Mediterranean Marine Science

Vol 11, No 2 (2010)

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doi: 10.12681/mms.77

Mediterranean Marine Science
Indexed in WoS (Web of Science, ISI Thomson)
The journal is available on line at http://www.medit-mar-sc.net

Research Article

Synechococcus dynamics in the Levantine basin shelf waters (northeastern Mediterranean)

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Received: 01 April 2010; Accepted: 14 June 2010; Published on line: 8 October 2010

Abstract

The abundance of picoplanktonic marine cyanobacteria *Synechococcus* was measured at weekly intervals over a period of one year in the northern Levantine basin shelf waters. *Synechococcus* was found more abundant during summer and early autumn and least during winter. Significant increases in abundances mostly occurred during very low nutrient concentrations either a week or two weeks after the nutrient enrichments. Cells were distributed homogenously in the water column due to intense mixing observed during winter. Despite the homogenous cell distribution attained during late autumn and winter, the magnitude of variation in cell abundances among depths was found greatest during August and September. Cell concentrations ranged from a minimum of 6.4×10^3 to a maximum of 9.2×10^4 cells ml^{-1} with an annual mean level of 2.5×10^4 cells ml^{-1} at surface. Below the surface, it ranged from a minimum of 5.6×10^3 to a maximum of 8.0×10^4 cells ml^{-1} with an annual mean level of 2.1×10^4 cells ml^{-1} at 25 m depth. Compared to surface and 25 m depth, lowest levels were attained at 50 m. At this depth, cell counts ranged from a minimum of 5.4×10^3 to a maximum of 3.2×10^4 cells ml^{-1} with an annual mean level of 1.4×10^4 cells ml^{-1}. Based on Pearson-product moment correlation analysis, a highly significant correlation between *Synechococcus* abundance and ambient temperature was observed.

Keywords: Picoplankton; Abundance; Physicochemical properties; Shelf dynamics; Mediterranean; Levantine basin.

Introduction

The first members of the picoplankton to be discovered were phycoerythrin containing unicellular cyanobacteria *Synechococcus* (WATERBURY *et al.,* 1979). Since then, it has been known to be a major contributor to the total phytoplankton biomass and chlorophyll, (BERMAN, 1975; WATERBURY *et al.,* 1979; JOHNSON & SIEBURTH, 1979; LI *et al.,* 1983; PLATT *et al.,* 1983; TAKAHASHI & BIENFANG, 1983; GLOVER *et al.,* 1986; BOOTH, 1988; LI *et al.,* 1992) as well as to the pelagic food

web of the oceans (ITURRIAGA & MITCHELL, 1986; JOHNSON *et al.,* 1982). In oligotrophic oceans this specific 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). This group is important as a primary producer, especially in the open ocean where the community structure is shifted so that smaller cells (<20 μm) dominate (GLOVER *et al.,* 1986). Even in the highly eutrophic Arabian Sea, the highest concentrations of this group that were ever reported may exist (BIDIGARE *et al.,* 1997; SHERRY & UYSAL, 1995; SHERRY & WOOD, 2001). The ecological success of *Synechococcus* in oceanic regions has been partly attributed to the increased efficiency of light-harvesting and nutrient uptake conferred by their small size and their negligible sinking rate. Despite the high number of publications dealing with almost all aspects of this group, crucial information regarding its weekly time series responses to rapidly changing ambient biological, chemical and physical properties of shelf waters over an extended period is still lacking. The aim of this study is to provide background information on the least studied fraction of the phytoplankton in the highly dynamic shelf waters of the Levantine basin.

Materials and Methods

Study area

The sampling station is situated offshore of the Institute of Marine Sciences of the Middle East Technical University (IMS-METU), located on the north-eastern coast of the Mediterranean (Fig. 1). The station is located approximately 5 km (34˚18' E, 36˚32' N) from the land and has a total depth of approximately 100 m. Weekly cruises were held on board R/V *Erdemli* of the Institute throughout the year, 1998. Sampling was conducted consistently during the same period of the day between 10:30 and 11:30 a.m.

Sampling, analysis of samples

Using closing bottles, water samples

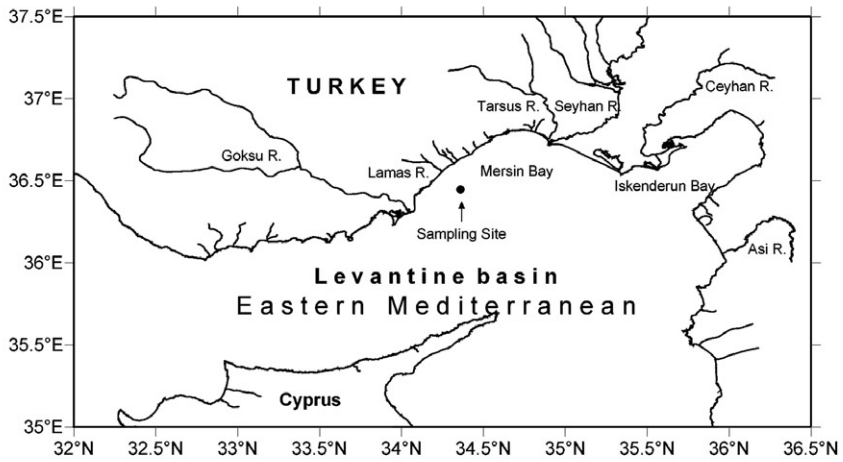

Fig. 1: Location of the sampling station in the Levantine Basin (north-eastern Mediterranean).

were collected from three different depths (surface, 25 m and 50 m depths within the euphotic zone), put into 100 ml dark-coloured polyethylene bottles and were then preserved with 4% buffered formalin (final concentration) on board. Depending on the amount required, 10 to 15 ml aliquots from each sample were filtered onto 25 mm diameter, black, polycarbonate, nuclepore membrane filters with a 0.2 μm pore-diameter (LI & WOOD, 1988; UYSAL 2000, 2001). The filters were then mounted on glass slides using immersion oil and counted using a Nikon epifluorescence microscope at 1000X with a filter combination of B-2A and G-1A. Since the main light harvesting pigment of *Synechococcus* is phycoerythrin, it fluoresces orange to red when excited with green light. A minimum of 20 microscope fields were chosen at random and counted on each slide for their cell contents. In search of a possible relationship between the *Synechococcus* abundance and the ambient biological, physical and chemical variables, the Pearson-product moment correlation analysis was applied.

