Marine Ecology. ISSN 0173-9565

ORIGINAL ARTICLE

The annual cycle of *Synechococcus* (cyanobacteria) in the northern Levantine Basin shelf waters (Eastern Mediterranean)

Zahit Uysal & İrem Köksalan

Institute of Marine Sciences, Middle East Technical University, Erdemli, Mersin, Turkey

Keywords
Eastern Mediterranean; growth factors; Levantine Basin; near-shore waters; population dynamics; *Synechococcus*.

Correspondence
Zahit Uysal, Institute of Marine Sciences, Middle East Technical University, Erdemli, Mersin 33731, Turkey
E-mail: uysal@ims.metu.edu.tr

Accepted: 17 July 2006

doi:10.1111/j.1439-0485.2006.00105.x

Abstract

Abundance of picoplanktonic chroococcoid marine cyanobacteria *Synechococcus* was monitored weekly over the year 1998 in shallow coastal waters of the northern Levantine Basin. The ambient physical, chemical and biological variables (temperature, salinity, Secchi disk depth, total suspended sediment, nitrate, phosphate, Chl *a* and phytoplankton) were also measured. *Synechococcus* was found to be more abundant during summer and early autumn and less during winter and early spring. At the surface and 15 m depth, cell concentrations were in the range 6.4×10^3–1.5×10^5 and 3.2×10^3–1.6×10^5 cells·ml^{-1}, respectively. Based on the Pearson product–moment correlation analysis, a highly significant correlation between *Synechococcus* abundance and ambient temperature was observed ($n = 40$, $r = 0.558$, $P < 0.01$). As *Synechococcus* forms blooms that usually do not last more than a week, the short time-scale survey achieved in this study was appropriate to reveal its abundance dynamics. Several factors such as rapid changes in nutrient concentration (especially nitrate), phytoplankton, light availability, temperature, salinity, freshwater input and vertical mixing played a relevant role on the abundance of *Synechococcus* over the year in the highly dynamic shallow coastal waters of the Levantine Basin.

Problem

Previous studies have established that larger phytoplankters were responsible for most of the primary production of organic matter in the marine environment. With the introduction of new techniques and instrumentation (single cell analysis by flow cytometry and pigment analysis by high-performance liquid chromatography), small cell phytoplankton (picoplankton, <2 μm) also was found to contribute significantly to the total biomass, photosynthesis and the pelagic food web in the world oceans (Berman 1975; Johnson & Sieburth 1979; Waterbury *et al.* 1979; Li *et al.* 1983; Platt *et al.* 1983; Takahashi & Bienfang 1983; Glover *et al.* 1986; Iturriaga & Mitchell 1986; Booth 1988; Li *et al.* 1992; Bell & Kalff 2001). The first picoplankton components discovered were phycoerythrin-containing unicellular cyanobacteria, *Synechococcus* (Waterbury *et al.* 1979). *Synechococcus* is regarded as an important component of the phytoplankton in the highly oligotrophic Mediterranean Sea (Li *et al.* 1993; Magazzu & Decembrini 1995; Mostajir *et al.* 1995; Vaulot *et al.* 1996; Agawin & Agusti 1997; Jacquet *et al.* 1998; Agawin *et al.* 2000; Moutin *et al.* 2002). In oligotrophic oceans, this group contributes up to an estimated 25% of photosynthetic carbon fixation (Waterbury *et al.* 1986) and accounts for 64% of the total photosynthesis in the North Pacific Ocean (Iturriaga & Mitchell 1986). *Synechococcus* is one of the main components of the microbial loop that regulates biogeochemical cycles (Burkill *et al.* 1993). It is important as a primary producer, especially in the open

ocean where >20-μm cells cannot thrive (Glover *et al.* 1986). *Synechococcus* possesses high specific growth rates (Bienfang & Takahashi 1983; Landry *et al.* 1984) and its ecological success in oceanic regions has been partly attributed to the increased efficiency of light harvesting and nutrient uptake conferred by its small size and its negligible sinking rate (Glover *et al.* 1988a,b).

Phytoplankton investigations conducted earlier in the Levantine Basin shelf waters mainly focused on the qualitative and quantitative aspects of diatoms, dinoflagellates and coccolithophorids among others, and their relationships to environmental factors (Eker & Kideys 2000; Eker-Develi *et al.* 2003; Uysal *et al.* 2003; Yılmaz *et al.* 2003). All these studies dealing with phytoplankton overlooked *Synechococcus*. Despite the large number of publications dealing with almost all aspects of this group in the world ocean (Bidigare *et al.* 1989; Bryant 1994; Cavender-Bares *et al.* 2001; Bertilsson *et al.* 2003), time series data at the scale of a week regarding its development under rapidly changing ambient biological, chemical and physical properties of both open seas and shelf waters are still insufficient. The aim of this study was to provide baseline information on *Synechococcus* dynamics in a rapidly changing coastal environment with respect to several physical, chemical as well as biological factors.

