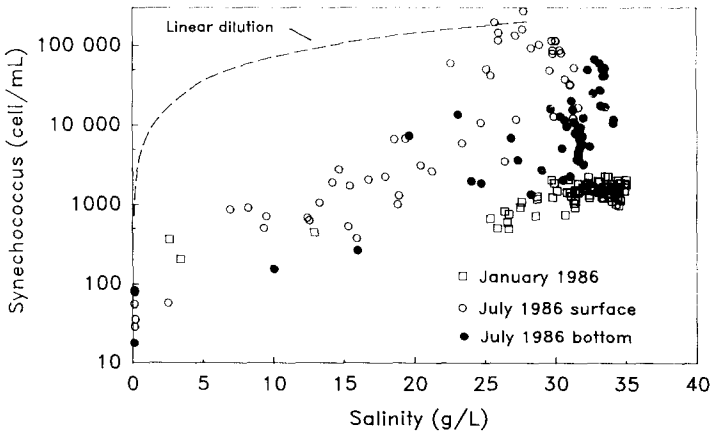

Fig. 10. Concentration of *Synechococcus* as a function of salinity in January and July 1986. The dashed line corresponds to the expected *Synechococcus* concentration if the maximum concentration (2.10^5 cell ml^{-1}) was linearly diluted in the direction of the river mouth.

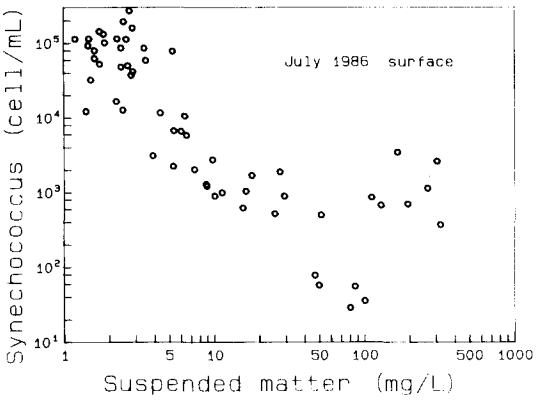

Fig. 11. Concentration of *Synechococcus* as a function of suspended matter in the surface layer in July 1986.

maximum value of 2.10^5 cell ml^{-1}, corresponding to nitrate concentrations of 10 µM and phosphate concentrations below the detection limit. Light limitation of phytoplankton growth due to suspended matter had been previously hypothesized indirectly for the Amazon (EDMOND *et al.*, 1981; DEMASTER *et al.*, 1986) and the Changjiang (EDMOND *et al.*, 1985) from observations of the consumption of nutrients such as NO_3 and SiO_3. In both cases, phytoplankton was assumed to be most abundant when suspended matter reached 10 mg l^{-1} (see also PETERSON and FESTA, 1984), a value somewhat larger than the one found here (5 mg l^{-1}). In our study, for all stations where suspended matter was below 5 mg l^{-1}, *Synechococcus* abundance was almost independent of nitrates, but inversely correlated to phosphates. Therefore *Synechococcus* could have been limited by phosphorus in the region of maximum densities.

The most striking feature of the denser *Synechococcus* populations was the small cell size in comparison to those encountered elsewhere (Fig. 9). This size difference could indicate the presence of two different strains. However, it is likely that small cell size was related to high population growth rates. GLIBERT *et al.* (1986) have recently shown that the cell size (measured by forward angle light scatter with flow cytometry) of a coastal clone of *Synechococcus* decreased in response to nutrient replenishment. Conversely they noted that cells subjected to nitrogen depletion were much bigger than actively growing cells. The same type of response might have been elicited in the field as slow-growing offshore cells encountered the high nutrient concentrations associated with the river plume.