Phytoplankton samples of 1 liter volume were collected into dark-colored glass bottles from surface, using closing bottles, and preserved in a final borax-buffered 4 % seawater-formalin solution for long term storage. Bottles were then kept standing in the laboratory over a period of 3-4 weeks for settling of phytoplankton. Supernatant water overlaying the settled particles was siphoned using fine tubes. The remnant (about 10-15 ml) was transferred to smaller tubes for further species identification and enumeration under proper microscopes (Nikon inverted microscope and Nikon Optiphot-2 light microscope). Both the Palmer-Maloney and Sedgewick-Rafter counting chambers were used during microscopic examinations. Each counting involved as far as possible at least 400 cells (VENRICK, 1978). Surface phytoplankters were composed primarily of diatoms, dinoflagellates, coccolithophorids, silicoflagellates and small flagellates with few species from cyanophyceae, euglenophyceae, chlorophyceae and cryptophyceae. It was attempted to identify cells at species level and related morphometric parameters (cell diameter, length and width) were also measured to calculate cell volumes (SENICHKINA, 1986; HILLEBRAND *et al.,* 1999). Volumes were then converted to biomass assuming one μm^3 equals to one pg.

Five litres of water were filtered through the GF/F filters (previously dried at 105 ± 5˚ C for three hours and pre-weighted) for their TSS (Total Suspended Sediment) contents. The filtrates were then kept at 105 ± 5˚ C overnight and weighed again and the difference was used in the calculations. One litre of seawater was filtered through GF/F filters and extracted into 90% acetone solution for the assessment of total chlorophyll content. The fluorescence intensity of clear extracts was then measured by the standard fluorometric method (HOLM-HANSEN *et al.,* 1978) using a Hitachi F-3000 model fluorometer.

Collection and analysis of physical and chemical parameters

Temperature, salinity and depth were measured using a Sea-Bird model CTD probe. This system contained sensors, batteries and tape recording units. The data recorded during the casts were later processed by the computers in the Institute laboratories. Nutrient samples from the bottle casts were stored in 50-100 ml capacity high density polyethylene bottles that were precleaned 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 by using a Technicon model two-channel auto-analyzer; the methods followed were very similar to those described in STRICKLAND & PARSONS (1972) and GRASSHOFF *et al.,* (1983). The detection limits achieved, using low concentration samples, were 0.02 µM and 0.05 µM for phosphate (PO^{3-}_{4}-P) and nitrate+nitrite (NO^{-}_{3}-N+NO^{-}_{2}-N), respectively.

Results

Temperature and salinity

Time profiles of temperature and salinity along depth during the year 1998 are given in Figure 2. Over the year, temperature varied in the range 16.5 - 29.6˚ C and salinity in the range 38.4 - 39.3. Surface water was coldest in March and warmest in August. Temperature and salinity was homogeneous from the surface to the bottom

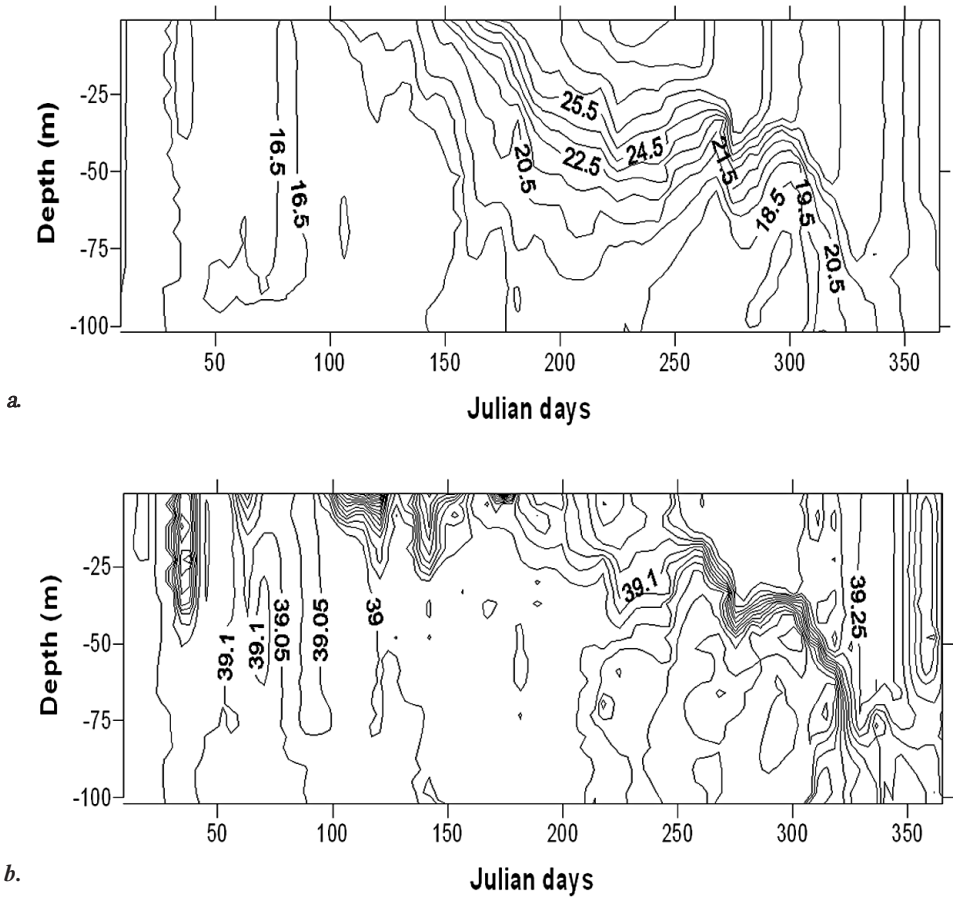

Fig. 2: Time profile of temperature (a) and salinity (b) *versus* depth.