Material and Methods

Sampling site and hydrological parameters

The sampling site is located at 34°16′ E, 36°33′50″ N in the north-eastern coast of the Mediterranean Sea/Levantine Basin (Fig. 1). The Levantine Basin is regarded as one of the most important regions of freshwater influence in the eastern Mediterranean Sea. The study area receives fresh water from the nearby Lamas River over most of the year. In addition to the river input, appreciable amounts of nutrients are supplied via the underground freshwater sources as well as from the upwelling events. Weekly sampling was done on board R/V Erdemli of the Institute of Marine Sciences of Middle East Technical University between January 1998 and January 1999. The station is located approximately 500 m from the shoreline and has a total depth of about 20 m. Closing bottles were used to sample water at the surface and at 15 m depth. Two depths were chosen as the surface waters receive freshwater from the nearby Lamas River for most of the time throughout the year. Although both stations are shallow, freshwater impact to the nutrient budget of the surface water was much greater compared with 15 m depth. Changes in temperature and salinity with depth were measured using a Sea-Bird SBE 9 Oceanographics CTD (Conductivity Temperature Depth) profiler (Sea-Bird Electronics, Bellevue, WA, USA) equipped with a fluorometer. This system contained sensors, batteries and internal data recording units (searam memory). The data recorded during the casts were later processed by the computers in the Institute laboratories.

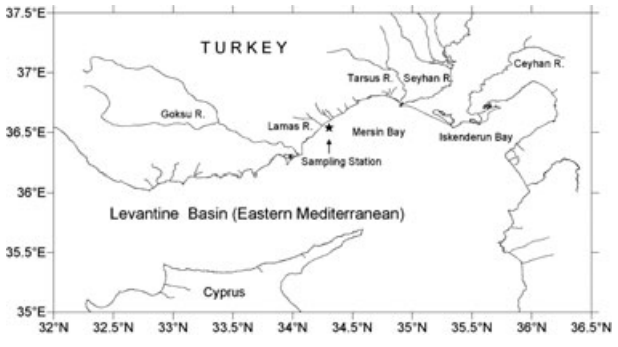

Fig. 1. Location of the sampling station in the Levantine Basin.

Nutrient, Chl *a* and total suspended sediment (TSS) analysis

Water samples for nutrients were collected into 50-ml high-density polyethylene bottles that were pre-cleaned with 10% HCl. Bottles for nitrate and phosphate analysis were kept frozen (−20 °C), whereas those for silicate were kept cool (+4 °C) in the dark until analysis. The nutrient measurements were carried out using a Technicon model two-channel auto-analyzer (SPX Corporation, Bran Luebbe Inc., Norderstedt, Germany); the methods followed were very similar to those described by Strickland & Parsons (1972) and Grasshoff *et al.* (1983). The detection limits achieved, using low-concentration samples, were 0.02 and 0.05 μM for phosphate (PO_4^{3-}-P) and nitrate + nitrite (NO_3^--N + NO_2^--N), respectively. One liter of seawater was filtered through GF/F filters and extracted into 90% acetone solution for Chl *a* measurements. The fluorescence intensity of clear extracts was then measured by the standard fluorometric method (Holm-Hansen & Riemann 1978) using a Hitachi F-3000 model fluorometer (Hitachi High Technologies America, Inc., Life Sciences Division, San Jose, CA, USA). For the TSS measurements, 5 l of seawater was filtered through dried (at 105 ± 5 °C for 3 h) and pre-weighed GF/F filters (Eaton *et al.* 1995). The filters were then kept at 105 ± 5 °C overnight and weighed again. The weight differences were used in the calculations. A 20-cm diameter Secchi disk was used for Secchi depth measurements.

Picoplankton analysis

Seawater samples for picoplankton analysis were drawn from closing bottles into 100-ml dark-colored polyethylene bottles and preserved onboard with pre-filtered

(through 0.22-μm Millipore filter; Millipore Corporate, Billerica, MA, USA) 4% buffered formalin. Aliquots (10 ml) from each sample were filtered onto 25-mm-diameter, black, polycarbonate, Nuclepore® (Whatman International Ltd, Maidstone, UK) membrane filters with 0.2-μm pore size. The filters were then placed onto glass slides for picoplankton counting on a Nikon epifluorescence microscope (Nikon Corporation, Tokyo, Japan) with a filter combination of B-2A (blue excitation, dichroic mirror DM 505, excitation filter EX 450–490, barrier filter BA 520) and G-1A (green excitation, dichroic mirror DM 575, excitation filter EX 546/10, barrier filter BA 580). The main light-harvesting pigment of *Synechococcus* is phycoerythrin which is responsible for the orange fluorescence of *Synechococcus* when excited with green light. Depending on the quality (fluorescence) and quantity of the cells, 600× or 1500× magnifications were used for enumerating the fluorescing cells. The 1500× magnification was used when *Synechococcus* was very abundant and its fluorescence was weak. On each filter, at least 20 randomly chosen microscope fields were counted for estimating the cell abundance.

