Phytoplankton size-based dynamics in the Aegean Sea (Eastern Mediterranean)

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Abstract

This study represents one component of the large MTP-II-MATER (MAST-III) multidisiplinary project in the Mediterranean supported by EU. Data were collected during three cruises performed in Spring and Autumn 1997 and Spring 1998 from six stations of the North and five stations of the South Aegean Sea. The work assessed the spatial, vertical and temporal variations of size fractionated chlorophyll α, primary production (in situ), photosynthetic parameters (in situ) and the taxonomic composition of phytoplankton. The population structure and dynamics were greatly influenced by the different hydrographic conditions prevailing in the Northern and Southern Aegean Sea due to the influence of Black Sea and Levantine Sea waters, respectively. The picoplankton fraction (0.2–1.2 μm) predominated and accounted for the 56% to 49% of total chl α and the 51% to 41% of total primary production in the N. and S. Aegean Sea, respectively. Throughout the sampling area, the levels of nano + microplankton (>3.0 μm) were next in abundance proportions of total chl α (21–31%) and primary production (20–33%) and the levels of the ultraplankton (1.2–3.0 μm) were the lowest, contributing the 18–22% of total chl α and the 20–23% of total primary production. There was a highly significant ($P \le 0.005$–0.01) spatial, vertical and temporal influence on the biomass and productivity of all size classes in the N. Aegean and of most of them in S. Aegean. Light utilization efficiency (ε%) and quantum yield (φ_{max}) exhibited a temporal trend having higher values in Spring than in Autumn as well as a trend affected by cell size, being higher for picoplankton in relation to ultraplankton and nano + microplankton. Assimilation ratios (P^B) increased with cell size. Daily primary production in the N. Aegean (81.36 mg C m^{-2} day^{-1}) was higher than that in the S. Aegean (38.88 mg C m^{-2} day^{-1}) but both are characterized as the most oligotrophic areas of the eastern Mediterranean. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Phytoplankton; Productivity; Biomass; Size fractionation; Photosynthetic parameters; Eastern Mediterranean; Aegean Sea

1. Introduction

The Eastern Mediterranean is one of the world's poorest seas characterized by Azov (1991) as a "marine desert", a concept based on the impoverished phytoplankton biomass and productivity levels mainly

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due to phosphorus deficiency (Berland et al., 1980; Krom et al., 1991). Recent investigations in the Mediterranean Sea (Dolan, 2000; Christaki et al., 2001; Pitta et al., 2001; Van Wambeke et al., 2002) demonstrated a distinct longitudinal gradient of increasing oligotrophy from west to east in terms of the biomass and production of bacteria, autotrophic picoplankton and nanoplankton as well as the standing stocks of ciliate communities.

The Aegean Sea is one of the Eastern Mediterranean basins displaying a complicated hydrographic and ecological structure due to its geographical position between the Black Sea and the Ionian and Levantine Seas (Siokou-Frangou et al., 2002; Zervakis et al., 2000). The Aegean Sea is separated by the Cyclades plateau into two subbasins, the North Aegean and the South Aegean, with significantly different hydrographic characteristics due to the influence of Black Sea waters and Levantine Sea waters, respectively.

A number of studies on phytoplankton communities have been carried out in the Southern Aegean, and the topics covered include the temporal variations in biomass, primary production, bacterial production, species composition and underwater light penetration (Becacos-Kontos, 1977; Ignatiades, 1976, 1998; Ignatiades et al., 1995; Gotsis-Skretas et al., 1996, 1999; Turley et al., 2000; Psarra et al., 2000; Van Wambeke et al., 2000). The results demonstrated the extremely oligotrophic status (annual primary production 24.79 g C m^{-2} $year^{-1}$), the high optical transparency (Jerlov's Optical Type I) of the S. Aegean Sea waters and the significant relationship between bacterial and primary production. However, information on the temporal and spatial distribution of picoplankton and ultraplankton is missing, although they are important components of the oligotrophic waters (Li et al., 1983) because of their major role on the microbial food web (Azam et al., 1983). In their review on picoplankton production in the Mediterranean, Magazzu and Decembrini (1995) emphasized the scarcity of the relevant data from the Eastern Mediterranean, whereas Li et al. (1993) pointed out the importance of ultraplankton in this area. Moreover, the importance of heterotrophic bacteria in carbon dynamics, particularly in the oligotrophic Aegean Sea, has been demonstrated by Christaki et al. (1999) and Van Wambeke et al. (2000) whereas a strong coupling between

primary and bacterial production in the eastern Mediterranean has been discussed by Turley et al. (2000).

Studies on phytoplankton community structure and/or dynamics in the Northern Aegean do not exist up to date with the exception of data for bacterial production (Christaki et al., 1999) and chlorophyll α (Kucuksezgin et al., 1995), both characterizing the area as oligotrophic. Thus, among the open questions was the size structure of phytoplankton communities in terms of biomass and productivity in the two hydrologically contrasting subbasins, the N. and S. Aegean. Another interesting aspect to investigate was the potential uniformity, both over time and space of biomass and productivity in the Aegean Sea, a situation characterizing the oligotrophic systems (Hayward et al., 1983).

The consideration of light as a photosynthetic substrate in the studies of phytoplankton dynamics has received increasing attention in recent research but, as yet, there is no information about the photosynthesis–irradiance fundamental parameters such as light utilization efficiency (ε) and the photosynthetic quantum yield (φ) from the Eastern Mediterranean. Questions on physiological limitation in the ocean could be potentially resolved by assessing the variability of these photosynthetic parameters (Greene et al., 1994).

This study represents a part of the large MTP-II-MATER (MAST-III) multidisciplinary project in the Mediterranean Sea supported by the EU. It was designed to assess the variability in spatial and temporal patterns of phytoplankton dynamics in the N. and S. Aegean Sea. The work focused on determinations of size fractionation of biomass, primary productivity (in situ) and taxonomic composition of phytoplankton, as well as photosynthetic parameters (in situ) and underwater light penetration. These data provide the first comprehensive knowledge of the phytoplanktonic ecosystem in the Eastern Mediterranean.

2. Methods

2.1. Sampling and measurements of physical and chemical parameters

The experimental work was performed during Spring and Autumn 1997 and Spring 1998 at the

stations of the N. and S. Aegean Sea given in Fig. 1. Certain experiments at some stations, although scheduled, were not performed because of unfavorable weather conditions. Samples were collected from routine hydrocasts using a CTD rosette sampler from 1, 5, 10, 20, 30, 40, 50, 75, 100 and 120 m. Temperature and salinity were recorded using a Seabird Electronics SBE-911 + CTD profiler and the data were quality controlled by comparing salinity with that from bottle samples analyzed by an AUTOSAL salinometer.

