

Vertical distribution of marine cyanobacteria *Synechococcus* spp. in the Black, Marmara, Aegean, and eastern Mediterranean seas

Zahit Uysal*

Institute of Marine Sciences, Middle East Technical University, P.O. Box 28, 33731 Erdemli, Turkey

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Abstract

The vertical distributions of the unicellular cyanobacteria *Synechococcus* were studied in several highly contrasting seas: the Black Sea, Sea of Marmara, Aegean Sea, and Mediterranean Sea. Cell abundances varied significantly on both vertical and horizontal scales in all physically and spatially discrete water masses. Epifluorescence microscope cell counts from all seas clearly showed that majority of the population remains suspended in the surface-mixed layer and decreases gradually towards the base of the euphotic zone. Surface spatial distributions in the Black Sea were heterogeneous. Salinity, rather than temperature, seemed to have the greatest impact on the surface distribution of cells in this highly eutrophic sea. Changes in abundance in the mixed layer were small compared to the abrupt changes below the halocline, especially in the Black Sea and the Sea of Marmara. In contrast to the Black Sea, the major population remains suspended above the depth of fluorescence maximum in the Aegean and eastern Mediterranean seas. Significant correlations ($r > P_{0.01}$) were observed between cell counts and physical and chemical parameters with depth in the Black Sea. In all seas, cells at subsurface chlorophyll-*a* maximum layer (SCML) reflected brighter and longer fluorescence than those present at the surface and below. Cell size derived from flow cytometry indicated the presence of larger cells at the surface mixed layer compared to those at depth.

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1. Introduction

The first members of the picoplankton to be discovered in the oceans were phycoerythrin-containing unicellular cyanobacteria *Synechococcus* (Waterbury et al., 1979; Johnson and Sieburth, 1979). The picoplanktonic, chroococcoid cyanobacteria, *Synechococcus* spp., are now known to be

major contributors to the total photosynthetic biomass in the oceans (Berman, 1975; Waterbury et al., 1979; Johnson and Sieburth, 1979; Li et al., 1983; Platt et al., 1983; Takahashi and Bienfang, 1983; Iturriaga and Mitchell, 1986; Glover et al., 1986; Booth, 1988; Li et al., 1992), especially in more oligotrophic regions such as the subtropical ocean gyres and the Mediterranean Sea (Li et al., 1993; Magazzu and Decembrini, 1995; Agawin and Agusti, 1997). *Synechococcus* spp. contribute from 15% to 25% and occasionally up to 45% of POC in the oligotrophic waters of the Arabian Sea

*Tel.: +90 324 5213434; fax: +90 324 5212327.

E-mail address: uysal@ims.metu.edu.tr.

(Burkill et al., 1993). In oligotrophic oceans, this group contributes up to 25% of photosynthetic carbon fixation (Waterbury et al., 1986). They account for 64% of the total photosynthesis in the North Pacific Ocean (Iturriaga and Mitchell, 1986). This group also possesses high specific growth rates (Bienfang and Takahashi, 1983; Douglas, 1984; Landry et al., 1984).

There have been few studies of picoplankton distributions in the highly contrasting Turkish seas. Recently, new data have become available on pigments, size, distribution, growth and diurnal variability of *Synechococcus* spp. in the Black Sea (Uysal, 2000, 2001). The aim of this study is to

compare the abundance distribution of this group in highly contrasting Turkish seas.

2. Material and methods

Samples were collected during various cruises conducted aboard R/V *Bilim* to the Black Sea during April–May 1994 (Fig. 1A) and September–October 1996 (Fig. 1B); to the Sea of Marmara, Aegean Sea and Mediterranean Sea during October 2000, aboard R/V *Erdemli* of the Institute of Marine Sciences—Middle East Technical University; to the Levantine basin during September 2002, and aboard the R/V *Knorr* during June 2001 (Fig. 2). Water