due to winter convectional mixing. The water column mean temperatures for December, January and February were 21.5, 18.2 and 16.7° C, respectively. Water column mean salinity remained stable during winter as well (having 39.2 salinity during December and January, and 39.1 salinity during February). With the onset of spring, a gradual warming of the surface waters was observed. With increasing irradiance, the surface waters started to warm up and the temperature gradient became much wider with depth during summer. Surface temperature reached its maximum level of 29.6° C on 18 August. In September, a well- defined surface mixed layer was observed in the top 15 meters. Underneath the thermocline occurs, to a depth of approximately 30 m. The surface mixed layer became thicker with further cooling and convectional mixing during October, yielding a much thinner and a deeper thermocline below it. The water column remained thoroughly mixed from December till March.

Nutrients

Over the year, surface nitrate and phosphate concentrations varied in the range 0.02 – 2.85 and 0.02 – 0.3 μM with annual surface averages of 0.6 and 0.05 μM, respectively (Fig. 3). These average values slightly decreased at 25 m. Nitrate and phosphate

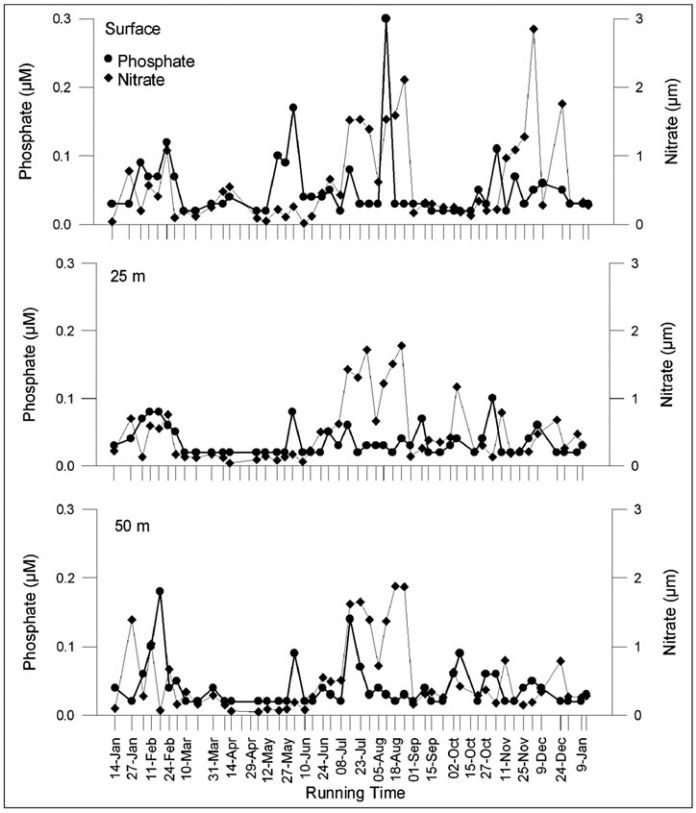

Fig. 3: Time series of phosphate (●) and nitrate (◆) levels at selected depths.

concentrations fluctuated between 0.04 – 1.78 and 0.02 – 0.1 μM with annual mean levels of 0.48 and 0.04 μM, respectively. Nutrient concentrations at 50 m almost mimic the levels observed at 25 m. At this depth, nutrient concentrations varied in the range 0.05 – 1.88 μM with an annual mean level of 0.51 μM for nitrate and in the range 0.02 – 0.18 μM with an annual mean level of 0.04 μM for phosphate. Winter mixing enhanced the nitrate and phosphate concentrations at all depths that were studied. Phosphate values were relatively low (near the detection limits) throughout the year except during mixing periods (late autumn, winter), river input (late spring) and during intrusion of Atlantic waters (from mid-July to the end of August) into the shelf area.

Phytoplankton biomass, total chlorophyll and total suspended sediment (TSS)

Total phytoplankton biomass ranged from 1.7 to 5607.5 μg l^{-1} with an annual average value of 224 μg l^{-1} at the surface (Fig. 4). Pronounced highs in biomass were observed mostly during winter and spring. Contribution of diatoms to total biomass was highest over the year in the shelf area. In addition to diatoms, dinoflagellates and coccolithophorids were the other important constituents of the phytoplankton assemblage.

Over the year surface chlorophyll concentration varied in the range 0.06 – 3.27 μg l^{-1} with an annual average value of 0.34 μg l^{-1} (Fig. 5). These average values tend to decrease with depth. Total chlorophyll con-

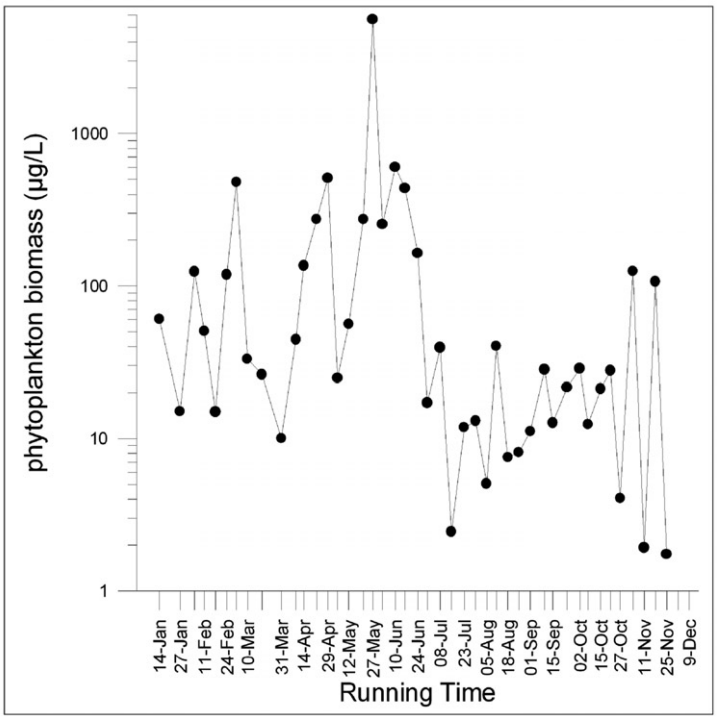

Fig. 4: Time series of phytoplankton biomass at surface.