Samples for nutrient analyses were collected with a rosette (12 Go-Flo bottles of 10 l fixed on a CTD probe) in 100 ml polyethylene bottles. Phosphate (Murphy and Riley, 1962) and ammonium (Koroleff, 1970) were measured on board by a Perkin Elmer Lambda 2S UV/VIS spectrophotometer in order to improve reliability. The samples for the analysis of nitrate + nitrite (Strickland and Parsons, 1968) and silicate (Mullin and Riley, 1955) kept continuously under deep freeze (− 20 °C) until their analysis in the laboratory by an ALPKEM Flow Solution III auto
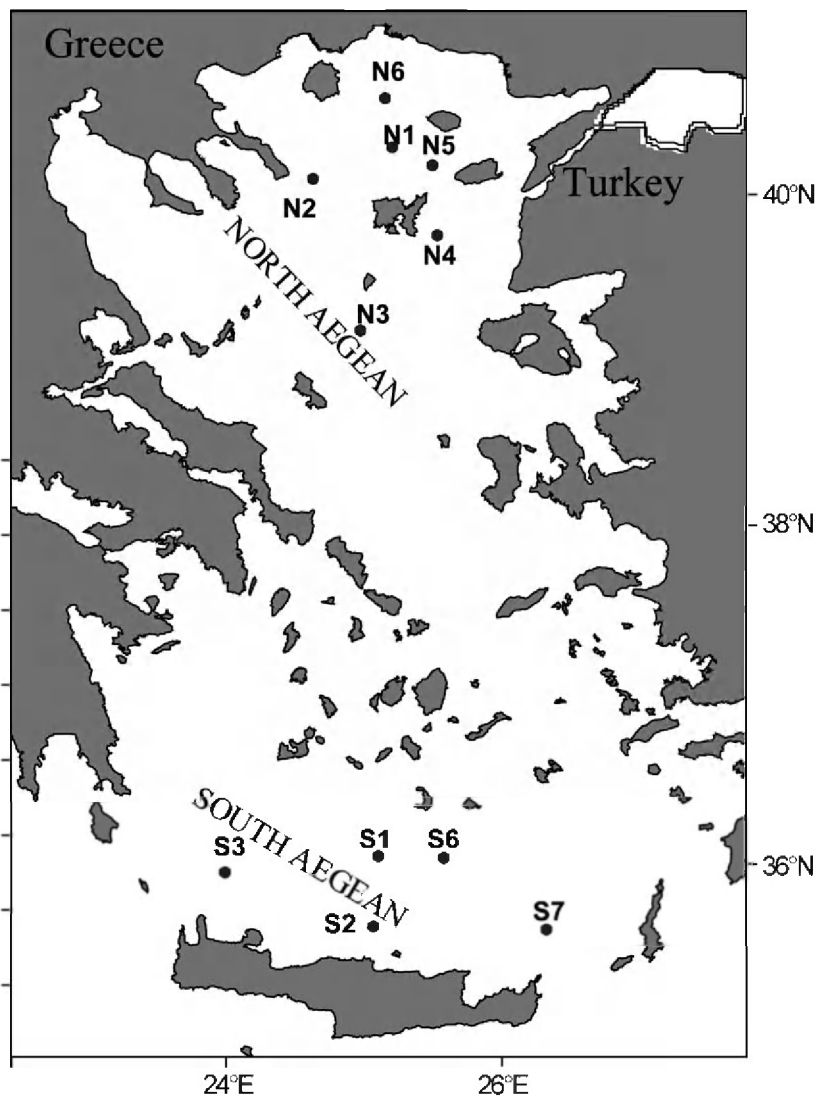

Fig. 1. Location of stations.

analyser. The precision was estimated at ± 0.1 μmol/l for nitrate and silicate and ± 0.02 μmol/l for phosphate and nitrite. The detection limit was 0.01 μmol/l for phosphate, 0.02 μmol/l for ammonia and 0.08 for nitrate + nitrite and 0.22 for the silicate.

Standard solutions of orthophosphate, nitrate and silicic acid prepared from Wako (Japan) were used additionally to the stock and working standards for the control of the methods precision. The NCMR nutrient laboratory has participated in several intercalibration exercises within the framework of POEM (Physical Oceanography of the Eastern Mediterranean) and of different MAST programs. It is also participating since 1993 in the EC intercalibration projects: QUA-SIMEME (Quality Assurance of Information in Marine Environmental Monitoring in Europe) and QUASH (Quality Assurance of Sampling and Sample Handling).

2.2. Size fractionated chlorophyll α

Water samples (2 l) collected from each sampling depth were size fractionated with separate filtration through polycarbonate Millipore filters having porosities 0.2, 1.2 and 3.0 μm. The filters were kept deep frozen and analyzed at the laboratory (Holm-Hansen et al., 1965) on a TURNER 00-AU-10 fluorometer (N. Aegean) and on a TURNER 112 fluorometer (S. Aegean). Since there is no internationally accepted definition, the chl α size fraction range 0.2–1.2 μm is referred to as picoplankton cells, the fraction range 1.2–3.0 μm as ultraplankton cells and the fraction >3.0 μm as nano + microplankton. These size classes approximate those given in the literature for the corresponding denominations (Murphy and Haugen, 1985; Joint, 1986).

2.3. Size fractionated primary production

Photosynthetic productivity was measured with the in situ ^{14}C method of Streeman-Nielsen (1952). The samples were dispensed in 250 ml transparent polycarbonate bottles (three light and one dark for each depth) and each one was inoculated with 5 μCi ^{14}C-NaHCO$_3$ and incubated at the collection depths for 2 h at noon time (closely to 12–2 p.m.). Fractionation was carried out by filtration through separate 0.2, 1.2 and 3.0 μm polycarbonate Millipore filters. Filters

were placed in scintillation vials, acidified with 0.5 N HCl and counted in a liquid scintillation counter (samples from the N. Aegean Sea in a BECKMAN LS6500 and from the S. Aegean Sea in a PACKARD TRICARB-2100TR). The daily production in each area was calculated by multiplying the mean depth-integrated production (derived from the three sampling periods at the six stations in N. Aegean and at the five stations in S. Aegean) by 12 h day^{-1} (Bienfang et al., 1984).

2.4. Quantitative and qualitative phytoplankton analysis

Phytoplankton samples were fixed with lugol solution and examined under an inverted light microscope (Utermohl, 1958) for phytoplankton (>5 μm).

2.5. Underwater light penetration

Underwater irradiance was measured with a LiCor 1800 quantum meter. The total diffuse attenuation coefficient, k_d, for downward irradiance was determined from the equation:

$$E_d(z) = E_d(0)e^{-k_d z}$$

where E_d (z) and E_d (0) are the values of downward photosynthetic available radiation (PAR, 400–700 nm) at z meters and just below the surface, respectively. The above equation is more satisfactory for monochromatic light but it can be used for a broad waveband as a useful approximation (Kirk, 1986). The average value of the attenuation coefficient $\bar{k}_d$ for the euphotic zone ($Z_{1\%}$ of surface irradiance) was used in this investigation (Kirk, 1986).

The photosynthetic parameters measured by the in situ experimentation were the assimilation number (P^B), the light utilization efficiency (ε) and the photosynthetic quantum yield (φ).

Assimilation number P^B is the photosynthetic rate per unit chl α:

$$P^B[\text{mg C (mg chl } \alpha)^{-1} \text{ h}^{-1}]$$

Light utilization efficiency (ε) was determined from the equation:

$$\varepsilon = \text{PSR} \cdot \text{PAR}^{-1} \cdot k_d^{-1}$$

where PSR is the photosynthetically stored radiation derived from the photosynthetic rate (mg C m^{-3} h^{-1}). The units used for PSR (mol C m^{-3} h^{-1}), PAR (mol quanta m^{-2} h^{-1}) and k_d (m^{-1}) produced a dimensionless ε quantity (Morel, 1978, 1982). The calculation of light utilization efficiency was performed using data of the photosynthetic rate collected near the maximum of daily irradiance and it was expressed as an overall temporal average in terms of percentage ($\bar{\varepsilon}$%).

The in situ photosynthetic quantum yield $\varphi_{\text{in situ}}$ (mol C mol quanta^{-1}) was calculated from the equation:

$$\varphi_{\text{in situ}} = \text{PSR} \cdot \text{PUR}^{-1}$$

PUR, the photosynthetically usable radiation (Morel, 1978) was estimated from the fractional absorbance of algae (Banister, 1974; Dubinsky, 1980; Dubinsky et al., 1984):

$$\text{PUR} = [(k_c\text{chl})(k_d)^{-1}][(\text{PAR}_{z_1} - \text{PAR}_{z_2})(z_2 - z_1)^{-1}]$$

where k_c is the spectral extinction coefficient for the absorption of light by phytoplankton pigments having the value 0.016 (m^2 mg^{-1} chl) that can be considered as constant (Banister, 1974; Smith and Baker, 1978) at a water layer between z_1 and z_2 meter depths. The estimation of the phytoplankton photosynthetic quantum yield denoted as φ_{max} in this study has derived from data of PSR and PUR at depth $Z_{1\%}$ since, accord-

ing to Dubinsky et al. (1984) and Kishino et al. (1986), the $\varphi_{\text{in situ}}$ at depth $Z_{1\%}$ approximates the φ_{max}.