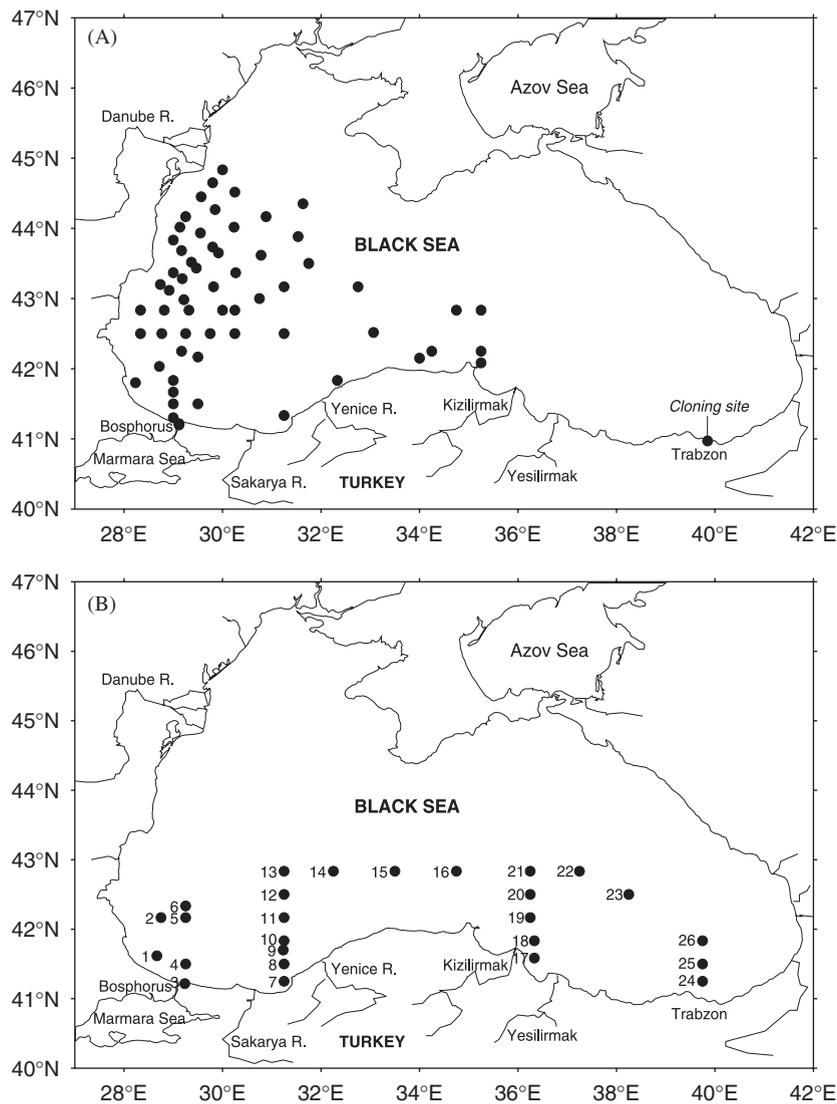


Fig. 1. Location of sampling stations in the Black Sea during April–May 1994 (A) and September–October 1996 (B) cruises.

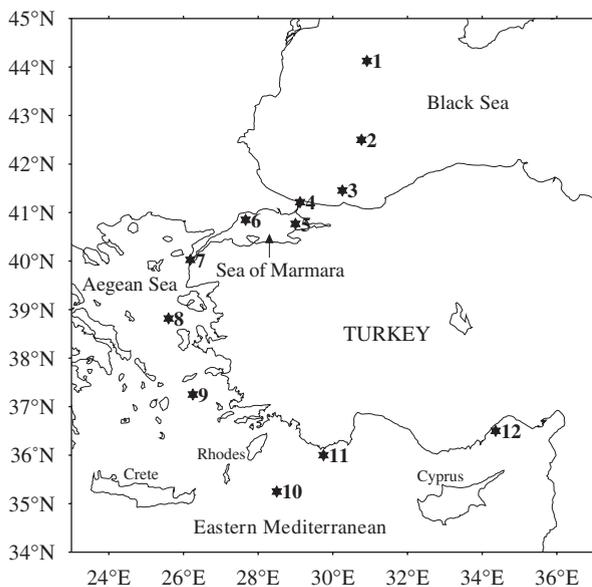


Fig. 2. Location of sampling stations visited by R/V *Knorr* (nos. 1–4) by R/V *Bilim* (no. 5–11) and by R/V *Erdemli* (no. 12).

samples were collected during all cruises from different depths within the euphotic zone with rosette samplers equipped with CTD probes. Sampling depths were chosen on the upcasts based on the details of the CTD profiles obtained during the downcast. Water samples were drawn into 100-ml dark coloured polyethylene bottles and preserved with 4% buffered formalin. Depending on the depth, 10–15-ml aliquots from each sample were filtered onto 25-mm diameter, 0.2- μ m pore-diameter, black, polycarbonate, nucleopore membrane filters. The filters were placed on glass slides for counting either on a Leitz Laborlux S epifluorescent microscope at 1000 \times with a Leitz M2 filter set at 546 nm excitation, >580 nm emission (at the University of Oregon, Eugene) or on a Nikon epifluorescent microscope at 1000 \times with a filter combination of B-2A (DM 505, EX 450–490, BA 520) and G-1A (DM 575, EX 546/10, BA 580) at Institute of Marine Sciences in Erdemli, Turkey. Cells were counted in at least 40 randomly chosen microscope fields.

3. Results

3.1. Distribution in the Black Sea

The Black Sea is characterized by a relatively shallow euphotic layer located above the main pycnocline. The thickness of this zone is greater in

the anticyclonic eddy fields in the Rim Current (about 35–40 m) and smaller in the central gyre cyclonic regions (30–35 m). In the central gyres, chlorophyll-*a* (chl-*a*) is distributed almost homogeneously in the euphotic zone without any subsurface or deep maxima (Yilmaz et al., 2006). In contrast, in the anticyclones, maxima are observed at 30–40 m, coinciding with the base of the euphotic zone. Nutrient input to the euphotic zone in the coastal Black Sea is mainly via the major rivers, which mostly discharge to the northwest shelf. In the central regions, primary production is driven mostly by the influx of nutrients due to mixing from the underlying pycnocline at 50–200 m.

3.1.1. April–May 1994

Cell counts were made on 101 samples collected from the surface mixed layer, the subsurface chl-*a* maximum layer (SCML), and the depth of nitrite maximum (between $\sigma_\theta = 15.8$ – 15.9 , which coincided with the phosphate minimum) in the western and southwestern Black Sea during April–May 1994. *Synechococcus* were present in varying quantities at all stations and depths studied. Minimum and maximum cell concentrations ranged from 9×10^2 to 1.45×10^5 cells/ml at the surface, from 2×10^3 to 1.23×10^5 cells/ml at the SCML, and from 1.3×10^2 to 3.5×10^2 cells/ml at the nitrite maximum. A pronounced spatial heterogeneity in surface cell abundances was apparent in the study area (Fig. 3). In this western region cell numbers decreased to about 9×10^2 cells/ml. Cell counts were as low as 1000 cells/ml at the Danube inflow area, and progressively increased towards more saline and colder offshore waters to a maximum 1.45×10^5 cells/ml. Lower cell counts also were observed in the less-saline Turkish coastal waters where temperatures were higher. In general, the rim current region was relatively low in cell numbers in comparison to the central western cyclone. Cell abundances averaged 4.5×10^4 cells/ml in the much warmer (15 $^\circ$ C) and saline ($S = 18.5$) offshore waters.

