

## ORIGINAL RESEARCH ARTICLE

# Size-fractionated primary production in the south-eastern Black Sea

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## KEYWORDS

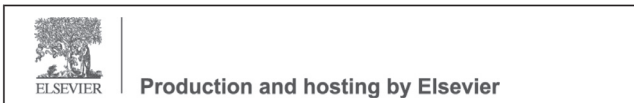
C-14;  
Phytoplankton;  
Primary production;  
Size-fractionated;  
South-Eastern Black  
Sea

**Abstract** Size-fractionated primary production (PP) and chlorophyll-*a* (Chl-*a*) with phytoplankton abundance and nutrients were investigated in the south-eastern Black Sea from November 2014 to August 2015. A <sup>14</sup>C radio-tracing technique was used to estimate phytoplankton primary production. C-14 experiments revealed that total PP ranged from 295 mgC m<sup>-2</sup> d<sup>-1</sup> to 5931 mgC m<sup>-2</sup> d<sup>-1</sup> along the study area. Size-fractionated PP varied from 84 to 1848 mgC m<sup>-2</sup> d<sup>-1</sup>, from 96 to 3156 mgC m<sup>-2</sup> d<sup>-1</sup> and from 56 to 3363 mgC m<sup>-2</sup> d<sup>-1</sup> for pico-, nano- and microphytoplankton, respectively. Overall, winter (4163 mgC m<sup>-2</sup> d<sup>-1</sup>) and spring (5931 mgC m<sup>-2</sup> d<sup>-1</sup>) were the most productive seasons, which coincided with high phytoplankton abundance. Contributions of microphytoplankton and nanophytoplankton were prominent in spring with maximum PP values. Winter was the second productive season with high contributions of nano- and microphytoplankton PP. Summer and autumn were less productive seasons, which were characterised by a high contribution of pico- and nanophytoplankton PP. Dinoflagellates were represented with the highest species richness (68 species, 53.54%) and diatoms were the second group along the area. Diatoms and other phytoplankton species (mainly *Emiliania huxleyi*) were the most abundant groups in terms of quantitative contribution. The results show that microphytoplankton along the study area are responsible for the majority of PP. However, the measured high Chl-*a* against low size-fractionated PP clearly indicates that smaller groups (i.e., pico- and nanophytoplankton) were dominant during these periods. Hence, the quantification of size-fractionated PP rates together with ecological indicators will allow for a more comprehensive assessment of the Black Sea ecosystem.

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## 1. Introduction

Phytoplankton community composition and size classes (i.e., pico-, nano- and micro-phytoplankton) affect biogeochemical processes, carbon fixation and transferring of organic matter to upper trophic levels via photosynthesis mechanism (Guidi et al., 2010; Kiørboe, 1993; Margalef, 1965; Uitz et al., 2010). This mechanism builds the base of the marine food web, and regulates trophic interactions, nutrient dynamics, and energy transfer to upper trophic levels (Paerl et al., 2003; Platt and Sathyendranath, 2008). Since phytoplankton physiologically quickly respond to environmental changes, this makes them sensitive indicators of environmental degradation in the aquatic ecosystems (Hays et al., 2005; McQuatters-Gollop et al., 2007).

Photosynthetic capacity, trophic role and physiology of the phytoplankton are closely related to their size structure (Song et al., 2019). Size structure of phytoplankton influences food web efficiency and carbon export in the pelagic ecosystem (Tilstone et al., 2017). For example, microphytoplankton (>20  $\mu\text{m}$  in size) are responsible for new production and contribute significantly (nearly 20% of annual primary production) to carbon fixation (Eppley and Peterson, 1979; Goldman, 1993; Michaels and Silver, 1988; Nelson et al., 1995; Tilstone et al., 2017). Nanophytoplankton (2–20  $\mu\text{m}$  in size) are responsible for most of the primary production (PP) in many shelf seas (Joint et al., 1986). Picophytoplankton are dominant in the low Chl-*a* areas of oligotrophic subtropical and tropical seas (Aiken et al., 2009; Veldhuis et al., 2005), and their contributions to annual PP are generally low when compared with other size groups (Curran et al., 2018). Moreover, phytoplankton size classes can be associated with different biogeochemical regions and trophic status for a given area. Oligotrophic waters are generally dominated by picophytoplankton with low Chl-*a* and PP rates (Curran et al., 2018; Platt et al., 1983; Viviani et al., 2011). Differently, nanophytoplankton have moderate Chl-*a* and PP rates in the mesotrophic regions. By contrast, the microphytoplankton inhabit eutrophic areas (i.e., nutrient replete waters) with high Chl-*a* and PP capacity (Cho and Azam, 1988; Eppley and Peterson, 1979; Falkowski et al., 1998, Tilstone et al., 2017). Moreover, microphytoplankton plays a major role in global carbon cycle (Tilstone et al., 2017). Hence, measuring of size-fractionated primary production and monitoring of changes in phytoplankton size structure have vital role in understanding biogeochemical carbon cycle, biological pump, ecosystem management strategies and sustainable ecosystem policies (Aumont et al., 2003; Le Quéré et al., 2005; Tilstone et al., 2017; Uitz et al., 2010).

The Black Sea is a biologically productive and the largest anoxic marine environment (Yilmaz et al., 2006; Yunev et al., 2002). However, due to ecological deteriorations, shifts in the ratio of major phytoplankton groups, qualitative and quantitative changes in community structure, phenological changes in bloom pattern and decline in PP rates have been observed over the decades (Agirbas et al., 2014; Bat et al., 2011; Feyzioglu and Seyhan, 2007; Kideys, 1994, 2002; Kopelevich et al., 2002). The Black Sea is characterized with two phytoplankton

blooms throughout the year. The major bloom (mainly diatoms) occurs in early spring, while a secondary bloom of coccolithophores appears in autumn (Sorokin, 1983; Vedernikov and Demidov, 1997). However, additional summer blooms of dinoflagellates and coccolithophores have frequently been reported from the Black Sea (Hay et al., 1990; Sur et al., 1996; Yayla et al., 2001; Yilmaz et al., 1998).

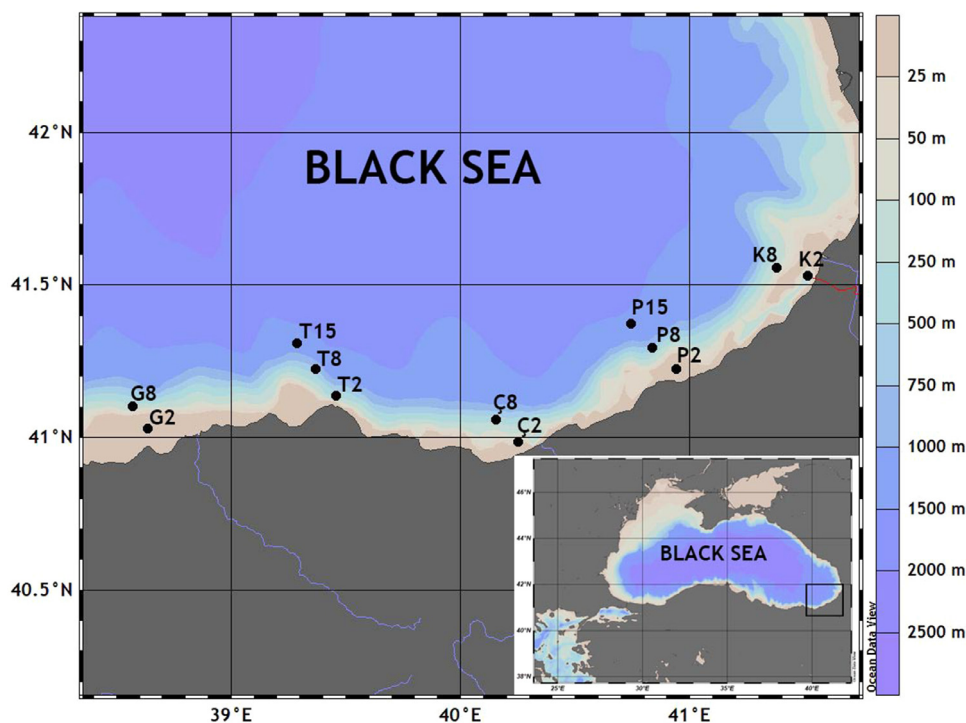
Production rates were generally high in the north-western Black Sea, they ranged from 570 to 1200  $\text{mgC m}^{-2} \text{d}^{-1}$ , whereas values varied from 320 to 500  $\text{mgC m}^{-2} \text{d}^{-1}$  in the regions of continental slope, 100 to 370  $\text{mgC m}^{-2} \text{d}^{-1}$  in the central deep-sea regions during 1960–1991 (Bologa et al., 1986; Demidov, 2008; Vedernikov and Demidov, 1997). On the contrary, PP rates along the southern Black Sea were reported as 247–1925  $\text{mgC m}^{-2} \text{d}^{-1}$  for spring, and 405–687  $\text{mgC m}^{-2} \text{d}^{-1}$  for summer-autumn period during 1995–1996 (Yilmaz et al., 2006). Recently, monthly production rates for the south-eastern coasts of the Black Sea were reported as 285–565  $\text{mgC m}^{-2} \text{d}^{-1}$  for coastal stations, and as 126–530  $\text{mgC m}^{-2} \text{d}^{-1}$  for offshore stations (Agirbas et al., 2014). Majority of studies have focused on the simultaneous analysis of size-fractionated PP in the oceans (Cermeño et al., 2005; Han and Furuya, 2000; Jochem and Zeitzschel, 1989; Tamigneaux et al., 1999), however, no studies that include size-fractionated PP rates were reported from the Black Sea, and therefore, it is essential to understand which size classes of phytoplankton are seasonally active and make a major contribution to primary production.

In this study, we consider the spatial and temporal variations in seasonal size-fractionated PP and Chl-*a* with phytoplankton abundance and nutrient data in the south-eastern Black Sea during the 2014–2015 sampling period. The present study also provides the first measurement of size-fractionated PP rates for the study area, and specifically focuses on determining the contribution of phytoplankton size classes to total PP rates in the study area throughout a seasonal cycle.

## 2. Material and methods

### 2.1. Study area and sampling regime

Samplings were performed seasonally at the 12 stations from November 2014 to August 2015 along the south-eastern Black Sea (Figure 1). The station coordinates and sampling details are given in Supplementary Material Table 1. Seawater samples were obtained from the particular depths (surface, 10 m, 20 m, 30 m and 40 m) by using a SBE 32 Carousel rosette sampler. A SBE 25 plus CTD probe was deployed (from surface to 100 m) to reveal the vertical profile of temperature, salinity and Chl-*a* during samplings. Similarly, photosynthetically active radiation (PAR) was measured seasonally by using a Li-Cor (LI-193 SA) sensor mounted to CTD (conductivity, temperature, depth) probe. The 1% light penetration depth was also calculated from PAR values in order to determine the base of euphotic zone along the study area. Variations of the parameters measured for the study area are summarized in Table 1.



**Figure 1** Map of study area and station locations (K2: Kemalpaşa 2 nm, K8: Kemalpaşa 8 nm, P2: Pazar 2 nm, P8: Pazar 8 nm, P15: Pazar 15 nm, Ç2: Camburnu 2 nm, Ç8: Camburnu 8 nm, T2: Trabzon 2 nm, T8: Trabzon 8 nm, T15: Trabzon 15 nm, G2: Giresun 2 nm, G8: Giresun 8 nm).