Due to malfunctioning of the equipment in March 1997, measurements of underwater light penetration were performed in September 1997 and March 1998.

3. Results

3.1. Physical and chemical parameters

An evaluation of the overall means of the physical and chemical parameters derived from combined data over stations and depths in Northern and Southern Aegean Sea are presented in Table 1. The data collected during three sampling periods, March–April and September, are designated as Spring and Autumn, respectively. In general, temperatures were lower in Spring (N. Aegean: 13.195–14.345 °C; S. Aegean: 15.089–15.871 °C) than in Autumn (N. Aegean : 16.859 °C; S. Aegean: 17.885 °C) in both regions and always more depressed in the N. than in S. Aegean Sea. Average salinity levels were also lower in N. Aegean (Spring: 38.248–38.250 psu; Autumn: 37.956 psu) than in the S. Aegean (Spring: 39.013–38.955 psu; Autumn: 39.108 psu).

A regional and temporal fluctuation was observed in the diffuse attenuation coefficient $\bar{k}_d$ and the depth $\bar{Z}_{(1\%)}$ where PAR is reduced to 1% of its surface value. In N. Aegean the $\bar{k}_d$ varied between 0.051 and 0.055

Table 1
Overall means and standard deviations (in parentheses) of physical, chemical and biological parameters in North and South Aegean Sea

Area	North Aegean			South Aegean		
Parameter	March 28–April 1, 1997	September 19–24, 1997	March 12–15, 1998	March 6–9, 1997	September 11–15, 1997	March 12–15, 1998
Temperature (°C)	13.195 (0.401)	16.859 (0.251)	14.341 (0.567)	15.089 (0.160)	17.885 (0.162)	15.871 (0.211)
Salinity (psu)	38.248 (0.322)	37.956 (0.503)	38.250 (0.756)	39.013 (0.014)	39.108 (0.069)	38.955 (0.191)
Attenuation coefficient, $\bar{k}_d$ (m^{-1})	–	0.051 (0.04)	0.055 (0.010)	–	0.037 (0.012)	0.040 (0.013)
Euphotic zone, $\bar{Z}_{(1\%)}$ (m)	–	100 (16)	80 (12)	–	147 (22)	110 (28)
P-PO$_4$ (µM)	0.031 (0.011)	0.032 (0.006)	0.019 (0.009)	0.023 (0.002)	0.049 (0.013)	0.013 (0.003)
N-NH$_3$ (µM)	0.135 (0.051)	0.067 (0.037)	0.162 (0.061)	0.397 (0.408)	0.316 (0.122)	0.215 (0.106)
N-(NO$_3$ + NO$_2$) (µM)	0.621 (0.153)	0.287 (0.035)	0.442 (0.216)	0.881 (0.217)	0.395 (0.139)	0.570 (0.254)
Si-SiO$_2$ (µM)	1.207 (0.349)	1.414 (0.157)	2.395 (0.694)	1.177 (0.199)	1.398 (0.228)	1.625 (0.134)
Chl α (mg m^{-3})	0.379 (0.262)	0.260 (0.126)	0.344 (0.327)	0.301 (0.105)	0.119 (0.091)	0.217 (0.032)
Primary production (mg C m^{-3} h^{-1})	1.842 (1.626)	0.261 (0.229)	0.478 (0.524)	0.508 (0.351)	0.167 (0.086)	0.335 (0.199)

m^{-1} and the $\bar{Z}_{(1\%)}$ between 100 and 80 m in Autumn 1997 and Spring 1998, respectively. In S. Aegean, the euphotic layer was thicker at both seasons since the Autumn–Spring range was for $\bar{k}_d$ 0.037–0.040 m^{-1} and for $\bar{Z}_{(1\%)}$ 147–110 m.

All nutrients exhibited very low concentrations not differing significantly between the N. and S. Aegean Sea and, without distinct temporal trends with the exception of N-$(NO_2 + NO_3)$ that showed somehow elevated values in Spring in relation to Autumn. The average levels in the entire area ranged for P-PO_4 from 0.013 to 0.049 μM, for N-NH_3 from 0.067 to 0.397 μM, for N-$(NO_3 + NO_2)$ from 0.287 to 0.881 μM and for Si-SiO_2 from 1.177 to 2.395 μM.

3.2. Water column structure

The average profiles (along with the corresponding standard deviation) of six CTD stations from the North and five stations from the S. Aegean Sea are presented in Fig. 2. In Spring 1997, the surface layer of the N. Aegean was characterized by lower temperatures (11–13 °C) than at depth 100 m (~ 14 °C), reflecting the influence of the Black Sea waters outflow. On the contrary, the upper 100 m of the South Aegean were completely homogenized with temperature of about 15 °C. In Autumn 1997, regular temporal thermoclines were developed both in the N. and S. Aegean Sea but the upper layer of the North (at 18–20 °C) was significantly colder than South Aegean (23 °C) due to large amounts of heat absorbed by the cold surface layer of the Black Sea water.

The salinity profiles also present a vertical structure and temporal variability. In both seasons, the surface layer of the N. Aegean was characterized by low salinity ranging from 33 to 36 psu. The salinity increased with increasing depth, to exceed 38 psu
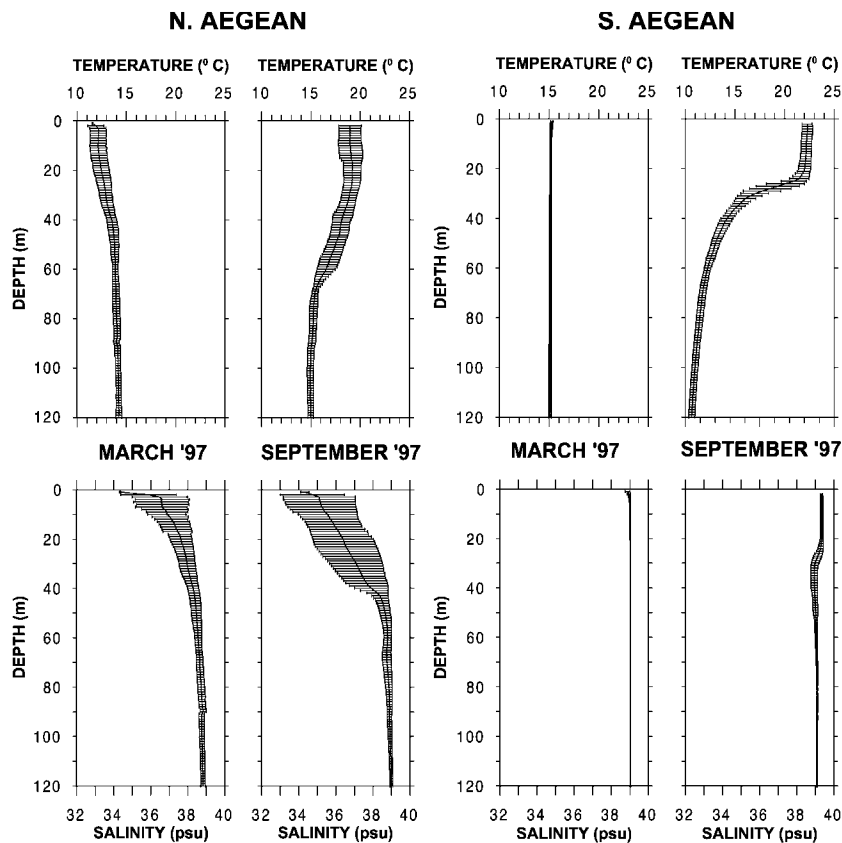

Fig. 2. Average temperature and salinity profiles (standard deviations are presented by horizontal lines) in the N. and S. Aegean Sea.

below 40 m, where waters of the Levantine and the S. Aegean constitute the water column. On the contrary, the S. Aegean was fully homogenized down to 120 m in Spring 1997, at a salinity of 39 psu. In Autumn, the 25-m-thick surface layer in the S. Aegean Sea was characterized by an increased salinity, at 39.2 psu, due to the increased evaporation of the region.