For phytoplankton analysis by optical microscopy, surface seawater samples were transferred into 1-l dark glass bottles and preserved with buffered formaldehyde to obtain a final concentration of 2%. These bottles were then allowed to settle for at least 1 week and the supernatant water was discarded with a Pasteur pipette (designed to minimize the disturbance of the settled material by convection currents; VWR Scientific, West Chester, PA, USA) until *ca.* 20-ml water remained at the bottom. A Nikon inverted microscope (Nikon Corporation) with phase-contrast attachment was used for the identification and enumeration of concentrated phytoplankton. Cells smaller than 15 μm were counted in two to three drops of the concentrate on a glass slide. Cells greater than 15 μm were enumerated using Nauman's counting chambers from 0.4 or 0.8 ml of the phytoplankton concentrate.

Statistical analysis

Each measured variable was checked for data normality by applying the test of randomness (index of dispersion). Pearson product–moment correlation analysis was applied to look for relationships between *Synechococcus* abundance and ambient biological, physical and chemical variables.

Results

Temperature and salinity

Time profiles of temperature and salinity along depth during the year 1998 are given in Fig. 2. Over the year, temperature varied in the range 15.20–30.48 °C at the surface and 15.46–29.78 °C at 15-m depth, and salinity in the ranges 37.94–39.34 and 38.4–39.34 practical salinity unit (psu) at the surface and 15-m depth, respectively (Table 1). Surface water was coldest in February and warmest in August. Both depths showed least salinity on March 31 and highest salinity on October 7. At the beginning of the study, water temperature was 15.5 °C. It fluctuated between 15.5 and 17.5 °C until late April because of heavy rains and storms. The colder freshwater input from the nearby Lamas River appeared to play a major role in the heat as well as the salinity budget of the water column at the sampling site. Quite heavy rains towards the end of March led to a 1 °C decrease in temperature in the water column. Beginning from May, temperature started to warm up and reached the highest level of 30.48 °C on August 18. Following this period, it started to cool down gradually towards winter again. As the total depth of the sampling site is about 20 m, it is difficult to talk about stratification at the site. An apparent temporary thermocline as well as a halocline formation could not be observed throughout the year.

Nutrient concentrations

The surface annual average for nitrate concentration was 0.98 μM, a relatively high value. Nitrate concentration reached its maximum level of 4.87 μM on December 24 (Fig. 3). It remained above the annual mean value during winter (December, January and February) and late spring (May). In early summer (June), nitrate concentrations remained close to the detection limits. Between late June and early September, the levels again exceeded the annual mean. This was followed by a period of low values until early November. By mid-November, nitrate concentrations were again well above the annual average and shortly decreased in early December. The annual cycle was completed with a relatively high value of 0.8 μM. At 15 m, the annual mean concentration was 0.68 μM with a maximum of 2.25 μM recorded on August 25. Except during the spring period (March, April and May), the annual patterns for surface and 15 m depth were similar. Between March 3 and June 16, nitrate concentrations remained at the detection limit at 15 m depth. In the following weeks, a summer maximum was followed by an early autumn minimum and then by a late autumn – early winter maximum as was the case at the surface. The annual mean concentration for phosphate at the surface was 0.06 μM with a maximum level of 0.15 μM recorded on February 5–11 and on July 23 (Fig. 3). The levels remained above the annual mean during the period January 14–August 25. After this period, phosphate values