**Table 1** Seasonal ranges of the parameters (mean, minimum and maximum values) obtained for the study area.

Parameters	Autumn	Winter	Spring	Summer	Overall
Temperature (°C)	12.27 (8.35-18.20)	8.67 (8.123-10.52)	10.37 (8.14-19.79)	13.06 (8.379-28.41)	11.08 (8.12-28.41)
Salinity (‰)	18.38 (17.43-19.98)	18.23 (17.354-18.88)	18.30 (16.13-19.54)	18.39 (17.63-19.71)	18.33 (16.13-19.98)
Chl- <i>a</i> (µg l <sup>-1</sup> )	1.25 (0.35-4.57)	1.60 (0.27-4.96)	0.68 (0.21-2.50)	0.60 (0.161-2.75)	1.03 (0.16-4.96)
Euphotic zone (m)	22.33 (19-26)	28.67 (18-36)	29.83 (23-45)	35.25 (31-40)	29.02 (18-45)
NO <sub>2+3</sub> -N (µM)	0.59 (0.001-2.12)	0.60 (0.014-1.55)	0.0449 (0.001-0.61)	0.23 (0.001-0.88)	0.37 (0.001-2.12)
PO <sub>4</sub> -P (µM)	0.060 (0.001-0.28)	0.059 (0.001-0.11)	0.030 (0.001-0.14)	0.029 (0.001-0.14)	0.04 (0.001-0.28)
SiO <sub>2</sub> -Si (µM)	4.24 (1.58-13.63)	2.04 (0.01-6.30)	1.94 (0.60-4.75)	1.55 (0.28-5.19)	2.444 (0.01-13.63)
Pico_PP (mgC m <sup>-2</sup> d <sup>-1</sup> )	347.67 (84-582)	433.50 (120-1143)	817.50 (275-1848)	486.33 (119-1335)	521.25 (84-1848)
Nano_PP (mgC m <sup>-2</sup> d <sup>-1</sup> )	409.25 (188-637)	947.42 (97-2095)	1318.17 (263-3156)	414.08 (96-1168)	772.23 (96-3156)
Micro_PP (mgC m <sup>-2</sup> d <sup>-1</sup> )	217.92 (86-529)	702.83 (56-1710)	1301.33 (169-3363)	444.42 (73-1204)	666.63 (56-3363)
Total_PP (mgC m <sup>-2</sup> d <sup>-1</sup> )	974.67 (521-1444)	2084.08 (323-4163)	3437.17 (951-5931)	1344.83 (295-2555)	1960.19 (295-5931)

## 2.2. Phytoplankton analysis

Samples (1 litre) for the phytoplankton analysis were preserved with 4% formalin, and later the samples were concentrated to 10 ml by sedimentation method after keeping the samples immobile for 2 weeks in a dark and cool place until microscopic analysis (Utermöhl, 1958). The excess seawater after settling was gently removed with a pipette. A subsample of 1 ml from the concentrated sample (10 ml) was counted by using a Sedgewick-Rafter cell under a phase-contrast binocular microscope (Leica DM4000). The phytoplankton groups (diatoms, dinoflagellates, other phytoplankton groups) were identified according to Balech (1988), Tomas (1996) and Rampi and Bernard (1978).

## 2.3. Nutrient analysis

Samples for nutrient ( $\text{NO}_{2+3}\text{-N}$ ,  $\text{SiO}_2\text{-Si}$  and  $\text{PO}_4\text{-P}$ ) analyses were filtered through 0.45  $\mu\text{m}$  cellulose acetate membrane filters. The filtrate was collected in 100 ml acid-washed high-density polyethylene bottles, and then was kept frozen ( $-20^\circ\text{C}$ ) until the analysis. An auto-analyser (SEAL) was used to measure nutrient concentrations. Nitrite and Nitrate ( $\text{NO}_{2+3}\text{-N}$ ) were analysed according to cadmium coil reduction method followed by sulfanilamide reaction in the presence of N-(1-naphthylethylenediamine) dihydrochloride (Std. Methods 4500- $\text{NO}_3\text{-F}$ , APHA, 1998). Ortho-phosphate ( $\text{PO}_4\text{-P}$ ) was detected according to OrthoAcidic molybdate/antimony with ascorbic acid reduction (phosphomolybdenum blue) method (Std. Methods 4500-P F, APHA, 1998). Reactive silicate ( $\text{SiO}_2\text{-Si}$ ) was measured by using acidic molybdate with ANSA reduction (silicomolybdenum blue) method (Std. Methods 4500- $\text{SiO}_2\text{ D}$ , APHA, 1998).

## 2.4. Size-fractionated primary production experiments

A  $^{14}\text{C}$  radio-tracing technique was deployed in order to estimate phytoplankton primary production (Steemann-Nielsen, 1952; Richardson, 1991). For this purpose, sea water samples from each depth were sub-sampled into 50 ml clear polycarbonate bottles. All bottles were pre-cleaned following JGOFS protocols to reduce trace metal contamination. Each bottle (50 ml) was inoculated with 50  $\mu\text{L}$   $\text{NaH}^{14}\text{CO}_3^-$  (1  $\mu\text{Ci}$ ; 2220000 dpm). After inoculations, the polycarbonate bottles were transferred to an on-deck incubation system (ICES Incubator HYDROBIOS) with simulated subsurface irradiance over depth to 97%, 55%, 33%, 20%, 14%, 7%, 3%, 1% or 0.1% of the surface value and incubated for two hours (between 10.00 and 12.00 pm).

After the incubation, each sample was filtered through 0.2, 2 and 10  $\mu\text{m}$  polycarbonate filters to measure the pico-, nano- and microphytoplankton primary production, respectively. The filters were exposed to concentrated hydrochloric acid (HCl) fumes for 12 hours. Then, the filters were transferred to scintillation vials and 4 ml of scintillation cocktail was added. The carbon activities (as disintegration time per minute, DPM) of each sample were measured with a liquid scintillation counter (LSC, PerkinElmer TriCarb

1550). Dark-bottle values were subtracted from the counts obtained from different light depths to calculate net production. Hourly rates of production were calculated from the measurements, and then these rates were converted to depth-integrated PP rates ( $\text{mgC m}^{-2} \text{d}^{-1}$ ) using the trapezoidal method (O'reilly and Zetlin, 1998). Hourly production rates were converted to daily rates depending on PAR measurements.

Following equation was used to calculate the rates of PP:

$$Pt = \frac{dpm(a).total\ CO_2(c).12(d).1.05(e).1.06(f).k1.k2.k3}{dpm(b)}$$

where  $Pt$  = carbon uptake,  $\text{mgC m}^{-3} \text{h}^{-1}$  and:

- (a) = sample dpm – background dpm = net dpm/sample
- (b) = the activity of the added  $^{14}\text{C}$  solution dpm
- (c) = concentration of total  $\text{CO}_2$  in experimental water,  $\mu\text{Mdm}^{-3}$
- (d) = 12: the atomic weight of carbon, converts  $\mu\text{Mdm}^{-3}$  to  $\text{mgdm}^{-3}$
- (e) = a correction for the effect of  $^{14}\text{C}$  discrimination
- (f) = a correction for the respiration of organic matter produced during the experiment
- $k1$  = a correction factor for sub-sampling
- $k2$  = a time correction factor
- $k3$  = a unit conversion factor

## 2.5. Evaluation of data

Kolmogorov-Smirnov test was applied to check whether the distribution of data was normal. One-way analysis of variance (ANOVA) test was used to test for significant differences between data sets (e.g., size-fractionated PP, Chl-*a*, phytoplankton abundance, inorganic nutrients and hydrography).

## 3. Results

### 3.1. Temperature and salinity profiles

Sea surface temperature (SST) ranged from  $8.58^\circ\text{C}$  (winter 2015) to  $28.41^\circ\text{C}$  (summer 2015) with a statistically significant difference (ANOVA,  $p < 0.001$ ) during the study period (Figure 2). The water column was uniform in winter due to the strong convective mixing, whereas thermal stratification was observed in summer and continued until autumn. The seasonal thermocline was detected between 20 and 50 m depths in summer and autumn. Surface salinity values revealed a typical Black Sea pattern and varied from 16.13‰ (spring 2015) to 18.18‰ (summer 2015) with seasonal differences (ANOVA,  $p < 0.001$ ). Depending on the depth, salinity increased to 20‰ which indicates the presence of Mediterranean origin waters at deeper depths (Figure 3). Surface salinity values clearly show that the upper layer of the study area is influenced by the river inflow, particularly during spring. Euphotic zone depth derived from PAR values ranged from 18 m (winter 2014) to 45 m (spring 2015) along the area. In general, the thickness of euphotic zone in summer and spring was greater than in other seasons (Table 1).

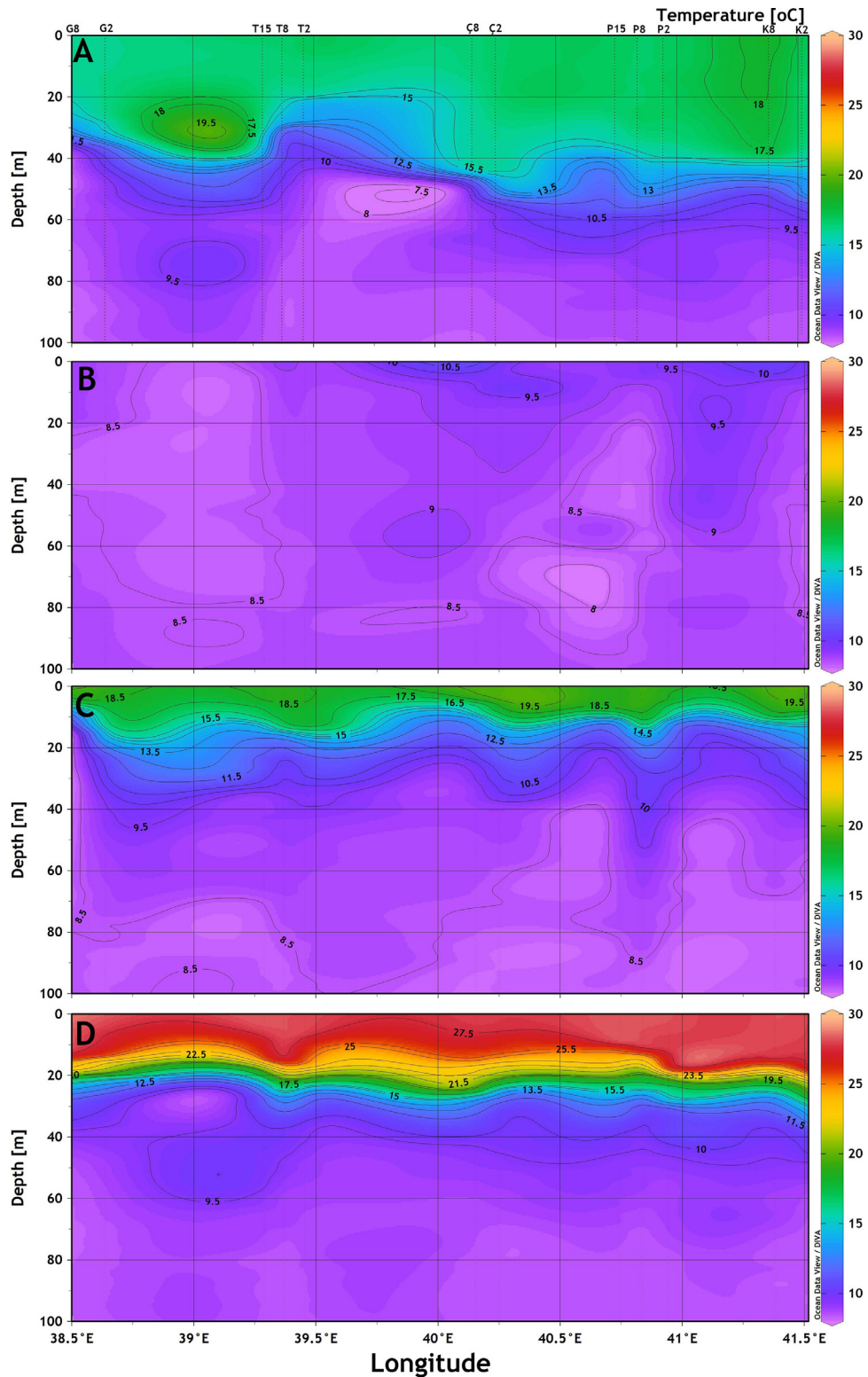


Figure 2 Spatio-temporal variations in temperature (A: autumn, B: winter, C: spring, D: summer).