3.3. Spatial distribution of chl α and primary production

The spatial distribution of size fractionated chl α and primary production (integral means over three sampling periods) including total values (sum of all fractions) at the six N. Aegean stations and the five S. Aegean stations are shown in Fig. 3A. Two important features characterized this distribution: (a) the N. Aegean stations N4 and N5 located close to the Dardanelle Straits (Fig. 1) showed elevated total chl α concentrations (38.55–50.65 mg m^{-2}) and total primary production rates (113.29–157.14 mg C m^{-2} h^{-1}) in relation to the other stations of this area and (b) in the N. Aegean the levels of total chl α concentrations (29.75–50.65 mg m^{-2}) and primary production rates (41.48–157.14 mg C m^{-2} h^{-1}) were higher than in the S. Aegean Sea (chl α: 20.12–30.76 mg m^{-2}; primary production: 29.99–42.39 mg C m^{-2} h^{-1}). The picoplankton fraction predominated and accounted for the 61% to 47% of total chl α and the 59% to 44% of total primary production in the N. and S. Aegean Sea, respectively. Throughout the sampling area, the levels of nano+microplankton were next in abundance proportions of total chl α (21–31%) and primary production (20–33%) and the levels of the ultraplankton were the lowest contributing the 18–22% of total chl α and the 20–23% of total primary production.

3.4. Temporal distribution of chl α and primary production

Biomass and productivity exhibited (Fig. 3B) a well expressed Spring maximum (Spring 1997 and Spring 1998) and an Autumn decline in 1997. The Spring 1997 total chl α values ranged from 39.15 to 34.28 mg m^{-2} and total primary production from 149.55 to 56.21 mg C m^{-2} h^{-1} in the N. and S. Aegean Sea, respectively. The values of these para-

meters were reduced in Autumn 1997 (chl α: 30.16 to 18.69 mg m^{-2}; primary production 43.80 to 21.67 mg C m^{-2} h^{-1}) and they had risen again in Spring 1998 (chl α: 38.25 to 25.62 mg m^{-2}; primary production 56.49 to 33.32 mg C m^{-2} h^{-1}) in the N. and S. Aegean Sea, respectively. Most of the biomass (51–59%) and the photosynthetic rate (43–61%) was due to the picoplankton fraction that showed a well expressed temporal variability and followed by the nano+microplankton fraction contributing the 23–30% of chl α and the 21–33% of primary production. There were less marked temporal changes in the ultraplankton μm fraction that accounted for the 18–24% of the total chl α and primary production.

Statistical analysis showed a weak temporal relationship only between the N-(NO$_2$+NO$_3$) concentrations and phytoplankton total biomass.

3.5. Vertical distribution of chl α and primary production

The vertical profiles of total chl α (Fig. 4) showed Spring maxima at 20–30 m (0.54–0.65 mg m^{-3}) in the N. Aegean and at 30–40 m (0.25–0.39 mg m^{-3}) in the S. Aegean but their Autumn maxima were found at deeper depths at both areas, e.g., at 40 m (0.37 mg m^{-3}) and 100 m (0.31 mg m^{-3}), respectively. Picoplankton was the main contributor in both areas consisting up to 71–75% of total chl α and predominating all fractions at most depths. Ultraplankton and nano+microplankton displayed no perceptible vertical patterns.

