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Size-fractionated phytoplankton chlorophyll in an Eastern Mediterranean coastal system (Maliakos Gulf, Greece)

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Abstract The dynamics of phytoplankton biomass were studied in an Eastern Mediterranean semi-enclosed coastal system (Maliakos Gulf, Aegean Sea), over 1 year. In particular, chlorophyll *a* (chl *a*) was fractionated into four size classes: picoplankton (0.2–2 µm), nanoplankton (2–20 µm), microplankton (20–180 µm) and net phytoplankton (>180 µm). The spatial and temporal variation in dissolved inorganic nutrients and particulate organic carbon (POC) were also investigated. The water column was well mixed throughout the year, resulting in no differences between depths for all the measured parameters. Total chl *a* was highest in the inner part of the gulf and peaked in winter (2.65 µg l^{-1}). During the phytoplankton bloom, microplankton and net phytoplankton together dominated the autotrophic biomass (67.2–95.0% of total chl *a*), while in the warmer months the contribution of pico- and nanoplankton was the most significant (77.5–93.4% of total chl *a*). The small fractions, although showing low chl *a* concentrations, were important contributors to the POC pool, especially in the outer gulf. No statistically significant correlations were found between any chl *a* size fraction and inorganic nutrients. For most of the year, phytoplankton was not limited by inorganic nitrogen concentrations.

Keywords Nutrients · Chlorophyll · Fractionation · Particulate carbon · Coastal · Mediterranean

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Introduction

Based on the size structure of primary producers, i.e. large (in the present paper, >2 µm) versus small (<2 µm), trophic pathways in the marine environment can be distinguished in those where primary production is dominated by large phytoplankton and others where primary production is dominated by small cells (Cushing 1989; Legendre and Le Févre 1989). In the former systems, production often depends in allochthonous inputs of nutrients (new production), while in the latter primary production is mainly driven by in situ remineralisation of nutrients (regenerated production). Light availability, temperature and salinity may also be partly responsible for the composition of phytoplankton assemblages (see Delgado et al. 1992; Claereboudt et al. 1995). Moreover, the dominance of phytoplankton by either large or small cells may be influenced by processes of loss (i.e. size-differential grazing by zooplankton or sinking of cell aggregates) and accumulation (i.e. hydrodynamic traps) (Smetacek 1985; Legendre and Le Févre 1989; Banse 1992).

Phytoplankton cell size has thus been recognised as a morphological parameter of prime physiological (Raven 1986) and ecological significance (Malone 1980; Fogg 1995), the size distribution of the phytoplankton community playing a fundamental role in determining the food web structure of the whole pelagic biota (Fenchel 1988). In general, small cells have a higher contribution to total phytoplankton biomass during periods of nutrient depletion (Raven 1986), with increased temperature and when total chlorophyll *a* (chl *a*) is low (Weisse 1993; Magazzú and Decembrini 1995). In addition, picophytoplankton is an important contributor to total phytoplankton biomass and productivity in oligotrophic environments (Fogg 1995). In these environments, the microbial loop (Azam et al. 1983) seems to be very important for the energetics of the pelagic trophic web (Legendre and Rassoulzadegan 1995), as it is responsible for more efficient energy transfer to higher levels. The investigation of small sized phytoplankton is, thus, of special interest in the Greek

seas which are some of the most oligotrophic of the Mediterranean Sea (Stergiou et al. 1997). On the other hand, non-eutrophicated coastal and estuarine systems in temperate latitudes offer favourable conditions for assessing the environmental factors leading to dominance by the large or small primary producers. Such systems seem to be characterised by a shift between two periods of different physical and chemical conditions that favour the dominance of large or small algal cells (see above), which in turn determines the fate of the primary production, i.e. grazing and/or loss via sedimentation (Banse 1992; Lignell et al. 1993).

In Maliakos Gulf, one of the most naturally productive coastal areas in the Aegean Sea (Kormas 1998), abundant data on chl *a* concentrations have been available since 1992 (Christou et al. 1995; Kormas 1998; Kormas et al. 1998). However, chl *a* content was not determined for the different size classes. Therefore, to better understand plankton processes in Maliakos Gulf, studies on the size structure dynamics of phytoplankton were undertaken. The principal aims of this study were: (1) to examine temporal and spatial variations in chl *a* of various size classes of phytoplankton in Maliakos Gulf, and (2) to investigate mechanisms controlling size structure dynamics, mostly related to inorganic nutrients.

Methods

The area of study, Maliakos Gulf (Fig. 1), is a semi-enclosed embayment on the east coast of Greece. It covers an area of about 110 km^2 and is divided by two headlands into two sections. In the SW it receives the waters of the Sperhios River. The western part forms a basin with a maximum depth of 27 m, although closer to the river mouth the depth does not exceed 10 m. In the east, the gulf is connected to the Aegean Sea through the Orei Channel and to the Evoikos Gulf through the Knimida Channel. This part has an average depth of 36 m. Three sampling stations (Fig. 1) were chosen as being representative (Kormas 1998) of the three ecological (inner, middle and outer) compartments of the gulf with 7, 23 and 23 m depth, respectively. Sampling depths were 1 and 5 m for the inner station and 1, 10 and 20 m for the other two. The stations were visited every month from September 1997 until August 1998. The autumn and winter sampling dates were chosen based on previous studies (Kormas 1998; Kormas et al. 1998), when increased levels of phytoplankton chlorophyll were expected.