### 3.2. Nutrient dynamics

Seasonal dynamics of nutrients (i.e., nitrite plus nitrate, phosphate and silicate) were given in Figures 4–6. Over the

study period, nutrient concentrations substantially varied, and revealed statistically significant seasonal differences (ANOVA,  $p < 0.001$ ). Extensive vertical mixing during autumn and winter seasons resulted in high nutrient concentrations

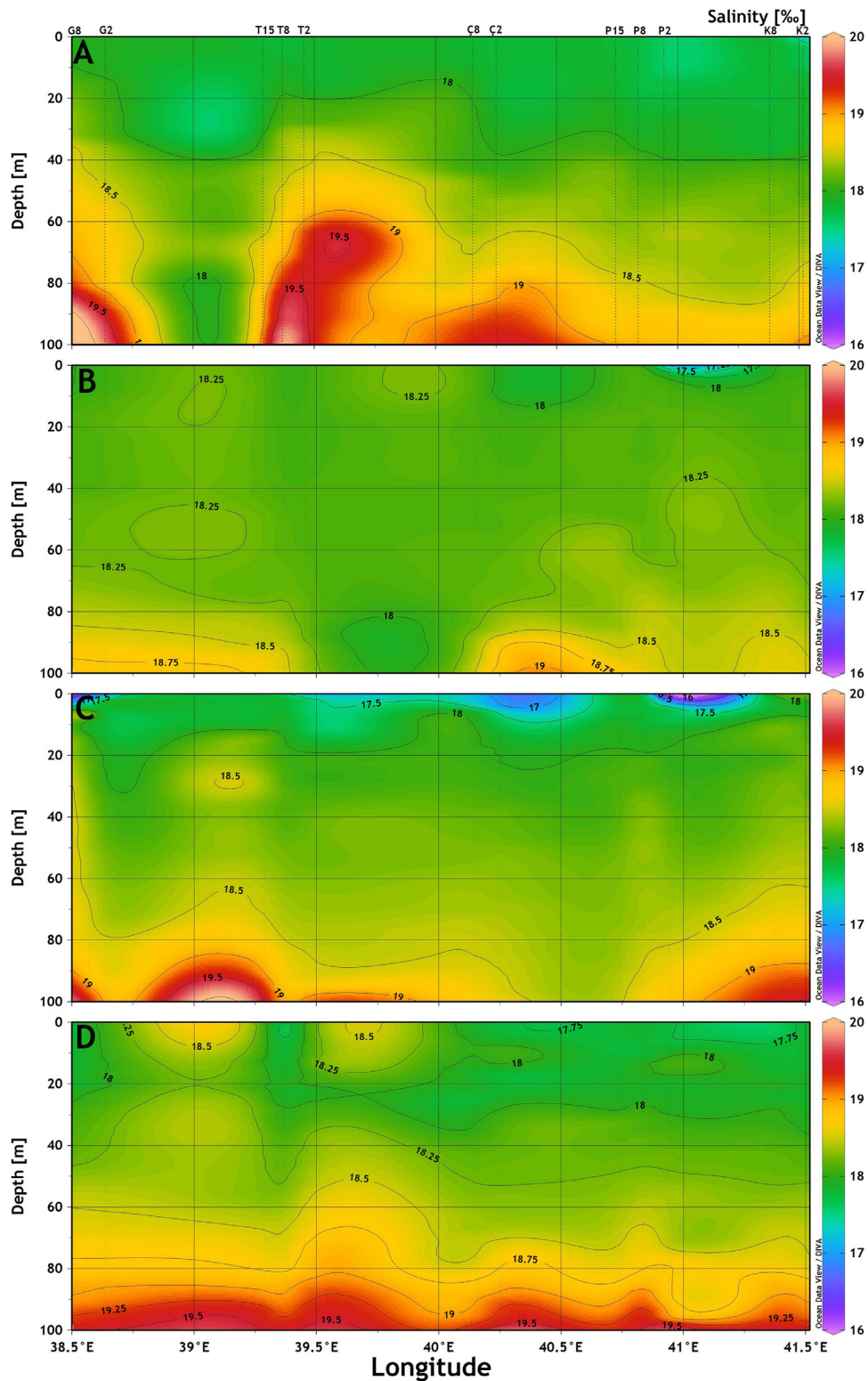


Figure 3 Spatio-temporal variations in salinity (A: autumn, B: winter, C: spring, D: summer).

in the euphotic zone. On the other hand, the concentrations were relatively low and showed a more uniform pattern during spring and summer along the study area. In general, the nutrient concentrations were high in the autumn and winter, and depending on phytoplanktonic

activity, the concentrations decreased in the spring and summer. Overall, phosphate concentrations ( $0.001\text{--}0.28 \pm 0.04 \mu\text{M}$ ) were very low, however, concentrations of  $\text{NO}_{2+3}$  ( $0.001\text{--}2.12 \pm 0.39 \mu\text{M}$ ) and silicate ( $0.01\text{--}13.63 \pm 1.93 \mu\text{M}$ ) were significantly high along the stations (Table 1).

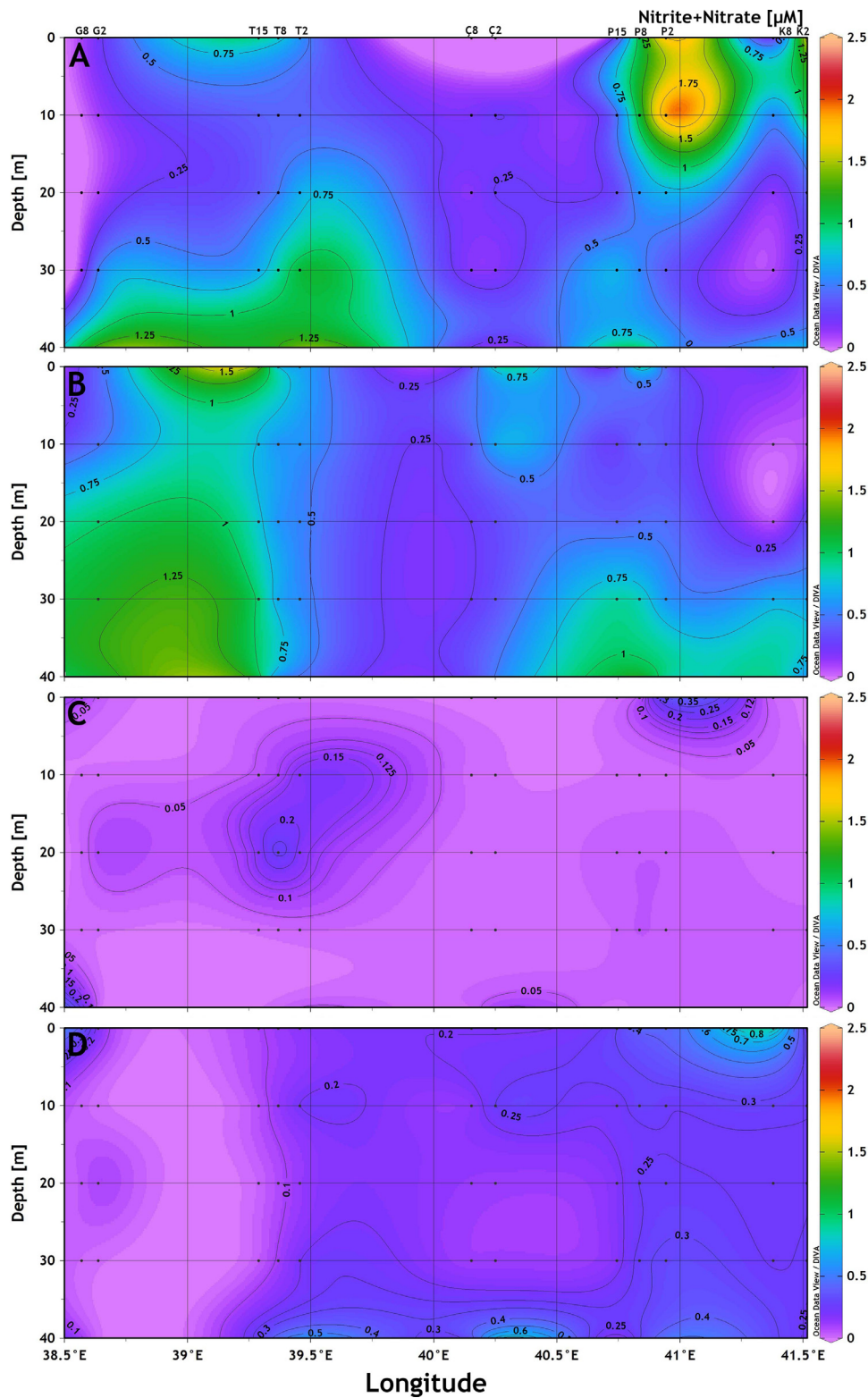


Figure 4 Spatio-temporal variations in nitrite and nitrate concentrations (A: autumn, B: winter, C: spring, D: summer).

$\text{NO}_{2+3}\text{-N}$  concentrations were generally high in autumn (0.001–2.12  $\mu\text{M}$ ) and winter periods (0.014–1.55  $\mu\text{M}$ ) when mixing process took place and phytoplanktonic activity were low, differently, the concentrations were low in

spring (0.001–0.61  $\mu\text{M}$ ) and summer (0.001–0.88) periods (Figure 4). Depending on the depth, high concentrations were recorded between 10 m and 20 m, except for the summer (Ç2 station, 40 m).

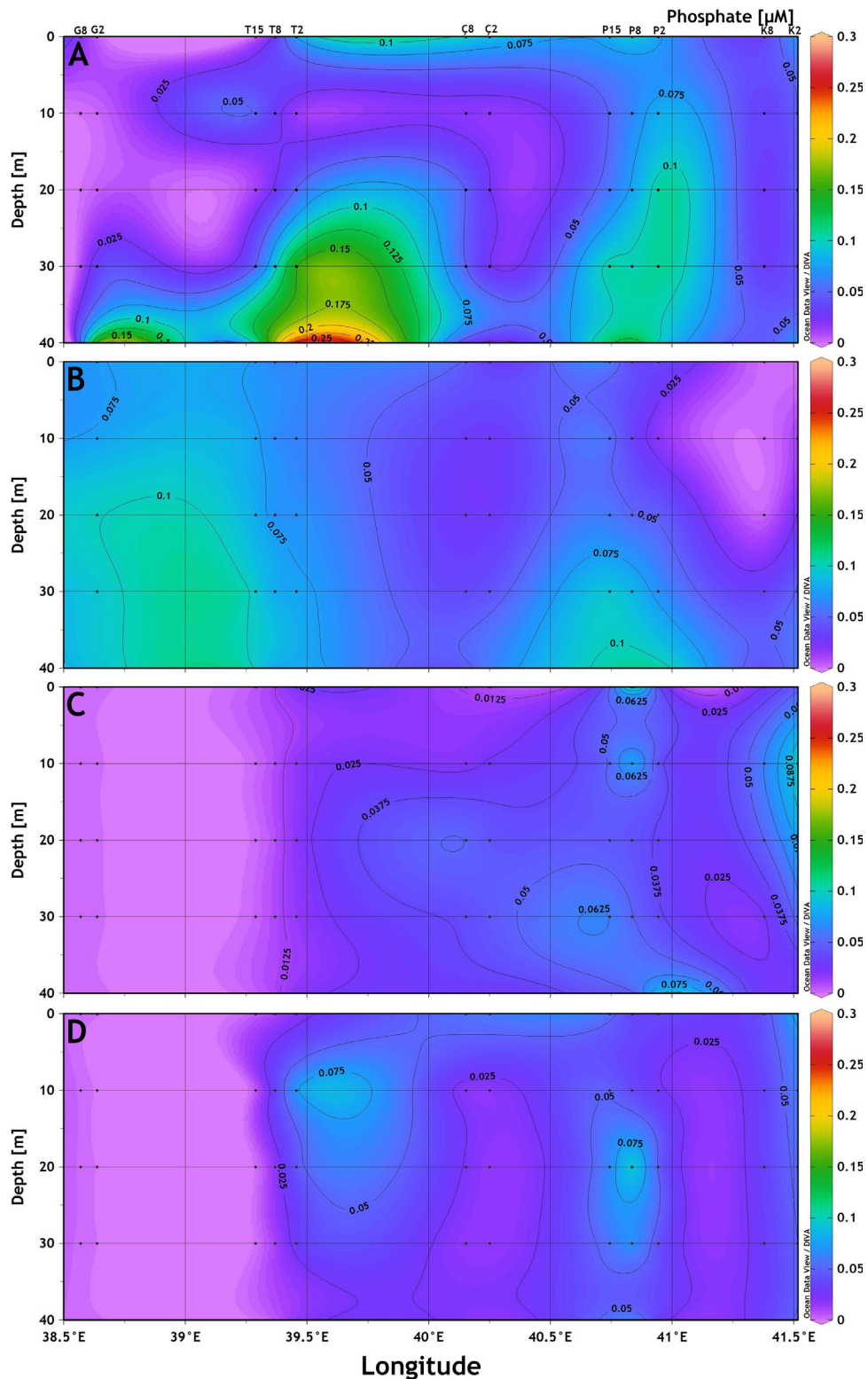
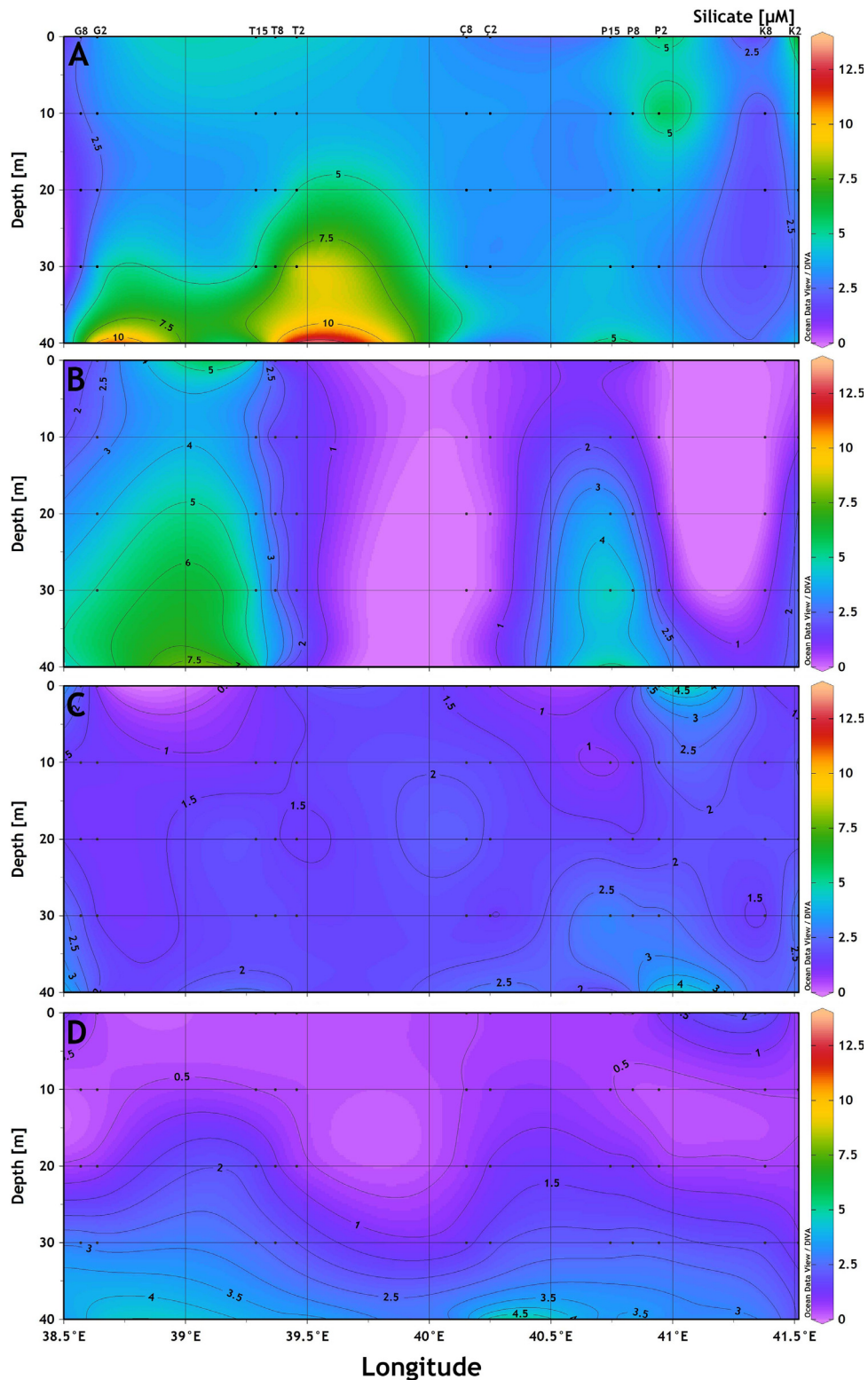