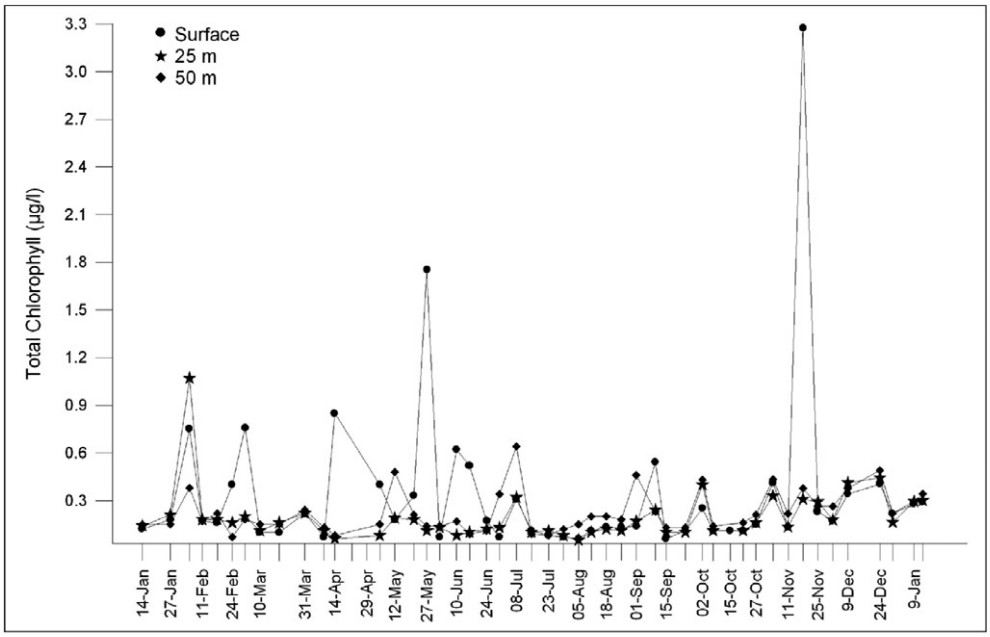

Fig. 5: Time series of total chlorophyll levels at selected depths.

centrations fluctuated between 0.05 – 1.07 µg l^{-1} and 0.07 – 0.64 µg l^{-1} with annual mean levels of 0.19 and 0.23 µg l^{-1}, at 25 and 50 m depths, respectively. Parallel to phytoplankton biomass, altered chlorophyll concentrations were observed during the winter and the spring at surface. Based on the Pearson-product moment correlation analysis, a highly significant correlation was obtained between phytoplankton biomass and total chlorophyll at surface ($n = 42$; $r = 0.517$; $p<0.01$).

The annual surface mean for the total suspended sediment (TSS) was 4.61 mg l^{-1} with minimum and maximum levels of 2.42 and 10.75 mg l^{-1} recorded on 18 February and 18 November, respectively (Fig. 6). TSS values made peaks during late spring and early summer in parallel to increased runoff from major rivers draining to the basin. The annual mean for 25 m depth was 4.25 mg l^{-1} with minimum and maximum levels of 1.48 and 9.36 mg l^{-1} recorded on 11 February and 10 June, respectively. Compared to surface and 25 m depth layers, fluctuations in weekly TSS amounts were more stable at the 50 m depth layer. The annual average TSS value was 3.86 mg l^{-1}, being lowest (2 mg l^{-1}) on 10 March and highest (10.5 mg l^{-1}) on 3 March.

Secchi disk depth (SDD)

The annual average SDD was 20 m, being lowest (3.2 m) both on 29 April and 18 November and highest (38.3 m) on 5 August (Fig. 7). SDD measurements increased significantly during July and early August as a result of invasion of the shelf waters by nutrient rich Atlantic deep waters. Low SDD values observed during spring and early summer coincided with high phytoplankton biomass levels obtained in the meantime.