Cell counts at the SCML ranged from 2×10^3 (at 10.4 $^\circ$ C and $S = 17.26$) to 1.2×10^5 cells/ml (at 7.46 $^\circ$ C and $S = 18.52$), with an average of 4.3×10^4 cells/ml. Low concentrations were observed in the northwestern sector, mainly in waters offshore from the Danube and along the shelf between the Bosphorus and Sakarya River. Despite the high range of temperature values at the SCML, there was little change in salinity, and its variability was much

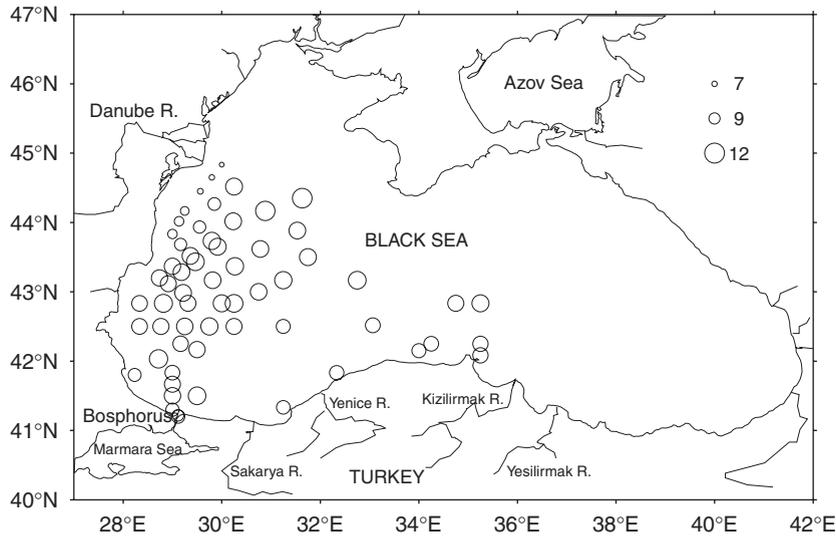


Fig. 3. Surface spatial distribution of *Synechococcus* cell abundance (ln of cells/ml) during April–May 1994 in the western Black Sea.

smaller than observed at the surface. Even these small changes in salinity seemed to cause spatial heterogeneity in cell concentrations. Based on Spearman’s rank correlation analysis, a negative correlation ($P = 0.06$, $n = 23$, $r = 0.75$) was observed between cell counts and salinity values in this layer. There were only a few samples from the nitrite maximum layer, and those had the lowest cell concentrations observed in the Black Sea.

Changes in *Synechococcus* abundance with depth in relation to temperature, salinity and fluorescence are shown in Fig. 4 for a station located offshore of the Bosphorus (41°50’N; 29°00’E). This figure illustrates that the majority of the *Synechococcus* cells were accumulated at the surface mixed and the SCML. The abundance increased twofold from the surface (2.7×10^4 cells/ml) to the SCML (5.0×10^4 cells/ml). Below this, there was a sharp decline in abundance at 50 m and deeper.

3.1.2. September–October 1996

Synechococcus cell counts during September–October 1996 also reflected the spatial heterogeneity in the region (Fig. 5). The average cell concentrations in surface waters were 1.09×10^5 cells/ml and ranged from 3.7×10^4 at station 2 in the west to 2.1×10^5 cells/ml at station 18 near Kizilirmak River. The observed average for surface water was much higher than that observed in April 1994 (4.5×10^4 cells/ml). In contrast to data from April 1994, nearshore stations had higher concentrations than offshore stations. On four of the transects,

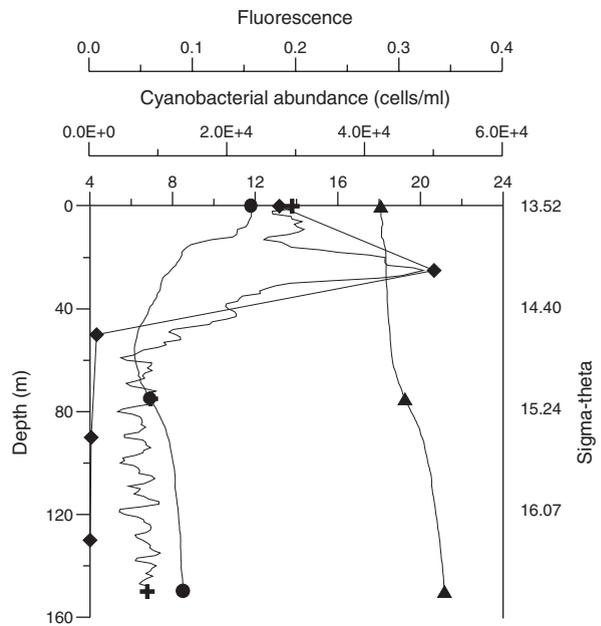


Fig. 4. Changes in abundance of *Synechococcus* (◆) temperature (°C, ●), salinity (ppt, ▲) and fluorescence (arbitrary unit, +) with depth at the station offshore Bosphorus (41°50’N, 29°00’E).

abundance decreased offshore. Cells were more abundant in the warmer and less-saline coastal waters along the cyclonically meandering rim current. Cell counts in the western and eastern central gyres remained low.