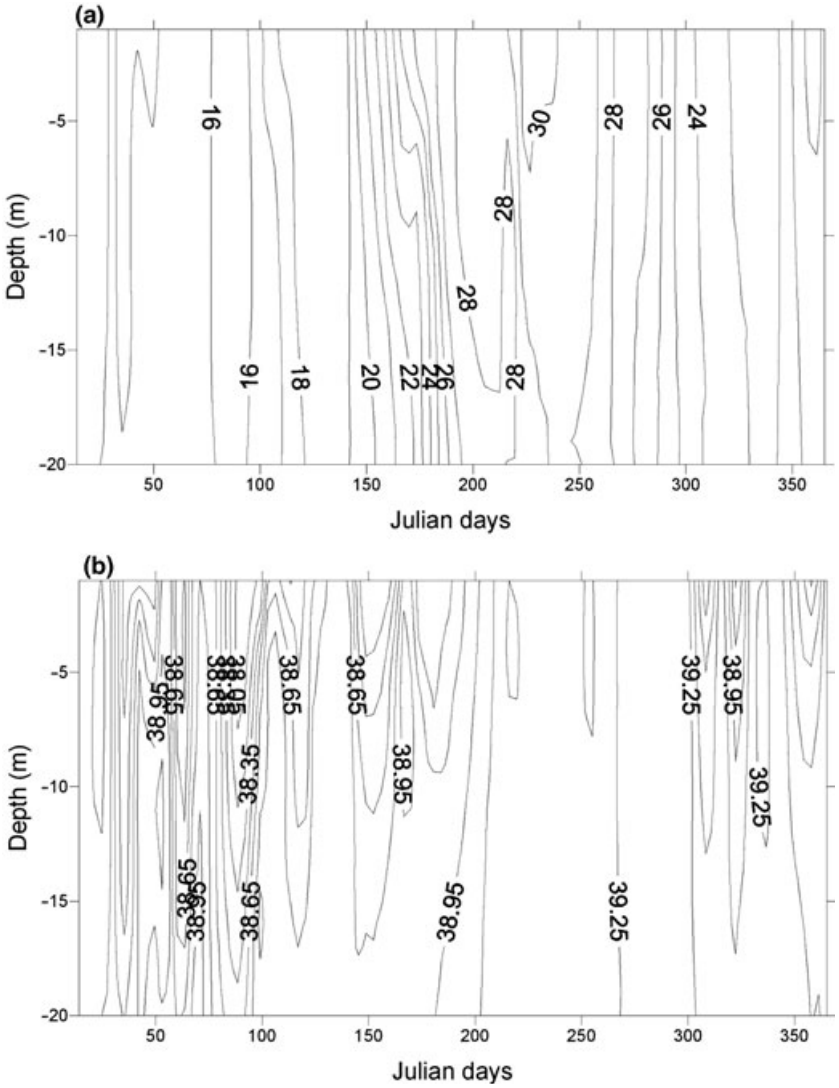

Fig. 2. Time profile of temperature (a) and salinity (b) *versus* depth.

stayed below the annual average except for the increase observed on November 4 (0.1 μM). The annual mean concentration at 15 m was 0.04 μM with a maximum of 0.12 μM recorded on February 5. Phosphate concentrations at this depth were lower than at the surface, especially during spring and early summer.

Table 1. Minimum, maximum and mean values of the physico-chemical and biological variables measured.

	minimum		maximum		average	
variables	surface	15 m	surface	15 m	surface	15 m
temperature [°C]	15.20	15.46	30.48	29.78	22.05	21.66
salinity [psu]	37.94	38.40	39.34	39.34	38.79	38.98
nitrate [μM]	0.07	0.04	4.87	2.25	0.98	0.68
phosphate [μM]	0.02	0.02	0.15	0.12	0.06	0.04
Chl *a* [$\mu g \cdot l^{-1}$]	0.12	0.08	2.93	2.86	0.83	0.57
total suspended sediment [$mg \cdot l^{-1}$]	1.76	2.38	17	14	5.29	5.45
Synechococcus [$cells \cdot ml^{-1}$]	6418	3220	153,562	160,099	36,224	38,152
phytoplankton [$cells \cdot l^{-1}$]	9864		5,633,458		483,444	
Secchi disk depth [m]	1.94		20.25		8.64	

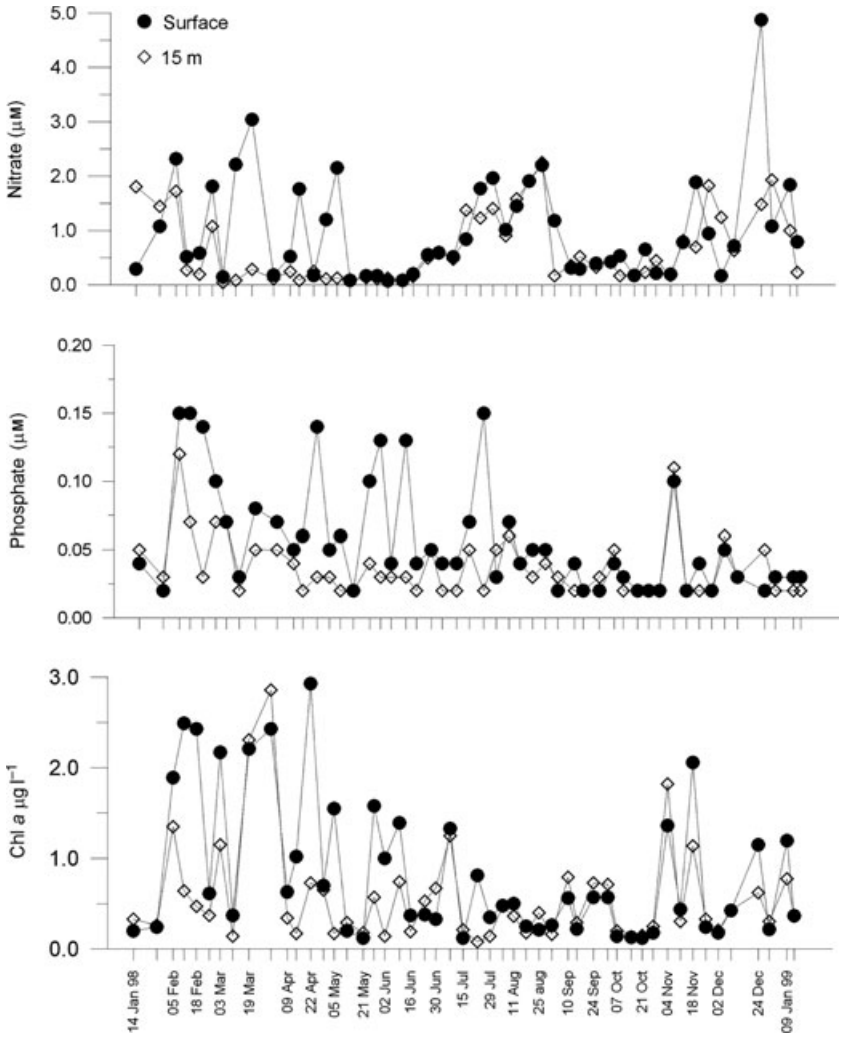

Fig. 3. Time series of nitrate [μM], phosphate [μM] and Chl *a* [$\mu g \cdot l^{-1}$] levels at the surface (●) and at 15-m depth (◇).