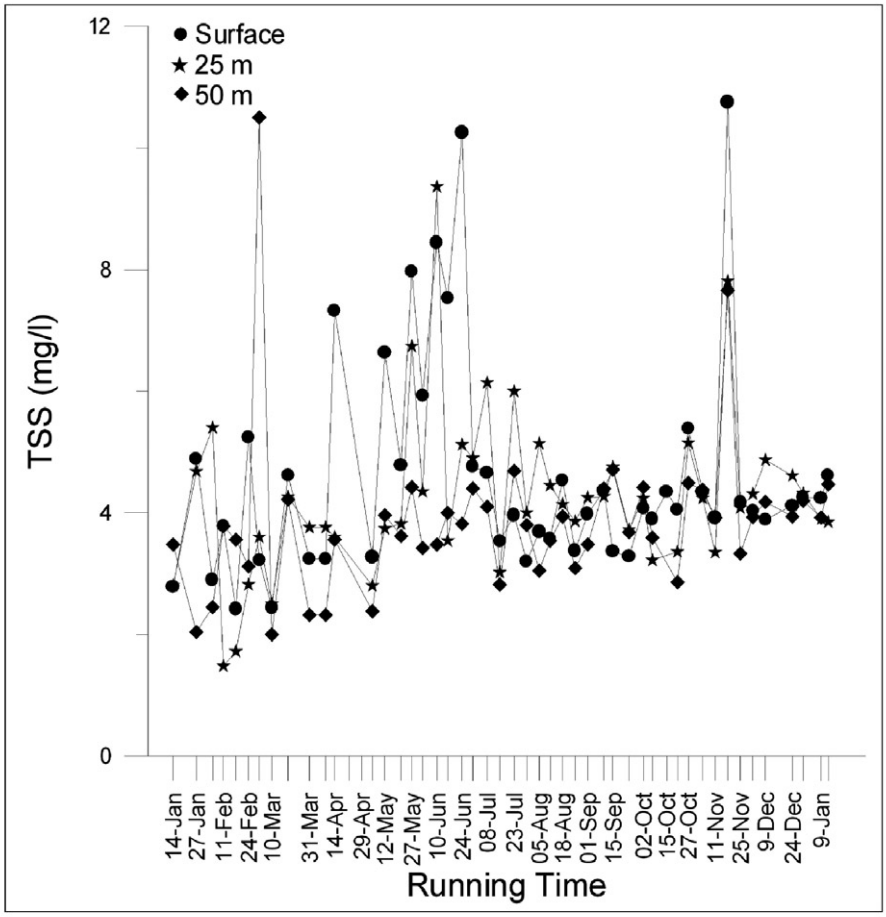

Fig. 6: Time series of total suspended sediment levels at selected depths.

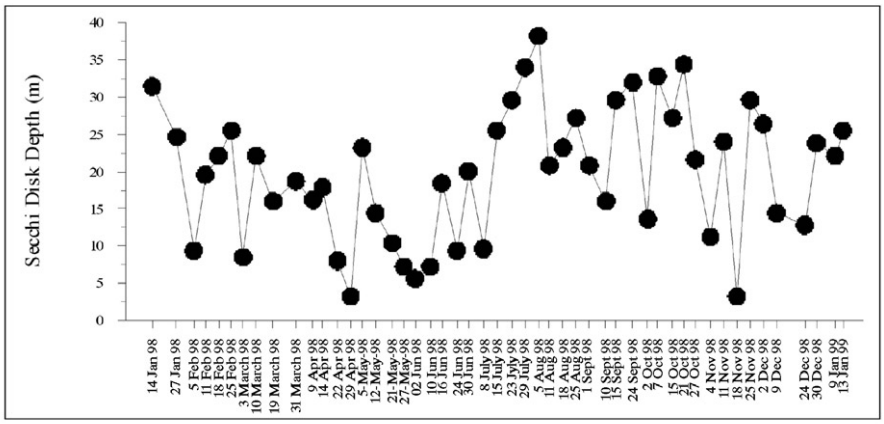

Fig. 7: Time series of Secchi disk depth at the sampling station.

Synechococcus abundance

Surface *Synechococcus* concentration ranged from a minimum of 6.4 x 10^3 to a maximum of 9.2 x 10^4 cells ml-1 with an annual mean level of 2.5 x 10^4 cells ml^{-1} at the shelf station (Fig. 8). Concentrations peaked on 29 April (7.7 x 10^4 cells ml^{-1}), 8 July (7.0 x 10^4 cells ml^{-1}), and 10 September (9.2 x 10^4 cells ml^{-1}). These peak levels were followed by rapid decreases in cell numbers shortly after. *Synechococcus* was found more abundant during warmer periods especially during late August and early September. During early winter, early spring and late autumn cell abundances remained below the annual mean except the high levels obtained on 25 November and on 2 December.

Below the surface, cell concentration ranged from a minimum of 5.6 x 10^3 to a maximum of 8.0 x 10^4 cells ml^{-1} with an annual mean level of 2.1 x 10^4 cells ml^{-1} at 25 m depth. Compared to the surface, fewer peaks were observed at 25 m. Two major increases in abundance were observed on 8 July (6.4 x 10^4 cells ml^{-1}), and on 10 September (8.0 x 10^4 cells ml^{-1}). Winter and late spring values stayed below the annual average. In general, except for the two major

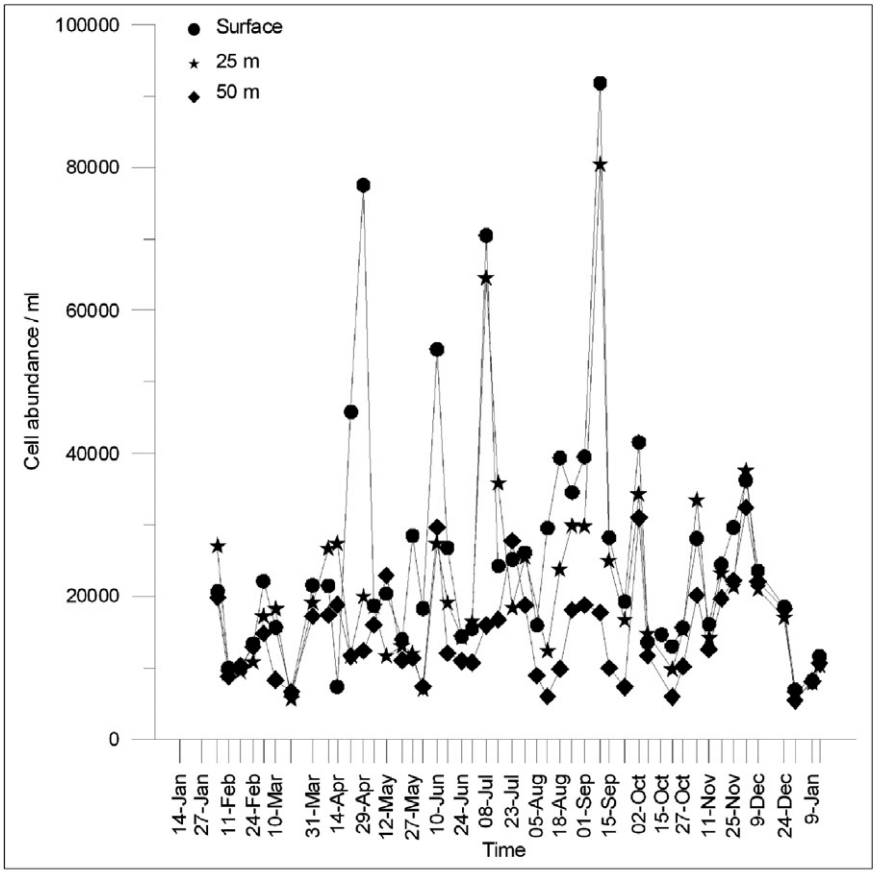

Fig. 8: Time series of *Synechococcus* abundance at selected depths.

peaks, cell abundances could be considered as stable throughout the year.