In the N. Aegean, the pattern of total primary production displayed similar shapes at both seasons with maximum (3.76 mg C m^{-3} h^{-1}) at 20 m depth in Spring 1997 and at 10 m in Autumn 1997 (0.52 mg C m^{-3} h^{-1}) and Spring 1998 (1.21 mg C m^{-3} h^{-1}). Picoplankton was the dominant fraction (48–63%) in Spring 1997 but in Autumn 1997 approached the concentrations of the two other fractions whereas in Spring 1998, it was surpassed quantitatively by nano+microplankton in the upper 10 m and shared proportions with the other fractions thereafter. In the S. Aegean, total primary production maximum was recorded at 10 m (0.84 mg C m^{-3} h^{-1}) in Spring 1997, at 30 m (0.27 mg C m^{-3} h^{-1}) in Autumn 1997 and along the 10–30 m (0.49 mg C m^{-3} h^{-1}) in Spring 1998. Nano+microplankton dominated the
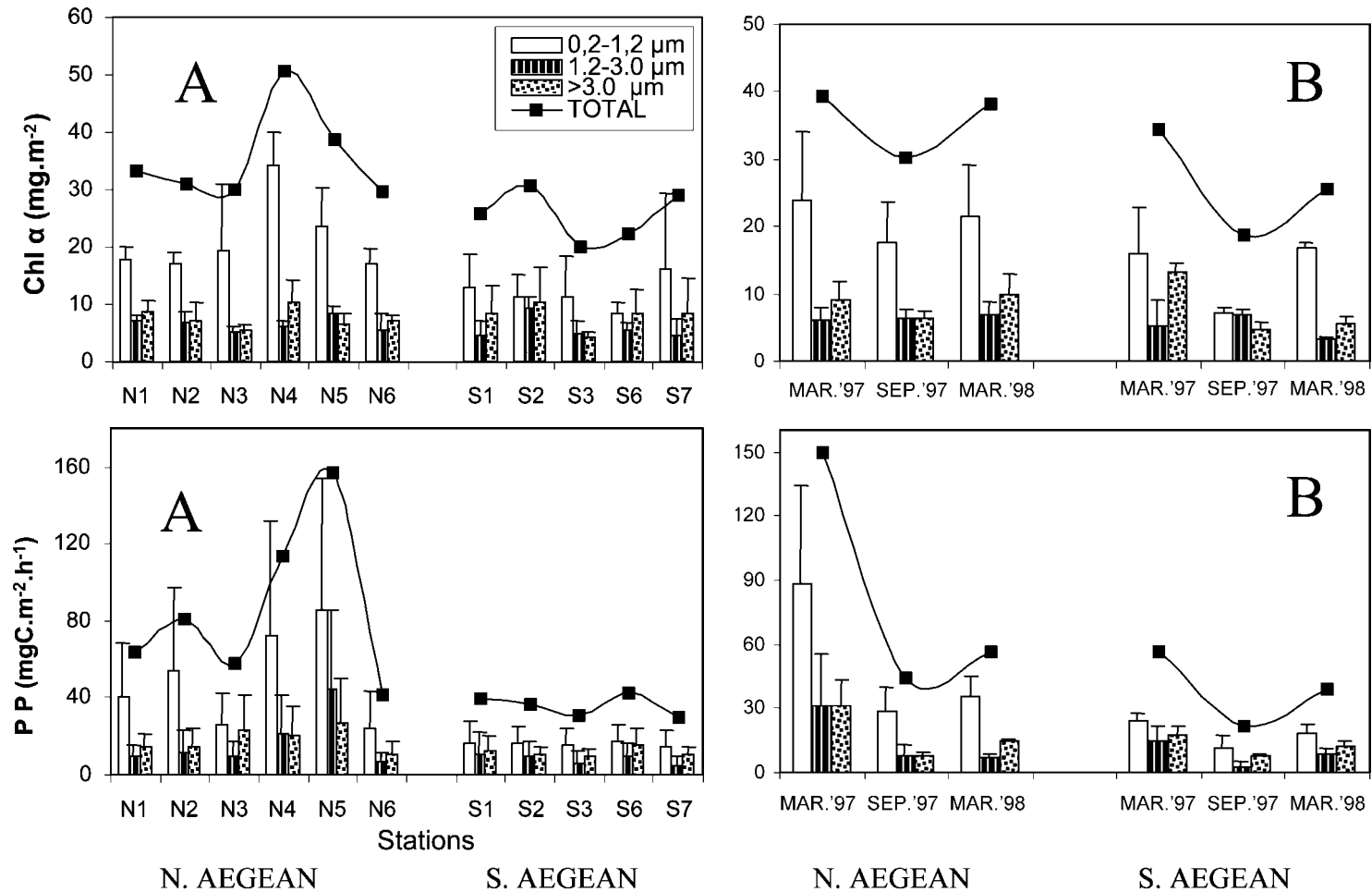
Fig. 3. Spatial (A) and temporal (B) distribution of chlorophyll a (chl a) and primary production (PP) fractions in the N. and S. Aegean Sea. [picoplankton (0.2–1.2 μm), ultraplankton (1.2–3.0 μm), nano+microplankton (>3.0 μm)].
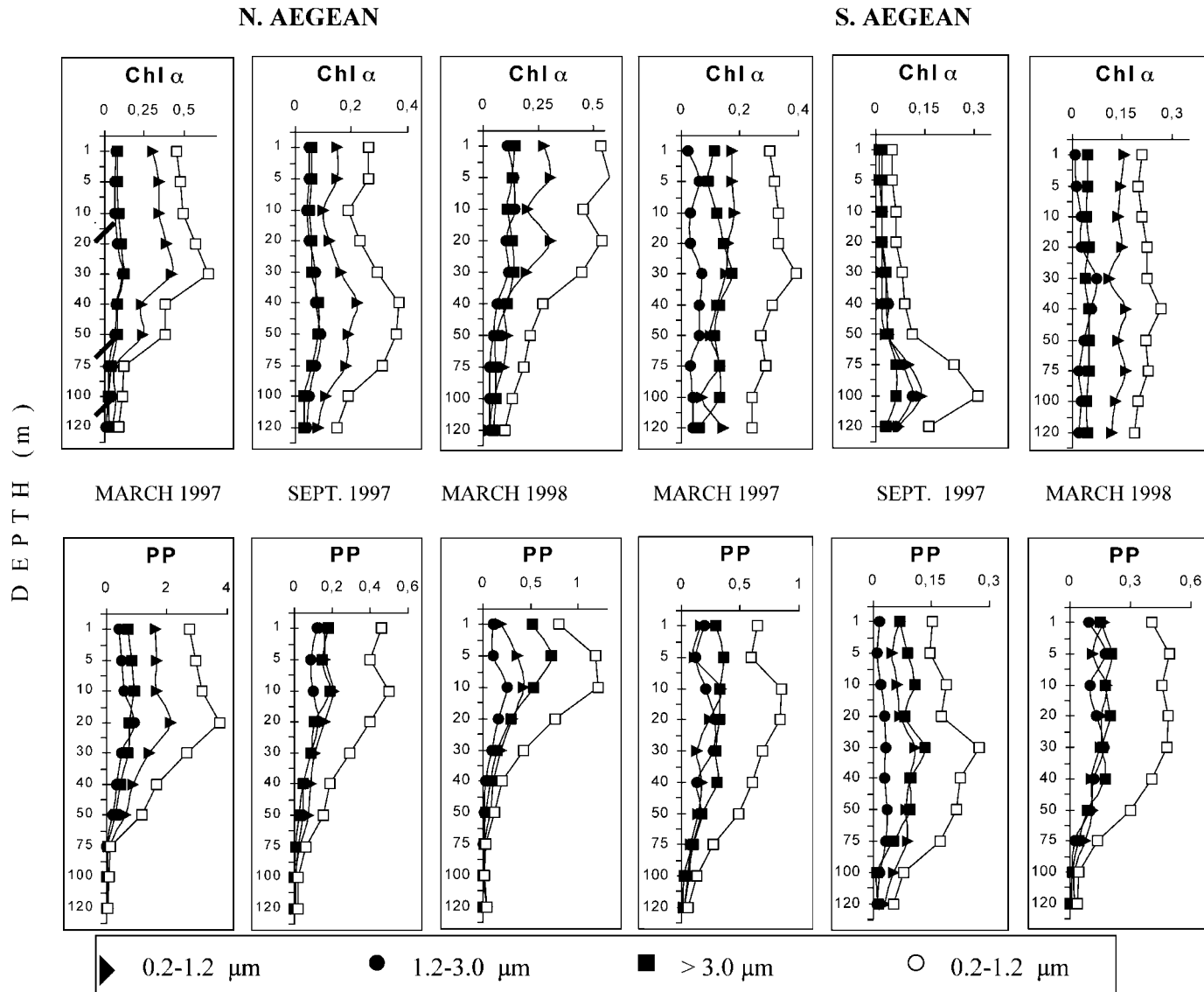
N. AEGEAN

S. AEGEAN

Fig. 4. Vertical distribution of chlorophyll α (chl a, mg m^{-3}) and primary production (PP, mg C m^{-3} h^{-1}) fractions in the N. and S. Aegean Sea. [picoplankton (0.2–1.2 μm), ultraplankton (1.2–3.0 μm), nano+microplankton (>3.0 μm)].

upper 10 m in only two occasions (Spring and Autumn 1997) but at deeper layers there was almost uniform distribution and relatively equal quantitative participation of the three fractions. A statistical analysis showed the lack of a relationship between the nutrient vertical distribution and phytoplankton biomass fractions.

Table 2 shows the results of the analysis of variance for testing the effect of station, depth and season on chl α and primary production fractions. In the N. Aegean, there was a highly significant ($P \leq 0.005$) spatial, vertical and temporal influence on the biomass and productivity of all size classes. Highly significant effects ($P \leq 0.01$) were also found in most S. Aegean size classes with the exception of certain nonsignificant relationships concerning the station versus the size class >3.0 μm of chl α, and the depth versus the size classes 0.2–1.2 and >3.0 μm of chl α.

3.6. Overall evaluations of size fractionated biomass and primary production data

An overall evaluation of the fraction's concentrations of chl α and primary production integrated over depth and averaged over station and season as well as their contribution to the total concentrations of these parameters in the N. and S. Aegean Sea is given in

Fig. 5. In the N. Aegean, approximately half of the total phytoplankton carbon was contributed by picoplankton constituting the 56% (18.43 mg chl α m^{-2}) of total biomass (32.84 mg chl α m^{-2}) and the 51% (34.58 mg C m^{-2}. h^{-1}) of total productivity (67.75 mg C m^{-2} h^{-1}). In the S. Aegean, the picoplankton was also the dominant fraction constituting the 49% (13.38 mg chl α m^{-2}) of total biomass (27.02 mg chl α m^{-2}) and the 41% (13.28 mg C m^{-2} h^{-1}) of total productivity (32.42 mg C m^{-2} h^{-1}). The relative contributions of the two other fractions showed a common pattern in both areas with an increased contribution of nano+microplankton (biomass: 23–31%, productivity: 28–32%) in relation to ultraplankton (biomass: 18–19%, productivity: 20–26%).

The comparison of N. versus S. Aegean Sea based on the overall data (Table 2) showed also a significant difference ($P \leq 0.05$) between all chl α and primary production fractions, thus making stronger the evidence of the effect of "space" on the productivity capacity in the Aegean Sea.