Chl *a* and TSS

Over the year, surface Chl *a* concentration varied in the range 0.12–2.93 $\mu g \cdot l^{-1}$, with an annual average value of 0.83 $\mu g \cdot l^{-1}$ (Fig. 3). The highest concentrations were achieved in February and March, followed by a decreasing trend towards late October. Values remained below the annual average between late July and late October. At 15 m depth, the Chl *a* concentration varied in the range 0.08–2.86 $\mu g \cdot l^{-1}$, with an annual average value of 0.57 $\mu g \cdot l^{-1}$. Chl *a* content of both depths showed the highest discrepancy during late winter and spring.

The annual surface mean for the TSS was 5.29 $mg \cdot l^{-1}$ with minimum and maximum levels of 1.76 and 17 $mg \cdot l^{-1}$ recorded on February 24 and April 29, respectively (Fig. 4). Winter values remained below the annual average, but in the following weeks, they started to increase and peaked on April 29. Following this, the values started to fluctuate while decreasing, and fell below the annual average towards late summer. A week-long increase on September 24 was followed by a decrease until November 11. This further continued to fluctuate until the end of the survey. The annual mean for 15 m depth was 5.45 $mg \cdot l^{-1}$ with minimum and maximum levels of 2.38 and 14 $mg \cdot l^{-1}$ observed on February 11 and April 29, respectively. The trend for both depths looked identical over the year.

Secchi disk depth (SDD)

The annual average SDD was 8.64 m, being lowest (1.94 m) on April 22 and highest (20.25 m; Fig. 4) on December 2. From the beginning of the survey until July 8, SDD readings remained low with an average value of 6.28 m. The SDD showed maxima on July 15 (18.7 m), August 18 (18.6 m), October 21 (19.4 m) and December 2 (20.2 m). From time to time, maximum values were always followed by minimum ones, and sometimes the

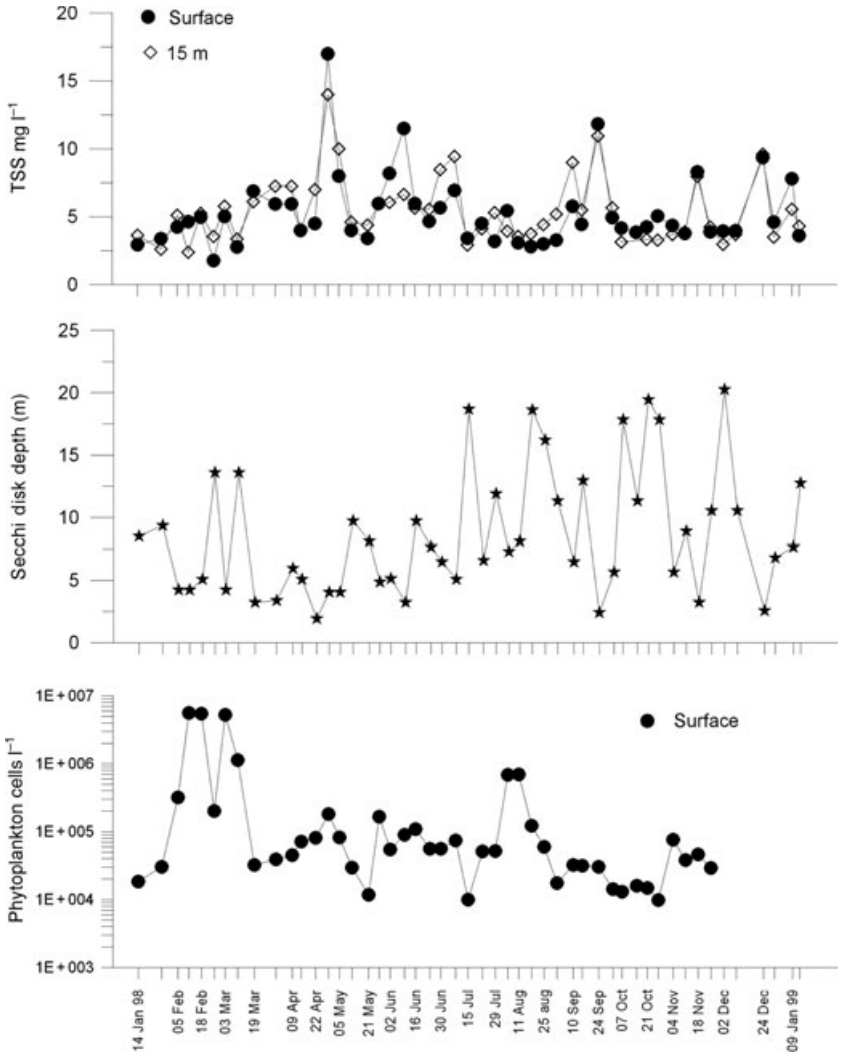

Fig. 4. Time series of total suspended sediment [mg·l^{-1}], Secchi disk depth [m] and phytoplankton abundance [number of cells·l^{-1}] at the surface (●) and at 15-m depth (◇).

values remained quite high over several weeks as observed during October.