Compared to surface and 25 m, the lowest levels were attained at 50 m. At this depth, the cell concentration ranged from a minimum of 5.4 x 10^3 cells ml^{-1} to a maximum of 3.2 x 10^4 cells ml^{-1} with an annual mean level of 1.4 x 10^4 cells ml^{-1}. Maximal counts were observed on 10 June (3 x 10^4 cells ml^{-1}), 2 October (3.1 x 10^4 cells ml^{-1}) and 2 December (3.2 x 10^4 cells ml^{-1}). In fact, weekly plots of abundances do not reveal any significant increases at this depth. At almost all depths, weekly variations in abundance occurred exclusively in the form of single point peaks rather than cycles or rhythms. Abundances fluctuated around annual mean throughout the year with no seasonal pattern.

Discussion

Surface maxima in cell concentrations were observed in only 39 of 52 weeks studied. Cells were found most abundant at 25 m depth for 10 weeks and at 50 m depth, surprisingly, only for 3 weeks. Distinct subsurface maxima in cell concentrations were also observed at both open-ocean and coastal stations in the North Atlantic and Pacific Oceans (OLSON *et al.,* 1990) as well as in the equatorial Pacific (VAULOT & MARIE, 1999). The authors related the occasional near-surface minima to different grazing pressures among sites or to the nutrient supply history of the sites.

The time of sampling is highly important for comparison of abundances obtained in this study with those obtained elsewhere. Samples were collected consistently between 10:30- 11:30 a.m. of each sampling day throughout the year. *Synechococcus* abundances given in this study correspond to daily minima (UYSAL, 2001; SHERRY & WOOD, 2001). Fluorescence intensities of this group also show diel evolution with clear signs of midday depression (VAULOT & MARIE, 1999). It has been widely shown that Synechococcus exhibit a characteristic synchronous division cycle, with cell division generally occurring near dusk (VAULOT *et al.,* 1996; JACQUET *et al.,* 1998, 2001; SWEENEY & BORGESE 1989; JOHNSON *et al.,* 1996). Consequently, it has been shown by other authors that numbers of *Synechococcus* can vary dramatically over the course of just a few hours or days (VAULOT *et al.,* 1996; JACQUET *et al.,* 1998, 2001; VAULOT & MARIE , 1999). Similar diel variations in abundance were also observed in the equatorial Pacific (DURAND & OLSON, 1996) and in the Sargasso Sea (OLSON *et al.,* 1990) where the maximum was found near dusk. From the field and on-board microcosm experiments conducted in the Black Sea (UYSAL, 2001) and field data obtained from the Arabian Sea (SHERRY & UYSAL, 1995; SHERRY & WOOD, 2001) it was found out that *Synechococcus* abundance decreases from midnight towards noon due to grazing and further begins to rebuild in the afternoon by dividing throughout the evening. In other words, cell division dominates during the latter half of the day, even if grazing continues throughout the day. Studies in the Arabian Sea have also shown that the diurnal change is greater than the differences between physically and spatially discrete water masses. In addition, *Synechococcus* spp have been shown to exhibit varying degrees of diurnal periodicity in cell division rates both in culture (CAMPBELL & CARPENTER, 1986) and in incubation experiments (CARPENTER & CAMPBELL, 1988; KUDOH *et al.,* 1990).

At all depths the abundance data showed a consistent pattern in which remarkable

weekly increases in cell abundance were essentially balanced by equally remarkable decreases in cell numbers throughout the year. It is possible that this variation may in fact be due to sporadic short term shifts and changes in other associated parameters (temperature, light, grazing, substrate supply, viral infection etc.,). The impact of viral infection and grazing was not measured in this study. Viral control of the phytoplankton especially of picoplankton has been well documented in the literature (SUTTLE & CHAN 1994; JACQUET *et al.,* 2002; MÜHLING *et al.,* 2005). However, sporadic changes in weekly evolution of nutrient salts, phytoplankton biomass, chlorophyll, total suspended sediment and secchi depth were observed in the area. Synechococcus was found most abundant during mid-spring, mid-summer and early autumn. Abundances remained below the annual mean level during the winter and mid-autumn. During late autumn and winter all depths showed almost similar trends in cell abundance with less variation in the cell contents. However, the magnitude of variation in cell abundances among depths was found greatest during August and September with the establishment of the thermocline at near surface.

During winter, *Synechococcus* was greatly affected by the natural forces that shape the water column structure. Cells were distributed homogenously in the water column due to strong mixing observed during winter (Fig. 2). This further enhanced the nitrate and phosphate concentrations at all depths that were studied. During winter, impact of the nearby Lamas River was negligible. Initially, cell concentration was found high in early December (water column mean is about 3.5×10^4 cells ml^{-1}) and this continued to decrease steadily towards January. Monthly average cell concentration for the water column was at its lowest level of 9.4 $\times 10^3$ cells ml^{-1} in January. In the following days an appreciable increase in cell concentration was seen on 5 February (water column mean was 2.2×10^4 cells ml^{-1}). In parallel to *Synechococcus* abundance, phytoplankton biomass (Fig. 4) was also found high on 5 February [of the total phytoplankton biomass of 124 mg m^{-3}, 113 mg m^{-3} was composed primarily of diatoms, (UYSAL *et al.,* 2003)]. Concomitant increase in phytoplankton and *Synechococcus* abundance eventually dropped the secchi depth to a lower value of 9.3 m. Higher phosphate and lower nitrate concentrations observed on 5 February indicate the preferential utilization of nitrate by existing flora at the site (Fig. 3). In terms of nutrient acquisition, *Synechococcus* are 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). In this study, phosphorus has been utilized extensively at surface by *Synechococcus* and to lesser extent by phytoplankton during the late summer - early autumn period. Phosphorus stress on this group during the summer months was demonstrated from the Red Sea (FULLER *et al.,* 2005).