Figure 5 Spatio-temporal variations in phosphate concentrations (A: autumn, B: winter, C: spring, D: summer).

PO<sub>4</sub>-P concentrations were generally low (generally less than 0.5 μM) with statistically significant differences (ANOVA,  $p < 0.05$ ) in the study area (Figure 5). The highest concentrations were measured in the autumn (0.001–

0.28 μM), while the lowest values were measured in spring and summer (0.001–0.14 μM). During the study period, deeper waters were characterized by high phosphate concentration in autumn (T2 station, 40 m) and winter (P8





**Figure 6** Spatio-temporal variations in silicate concentrations (A: autumn, B: winter, C: spring, D: summer).

station, 40 m), while the surface waters had much phosphate in spring (P8 station surface) and summer (P8 station, 20 m).

In general,  $\text{SiO}_2\text{-Si}$  concentrations revealed an increasing pattern with depth (Figure 6), and varied significantly

(ANOVA,  $p < 0.05$ ) along the study area. The highest concentrations were generally recorded in autumn (1.58–13.63  $\mu\text{M}$ ) and winter (0.01–6.30  $\mu\text{M}$ ). On the other hand, the concentrations decreased in spring (0.60–4.75  $\mu\text{M}$ ) and summer (0.28–5.19  $\mu\text{M}$ ).

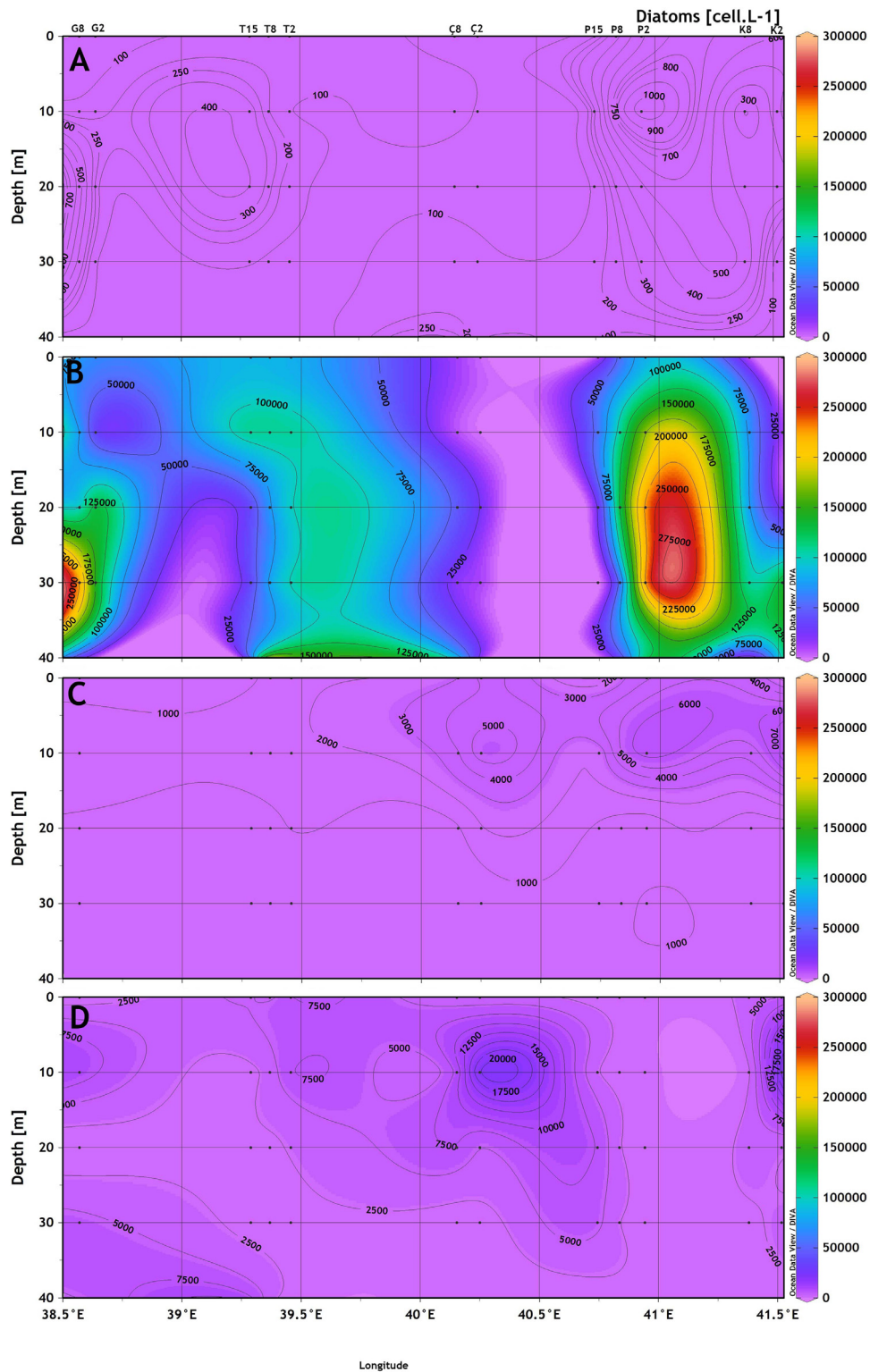


Figure 7 Spatio-temporal variations in diatom abundance (A: autumn, B: winter, C: spring and D: summer).

### 3.3. Phytoplankton composition and abundance

A total of 127 species were identified along the study area. 53.54% of these were dinoflagellate species (68 species), 40.94% were diatom species (52 species) and

5.51% consisted of other species (7 species), mainly coccolithophores (*Emiliana huxleyi*). The most dominant and common species were *Chaetoceros decipiens*, *Coscinodiscus granii*, *Coscinodiscus radiatus*, *Pseudo-nitzschia delicatissima*, *Rhizosolenia calcar-avis*, *Rhizosolenia setig-*

era, *Thalassionema nitzschioides*, *Thalassiosira angustilineata*, *Alexandrium minutum*, *Ceratium furca*, *Ceratium fusus*, *Ceratium tripos*, *Dinophysis acuminata*, *Dinophysis acuta*, *Dinophysis ovata*, *Gymnodinium* sp., *Noctiluca scintillans*, *Prorocentrum compressum*, *Prorocentrum micans*, *Prorocentrum minimum*, *Protoperidinium depressum*, *Protoperidinium steinii*, *Scrippsiella triquedum* and *Emiliania huxleyi* along the study area.

Quantitative phytoplankton distribution along the study area varied seasonally. Dinoflagellates (up to  $5 \times 10^3$  cells  $l^{-1}$ ) and other taxonomic groups (up to  $1.5 \times 10^5$  cells  $l^{-1}$ ) were in notable abundance during the autumn. On the other hand, diatoms (up to  $3 \times 10^5$  cells  $l^{-1}$ ) abundance remarkably increased in winter (Figures 7–9). In spring, dinoflagellates abundance (up to  $10 \times 10^3$  cells  $l^{-1}$ ) and other taxonomic groups (maximum  $4 \times 10^4$  cells  $l^{-1}$ ) were remarkably high, however, a decrease in diatom abundance was detected when compared to the previous sampling period. Quantitative phytoplankton density significantly decreased in the summer, and the abundance remained below  $3 \times 10^3$  cells  $l^{-1}$  when compared to other seasons (Figures 7, 8 and 9).

In terms of total cell number, winter was the most prominent period with a maximum of  $4.1 \times 10^5$  cells  $l^{-1}$ , followed by autumn (up to  $1.5 \times 10^5$  cells  $l^{-1}$ ) and spring (up to  $5 \times 10^4$  cells  $l^{-1}$ ), respectively (Figure 10). Over the study period, the abundance of diatoms revealed statistically significant differences among all seasons, while dinoflagellates were statistically different in spring and summer, other taxonomic groups were only statistically different in the autumn and summer (ANOVA,  $p < 0.05$ ). Similarly, total cell numbers also showed statistically significant differences between all seasons except for the autumn and spring seasons (ANOVA,  $p < 0.05$ ).

### 3.4. In-situ Chlorophyll-*a*

In-situ Chl-*a* concentrations ( $0.16\text{--}4.96 \pm 0.87$   $\mu\text{g } l^{-1}$ ) significantly varied (ANOVA,  $p < 0.01$ ) over the study period. In the autumn ( $0.35\text{--}4.57$   $\mu\text{g } l^{-1}$ ), the first 20 m of the water column was rich in terms of Chl-*a*, and its concentrations reached up to  $4.57$   $\mu\text{g } l^{-1}$  (Figure 11A). After these depths, Chl-*a* profile showed a more uniform pattern. In the winter ( $0.27\text{--}4.96$   $\mu\text{g } l^{-1}$ ), Chl-*a* was much patchy due to the intensive vertical mixing process (Figure 11B). In this period, Chl-*a* concentration reached up to  $5$   $\mu\text{g } l^{-1}$ . In the spring ( $0.21\text{--}2.50$   $\mu\text{g } l^{-1}$ ), the first 20–40 m of the water column was much richer in terms of Chl-*a* concentration. However, Chl-*a* concentration did not exceed  $2.50$   $\mu\text{g } l^{-1}$  during this period when the river runoff was intense, and the nutrient concentration was high (Figure 11C). In the summer ( $0.16\text{--}2.75$   $\mu\text{g } l^{-1}$ ), Chl-*a* concentrations were lower than other seasons, and the highest concentrations ( $2.75$   $\mu\text{g } l^{-1}$ ) were generally detected at 20–25 m (Figure 11D).