3.7. Photosynthetic in situ parameters

Light utilization efficiency ($\bar{\varepsilon}$%). and quantum yield ($\bar{\varphi}_{max}$) exhibited a temporal trend having higher values in Spring than in Autumn as well as a cell size

Table 2
Summary of the analysis of variance statistics for testing the differences in chlorophyll α concentrations (CHL A) and in primary production rates (PR.PR.) of the three fractions and the corresponding TOTAL values in N. and S. Aegean Sea

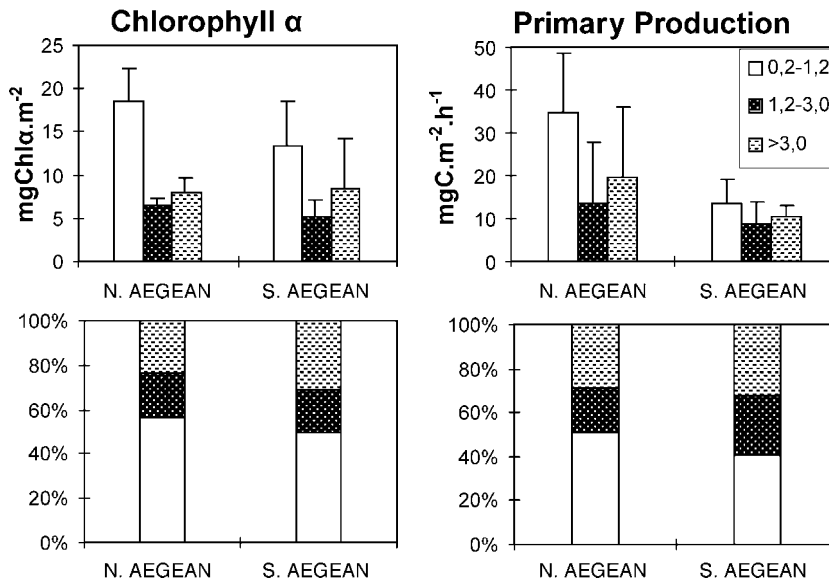| Area	Variable	Fractions		0.2–1.2 μm		1.2–3.0 μm		>3.0 μm		Total	
		Source	df	F	P	F	P	F	P	F	P
N. Aegean	CHL A	Station	6	5.08	0.0001	3.21	0.0053	11.70	0.0001	6.29	0.0001
		Depth	9	11.50	0.0001	6.69	0.0001	15.56	0.0001	14.62	0.0001
		Season	2	18.38	0.0001	5.44	0.0052	34.72	0.0001	10.09	0.0001
	PR.PR.	Station	4	4.41	0.0024	4.72	0.0015	5.59	0.0004	5.13	0.0008
		Depth	9	14.41	0.0001	7.11	0.0001	29.51	0.0001	26.24	0.0001
		Season	2	11.55	0.0001	31.51	0.0001	54.61	0.0001	130.49	0.0001
S. Aegean	CHL A	Station	3	5.87	0.0011	12.89	0.0001	1.28	0.2863*	0.87	0.0524
		Depth	9	0.79	0.6258*	8.59	0.0001	1.36	0.2221*	1.44	0.0532
		Season	2	54.64	0.0001	9.12	0.0003	74.56	0.0001	74.95	0.0001
	PR.PR.	Station	3	3.32	0.0237	1.51	0.0198	8.75	0.0001	7.21	0.0002
		Depth	9	5.81	0.0001	5.75	0.0001	12.11	0.0001	19.45	0.0001
		Season	2	9.76	0.0002	33.46	0.0001	31.44	0.0001	62.95	0.0001
North vs. South	CHL A	Overall	1	8.28	0.0183	6.14	0.0351	5.12	0.0537	6.31	0.0333
	PR.PR.	Overall	1	11.91	0.0072	5.89	0.0510	6.35	0.0327	10.72	0.0096

* Not statistically significant.

Fig. 5. Chlorophyll α and primary production (values integrated over depth and averaged over station and season) of the three fractions and their corresponding percentage in the N. and S. Aegean Sea. [picoplankton (0.2–1.2 μm), ultraplankton (1.2–3.0 μm), nano + microplankton (>3.0 μm)].

trend being higher for picoplankton in relation to ultraplankton and nano+microplankton (Table 3). In the N. Aegean, the levels of the three factions of $\bar{\varepsilon}\%$ fluctuated from 0.64–0.48–0.44% (Autumn 1997) to 2.53–1.79–0.96% (Spring 1998) and in S. Aegean from 0.62–0.31–0.22% (Autumn 1997) to 1.54–1.15–0.95% (Spring 1998).

The $\bar{\varphi}_{max}$ values of the three fractions in the N. Aegean were 0.046–0.36–0.024 mol C mol quanta^{-1} in Autumn 1997 whereas in Spring 1998, the values of this parameter increased (0.056–0.057–0.034 mol C mol quanta^{-1}). In the S. Aegean, the $\bar{\varphi}_{max}$ levels recorded in Autumn were 0.039–0.031–0.015 mol C mol quanta^{-1} and in Spring 1998, these values also

Table 3
Seasonal overall mean and standard deviation (in parenthesis) of in situ photosynthetic parameters in N. and S. Aegean Sea

Fractions (μm)	Season					
	September 1997			March 1998		
	Photosynthetic parameters					
	$\bar{\varepsilon}\%$	$\bar{\varphi}_{(max)}$ (at ~ $Z_{1\%}$)	$\bar{P}^B$	$\bar{\varepsilon}\%$	$\bar{\varphi}_{(max)}$ (at ~ $Z_{1\%}$)	$\bar{P}^B$
North Aegean						
0.2–1.2	0.64 (0.06)	0.046 (0.002)	1.06 (0.90)	2.53 (0.81)	0.056 (0.008)	1.44 (0.37)
1.2–3.0	0.49 (0.09)	0.036 (0.008)	1.44 (0.82)	1.79 (0.12)	0.057 (0.010)	1.54 (0.50)
>3.0 (μ)	0.44 (0.18)	0.024 (0.009)	1.62 (0.69)	0.96 (0.09)	0.034 (0.002)	1.81 (0.46)
South Aegean						
0.2–1.2	0.62 (0.08)	0.039 (0.004)	1.02 (0.41)	1.54 (0.06)	0.047 (0.005)	1.32 (0.44)
1.2–3.0	0.31 (0.05)	0.031 (0.003)	1.77 (0.63)	1.15 (0.10)	0.038 (0.005)	2.66 (0.53)
>3.0	0.22 (0.09)	0.015 (0.004)	1.82 (0.62)	0.95 (0.05)	0.033 (0.004)	2.74 (0.28)

Units of photosynthetic parameters: ε = dimensionless, φ = mol C (mol quanta^{-1}), P^B = mg C mg chl α^{-1} h^{-1}.

increased $(0.047-0.038-0.033$ mol C mol quanta^{-1}) in all three fractions. These data demonstrate also that both light utilization efficiency and quantum yield had higher values in the North than in the South Aegean Sea.

Assimilation ratio ($\bar{P}^B$) was also determined for the three fractions regionally and temporally (Table 3). The values of this parameter in N. Aegean were 1.06–1.44–1.62 mg C mg chl α^{-1} h^{-1} for the three fractions in Autumn 1997 and they were somehow increased in Spring 1998 (1.44–1.54–1.81 mg C mg chl α^{-1} h^{-1}). In S. Aegean, the Autumn 1997 values (1.02–1.77–1.82 mg C mg chl α^{-1} h^{-1}) increased also in Spring 1998 (1.32–2.66–2.74 mg C mg chl α^{-1} h^{-1}).