With the onset of spring, a gradual warming of surface waters was observed. In this season the impact of the local Lamas River was more pronounced, especially during April. Local river runoffs reached the station in mid-April, and as a consequence, the surface nitrate values increased from 0.2 to 0.6 μM. Following this, the concentrations

again dropped and stayed at low levels until 24 June. Phosphate values were relatively low (near the detection limits) throughout the year except during mixing periods (late autumn, winter), river input (late spring) and during intrusion of the Atlantic waters (from mid-July to the end of August). Except in late April, the cell concentrations remained relatively higher in March and May, compared to the winter. The water column mean cell concentration for March, April and May were 1.4 x 10^4 cells ml^{-1}, 2.5 x 10^4 cells ml_{-1} and 1.6 x 10^4 cells ml^{-1} respectively. In April, a marked invasion of the surface waters by Lamas River water was observed. Consequently, an extraordinary increase in surface *Synechococcus* concentration from 7.3 x 10^3 cells ml^{-1} on 14 April to 4.6 x 10^4 cells ml^{-1} on 22 April and to 7.7 x 10^4 cells ml-1 on 29 April was observed. This was not true for the 25 m and 50 m depths. Surface phytoplankton biomass was also found very high at the same time (273 and 508 mg m^{-3} on 22 and 29 April, respectively). This indicated the ready response of the flora to sudden nutrient pulses.

During summer, with increasing irradiance, the surface waters started to warm up and the temperature gradient became much wider with depth. Surface temperature reached its maximum level of 29.6° C on 18 August. Less than 39 salinity waters occupied the top few meters of sea surface in June due to local Lamas River input. On 2 June, an increase in phosphate and nitrate concentrations was observed. In the following week, on 10 June, a threefold (from 1.8 x 10^4 cells ml^{-1} to 5.4 x 10^4 cells ml^{-1}) increase in surface cell concentration was observed. This increase was fourfold at 25 m and 50 m depths. Starting from 10 June, a steady increase in both phosphate and nitrate concentrations towards 30 June was observed. Despite this increase in nutrient levels, no significant increase in cell concentrations at any depth was observed until 8 July. Enormous increases in cell abundances at the surface (7 x 10^4 cells ml^{-1}) and at 25 m (6.4 x 10^4 cells ml^{-1}) were observed on 8 July. This sudden outburst of cell numbers resulted in a decrease in phosphate levels in particular in the water column. Extremely high nitrate levels (up to 2 μM) observed in the whole water column between 15 July and 25 August in shelf waters was considered a unique event for the region. In general, the basin waters are regarded as nutrient poor and the average nitrate concentration for the surface waters is around 0.2 μM. During this period 38.9 salinity waters occupied the entire shelf, indicating an intense advection of nutrient-rich Atlantic deep waters towards the shelf. It was so intense that the signs of this were also detected in the coastal, much shallower (20 m) shelf areas (UYSAL & KOKSALAN, 2006). Indeed, this relatively lower salinity water in the Levantine basin may hold elevated nitrate levels up to 4 - 6 μM (YILMAZ & TUGRUL, 1998). This nutrient-rich water remained in the basin more than a month leading to a 'high nutrient, low chlorophyll' case. This was also evident from lower total phytoplankton biomass (Fig. 4), chlorophyll (Fig. 5) and TSS (Fig. 6), as well as inversely from the very high secchi depth readings (Fig. 7) observed during this period. As these water masses were advected from deep below the euphotic zone, they initially do not contain any live photosynthetic cells at all. Therefore, it takes a relatively longer time for both the picoplankton and net-phytoplankton to redevelop shortly after and to further flourish in such water masses. In the case *of Synechococcus,* due to their large surface-to-volume ratio, it takes a relatively short time to adapt to such disadvantages compared to larger cells. With

the intrusion of nutrient-rich deep Atlantic waters an apparent decline in cell numbers from 15 July to 5 August was observed (initial *Synechococcus* population being diluted in time). A sharp decrease in nitrate concentration at all depths was observed from 29 July to 5 August. Despite this decrease in nitrate concentration, neither the *Synechococcus* nor the phytoplankton biomass was observed to have increased. After 5 August, with increasing nitrate concentrations, a fast growth in the *Synechococcus* population at all depths was achieved until early September. The water column mean cell concentrations for June, July and August were 1.9×10^4 cells ml^{-1}, 3.1×10^4 cells ml^{-1} and 2.1×10^4 cells ml^{-1} respectively. These counts remained above the spring values.

During late spring and summer, cells in the top 25 m started to yield low fluorescence under the microscope due to increases in the intensity of irradiance. Fluorescence yield of the cells on 8 July was much better compared to the previous week and those after , parallel to the low secchi depth reading (about 10 m). Reduced illumination, in general, provided an optimal environment for surface and subsurface cells to grow. In a study conducted in the North Atlantic and Pacific Oceans, phycoerythrin fluorescence intensity per cell was found to be increasing dramatically with depth in the lower euphotic zone at all stations, and at some open-ocean stations, deep cells that are as much as 100 times brighter than those at the surface were recorded (OLSON *et al.,* 1990). It was shown that at low irradiance levels cells adapt themselves by increasing their phycoerythrin and chlorophyll-*a* content in order to harvest available light efficiently. Such cells yield a relatively long lasting, bright orange fluorescence under the microscope. This favourable condition was interrupted by a sudden 2.5 fold increase in secchi depth in the following week. These fast growing cells could adapt their phycoerythrin contents rapidly in their natural environments by decreasing their phycoerythrin and chl-*a* contents in high light intensities (IKEYA *et al.,* 1994; KANA & GLIBERT, 1987; GLOVER *et al.,* 1988; GIESKES & KRAAY, 1986). During mid-August, the fluorescence yields of the cells had somewhat recovered against high secchi depth readings.