### 3.5. Total and size-fractionated primary production

During the study period, total PP revealed significant seasonal variations (Figure 12, Table 1). Total and group-specific depth-integrated Primary Production rates for the

stations are given in Supplementary Material Table 2. Spring was the most productive season with the highest total PP rates ( $5931$   $\text{mgC m}^{-2} \text{d}^{-1}$ ) over the study period. Winter was the second productive period, and total PP rates reached up to  $4163$   $\text{mgC m}^{-2} \text{d}^{-1}$ . Summer and autumn had relatively low total PP levels when compared to other seasons, and their PP rates were  $2555$   $\text{mgC m}^{-2} \text{d}^{-1}$  and  $1444$   $\text{mgC m}^{-2} \text{d}^{-1}$ , respectively. Among the stations, Kemalpaşa and Pazar stations, which are under the effect of river runoff, were the most productive stations, whereas Camburnu station had the lowest production rates in terms of total primary production rates.

The rates of size-fractionated PP varied remarkably throughout the study period (Figure 13, Table 1). In general, the rates of PP varied from  $84$  to  $1848$   $\text{mgC m}^{-2} \text{d}^{-1}$ ,  $96$  to  $3156$   $\text{mgC m}^{-2} \text{d}^{-1}$  and  $56$  to  $3363$   $\text{mgC m}^{-2} \text{d}^{-1}$  for pico-, nano- and microphytoplankton, respectively. The autumn period was characterised with high nanophytoplankton PP ( $637$   $\text{mgC m}^{-2} \text{d}^{-1}$ ) and followed by picophytoplankton PP ( $582$   $\text{mgC m}^{-2} \text{d}^{-1}$ ) along the study area (Figure 13A, Table 1). A substantial increase in PP rates of nano- ( $2095$   $\text{mgC m}^{-2} \text{d}^{-1}$ ) and microphytoplankton PP ( $1710$   $\text{mgC m}^{-2} \text{d}^{-1}$ ) were recorded in the winter (Figure 13B). In this period, PP rates increased by almost 2–3 folds compared to the autumn period. In the spring, the highest size-fractionated production rates were detected, and reached up to  $3000\text{--}3500$   $\text{mgC m}^{-2} \text{d}^{-1}$  along the stations (Figure 13C). In this period, the most significant contribution was made by microphytoplankton ( $3363$   $\text{mgC m}^{-2} \text{d}^{-1}$ ). The second group was nanophytoplankton with the rates of  $3156$   $\text{mgC m}^{-2} \text{d}^{-1}$  levels. Picophytoplankton was the last group with the maximum rate of  $1848$   $\text{mgC m}^{-2} \text{d}^{-1}$  in spring (Table 1). Summer period was characterized by picophytoplankton, and the production rates reached up to  $1335$   $\text{mgC m}^{-2} \text{d}^{-1}$  (Figure 13D). In terms of spatial variation, microphytoplankton was generally dominant along the coastal stations, however their production rates ( $1200$   $\text{mgC m}^{-2} \text{d}^{-1}$ ) was less than picophytoplankton. Nanophytoplankton were high in offshore stations with the rates of  $1168$   $\text{mgC m}^{-2} \text{d}^{-1}$  during summer (Table 1).

## 4. Discussion

The present study facilitates to examine the spatio-temporal changes in size-fractionated PP, total PP, and *in-situ* Chl-*a* with phytoplankton abundance and nutrient data along the south-eastern Black Sea. More importantly, this work is also the first study that revealed size-fractionated primary production rates with a seasonal basis for the Black Sea.

### 4.1. Spatio-temporal variations in nutrients

The surface waters of the southern coasts of the Black Sea are characterised with low nutrient concentrations especially during stratified periods (Basturk et al., 1994; Bingel et al., 1993; Codispoti et al., 1991). The concentrations are mostly affected by sub-surface nutricline and vertical mixing processes (Yayla et al., 2001). Besides, regional rivers are also the primary resources of nutrients, especially in coastal areas. Nutrient concentrations in the

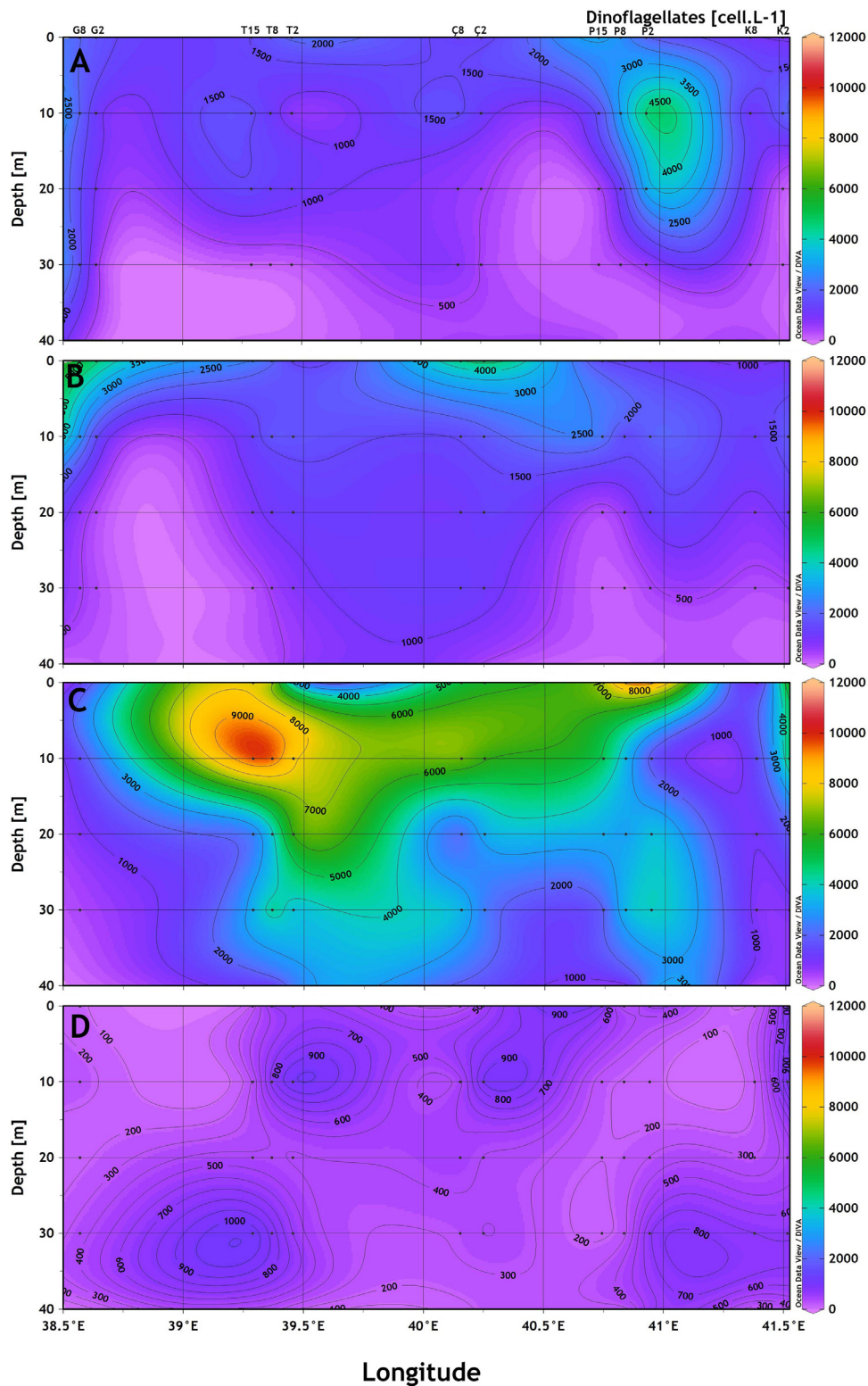
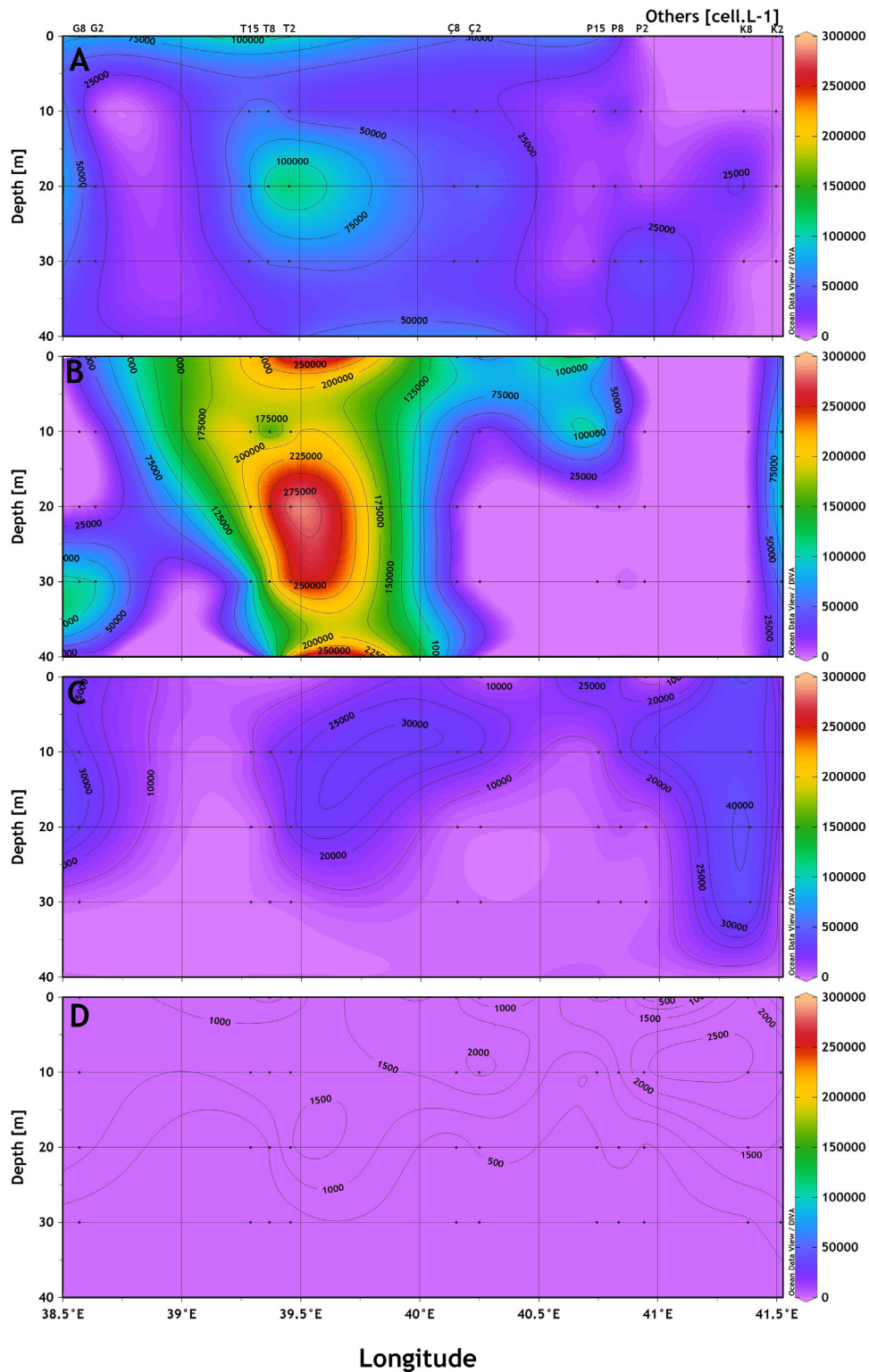


Figure 8 Spatio-temporal variations in dinoflagellates abundance (A: autumn, B: winter, C: spring and D: summer).

euphotic zone varied seasonally from 0.16 to 1.5  $\mu\text{M}$  for TNO<sub>x</sub>, and from 0.03 to 0.35  $\mu\text{M}$  for phosphate in the spring-autumn period of 1995–1996 (Yilmaz et al., 1998). During July 1997–September 1998 period, concentrations in the euphotic zone were detected as <0.35  $\mu\text{M}$  for PO<sub>4</sub>, <0.5

$\mu\text{M}$  for NO<sub>2+3</sub> and 5  $\mu\text{M}$  for silicate along the southern Black Sea (Yayla et al., 2001). In the present study, nutrient concentrations varied seasonally, and detected as 0.001–2.12  $\mu\text{M}$ ; 0.001–0.28  $\mu\text{M}$  and 1.58–13.63  $\mu\text{M}$  for NO<sub>2+3</sub>-N, PO<sub>4</sub>-P and SiO<sub>2</sub>-Si, respectively. Throughout the seasons, au-



**Figure 9** Spatio-temporal variations in other phytoplankton groups abundance (A: autumn, B: winter, C: spring and D: summer).

tumn was detected as the richest period in terms of nutrient concentrations along the study area. In the study area, coastal stations were richer in terms of nutrient concentrations than offshore stations. In particular, some stations (e.g., T2 and P2) are under influence of major river runoffs (e.g., Değirmendere and Firtına Rivers) which lead to de-

tect high nutrient concentrations even at the base of the euphotic zone.