Synechococcus cell counts in the SCML were much less variable than in the surface layer, and the

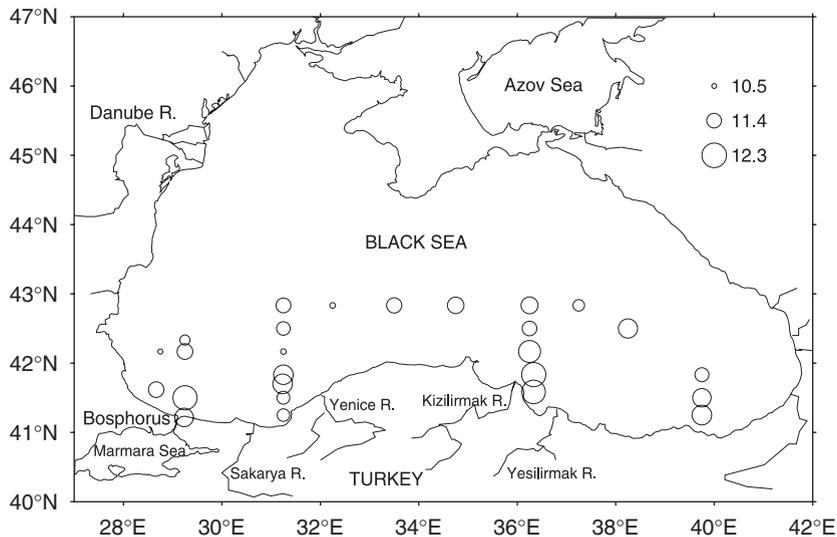


Fig. 5. Surface spatial distribution of *Synechococcus* cell abundance (ln of cells/ml) during during September–October 1996 in the southern Black Sea.

average cell concentrations (1.26×10^5 cells/ml) were higher than at the surface. In contrast to the surface distributions, which were higher near the coast, the offshore stations (especially in the western central gyre) had higher concentrations in the SCML. Only the coastal stations of the transect between the Kizilirmak and Yesilirmak rivers had higher abundances.

The largest heterogeneity in cell abundances between stations was observed at the chl-*a* minimum layer, in spite of the fact that it had homogeneous temperature and salinity. The average cell concentration was lower (1.18×10^4 cells/ml) than in the surface water. Vertical profiles for different areas (coastal, offshore, rim current, western gyre) of the Black Sea also showed that most *Synechococcus* cells were suspended in the surface mixed layer above the thermocline. At some stations the maximum corresponded to the SCML.

3.1.3. June 2001

Changes in *Synechococcus* abundance with depth at station 2 visited by R/V *Knorr* during June 2001 is shown in Fig. 6. Profiles of temperature, salinity and fluorescence are shown for comparison. The common feature in all profiles for this cruise was the presence of a pronounced maximum in the thermocline. At this time, the average abundance in the surface mixed layer was small compared to the population present in the thermocline, probably due

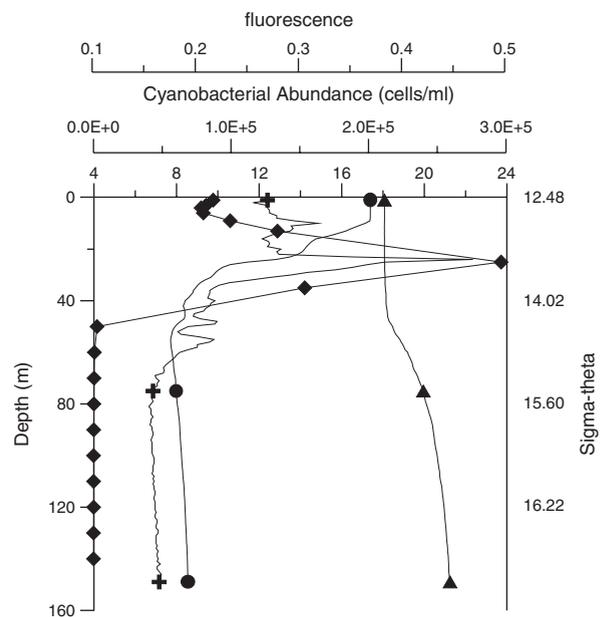


Fig. 6. Changes in abundance of *Synechococcus* (♦) temperature (°C, ●), salinity (ppt, ▲) and fluorescence (arbitrary unit, +) with depth at station 2 in the Black Sea in June 2001.

to the strong light inhibition that occurs during the summer. Inspection of individual cells under the epifluorescence microscope showed that cells inhabiting the top 10 m fluoresced very weakly over a short time period, indicating an unhealthy population.

3.2. Distribution in the Sea of Marmara

Located between the Black Sea and the Aegean Sea, the Sea of Marmara exhibits unique physical properties. Less-saline ($S \sim 22\text{--}25$) waters from the Black Sea occupy the top 20–25 m and more-saline ($S = 38.5$) waters of Mediterranean origin fill the deep basin. The presence of a permanent halocline at 20–25 m is the main feature that determine the lower limit of the euphotic zone in this two-layered system. In contrast to other seas, the strong halocline in the Sea of Marmara prevents mixing between the upper and lower layers. This halocline behaves like a barrier and almost all particles produced in the euphotic zone remain suspended above it. Accumulation of particles in this narrow layer limits light penetration to greater depths and results in a shallow euphotic zone with a remarkable increase in the downward attenuation coefficient of light at depths of 25–30 m (Ediger and Yilmaz, 1996a). The depth of the 1% of surface light penetration coincides with the depth of halocline.