In fact, it is difficult to suggest a one-to-one correspondence between *Synechococcus* abundances and other environmental variables. We know that *Synechococcus* make transient blooms when the nitrate concentration increases suddenly. This is due to the quick response mechanism of *Synechococcus,* having greater surface-to-volume ratio, over other organisms (LANDRY *et al.,* 1995). However, our major peaks of abundance did not coincide with nutrient maxima. Significant increases in abundance mostly occurred during very low nutrient concentrations either a week or two weeks after the nutrient enrichments. Overall, phytoplankton response to nutrient pulses was found to be much quicker and more intense than the *Synechococcus* at the site. There were times when *Synechococcus* and phytoplankters grew parallel to each other. In some cases there was a sudden decrease in phytoplankton biomass followed by a rapid increase in *Synechococcus* abundance. It may be possible that at diminished nutrient levels *Synechococcus* may be more favourable compared to other phytoplankton. Moreover, excess nutrient did not always yield higher biomass as observed during summer. Besides *Synechococcus,* other small phytoplankters (e.g. the coccolithophorid *Emiliania huxleyi*) also responded to these low nutrient levels simultaneously, which brought up the phenomenon of smaller species succeeding over the bigger ones in time.

During 1998 the basin waters underwent a period of extreme cold in winter and extreme heat in summer. A considerable delay in the formation of the thermocline was observed during this year. In September a well defined surface mixed layer was observed at the top 15 meters. Underneath the thermocline occurred to a depth of approximately 30 m. In October, the surface mixed layer (SML) deepened to as much as 30 m due to continuing mixing and cooling processes. Below 30 m, a sharp decline in both the salinity and temperature was observed. In November, the SML covered almost the top 50 m, and a gradual decrease in both temperature and salinity below it was observed. Changes in the physical structure of the water column influenced both the biology and chemistry of the ambient waters as well. Except October, the cell concentrations remained very high in September and November. The water column mean cell concentration for September, October and November were 3.2×10^4 cells ml^{-1}, 1.8×10^4 cells ml^{-1} and 2.2×10^4 cells ml^{-1} respectively. On 10 September *Synechococcus* marked its peak levels at the surface (9.2×10^4 cells ml^{-1}) and at 25 m depth (8.0×10^4 cells ml^{-1}).

Based on the Pearson-product moment correlation analysis, a highly significant correlation was obtained between *Synechococcus* abundance and water temperature ($n = 114$; $r = 0.382$; $p<0.01$). With increasing temperature, an increase in cell concentration was observed. *Synechococcus* was found most abundant during warmer periods especially during late August and early September and least during early winter, early spring and late autumn. In surface waters of diverse marine habitats, the annual average abundances of both heterotrophic bacteria and *Synechococcus* were found to be directly related to annual average temperature below 14˚ C (LI, 1998). However the surface temperature in the site ranged between 16.5 – 29.6˚ C throughout the year, being coldest in March and warmest in August. Weekly observations carried out in the Bedford basin indicated that the time scale at which *Synechococcus* responded to temperature, light, grazing, substrate supply, and viral infection was in the order of days or less (LI, 1998). Although *Synechococcus* was found most abundant at high temperatures, they were not least abundant at low temperatures. For this reason, the author stated that the role of temperature in setting the net seasonal abundance of *Synechococcus* is less clear than it is for bacteria. *Synechococcus* abundance peaked in September both in the Levantine and in the Bedford Basins. The peak observed in timely development in *Synechococcus* population size had no direct relationship to changes in nutrient concentrations, as well as in salinity in time. However, a strong response of the *Synechococcus* to narrow range (15 - 20 salinity) changes in salinity has been reported from Florida Bay (PHLIPS & BADYLAK, 1996) and from the Black Sea (UYSAL, 2000, 2001). Results obtained in this study contrast with those suggesting that *Synechococcus* are more tolerant of mixed water conditions (LINDELL & POST, 1995) and lower temperatures.

Conclusion

Timely response of *Synechococcus* to rapidly changing physical, chemical and biological conditions, at weekly intervals, is reported for the least studied shelf waters of the Levantine basin. *Synechococcus* was found more abundant during summer and early autumn and least during winter. Maximal abundances mostly coincided with very low nutrient concentrations either a week

or two weeks after the nutrient enrichments. Overall, phytoplankton response to nutrient pulses was found to be much quicker and more intense than the *Synechococcus* at the site. Abundance distribution exhibited a consistent pattern in which remarkable weekly increases in cell abundance were essentially balanced by equally remarkable decreases in cell numbers at all depths. Homogenous distribution of the *Synechococcus* population was observed during winter due to the intense mixing observed during this period. Despite the homogenous cell distribution attained during late autumn and winter, the magnitude of variation in cell abundances among depths was found greatest during August and September with the establishment of the thermocline at the near surface. Fluorescence yield of surface cells under an epifluorescent microscope was higher during winter compared to summer. Among all the physical, chemical and biological parameters collected throughout this study, a highly significant correlation was observed only between *Synechococcus* abundance and the ambient temperature.

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). Sincere thanks go to Paul Fucile (WHOI - MA, U.S.A.) for his kind help in editing the manuscript. We also would like to thank the academic and technical staff and the crew of R/V *Erdemli* of the Institute of Marine Sciences of the Middle East Technical University for their assistance and help.

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