Phytoplankton abundance

Total phytoplankton cell numbers ranged from 9.86×10^3 to 5.63×10^6 cells·l^{-1} with an annual average level of 4.83×10^5 cells·l^{-1} at the surface. Phytoplankton was the most abundant during late winter (February) and early spring (March). Blooms with concentrations of 5.6×10^6, 5.4×10^6 and 5.2×10^6 cells·l^{-1} were observed on February 11 and 18 and on March 3, respectively (Fig. 4). Diatoms were largely dominant during winter. Besides diatoms, dinoflagellates and coccolithophorids were the other important constituents of the phytoplankton assemblage. Phytoplankton abundance exhibited little increases during summer, especially during August, but remained very low during the rest of the year. Dinoflagellates were the most abundant during spring and late summer, reaching a maximum of 4.3×10^5 cells·l^{-1}. Cryptomonads were most abundant in April and in June with a maximum value of 9.4×10^3 cells·l^{-1} observed on April 14. Small flagellates were almost absent and only found in appreciable amounts during February, September and October. Based on annual averages, diatoms made up almost 90% of the total phytoplankton biomass (excluding *Synechococcus*) at the site (Uysal *et al.* 2003).

Synechococcus abundance

The time series of *Synechococcus* abundance at the surface and at 15 m depth are displayed in Fig. 5. At the surface, cell concentrations varied in the range 6.42×10^3–1.53×10^5 cells·ml^{-1}. The annual average was 3.9×10^4 cells·ml^{-1} with a maximum of 1.53×10^5 cells·ml^{-1} recorded on September 10. *Synechococcus* was more

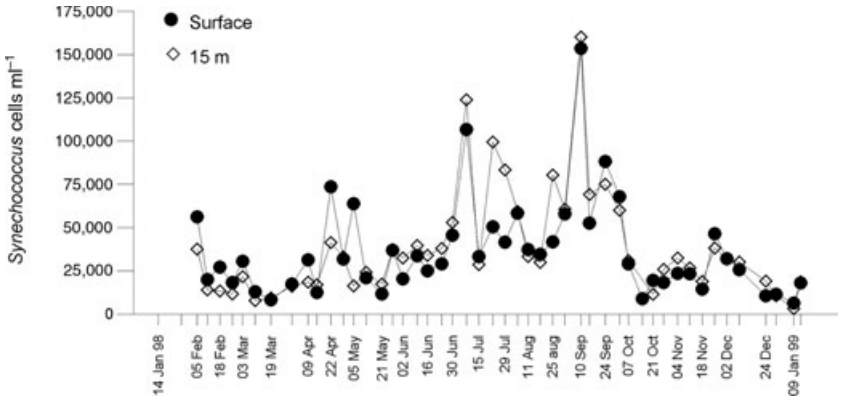

Fig. 5. Time series of *Synechococcus* abundance at the surface (●) and at 15-m depth (◇).

abundant during summer (June, July and August) and early autumn (September) and less during winter (December, January and February) and early spring (March and April). During late autumn and winter, *Synechococcus* abundance remained below the annual average. Cell abundances peaked on July 8 and 23 and on September 10 and 24, respectively. Increases in cell numbers on July 8 and September 10 lasted for a week. The peak observed on September 10 was followed by a lasting decrease. Surface cell counts remained below the annual average from February until mid-April, from mid-May to late June and from mid-October towards the end of the sampling.

At 15 m depth, *Synechococcus* concentrations were in the range 3.22×10^3–1.60×10^5 cells·ml^{-1}. The annual average for this depth was 4×10^4 cells·ml^{-1} with a maximum of 1.60×10^5 cells·ml^{-1} recorded on September 10, as was the case at the surface. *Synechococcus* abundance showed a summer–early autumn increase followed by a decrease for the rest of the year. Major peaks were observed on July 8 and 23 and on September 10. In general, surface cell counts during winter and spring were higher than counts at 15 m. This situation was then reversed in the following months. *Synechococcus* abundance was slightly higher at 15 m depth than at the surface during summer, with larger differences in late July and August. Size (length) of *Synechococcus* varied in the range 0.8–2 μm with an average size of 1.4 μm.

The Pearson product–moment correlation analysis showed that *Synechococcus* abundance was positively correlated ($n = 40$, $r = 0.558$, $P < 0.01$) to water temperature. No correlation was observed between *Synechococcus* abundance and TSS, nutrients, salinity, SDD and phytoplankton abundance.