Changes in *Synechococcus* abundance with depth in October 2000 are compared with temperature, salinity and fluorescence in Fig. 7. *Synechococcus* populations were high in the top 15–20 m. The vertical distributions of cell abundances correlate well with fluorescence. Cell abundances decreased

sharply below the halocline. Changes in cell abundance between 40 and 100 m were insignificant, and remained low.

3.3. Distribution in the Aegean Sea

The Aegean Sea is considered as the least productive, oligotrophic basin in the Mediterranean (Ignatiades, 1998; Ignatiades et al., 1995). Pico-plankton dominate the plankton community and account for 56–49% of total chl-*a* and 51–41% of total primary production in the north and south Aegean Sea, respectively.

Synechococcus cell abundances obtained at two stations in the Aegean Sea were low compared to the stations in the Sea of Marmara. At station 8 (October 2000), the average concentration in the top 20 m was 1.8×10^4 cells/ml. Since there seems to be no significant, abrupt changes in the temperature and salinity profiles, the reason for the sharp decrease in cell abundances below 20 m remains unclear (Fig. 8). The highest fluorescence values occurred at ~50 m, but *Synechococcus* were very low (about less than 1000 cells/ml) at these depths. This station was probably located near the edge of an upwelling region rather than the central part (on the dome) of it. The SCML was shallower there than at station 10. Sea-surface temperature (SST)

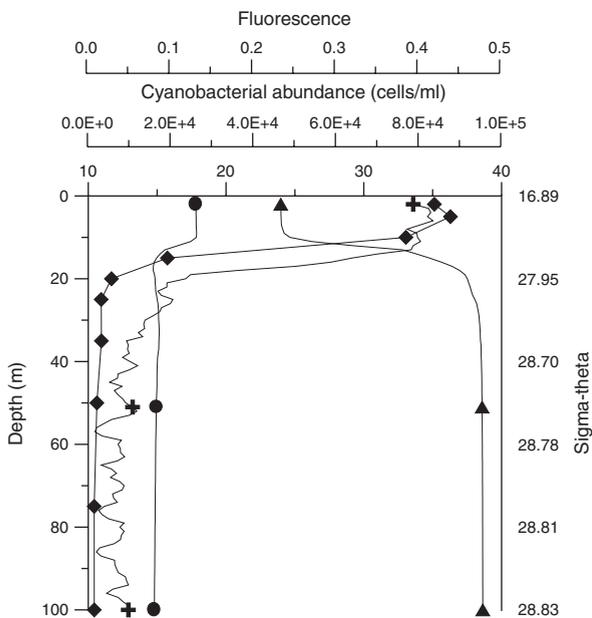


Fig. 7. Changes in abundance of *Synechococcus* (◆) temperature (°C, ●), salinity (ppt, ▲) and fluorescence (arbitrary unit, +) with depth at station 5 in the Sea of Marmara in October 2000.

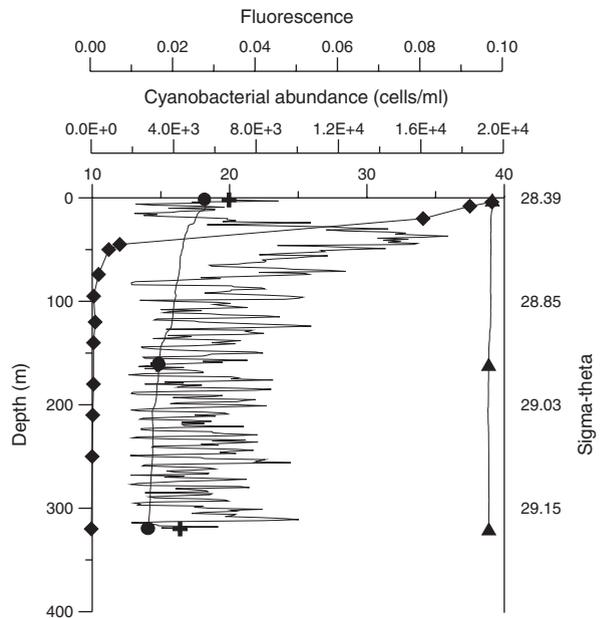


Fig. 8. Changes in abundance of *Synechococcus* (◆) temperature (°C, ●), salinity (ppt, ▲) and fluorescence (arbitrary unit, +) with depth at station 8 in the Aegean Sea in October 2000.

images indicated that surface water was colder (18.22 °C) in the northern Aegean Sea than in the south. However, at station 9, the majority of the population occupied the upper 55 m of the water column. The surface mixed layer extended to about 40 m, and the average cell abundance for the top 55 m was 1.43×10^4 cells/ml. In contrast to the Black Sea, the major *Synechococcus* population was located above the depth of fluorescence maximum at all stations in the Aegean Sea and in the eastern Mediterranean.

3.4. Distribution in the Levantine Basin (eastern Mediterranean)

The eastern Mediterranean has some of the world's most optically clear waters (Ediger and Yilmaz, 1996a). The depth of SCML is found as deep as 120 m, and in some cases, the SCML is deeper than the compensation depth. In this region, cyclonic (upwelling) and anticyclonic (downwelling) eddies determine the depth of the SCML and the vertical distribution of chl-*a*. The SCML was present at shallower depths in the cyclonic eddies and coincided with the top of the nutricline (Ediger and Yilmaz, 1996b). In contrast, the SCML in the anticyclonic regions had much reduced concentrations and was observed at the base of the euphotic zone (much shallower than the nutricline).