3.8. Structure of phytoplankton communities

Cell abundances (means over depth and station) exhibited a temporal variation (Fig. 6A) in both areas with maxima in Spring (N. Aegean: $4.5 \times 10^3 - 1.5 \times 10^4$ cells l^{-1}; S. Aegean: $1.7 \times 10^4 - 5.1 \times 10^4$ cells l^{-1}) and minima in Autumn (N. Aegean: 1.1×10^3 cells l^{-1}; S. Aegean: 5.8×10^3 cells l^{-1}). Qualitative comparisons in terms of percentage (Fig. 6B) showed that the spectrum of the major taxa, e.g., diatoms, dinoflagellates, coccolithophores, others (flagellates, silicoflagellates) in Spring 1997 differed from that in Spring 1998 in both areas. Thus, in Spring 1997, coccolithophores dominated in North (46%) and South (40%) Aegean Sea whereas in
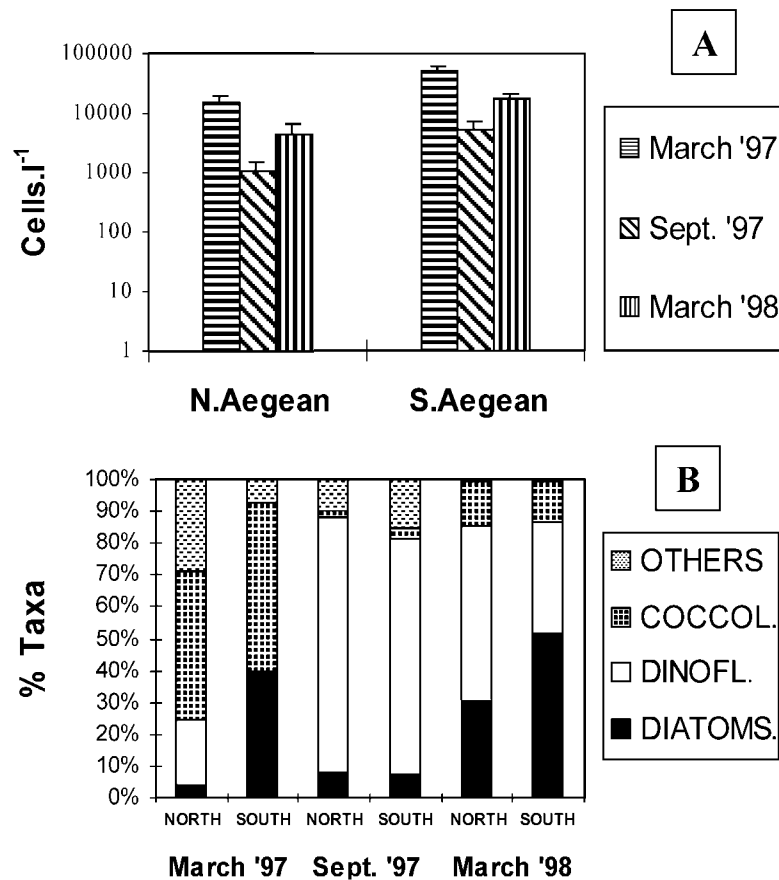

Fig. 6. Temporal variation of mean (over depth and station) phytoplankton concentrations and the corresponding percentage of taxa composition the N. and S. Aegean Sea.

Spring 1998, dinoflagellates (54%) and diatoms (51%) dominated, respectively. In Autumn, dinoflagellates were the dominant taxa in both areas consisting the 80% and 74% of the population in the North and South Aegean Sea, respectively.

4. Discussion

The hydrological characteristics of the N. and S. Aegean Sea have been described in detail by a number of investigators (Theocharis and Georgopoulos, 1993; Balopoulos et al., 1999; Georgopoulos et al., 1999; Theocharis et al., 1999; Zervakis et al., 2000). The water-column structure of the N. Aegean is influenced by the input of brackish waters from the Black Sea through the Dardanelles generating a strong salinity stratification in the upper layers during both seasons (Fig. 2). Furthermore, the Black Sea waters being significantly colder in Spring produced in the N. Aegean a 20-m thick surface layer cooler than the subsurface waters at that season. On the contrary, the S. Aegean was characterized by a different water-column structure since in Spring, the upper 120 m were homogeneous in terms of temperature and salinity whereas in Autumn a well defined thermocline and a weaker halocline was developed below 25 m depth.

According to several studies, the extremely oligotrophic character of the Eastern Mediterranean Sea is mainly due to phosphorus depletion (Krom et al., 1991, 1993; Kucuksezgin et al., 1995) but it has also been attributed to nitrogen limitation (Ignatiades and Moschopoulou, 1988; Dugdale and Wilkerson, 1988). The levels of phosphorus and nitrogen found in this study (Table 1) are comparable to those reported by the above investigators, thus confirming the poverty of both nutrients in the Aegean Sea. In this oligotrophic environment, the overall average level of chl α ranged from 0.119 to 0.371 mg m^{-3} and that of primary production from 0.167 to 1.842 mg C m^{-3} h^{-1} (Table 1). These estimates approach the values given for the Eastern Mediterranean (Azov, 1986, 1991; Berman et al., 1986) as well as for other oligotrophic areas of the tropical N. Atlantic (Claustre and Marty, 1995) and the equatorial Pacific (Everitt et al., 1990).

The optical transparency of the Aegean Sea waters is a further indication of the oligotrophic character of

this area. Jerlov (1997) defined (in terms of quanta 350–700 nm) the most transparent Optical Water Type I to have the depth of the euphotic zone $\bar{Z}$ (1%) m at 100–120 m depth and the average attenuation coefficient $\bar{k}_d$ to be 0.052 m^{-1} (for 0–100 m depth). On the basis of the present data (Table 1), the S. Aegean Sea waters belong to Optical Water Type I since the Autumn–Spring range was for $\bar{k}_d$ 0.037–0.040 m^{-1} and for $\bar{Z}_{(1\%)}$ 147–110 m and these results are in agreement with the results of a previous investigation in this area based on the estimation of spectral diffuse attenuation coefficient (Ignatiades, 1998). The N. Aegean Sea waters, having $\bar{k}_d$ 0.051 m^{-1} and $\bar{Z}_{(1\%)}$ 100 m in Autumn belong also to Type I but in Spring, the levels of $\bar{k}_d$ (0.055 m^{-1}) and $\bar{Z}_{(1\%)}$ (80 m) may indicate a shift to the Optical Type IA.

Previous investigations of phytoplankton size class structure in the oligotrophic waters of the equatorial oceanic ecosystems characterized them as the most favorable environments for the growth of picoplankton and they estimated its contribution to total chl α up to 70% (Herbland et al., 1985) and to total primary production up to 80% (Li et al., 1983). A review on picoplankton studies (Magazzu and Decembrini, 1995) in the Mediterranean Sea reported that its share to total chl α ranged from 35% (straits of Messina) to 75% (Ligurian Sea) and to total primary production from 31% (straits of Messina) to 92% (Ionian Sea). In the Aegean Sea, according to the results of this work, picoplankton dominated the size class structure, accounting on average (N. and S. Aegean) for 53% of total chl α and 46% of total primary production.

Light utilization efficiency (ε), photosynthetic quantum yield (φ_{max}) and assimilation number P^B are fundamental parameters of photosynthesis. There are two different but equally important experimental techniques applied for the determination of the photosynthetic parameters: one is based on in situ measurements of photosynthesis and underwater light irradiance (Dubinsky et al., 1984; Kishino et al., 1986; Morel et al., 1996) and the second is based on shipboard incubation experiments designed to determine the photosynthesis–irradiance relationships ($P–I$ curves) employed in modeling of primary production (Fasham and Platt, 1983; Maranon and Holligan, 1999). In this work, the determination of photosynthetic parameters was made within the framework of the in situ measurements of primary production and underwater light

penetration; the advantage of this method lies in the ability to determine the carbon fixation rate in the natural environment without introducing artificial temperature and light conditions (Bannister and Weidemann, 1984).

Examination of published data showed a lack of studies determining in situ the light utilization efficiency ($\bar{\varepsilon}$) and quantum yield ($\bar{\varphi}_{max}$) in different phytoplankton size fractions. The most important feature of the present data is that both $\bar{\varepsilon}$ and $\bar{\varphi}_{max}$ were affected by cell size since values of these parameters were higher for picoplankton in relation to ultraplankton and nano+microplankton (Table 3). This trend might be attributed to pigment "package effect" phenomenon, i.e., the diminution of the light collection efficiency as cell size increases. This phenomenon makes the picoplankton cells more efficient in utilizing light and converting the absorbed quanta to photosynthetic products than cells of bigger sizes (Kirk, 1986).