Discussion

Significant fluctuations in nitrate and phosphate concentrations were observed over most of the year. Fluctuations observed during winter were mainly due to storms and turbulence that helped mixing of the water column. High nitrate and phosphate levels observed at the surface were due to intense Lamas River input during spring (March, April and May).

During winter, *Synechococcus* abundance at the surface exceeded the annual average only once on February 5 when the phosphate (0.15 μM) and nitrate (2.32 μM) concentrations were high. A net increase in total phytoplankton abundance was also observed during this week. Phytoplankton standing stock at the surface remained at its peak levels until March 10 due to surface fertilization mainly by phosphate and less by nitrate. During this period, phosphate concentration dropped steadily from a very high level of 0.15 μM on February 5 to a low level of 0.03 μM on March 10. Meanwhile, *Synechococcus* maintained a small standing stock compared with that of phytoplankton. Factors such as insufficient irradiance and intense competition with phytoplankton for nutrients could have played a major role during this period. Compared with February, a net increase in *Synechococcus* was observed at both depths in April. Phytoplankton abundance, on average, was about 30 times less in April than in February. Lower phytoplankton abundance as well as increasing temperature could have possibly favored the *Synechococcus* in the meantime, although the nutrients were scarce compared with February. The observed *Synechococcus* as well as phytoplankton peaks in late April and early May were due to increased nutrient levels introduced from the nearby Lamas River whose influence was felt over most of the year. TSS was found to be maximum (17 mg·l^{-1}) on April 29. This increase lasted for about 3 weeks and then fell below the annual average again until late June, when the nutrients increased again and were above the detection limits.

Between June 30 and October 2, *Synechococcus* sustained a biomass well above the annual average. The two major increases observed on July 8 and September 10

were not directly influenced by the high nutrient levels. Indeed, they took place just before and after the nutrient enrichment. An increase in nitrate concentration towards the end of June favored *Synechococcus* in early July against other phytoplankton. *Synechococcus* minima observed between August 5 and 18 were compensated by a rapid increase in phytoplankton abundance. The fall observed in nitrate concentration on August 5 was mainly due to phytoplankton consumption. In terms of nutrient acquisition, *Synechococcus* is able to utilize nitrate, nitrite, ammonium, urea, and some amino acids (Moore *et al.* 2002). Under nitrogen deprivation, *Synechococcus* will degrade the major light-harvesting pigment protein phycoerythrin as an internal nitrogen source (Wyman *et al.* 1985). Phosphorus utilization is *via* the uptake of phosphate and numerous organic P sources (Scanlan *et al.* 1997) as well as of novel organic sources of N and P, such as cyanates and phosphonates (Palenik *et al.* 2003). Phosphorus stress on this group during the summer months was demonstrated from the Red Sea (Fuller *et al.* 2005).

The very high nitrate levels (up to 2 μM) observed in the water column between mid-July and late August in shelf waters may be regarded as a very unique event. Indeed, the Basin waters are known to be usually nutrient poor and the average nitrate concentration for the surface waters is around 0.2 μM. Starting from mid-July, 38.9 salinity waters occupied the entire shelf area indicating an intense advection towards the coast of nutrient-rich Atlantic deep waters. Low salinity waters in the Levantine Basin may contain elevated nitrate levels up to 4–6 μM (Yılmaz & Tuğrul 1998). The near surface contours with salinities of 38.9 or less are used to identify the Atlantic water, and salinities of 39.0 and greater at intermediate depths are used to characterize the Levantine intermediate water, despite difficulties in assigning any absolute limits to either water mass (Özsoy *et al.* 1989). The nutrient-rich water remained in the basin for more than a month, leading to a 'high nutrient, low chlorophyll' (HNLC) situation. The low TSS and Chl *a* contents as well as the high SDD observed during this period were supporting the occurrence of an HNLC situation. As the low-salinity water masses were advected from deep below the euphotic zone, they were initially deprived of photosynthetic cells. Consequently, a relatively long period of time was required for autotrophic cells to develop after the advection, generating a transitory HNLC situation. In the case of *Synechococcus*, its large surface-to-volume ratio reduced the adaptation delay compared with larger cells. During the first week of the event, an apparent decline of *Synechococcus* abundance in the water column from July 8 to July 15 was observed. In the following 2 weeks, *Synechococcus* exhibited a maximum concentration at 15 m depth which was further replaced by a phytoplankton maximum at the surface in early August. The rapid decrease in nitrate concentration at both depths observed on August 5 was mainly due to phytoplankton uptake. The presence of more cells at 15 m than at the surface during the summer months can be attributed to light inhibition rather than to any other factor. When TSS was low and SDD high, higher *Synechococcus* abundances were observed at 15 m, implying that the increasing light penetration helped subsurface cells to develop. In such coastal regimes, strong vertical mixing, rapid freshwater intrusion and light inhibition control much of the *Synechococcus* abundance. As we did not carry out any specific study on grazers, it would be speculation to talk about the impact of grazers on *Synechococcus*. From September to mid-October, a gradual decrease in cell abundance was observed. Although a slight increase in cell numbers occurred in late November, abundances remained below the annual average value during winter, the period of complete mixing of the water column.