Station 10 (Fig. 9) was most likely located in a cyclonic regime with a much thinner surface mixed layer (~20 m). Cells were distributed homogeneously at the top 30 m, and most of the population was above the SCML. Cell abundance decreased significantly at 65 m while the fluorescence maximum occurred between 45 and 85 m. The coastal station 11 (Fig. 2) was most likely located in an anticyclone region with a warmer and deeper (~55 m) surface mixed layer. Surface abundances were lower than at station 10. Because this was a downwelling regime, a considerable number of cells were carried below the surface mixed layer. There was a slight increase in fluorescence between 50 and 90 m, but as a whole, the profile was much more homogeneous down to 250 m.

Changes in *Synechococcus* abundance with depth at station 12 (Fig. 2) located at the continental shelf border in the northern Levantine basin during September 2002 is shown in Fig. 10. The total depth at this station was 210 m and the mixed layer depth was 40 m. The SCML was deeper at this station (about 110 m) than at any other sampled.

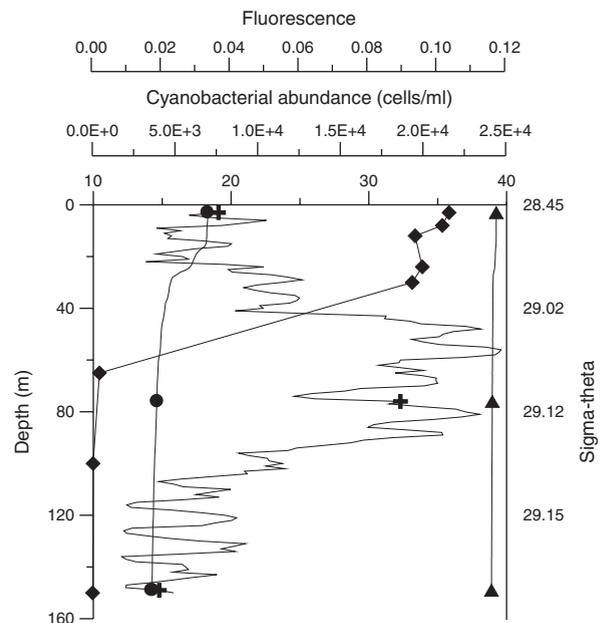


Fig. 9. Changes in abundance of *Synechococcus* (◆) temperature (°C, ●), salinity (ppt, ▲) and fluorescence (arbitrary unit, +) with depth at station 10 in the northeastern Mediterranean in October 2000.

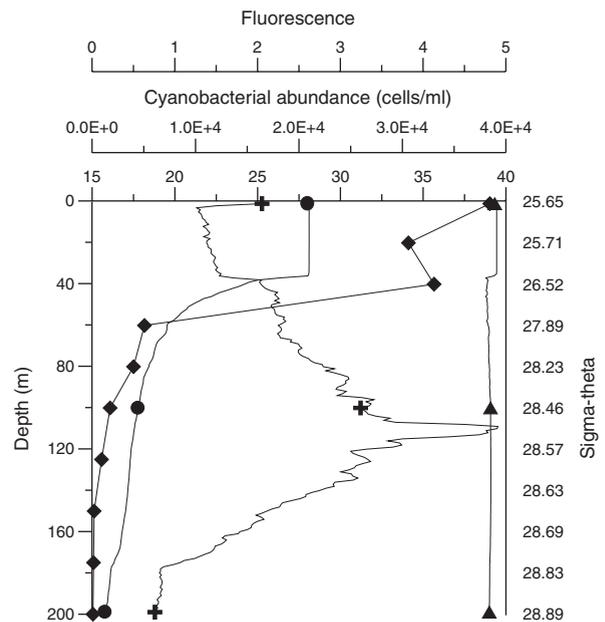


Fig. 10. Changes in abundance of *Synechococcus* (◆) temperature (°C, ●), salinity (ppt, ▲) and fluorescence (arbitrary unit, +) with depth in Levantine basin during September 2002.

This station was also influenced occasionally by the highly eutrophic Mersin and Iskenderun Bays, enriched by Seyhan and Ceyhan rivers, via the

westerly flowing Asia Minor Current (Ozsoy et al., 1993). As a result high fluorescence values were obtained at this station. Most *Synechococcus* were present in the top 40 m and then decreased significantly below the surface mixed layer.

4. Cell size

Live samples were collected from a single station in the southern Black Sea (near Trabzon) for flow cytometric analysis. Water samples collected at 10-m intervals down to 60 m were sent to the Bedford Institute in Dalhousie, Canada, immediately after the cruise for flow cytometric analysis. Analyses were performed with a FACSort Becton Dickinson flow-cytometer. Cell size, related to the cross-sectional area of each particle, was estimated from a 488-nm laser light scattered in the forward narrow angle direction. Calibration of the light scatter signals was done utilizing commercially available plastic spherical beads of known diameters. The results are given in terms of ESD 'Equivalent Spherical Diameter' in micrometers. Results indicate that the cell size of *Synechococcus* gets smaller with increasing depth in the euphotic zone. The majority of cells in the surface mixed layer were in the 0.7–0.8 μm size group while the dominant cell size at greater depths between 20 and 60 m was about 0.5 μm .