Inorganic nitrogen status was not uniform in the region of maximum cell densities. While NO_3 was abundant in the south (Sta. 16), it was completely depleted at the northernmost stations (e.g. Sta. 21), probably as a result of biological consumption. This had no visible influence on cell size (Fig. 9), indicating that cells probably kept dividing, but had a direct effect on cell PE content, which decreased by a factor of 5 between Sta. 16 ($N\text{–}NO_3$ = 16 µM) and Sta. 21 ($N\text{–}N0_3$ = 0.11 µM). This is in agreement with the observations of GLIBERT *et al.* (1986) on a coastal clone of *Synechococcus*, which continued to divide for 48 h in the absence of nitrogen, while PE content decreased sharply.

Away from the region of maximum densities, cells were larger (Fig. 9) and had probably a much lower division rate. Cell densities fell more rapidly in the inshore direction than could be explained by dilution alone (Fig. 10), indicating high cell loss rates resulting probably from *Synechococcus* cell sensitivity to low salinity and low light conditions. At the surface the increase in cell pigment concentration towards the river mouth was probably a response to low light conditions (KANA and GLIBERT, 1987) resulting from increasing sediment load, as suggested by the relationship existing between cell PE and suspended matter concentration (Fig. 12).

The dynamics of *Synechococcus* in the bottom layer appeared to be completely uncoupled from those in the surface layer. There, the highest cell concentrations corresponded to the highest salinities (Fig. 10) associated with the intrusion of Taiwan Current water along the southeast submarine canyon. The low rates of mixing and sedimentation between the surface and the bottom layers was evident from depth profiles of cell concentration (Fig. 7a), but also from the absence of small, presumably fast-growing cells in the bottom layer (Fig. 8). The increase in cell PE in the bottom direction (Fig. 7a) was a likely result of photoadaptation (OLSON *et al.*, 1985). The time scale of this photoadaptation might be, however, of the order of several days (KANA and GLIBERT, 1987), since when rapid mixing events occurred, such as the one recorded at Sta. 14 (Fig. 7b), where a saline layer rich in *Synechococcus* was buried under a layer of fresher water poor in *Synechococcus*, photoadaptation might not have had the time to take place as suggested by the lower value of cell PE in the saline layer.

In summary, we have shown that marine *Synechococcus* was very abundant in summer in a narrow region located 80 km off the mouth of the Changjiang, while in winter it was not very abundant nor presumably very active. The summer maximum was associated with the deepening of the euphotic zone, as a result of particulate matter sedimentation, within the nutrient-rich plume. The cellular characteristics of *Synechococcus* observed in the field were consistent with the controls observed in the laboratory (GLIBERT *et al.*, 1986; KANA and GLIBERT, 1987): size appeared to be related to growth conditions and PE content to light availability and nutrient levels.

Many questions remain to be addressed concerning the physiology of this organism in this very contrasted region. It would be necessary to measure *in situ* growth rates in order

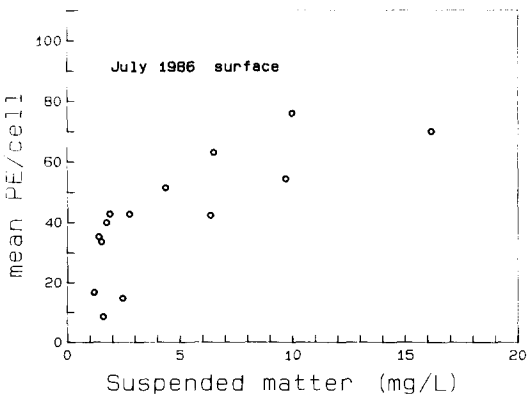

Fig. 12. *Synechococcus* cell PE as a function of suspended matter in the surface layer in July 1986.

to relate them to cell size and pigment content and to compare the region of maximum cell densities with the onshore region where cells become limited by light and the offshore region where they are subjected to nutrient limitation. Another element regulating *Synechococcus* cell densities, microzooplankton grazing (CAMPBELL and CARPENTER, 1986; WATERBURY *et al.*, 1986), was not measured here but was probably important offshore (COURTIES *et al.*, in preparation).

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