Usually, open ocean waters (oligotrophic) exhibit lower *Synechococcus* abundances than eutrophic coastal waters. *Synechococcus* abundances were reported in the range 1.7–13×10^3 cells·ml^{-1} (Agawin & Agusti 1997) in the stratified north-west Mediterranean, and in the range 1.7×10^3–8×10^3 cells·ml^{-1} (Glover *et al.* 1988a,b) in the Sargasso Sea. Counts from the eutrophic, mesotrophic and oligotrophic regions of the north-eastern Atlantic Ocean yielded 2.2×10^5, 1.7×10^5 and 1.3×10^5 cells·ml^{-1}, respectively (Lantoine & Neveux 1997). In the north-west Mediterranean (Bay of Blanes), *Synechococcus* abundances increased from winter levels of 5×10^2 to 7×10^4 cells·ml^{-1} towards summer (Agawin *et al.* 1998). In the western Pacific Coast, Chang *et al.* (1996) reported abundances in the range 2×10^3–1.1×10^5 cells·ml^{-1}. In the Black Sea eutrophic waters, *Synechococcus* concentrations was found in the range 9×10^2–1.45×10^5 cells·ml^{-1} at the surface, 2×10^3–1.23×10^5 cells·ml^{-1} at the chlorophyll maximum subsurface layer and 1.3×10^2–3.5×10^2 cells·ml^{-1} at the nitrite maximum layer (Uysal 2000, 2001). The decreasing trend in abundance from eutrophic to oligotrophic sites was also observed by other authors (Davis *et al.* 1985; Partensky *et al.* 1996; Lantoine & Neveux 1997). *Synechococcus* concentrations may range from a few thousand cells per milliliter in oligotrophic systems such as the Sargasso Sea to almost 1×10^6 cells·ml^{-1} in nutrient-rich coastal waters (Gallager *et al.* 1994). The highest abundances of *Synechococcus* were always found in the mixed layer (Gieskes & Kraay 1986; Karrasch *et al.* 1996). Maximum abundances were frequently observed at the surface (Murphy & Haugen 1985; Landry *et al.* 1996) and near the deep chlorophyll maximum, particularly in oligotrophic waters (Iturriaga & Marra 1988). Average cell counts determined in the present

study are similar to abundances observed in other coastal regimes and appear larger than the values in open waters.

Generally, both heterotrophic bacteria and *Synechococcus* are more abundant in summer than in winter (Li 1998). Factors other than temperature, such as nutrient supply, may be important in warmer waters (annual average temperature higher than 14 °C) (Li 1998). However, abundance and distribution of picoplankton, especially *Synechococcus*, are relatively stable and conservative, while other populations, such as diatoms, respond more dramatically to environment forcing (Landry *et al.* 1996). No significant correlation was found between *Synechococcus* abundance and salinity, although strong responses of *Synechococcus* even to small-scale fluctuations in salinity were observed. As the sampling station is located nearby the Lamas River, freshwater input to the sampling site governs most of the biological, chemical and physical processes. In addition to phytoplankton blooms, TSS carried by the Lamas River throughout the sampling period also reduced the efficient utilization of available nutrients and light by *Synechococcus*.

Synechococcus distribution throughout the water column is generally controlled by three main factors, namely temperature, nitrate availability and light conditions (Lantoine & Neveux 1997). But the factors that regulate long-term (and broad-scale) variations of *Synechococcus* abundance (*e.g.* nutrients, light and temperature) are different from those that result in short-term (and small-scale) variations (*e.g.* grazing and advection) (Binder *et al.* 1996). Relationships with other planktonic groups on a time basis and in different water bodies are also important in understanding the dynamics of *Synechococcus*. For example, there is a seasonal shift between diatoms (*Chaetoceros*, *Thalassiosira*, *Nitzschia*) in winter and smaller autotrophs in summer (Agawin *et al.* 1998). It was also observed that *Synechococcus* is depressed when large buoyant diatoms are present in the system.

As *Synechococcus* frequently forms transient blooms lasting up to a week under favorable conditions (Glover *et al.* 1988a,b; Iturriaga & Marra 1988), the short timescale survey achieved in this study appears relevant to document the dynamics of this picoplanktonic group. As reported by Li (1998), *Synechococcus* was found more abundant during summer and early autumn indicating a strong response to increasing water temperature in the long term. As a response to nutrient pulses, transient increases in abundance were also revealed from time to time in the region. The observed fluctuations in abundances were due to multiple factors that are characteristic of the shallow coastal waters, with rapidly changing environmental conditions, including in this specific case river input.

Acknowledgements

This work was part of a time series sampling program carried out in the northern Levantine Basin in connection with the projects supported primarily by the Turkish Scientific and Technical Research Council (TUBITAK – YDABCAG 615/G) and partially by UNESCO-IOC (SC.214.124.9). We thank the academic and technical staff and the crew of R/V Erdemli of the Institute of Marine Sciences of Middle East Technical University for their help in various ways.

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