Total  $\text{NO}_{2+3}\text{-N}$  concentrations for the southern Black Sea were reported as  $0.11\text{--}0.59\ \mu\text{M}$  (Eker-Develi et al., 2003). In another study, total  $\text{NO}_{2+3}\text{-N}$  concentrations were reported as  $0.02\text{--}4.14\ \mu\text{M}$  for the Anatolian coast of the Black Sea

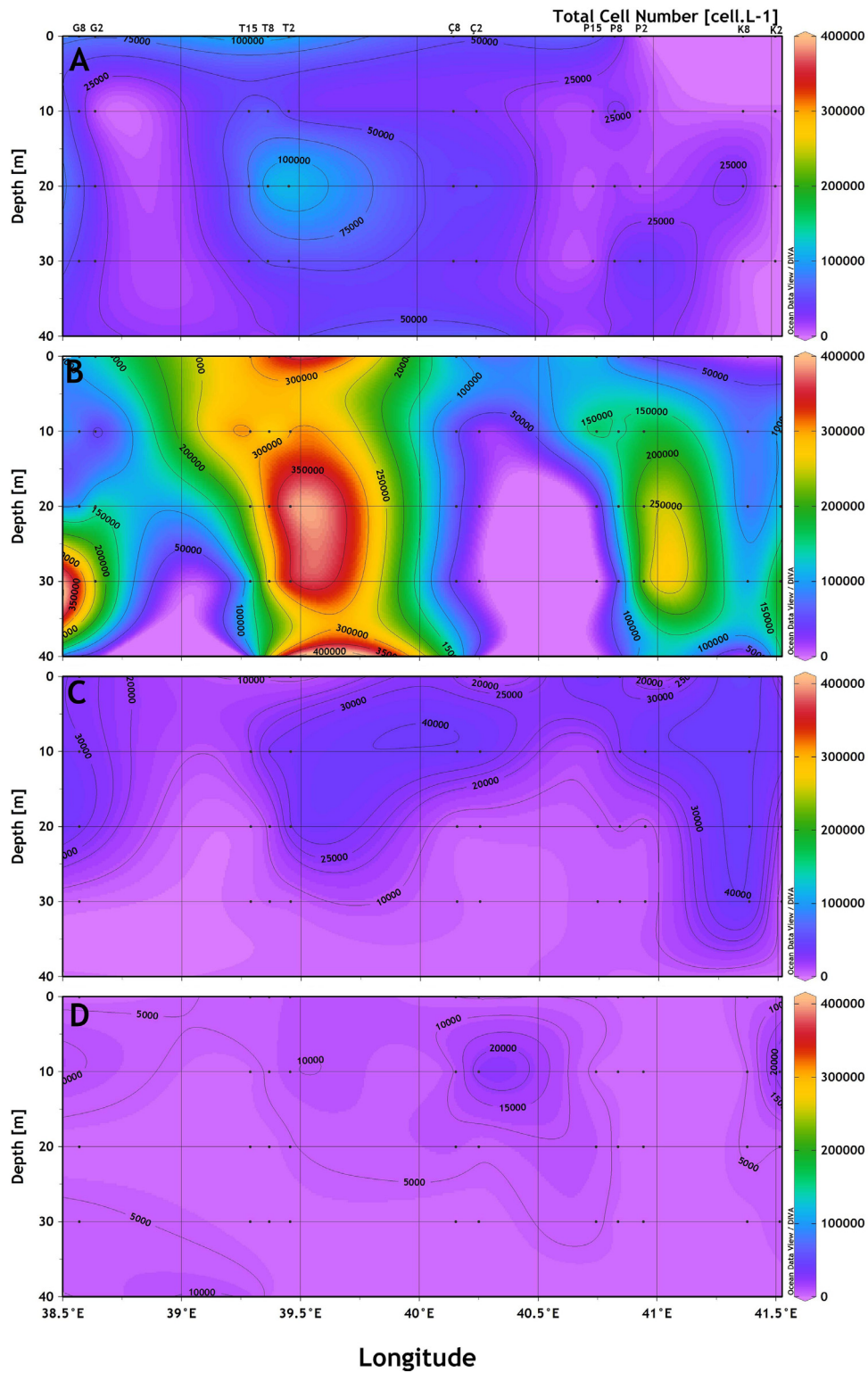


Figure 10 Spatio-temporal variations in total phytoplankton cell numbers (A: autumn, B: winter, C: spring and D: summer).

(Coban-Yildiz et al., 2000). Along the south-eastern Black Sea coasts, the total  $\text{NO}_{2+3}\text{-N}$  concentrations varied between 0.37 and 4.71  $\mu\text{M}$  in coastal waters and ranged from 0.31 to 4.46  $\mu\text{M}$  in open waters (Agirbas, 2010). In a study conducted by Koca (2014),  $\text{NO}_{2+3}\text{-N}$  concentrations were de-

tected between 0.52 and 9.88  $\mu\text{M}$  along the south-eastern Black Sea (Rize) (Koca, 2014). In the present study, the total  $\text{NO}_{2+3}\text{-N}$  concentration varied between 0.001 and 2.12  $\mu\text{M}$  with significant seasonal variations. Compared to previous studies,  $\text{NO}_{2+3}\text{-N}$  concentrations were found to be lower

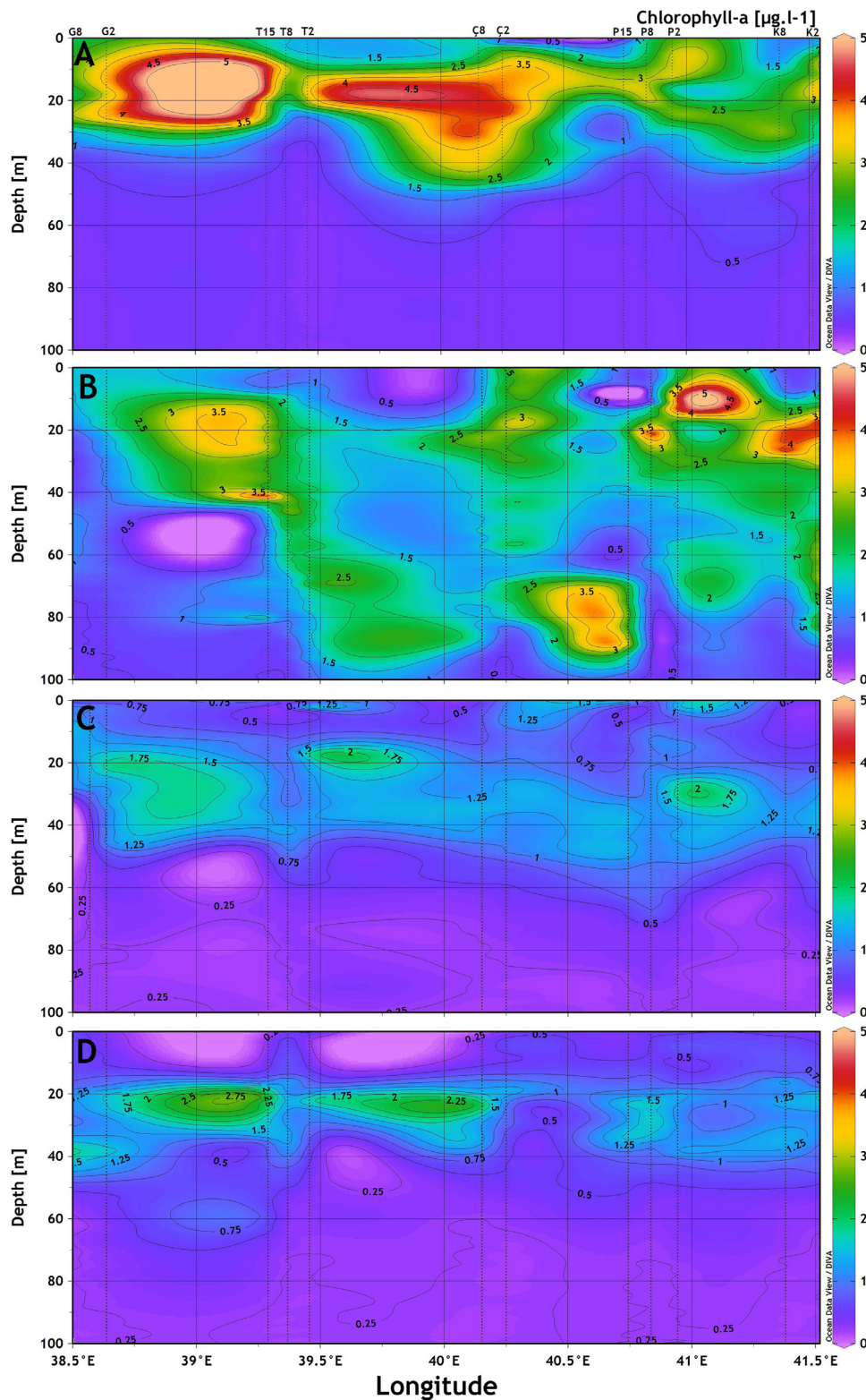
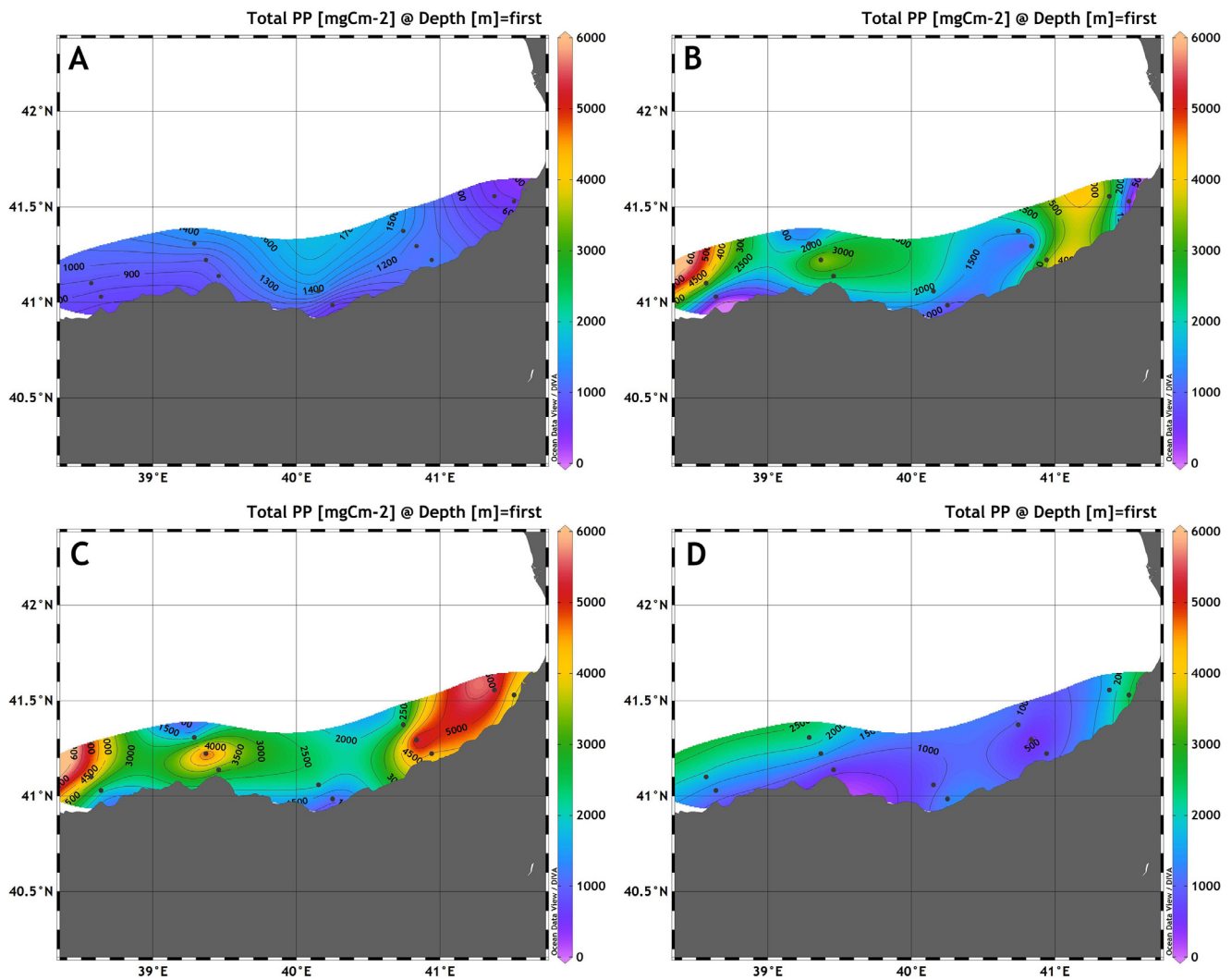


Figure 11 Spatio-temporal variations in *in-situ* Chl-*a* concentrations (A: autumn, B: winter, C: spring and D: summer).

than those of studies conducted along southern coasts of the Black Sea.