5. Discussion

During April 1994, surface *Synechococcus* cells were more abundant in the surface waters of the western central gyre area than the area occupied by the cyclonic boundary current (Rim Current) under direct influence of the Danube river. Lower cell counts were also characteristic of the less-saline Turkish coastal waters where temperature contrast was high. During this period, fluctuations in surface salinity seemed to have a greater impact than temperature on *Synechococcus* abundance. These distributions suggest that cell abundance is not directly related to the nutrient availability, especially in the highly eutrophic north-western shelf area. It is well known that the western margin of the Black Sea is fed by a rich supply of nutrients, as well as detritus and terrigenous pollutants from the Danube. Total inorganic phosphate and nitrogen loads of the Sulina branch of the Danube River increased from the 1960s to 1992 by two- and five-fold, respectively. Input of silicate from the Danube

decreased by about 1/3 (Cociasu et al., 1996). As a result of this nutrient input the frequency and the amplitude of algal blooms increased on the north-west shelf (Bodeanu, 1991, 1993, 1995; Bologa et al., 1995; Moncheva, 1991, 1992; Moncheva et al., 1991; Petrova-Karadjova, 1984, 1990, 1992; Sorokin, 1983; Sukhanova et al., 1988) and south of the Rim Current along Turkish coast (Uysal and Sur, 1995). However, such variability was not observed for the *Synechococcus* population over this sampling period.

Salinity rather than temperature seemed to have the most important influence on the surface spatial distribution of *Synechococcus* in the Black Sea. A highly significant ($P = 0.00$, $n = 61$, $r = 0.75$) positive correlation (based on Spearman's Rank Correlation) was observed between cell abundance and salinity. A similar strong correlation of *Synechococcus* to salinity gradient also has been reported in Florida Bay (Phlips and Badylak, 1996).

Several factors other than temperature and salinity also affect *Synechococcus* abundance. These include differences in grazing pressure or time of sampling during the day. Field and experimental data collected in the Black Sea have shown that synchronous cell division occurs between noon and midnight, with apparent grazing pressure greatest from midnight to noon (Uysal, 2001). Similar trends also have been observed in the Arabian Sea (Sherry and Uysal, 1995), where the magnitude of the diurnal change was found to be greater than the differences between discrete water masses. *Synechococcus* exhibit varying degrees of diurnal periodicity in cell division rates both in culture (Campbell and Carpenter, 1986) and in incubation experiments (Carpenter and Campbell, 1988; Kudoh et al., 1990). Significant differences also were observed in the acclimated growth rates of *Synechococcus* clones from the Black Sea (Uysal, 2001). Clonal isolates from deeper parts of the euphotic zone exhibited higher growth rates compared to clones from the surface mixed layer. This also may be regarded as a factor affecting heterogeneous abundance distribution of this group. Studies of isolates and field samples suggest that physiologically and genetically different *Synechococcus* groups may exist at the same site (Palenik, 1994).

During September–October 1996, significant correlations ($r > P_{0.01}$) were observed between cell counts and physical and chemical parameters (Table 1). Highly significant negative correlations

Table 1
Relationships between physical, chemical parameters and *Synechococcus* spp. abundance based on Spearman's rank correlation coefficient

Parameter	Temperature	Salinity	Dis. oxygen	Depth	Time
Cell abundances	0.6695	-0.6298	0.3307	-0.7164	0.0548
	117	117	117	117	117
	0.0000	0.0000	0.0004	0.0000	0.5552
Parameter	Phosphorus	Nitrogen	Silicium	Fluorescence	Chl- <i>a</i>
Cell abundances	-0.2980*	-0.6761	-0.5947	0.7132	0.6880
	117**	117	117	117	46
	0.0013***	0.0000	0.0000	0.0000	0.0000

*Correlation coefficient.

**Sample size.

***Significance level.

were observed between cell counts and salinity, depth and nutrients (phosphate, nitrate, silicate). This could be summarized as the decrease in cell counts and increase in such parameters with depth. The positive correlation between cell counts and temperature, dissolved oxygen, in-situ fluorescence and chl-*a* denotes a decrease in all with depth. Briefly, we can conclude that, besides grazing pressure and time of sampling during the day, the abundance distribution of the cyanobacterium *Synechococcus* in the water column was very dependent on the ambient physico-chemical factors. From our field and microcosm experiments conducted on board R/V *Bilim* in the Black Sea (Uysal, 2001) and field data collected during the Arabian Sea expedition (Sherry and Uysal, 1995), we found that cells of *Synechococcus* in general are under grazing pressure starting from midnight till noon and slowly begin to rebuild their population in the afternoon via dividing throughout the evening (Uysal, 2000, 2001). In other words, cell division dominates during the latter half of the day even if grazing continues throughout the day. This balance between growth and grazing observed in the surface layer also applies to the SCML and the chlorophyll minimum layer in the Black Sea. Similar diel variations in *Synechococcus* abundances have been observed in the equatorial Pacific (DuRand and Olson, 1996), Arabian Sea (Sherry and Wood, 2001), and Sargasso Sea (Olson et al., 1990), where the maximum abundance was observed near dusk. Similar to this study, the amplitude of the diel variation tended to decrease with depth in the equatorial Pacific (DuRand and Olson, 1996).

Among all these contrasting water bodies, the highly eutrophic Black Sea and the Sea of Marmara appeared to contain the highest *Synechococcus* concentrations at all depth layers studied (Table 2). Highest concentration (5.19×10^5 cells/ml) was observed at the SCML during September–October 1996 in the Black Sea. Most important is that the concentrations at the SCML in the Aegean Sea, north-eastern Mediterranean as well as in the Levantine remained much lower than the concentrations obtained in the Black Sea and the Sea of Marmara. From here we can conclude that deepening of this layer may limit the populations growth to a certain degree. Light rather than nutrients will be the limiting factor at such depths. For example, SCML occurred at ~110 m in the Levantine (see Fig. 10) whereas the maxima was so close to the surface (between 5 and 15 m) in the Sea of Marmara (Fig. 7).