Existing information has shown that environmental conditions such as optical water type (Morel, 1978), nutrient limitation (Kolber et al., 1994; Babin et al., 1996), irradiance levels (Moisan and Mitchell, 1999) and changes in community composition (Schofield et al., 1993) affect the photophysiology of phytoplankton. The results of this work have also demonstrated a temporal and regional variability of both $\bar{\varepsilon}$ and $\bar{\varphi}_{max}$ at all size fractions. Thus, all fractions of these parameters were higher in Spring than in Autumn and in the N. Aegean than in the S. Aegean Sea. These differences could be associated with the recorded differences in the synthesis of species and as well as in the levels of the incident radiation between the two seasons and areas. The range of variability in $\bar{\varepsilon}$ and $\bar{\varphi}_{max}$ observed in the different size fractions of this study is as large as has been reported previously for phytoplankton natural assemblages (Morel, 1978; Kishino et al., 1986; Babin et al., 1996).

The few reported assimilation numbers (P_{max}^{B}) for phytoplankton size classes have been derived from the $P-I$ curves. Their values representing assimilation at the maximum photosynthetic rate and light saturation cannot be compared with the in situ $\bar{P}^{B}$ values of this work that were estimated on overall spatial and temporal statistical means, but it is interesting to look at their trends. Thus, Platt et al. (1983) and Herbland et al. (1985) demonstrated that the assimilation num-

bers were higher for picoplankton than for larger phytoplankton, because of the lower chlorophyll content of picoplankton. However, the data of Joint and Pomroy (1986) showed that, depending on the species composition, irradiance and nutrient supply, assimilation number values could be either bigger or smaller for picoplankton in relation to the other examined fractions (>5, <5 to >1 μm) and in several cases almost identical for all fractions. In this work, the recorded values of $\bar{P}^{B}$ increased with the cell size, in agreement with Joint and Pomroy's relevant results.

Vertical gradients of biomass and photosynthetic activity of picoplankton are of particular ecological interest in oligotrophic waters dominated by this size fraction. The vertical profile of picoplankton biomass has been described in many studies by conflicting data. Some investigators reported a decrease of picoplankton chl α abundance with depth (Pena et al., 1990; Happey-Wood, 1993) and others an increase towards the base of the euphotic zone that was attributed to the thermocline or nitracline depth (Partensky et al., 1996) or to cell preference of dim light (Li, 1994; Huang et al., 1999). In this work, the picoplankton chl α maxima although not occurring near the depth of the euphotic zone, showed a tendency to be formed at decreased light levels, e.g., at water layers where the surface irradiance was reduced to 10% (Spring 1998) and 5% (Autumn 1997) in the N. Aegean and to 7% (Spring 1998) and 3% (Autumn 1997) in the S. Aegean. The lack of a significant relationship between the vertical distribution of picoplankton biomass and nutrient concentration is comparable with several other data sets from the oligotrophic Pacific (Hayward, 1987; Pena et al., 1990).

The contribution of picoplankton to primary production with increasing depth has been also described by contradictory data since some investigators reported that picoplankton accounted for a larger share of primary production in deeper waters (Platt et al., 1983) and others in surface layers (Gieskes and Kraay, 1986). The results of this work showed no defined depth boundaries in the percentage of picoplankton to total production because, with a few exceptions (Fig. 4); it generally shared proportions with the other fractions and there is no clear explanation for this pattern. The maxima of total productivity were always recorded over the corresponding depths of biomass

maxima (Fig. 4). These results are in agreement with those discussed by Morel and Berthon (1989) for oligotrophic waters and confirm their theory of the nonuniform vertical structure of pigments in relation to estimates of production. It must be noted that the photosynthetic maxima were always recorded at depths located within the light-saturated layer characterized by irradiance levels exceeding 90–100 μE $m^{-2} s^{-1}$ (Harris, 1986).

Analysis of variance showed statistically significant temporal variation of all biomass and productivity fractions of phytoplankton in N. and S. Aegean Sea in response to temporal changes in the physical environment (mixing, vertical motions), the N-($NO_2 + NO_3$) concentrations and possible grazing effects. The well-defined Spring maxima and Autumn minima of total chl α and photosynthetic activity (Fig. 3B) and the role of picoplankton as the main contributor to both parameters were properties similar to those reported for the equatorial Atlantic (Herbland et al., 1987) the Sargasso Sea (Olson et al., 1990) and the tropical Pacific (Le Bouteiller et al., 1992).

The spatial variation of total and fractionated biomass and productivity levels (Fig. 3A) was also statistically significant (Table 2) indicating a north–south gradient of increasing oligotrophy in the Aegean Sea. In the N. Aegean, higher values of both parameters were recorded at stations N4 and N5, influenced by the Black Sea waters. Although there were no detectable differences in nutrient concentrations among stations during the sampling periods of this work, existing information indicated that the input of Black Sea waters through the Dardanelles was rich in dissolved organic carbon (Lykousis et al., 2002) as well as nutrients producing higher concentrations of chl α (Kucuksezgin et al., 1995; Orhon, 1995) in the neighboring Aegean Sea waters. ANOVA showed statistically significant variability among stations of both chl α and primary production in the S. Aegean Sea, confirming results of a previous investigation in this area (Ignatiades, 1998). No statistically significant relationship was found between the data of primary production and the contemporary data of bacterial production estimated by Christaki et al. (1999) in N. and S. Aegean Sea.

The monitoring of the major taxonomic groups of phytoplankton (size >5 μm) verified their quantitative

poverty (Fig. 6A) as recorded previously (Ignatiades, 1976; Ignatiades et al., 1995; Psarra et al., 2000). The remarkable growth of coccolithophores throughout the studied area in Spring 1997 is in agreement with the data of other studies from the E. Mediterranean (Kimor et al., 1987; Gotsis-Skretas et al., 1996). On the other hand, the higher abundance of diatoms during Spring 1997 as well as Spring 1998 in the S. Aegean in relation to that in the N. Aegean did not show any relationship with the recorded chemical and/ or physical conditions and it might be due to a lag phase in their bloom between the two areas or, to the existing different grazing pressures (Siokou-Frangou et al., 2002). The dominance of dinoflagellates in Autumn 1997 throughout the studied area has been also reported by other investigators (Siokou-Frankou et al., 1999).

A daily evaluation (mean integrals over depth, station and season) of the productivity status of the Aegean Sea comes from comparing the data analyzed here with those from other oceanic regions in the Mediterranean. Daily primary production in the N. Aegean (81.36 mg C m^{-2} day^{-1}) is higher than that in the S. Aegean (38.88 mg C m^{-2} day^{-1}) but both areas are oligotrophic as having productivity values lower than 270 mg C m^{-2} day^{-1} (Nixon, 1995). The productivity levels recorded in the Aegean Sea are consistent with those (20–115 mg C m^{-2} day^{-1}) reported for the oligotrophic Levantine Sea (Berman et al., 1984; Azov, 1991) but much lower than the levels (160–760 mg C m^{-2} day^{-1}) recorded in Northwestern Mediterranean (Estrada et al., 1993) and those (330–600 mg C m^{-2} day^{-1}) in Southwestern Mediterranean (Lohrenz et al., 1988). The results of this investigation are also in agreement with the recent data of other investigators (Dolan, 2000; Christaki et al., 2001; Pitta et al., 2001; Van Wambeke et al., 2002) on the existence of strong oligotrophic conditions in the eastern Mediterranean Sea.

Oligotrophic systems dominated by picoplankton are often assumed to be at steady state (Goldman et al., 1979; Hayward et al., 1983). The present data demonstrate that the Aegean Sea ecosystem could not be characterized as being at steady state because of the spatial and temporal heterogeneity in the magnitude and patterns of the examined phytoplanktonic parameters. In this nonsteady state environment, the space–time structure of phytoplankton communities is sub-

ject to fluctuations in species composition, dominance, succession and diversity and according to Harris (1986) these fluctuations characterize temperate waters.

Acknowledgements

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