Average  $PO_4\text{-P}$  concentration in surface waters was reported as  $0.419 \mu\text{M}$  in the Black Sea (Sorokin, 1983). In a time-series study conducted along the Romanian coasts, av-

erage  $PO_4\text{-P}$  concentrations were measured as  $0.26 \mu\text{M}$  for the period of 1959–1965,  $6.54 \mu\text{M}$  for the period of 1983–1990 period,  $1.86 \mu\text{M}$  for the period of 1991–2000 and  $0.49$  for the period of 2001–2005 (Oguz et al., 2008). The average  $PO_4\text{-P}$  concentration was reported as  $0.002 \mu\text{M}$  (Novem-



**Figure 12** Spatio-temporal variations in integrated size-fractionated primary production rates (A: autumn, B: winter, C: spring and D: summer).

ber 2009) to  $0.052 \mu\text{M}$  (June 2009) at the coastal stations in the south-eastern Black Sea (Agirbas, 2010). In the open waters, concentrations varied between  $0.002 \mu\text{M}$  (November 2009) and  $0.068 \mu\text{M}$  (June 2009). Similarly, the phosphate concentration for the south-eastern Black Sea varied between  $0.01$ – $0.06 \mu\text{M}$  (Kopuz, 2012). Along the south-eastern coasts (Rize),  $\text{PO}_4\text{-P}$  concentration varied between  $0.03$  and  $0.90 \mu\text{M}$  (Koca, 2014). In this study,  $\text{PO}_4\text{-P}$  concentrations ranged from  $0.001$  to  $0.28 \mu\text{M}$ . The highest  $\text{PO}_4\text{-P}$  concentrations were observed in autumn while, the lowest values were measured in winter. Overall, a significant decrease was observed in  $\text{PO}_4\text{-P}$  concentrations over the years when compared to the previous decades along the study area.

As a general trend,  $\text{SiO}_2\text{-Si}$  concentration of seawater varies between  $7$ – $15 \mu\text{M}$  in surface waters during the winter period, concentrations may decrease down to  $0.35 \mu\text{M}$  in the summer period (Tait, 1988). Depending on phytoplankton activity,  $\text{SiO}_2\text{-Si}$  concentrations decrease especially after intense diatom blooms in the Black Sea, and its concentration increases again with river inputs and precip-

itation (Bologa, 1986). The average annual surface water  $\text{SiO}_2\text{-Si}$  concentrations were reported as  $40.5 \mu\text{M}$  for the period of 1959–65;  $11.0 \mu\text{M}$  for the period of 1983–1990;  $12.6 \mu\text{M}$  for the period of 1991–2000 and  $13.7 \mu\text{M}$  for the period 2001 of 2005 along the Romanian coasts (Oguz et al., 2008). Particularly, after the 70's, reactive silicate concentration in surface waters of Black Sea decreased by 60% due to dam constructions on river Danube, and this decline led to dramatic changes in phytoplankton compositions especially in diatoms in the early 1990s (Kideys et al., 2000). It was reported that  $\text{SiO}_2\text{-Si}$  concentrations varied between  $1.20$  and  $14.08 \mu\text{M}$  in the south-eastern Black Sea coast (Agirbas, 2010). In another study conducted in the same region,  $\text{SiO}_2\text{-Si}$  concentrations ranged from  $0.37$  to  $16.63 \mu\text{M}$  (Kopuz, 2012). Similarly, silicate concentrations were reported between  $1.92$  and  $16.25 \mu\text{M}$  along the south-eastern Black Sea (Koca, 2014). In the present study,  $\text{SiO}_2\text{-Si}$  concentrations varied between  $1.58$  and  $13.63 \mu\text{M}$ . The highest concentrations were detected in the autumn due to vertical mixing and low phytoplanktonic activity.



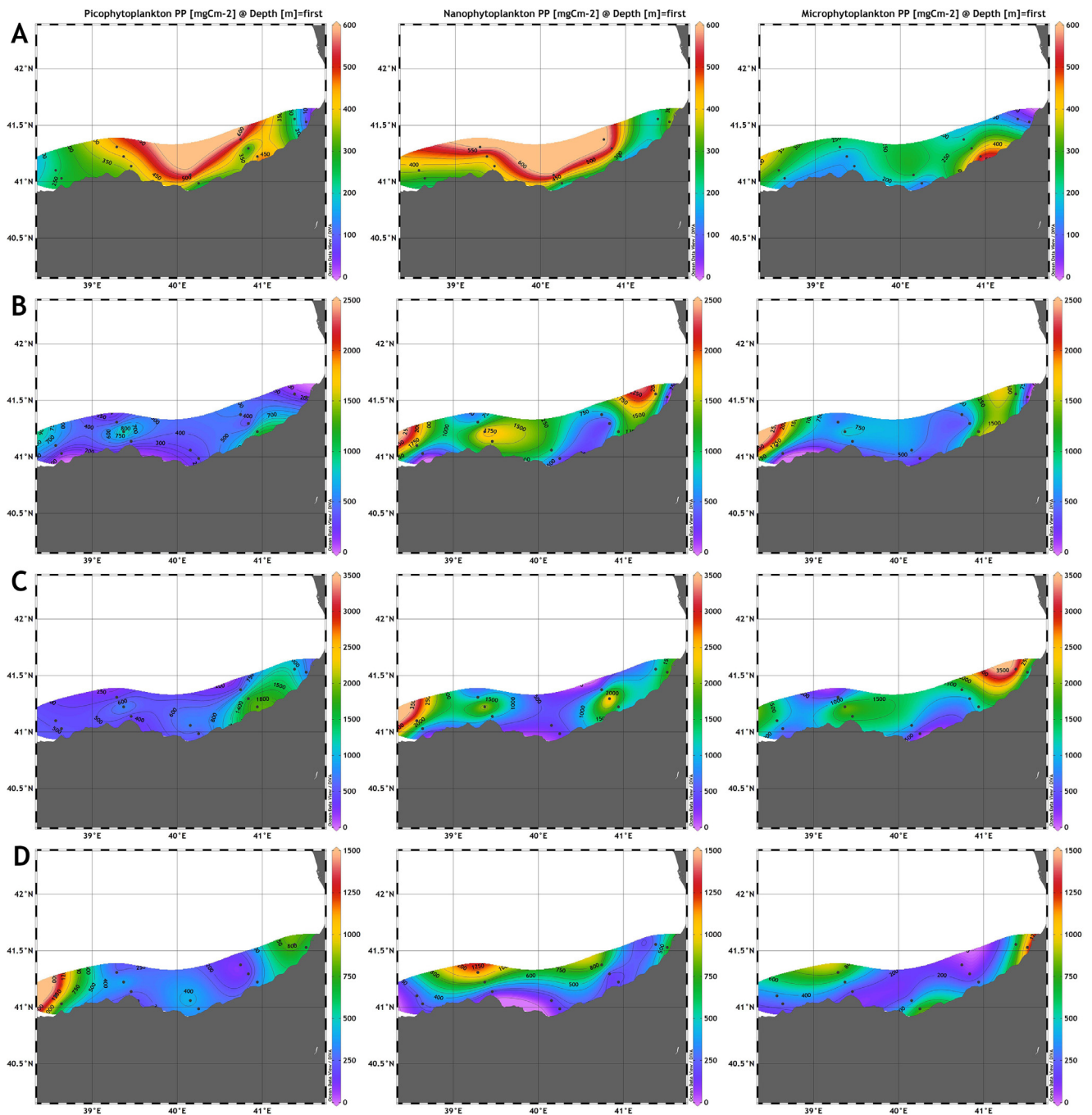


Figure 13 Spatio-temporal variations in total integrated primary production rates (A: autumn, B: winter, C: spring and D: summer).

#### 4.2. Spatio-temporal variations in phytoplankton

The seasonal dynamics of the Black Sea phytoplankton exhibit a typical spring bloom of which diatom are main responsible groups, whereas in the autumn bloom is stimulated by the coccolithophore *Emiliana huxleyi* (Honjo et al., 1987; Oguz and Ediger, 2006; Sorokin, 1983; Vedernikov et al., 1993). However, ecological changes occurred in the ecosystem after the 80's have led to unusual summer phytoplankton blooms (Hay et al., 1990; Sur et al., 1996; Yayla et al., 2001; Yilmaz et al., 1998).

Moreover, these changes have also caused significant shifts in phytoplankton composition and bloom patterns along the Black Sea. In general, diatoms were considered as the main group (46%) contributing to the total phytoplankton biomass, followed by dinoflagellates with a rate of 27% (Zaitsev and Alexandrov, 1997). However, after eutrophication and the retention of inorganic nutrients (mainly silicate) caused shifts in phytoplankton group ratios in favour of coccolithophores and dinoflagellates rather than diatoms (Bodeanu et al., 1998; Bologa et al., 1995; Cociasu et al., 1996; Humborg et al., 1997; Moncheva and

Krastev, 1997). Qualitative changes were also reported in the phytoplankton composition during the eutrophication period, in which the diatom ratio decreased from 67% (209 species) to 46% (172 species) between 1960–1970 and 1972–1977 (Bologna, 1986). In addition, the gradual increases in number of dinoflagellates species in recent years, especially during summer, have made them the dominant group along the Black Sea (Mikaelyan et al., 2013; Moncheva et al., 2001; Uysal and Sur, 1995; Uysal et al., 1998; Zaitsev and Alexandrov, 1997). Similarly, a high dinoflagellate species number (81% of total species number) were reported from south-western Black Sea (Ediger et al., 2006). Agirbas et al. (2015) also reported a high dinoflagellate dominance (71%) from the south-eastern Black Sea for the period of February–December 2009. In the present study, a high dinoflagellate dominance (53.54%) was also observed throughout the study period. Overall, the results are consistent with recent trends reported from previous studies thus suggesting the dinoflagellate species have become the dominant group in terms of species richness in the study area.

During the study period, two distinct phytoplankton bloom were identified in terms of phytoplankton abundance. These periods were autumn ( $1.5 \times 10^5$  cells  $l^{-1}$ ) and winter ( $4.1 \times 10^5$  cells  $l^{-1}$ ). Especially in winter, diatoms were represented with the high cell abundance, followed by *E. huxleyi*. In the autumn, major contributions were made by *E. huxleyi* and dinoflagellates. Throughout the study period, diatoms reached the highest abundance ( $3 \times 10^5$  cells  $l^{-1}$ ) in the winter, whereas dinoflagellates reached the highest abundance ( $1 \times 10^4$  cells  $l^{-1}$ ) in the spring. *E. huxleyi* was the most abundant species represented in the other groups and reached the highest abundance ( $1.5 \times 10^5$  cells  $l^{-1}$ ) in winter.

The north-western shelf of the Black Sea was characterized with higher phytoplankton abundance than other parts of the region. However, the abundance of phytoplankton along the south-eastern Black Sea is quite low when compared with north-western coasts. Phytoplankton abundance, ranged from  $3 \times 10^4$  to  $4.1 \times 10^5$  cells  $l^{-1}$ , obtained from the present study were found to be similar to those of previous studies conducted on the Anatolian coasts of the Black Sea (Bat et al., 2007; Eker, 1999; Feyzioglu, 1996), however, values were lower than the studies carried out on the north-western continental shelf.

### 4.3. Spatio-temporal variations in Chl-*a*

Chl-*a* concentrations vary spatially and temporally along the Black Sea. The concentrations in the Black Sea were reported as  $0.15 \pm 0.04$   $\mu\text{g/l}$  for the period of 1964–1986 (Kideys, 1994; McQuatters-Gollop et al., 2008; Mikaelyan et al., 2013; Vinogradov et al., 1999; Yunev et al., 2002). However, the seasonal variations in Chl-*a* are not spatially uniform in the Black Sea (McQuatters-Gollop et al., 2008). The average Chl-*a* concentrations for the entire Black Sea varied between 0.59 and 0.69  $\mu\text{g l}^{-1}$  (Kopelevich et al., 2004). In the shelf region, winters were generally characterised with low Chl-*a* concentrations (McQuatters-Gollop et al., 2008). On the other hand, maximum concentrations in Chl-*a* are generally observed during autumn and winter in the open areas of the Black

Sea, while reaches to minimum concentrations in summer (Vinogradov et al., 1999).