Synechococcus is known to be a major contributor to the total photosynthetic biomass in the more oligotrophic Mediterranean Sea (Li et al., 1993; Magazzu and Decembrini, 1995; Agawin and Agusti, 1997). Plenty of productivity measurements have been carried out in the region, but all cover the whole phytoplankton size range and none includes size fractionation to determine the relative contribution of picoplankton to total biomass in these contrasting water bodies. However, comparison of results of a time series study conducted on phytoplankton during 1997–1998 (Uysal et al., 2003) and on *Synechococcus* during 2002–2003 (Uysal et al., 2004, unpublished technical report) at station 12 in the Levantine Basin indicated that the contribution of *Synechococcus*

Table 2
Changes in *Synechococcus* abundance at different layers in the Black, Marmara, Aegean and north-eastern Mediterranean Seas

Depth/ layer	Black Sea (April 1994) <i>n</i> = 61	Black Sea (September 1996–October 1996) <i>n</i> = 26	Black Sea (June 2001) <i>n</i> = 4	Marmara Sea (October 2000) <i>n</i> = 3	Aegean Sea (October 2000) <i>n</i> = 2	NE Mediter. (October 2000) <i>n</i> = 2	Levantine (September 2002–August 2003) <i>n</i> = 11
<i>Surface</i>							
Min	9.00×10^2	3.73×10^4	2.01×10^4	5.58×10^4	1.50×10^4	9.27×10^3	5.21×10^3
Max	1.45×10^5	2.11×10^5	8.69×10^4	1.61×10^5	1.94×10^4	2.15×10^4	7.31×10^4
Avg	4.50×10^4	1.09×10^5	4.40×10^4	1.00×10^5	1.72×10^4	1.54×10^4	2.25×10^4
		<i>n</i> = 61	<i>n</i> = 14	<i>n</i> = 8	<i>n</i> = 6	<i>n</i> = 7	<i>n</i> = 26
<i>Surface mix</i>							
Min		2.28×10^4	2.01×10^4	3.48×10^4	1.39×10^4	7.91×10^3	4.77×10^3
Max		2.60×10^5	9.93×10^4	1.81×10^5	1.94×10^4	2.15×10^4	7.51×10^4
Avg		9.10×10^4	4.92×10^4	1.06×10^5	1.64×10^4	1.42×10^4	1.97×10^4
	<i>n</i> = 22	<i>n</i> = 25	<i>n</i> = 5	<i>n</i> = 3	<i>n</i> = 3	<i>n</i> = 4	<i>n</i> = 22
<i>Chl. max</i>							
Min	2.00×10^3	3.63×10^4	3.47×10^4	5.58×10^4	8.51×10^2	4.32×10^2	2.75×10^2
Max	1.20×10^5	5.19×10^5	2.96×10^5	1.67×10^5	4.51×10^3	7.34×10^3	1.50×10^4
Avg	4.30×10^4	1.26×10^5	1.05×10^5	1.03×10^5	2.25×10^3	5.20×10^3	6.12×10^3
		<i>n</i> = 24	<i>n</i> = 16	<i>n</i> = 9	<i>n</i> = 7	<i>n</i> = 3	<i>n</i> = 18
<i>Chl. min</i>							
Min		1.97×10^3	2.80×10^2	1.85×10^3	2.70×10^1	1.8×10^1	5.30×10^1
Max		3.25×10^4	1.96×10^4	5.59×10^3	1.92×10^2	6.4×10^1	5.65×10^3
Avg		1.18×10^4	5.09×10^3	2.87×10^3	1.01×10^2	3.6×10^1	1.33×10^3

to total phytoplankton biomass in terms of carbon varies significantly. During phytoplankton blooms this percentage ratio decreased to as low as 0.2%. During steady state (under normal conditions) it increased up to 60%. Minimum and maximum phytoplankton and *Synechococcus* biomasses ranged between ~3–1875 and 0.6–5.1 $\mu\text{gC/l}$, respectively, in the Levantine shelf waters.

6. Conclusions

Abundance distribution of *Synechococcus* varied significantly both in the vertical and horizontal scales in all physically and spatially discrete Turkish seas, ranging from the highly eutrophic brackish waters of the coastal Black Sea to highly oligotrophic saline eastern Mediterranean waters. In these contrasting ecosystems, the bulk of the population remained suspended in the surface mixed layer and decreased gradually towards the base of the euphotic zone. Salinity rather than temperature had more control on the heterogeneous surface spatial distribution of cells in the Black Sea.

An abrupt decline in cell abundances was noted below the halocline, especially in the Black Sea and the Sea of Marmara. In contrast to abundance profiles obtained in the Black Sea, majority of the population remain suspended above the depth of fluorescence maximum in the Aegean Sea and in the eastern Mediterranean. Besides grazing pressure and the time of sampling, the abundance distribution of the cyanobacterium *Synechococcus* in the water column was very dependent on physico-chemical factors. Highly significant negative correlations were found between cell counts and salinity, depth and nutrient salts in the Black Sea. The positive correlation between the cell counts and the temperature, dissolved oxygen, in-situ fluorescence, and chl-*a* denotes decrease in all with depth. In all seas, cells at the SCML reflected brighter and longer fluorescence than those present at and just below the surface. Cell size was found to decrease with increasing depth. Lastly, it was seen that the contribution of *Synechococcus* to total phytoplankton biomass may exceed 50% under normal conditions in the Levantine.

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