For the Anatolian coasts of the Black Sea, Chl-*a* concentrations ranged from 0.1 to 1.5  $\mu\text{g/l}$  during 1995–1996 (Yilmaz et al., 1998). In another study, the surface Chl-*a* values along the coast of Turkey for the period of 1996–1998 ranged from 0.34 to 0.42  $\mu\text{g l}^{-1}$  (Eker-Develi et al., 2003). Ediger et al. (2006) reported that the mean Chl-*a* concentration for the south-western Black Sea varied between 0.15 and 1.23  $\mu\text{g l}^{-1}$ . In the SE Black Sea, surface water of Chl-*a* values was reported as 1.97  $\mu\text{g l}^{-1}$  and 1.84  $\mu\text{g l}^{-1}$  for coastal (2 miles) and offshore (8 miles) stations, respectively (Agirbas, 2010). In another study, Chl-*a* concentrations along the SE Black Sea changed between 0.34 and 2.71  $\mu\text{g l}^{-1}$  (Koca, 2014). Along the south-eastern Black Sea ecosystem, the average surface Chl-*a* concentrations for the period of November 2014–August 2015 were reported as 0.37–2.68  $\mu\text{g l}^{-1}$ ; 0.16–2.04  $\mu\text{g l}^{-1}$  and 0.32–1.79  $\mu\text{g l}^{-1}$  for 2, 8, and 15 miles, respectively (Turkmen, 2016). In another study, monthly surface Chl-*a* concentrations varied between 0.51 and 3.97  $\mu\text{g l}^{-1}$  for river mouth, between 0.16 and 2.47  $\mu\text{g l}^{-1}$  for coastal and 0.18 and 3.04  $\mu\text{g l}^{-1}$  for offshore stations (Genc, 2018). Karadeniz (2019) reported that mean surface water *in-situ* Chl-*a* concentrations varied between 2.61  $\mu\text{g l}^{-1}$ , 2.56  $\mu\text{g l}^{-1}$  and 2.23  $\mu\text{g l}^{-1}$  for 2, 8 and 15 miles, respectively. Overall, the Chl-*a* concentrations obtained from the present study exhibited a distinct seasonal pattern, autumn and winter were characterized with high Chl-*a* concentrations (0.35–4.57 and 0.27–4.96 for autumn and winter, respectively), however, the lowest values were detected during spring and summer when the stratification started in spring and strengthened in summer along the study area. The differences in Chl-*a* values observed between the present study and previous studies emphasise that regional differences, study period, sampling regime and frequency as well as changes in phytoplankton communities under changing ecosystem conditions are the main factors.

### 4.4. Spatio-temporal variations in total and size-fractionated primary production

The Black Sea is commonly reported one of the largest eutrophic (greater than 500  $\text{gC m}^{-2} \text{y}^{-1}$ ) marine environment in the world (Arai, 2001). Over the decades, considerable changes in nutrient input (especially silicate) and other ecological factors altered trophic food web structure of the Black Sea. These changes affected the succession, intensity, frequency, and extension of phytoplankton besides the rates of PP throughout the Black Sea (Oguz, 2005). Previous studies in the Black Sea on the PP reported that the values for the north-western shelf as 570–1200  $\text{mgC m}^{-2} \text{d}^{-1}$ , for the continental slope as 320–500  $\text{mgC m}^{-2} \text{d}^{-1}$  and for deep-sea regions as 100–370  $\text{mgC m}^{-2} \text{d}^{-1}$  for the period of 1960–1991 (Bologna, 1986; Demidov, 2008; Vedernikov and Demidov, 1993). PP values were reported for the nearshore as 785  $\text{mgC m}^{-2} \text{d}^{-1}$  in July 1997 in the western Black Sea, and the rates of PP for the deep regions of the Black Sea were reported as 62–461  $\text{mgC m}^{-2} \text{d}^{-1}$  during the spring 1998 period (Yayla et al., 2001). For the southern coasts of the Black Sea, PP rates were measured as 247–1925  $\text{mgC m}^{-2} \text{d}^{-1}$  for

spring period, and 405–687 mgC m<sup>-2</sup> d<sup>-1</sup> for summer and autumn periods from 1995 to 1996 (Yilmaz et al., 2006). In another study, monthly PP rates for the south-eastern coasts of the Black Sea were calculated as 285–565 mgC m<sup>-2</sup> d<sup>-1</sup> for the coastal station, and as 126–530 mgC m<sup>-2</sup> d<sup>-1</sup> for the offshore station (Agirbas et al., 2014). Recently, a time-series study obtained from the Wavelength Resolving Model (WRM) for the period of 1998–2011 using SeaWiFS data revealed spatial and temporal variations in mean annual PP values for the open Black Sea. PP rates were significantly higher in the western Gyre (110–2196 mgC m<sup>-2</sup> d<sup>-1</sup>) than the eastern Gyre (111–1806 mgC m<sup>-2</sup> d<sup>-1</sup>) (Agirbas et al., 2017). In the present study, total PP production rates were significantly varied, and values ranged from 1444 mgC m<sup>-2</sup> d<sup>-1</sup> (autumn) to 5931 mgC m<sup>-2</sup> d<sup>-1</sup> (spring) along the study area. The differences observed in PP values along the different parts of the Black Sea are thought to be due to nutrient concentrations (Cociasu et al., 1997). In addition, variability in the rim current and the physics of the gyres also play a significant role in regional differences of PP (Enriquez et al., 2005; Zatsépin et al., 2003). The cyclonic boundary of rim current which constitutes a biogeochemical barrier between coastal and offshore areas, and frontal jet instabilities between the rim current and the interior eddy fields affect the spatial variability in PP around the Black Sea (Oguz et al., 1994; Yilmaz et al., 1998). Moreover, Batumi anticyclone along the eastern Gyre, which appears as warm core rings during summer, may also led to decrease in PP (Oguz et al., 1993). Similarly, low PP rates detected in the summer period coincided with low nutrient concentrations and phytoplankton abundance along the stations. Changes in PP rates could be also related to community structure than abiotic factors (Richardson and Schoeman, 2004). In the study area, rates of PP closely coupled with phytoplankton abundance in some seasons. Spring was the most productive period which coincided with high dinoflagellates number. The second productive period was winter, which concur with high diatom abundance along the study area.

The main contribution of this study, which sets the current study apart from those of previous ones is the no studies on the size-fractionated PP have been conducted in the Black Sea so far. In this respect, this study includes comprehensive data on spatio-temporal variations in size-fractionated PP measurements in the Black Sea for the first time. In general, the rates varied from 84 to 1848 mgC m<sup>-2</sup> d<sup>-1</sup>, 96 to 3156 mgC m<sup>-2</sup> d<sup>-1</sup> and 56 to 3363 mgC m<sup>-2</sup> d<sup>-1</sup> for pico-, nano- and microphytoplankton fractions, respectively. During the study period, the contribution of each size class to total PP changed seasonally along the study area. Overall, microphytoplankton was the major group contributing to total PP in the study area. The PP values for the microphytoplankton were high in spring (3363 mgC m<sup>-2</sup> d<sup>-1</sup>) and in winter (1710 mgC m<sup>-2</sup> d<sup>-1</sup>). The second important group was nanophytoplankton, and their contribution was generally high in winter (2095 mgC m<sup>-2</sup> d<sup>-1</sup>) and spring (3156 mgC m<sup>-2</sup> d<sup>-1</sup>). The production rates for the picophytoplankton were generally low along the study area, however, their contribution was substantial in summer, and occasionally detected in spring.

In terms of spatial variability, coastal stations were generally dominated by microphytoplankton. On the other

hand, offshore stations were characterised by nano- and picophytoplankton during the study period (Figure 13). Earlier studies reported that picophytoplankton biomass and PP rates are lower than larger size classes, however, high in oligotrophic gyres. On the other hand, nanophytoplankton significantly contribute to total PP in coastal upwelling areas due to ability of light utilisation (Hirata et al., 2009; Moreno-Ostos et al., 2011; Maranon et al., 2001; Tilstone et al., 1999; Uitz et al., 2010). The differences in size-fractionated PP values between coastal and offshore areas evidently emphasize that physical factors are the major drivers in PP rates along the study area. Coastal ecosystems of the Black Sea are principally governed by freshwater inflow and climatic factors (Bodeanu, 2002, 2004), however, the open sea areas are controlled by stratification, mixing and circulation processes (Sorokin, 2002). Moreover, spatial and temporal variation in PP of different size classes vary greatly in the oceans with respect to hydrography, irradiance, nutrient availability and biogeochemistry (Bricaud et al., 2004; Poulton et al., 2006).

Water column stratification decreases nutrients input from below the thermocline to the euphotic zone, thus possibly limiting PP especially in the micro- and nanophytoplankton in the oligotrophic areas of Atlantic Ocean (Aldridge et al., 2014; Maranon et al., 2003). Especially, diatoms due to their nitrogen metabolism can respond rapidly to nitrate enrichment (Fogg, 1991), any deficiencies in nutrient affect the PP rates of diatoms and microphytoplankton. Similarly, due to high nutrient concentrations in spring, the highest PP rates were recorded with dominance of microphytoplankton along the study area. A significant relationship between abiotic factors and spring PP rates, were detected, particularly in silicate and nitrate concentrations with high PP rates in Western English Channel (WEC). Besides, high nutrient concentrations are generally thought to promote larger cells such as diatoms (Barnes et al., 2015; McAndrew et al., 2007; Poulton et al., 2006). Moreover, nanophytoplankton may have a moderate PP capacity in low Chl-*a* areas because of their mixotrophic characteristic (Riemann et al., 1995).

## 5. Conclusions

The data presented here contribute to our understanding of spatio-temporal variations in total PP, size-fractionated PP and Chl-*a* with phytoplankton abundance and nutrient data along the south-eastern Black Sea. More importantly, the study mainly focuses on the revealing the PP rates of size-classes in the study area throughout a seasonal cycle. We observed that microphytoplankton had the highest PP rates (3363 mgC m<sup>-2</sup> d<sup>-1</sup>), followed by nanophytoplankton (3156 mgC m<sup>-2</sup> d<sup>-1</sup>) and picophytoplankton (1848 mgC m<sup>-2</sup> d<sup>-1</sup>) along the study area. Overall, winter (4163 mgC m<sup>-2</sup> d<sup>-1</sup>) and spring (5931 mgC m<sup>-2</sup> d<sup>-1</sup>) were the most productive seasons in terms of total PP which coincided with high phytoplankton abundance. Earlier studies on PP reported two distinct periods in early spring and autumn, however, summer blooms have been also detected along the Black Sea (Hay et al., 1990; Sur et al., 1996; Yilmaz et al., 1998). Similarly, two distinct periods in PP rates were also detected in the present study, however, seasonality of bloom timing was

different from previous studies. Mikaelyan et al. (2017) have reported similar phenological changes in phytoplankton bloom pattern along the Black Sea.

Chl-*a* concentrations were high in autumn ( $4.57 \mu\text{g l}^{-1}$ ) and winter ( $4.96 \mu\text{g l}^{-1}$ ); however, its values were relatively low in spring and summer. Along the study area, dinoflagellates were the dominant group in terms of species richness (68 species, 53.54%), and diatoms was the second most abundant group. On the other hand, diatoms and other phytoplankton species (mainly *E. huxleyi*) were the most abundant groups in terms of quantitative contribution. SST varied seasonally between 8.58 and 28.41°C is an important factor which affects the hydrography. Along the study area, depending on the seasonal thermocline and phytoplankton activity, nutrient concentrations were low in spring and summer when compared with autumn and winter. On the other hand, high nutrient concentrations (especially  $\text{NO}_{2+3}\text{-N}$  and  $\text{SiO}_2\text{-Si}$ ) provoke productivity of microphytoplankton in coastal waters. The coastal stations of the southern Black Sea have different characteristics (e.g., river inflow, hydrography, light conditions and current properties etc.) and were separated statistically from the offshore stations with high production rates, phytoplankton abundance and nutrient concentrations. The results suggest that microphytoplankton along the study area are responsible for the majority of PP. However, the measured high Chl-*a* against low size-fractionated PP clearly indicates that smaller phytoplankton size classes (i.e., pico- and nanophytoplankton) were dominant during these periods. Hence, the quantification of size-fractionated PP rates with ecological drivers (hydrography, nutrient availability, irradiance etc.) will give a more comprehensive picture for the Black Sea ecosystem.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.oceano.2021.11.002>.

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