Vertical profiles of temperature and salinity (expressed in practical salinity units, psu) in each station were obtained with a Sea-Bird CTD sensor module. Water was collected with a 5.5 l Limnos water sampling bottle. Samples for nutrients (phosphate, nitrate, nitrite, ammonium and silicate) were kept in polyethylene bottles and stored frozen (–20°C) (Dore et al. 1996) until analysis within 2 days of collection. Phosphate, nitrate, nitrite and silicate concentrations were determined as described by Parsons et al. (1984a), and ammonium concentrations according to Liddicoat et al. (1974), after filtration through a 200 µm mesh to retain large particles and zooplankton. Although filters with higher retaining capacities are more efficient at removing particulate material and organisms, 200 µm mesh has been used successfully by other researchers in chl *a* size fractionation studies (e.g. Bradford-Grieve et al. 1997) and allowed us to compare our data with those of previous studies in the same area (Kormas 1998). In addition, occasional tests showed no significant differences in nutrient concentrations after filtration with 200 µm and GF/C filters in Maliakos Gulf (data not shown).

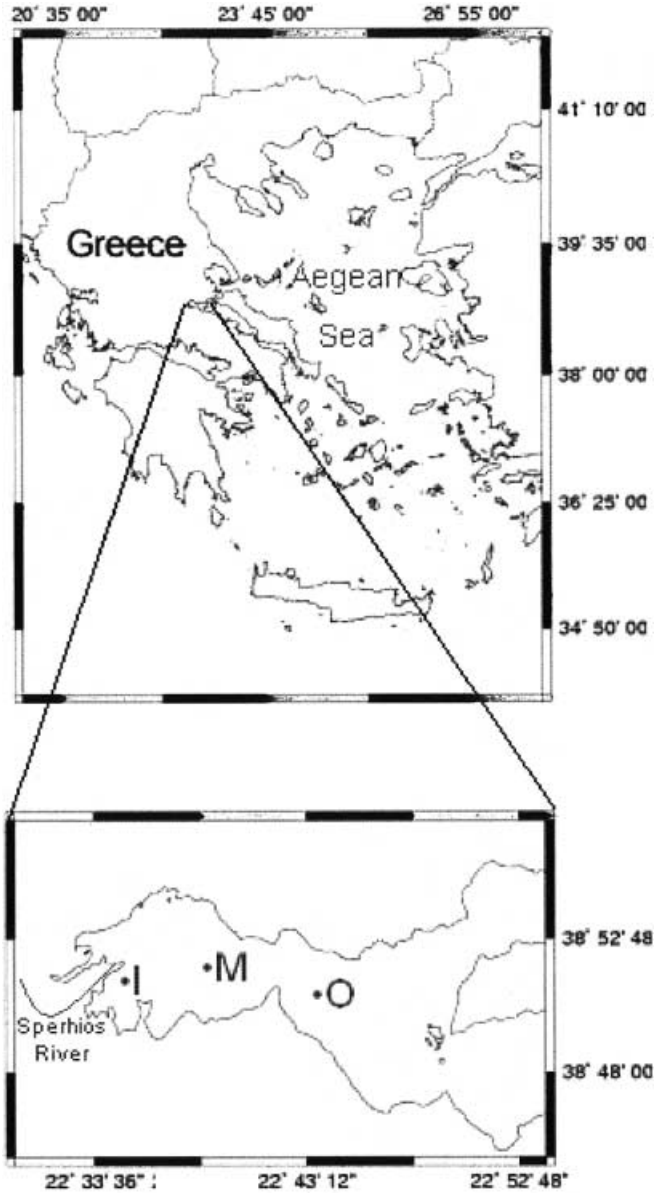

Fig. 1 Map of Maliakos Gulf with sampling stations: *I* inner, *M* middle and *O* outer stations

Water for phytoplankton pigment analyses was collected in polyethylene bottles wrapped in black plastic bags and kept cool until filtering, usually a few hours after sampling. The size fractions of chl *a* were chosen according to Fenchel (1988): 0.2–2 µm (picoplankton), 2–20 µm (nanoplankton) 20–200 µm (microplankton). In this study, the fractions of microplankton and net phytoplankton (>200 µm) were determined by using 180 µm mesh-size filters. Samples (1–1.5 l) were filtered successively through 180 and 20 µm mesh-size nylon Millipore filters, and 2 and 0.2 µm pore size isopore polycarbonate Millipore filters. Gravity filtration was applied for the 180 and 20 µm filtrations, while for the 2 and 0.2 µm filtration a vacuum of ≤150 mm Hg was applied. The volumes of sea-water filtered did not cause clogging of the filters as was seen by occasional microscopic observations of the filters. Chl *a* and phaeopigments (phaeo) were extracted in acetone, as described by Parsons et al. (1984a), immediately after filtration. Prior to the experiments, all the filters were checked for solubility in acetone by leaving blank filters in 90% acetone overnight at

Table 1 Surface water (*top value*) and bottom water (*bottom value*) temperature and salinity at the three sampling stations in Maliakos Gulf; *na* not available

Month	Inner		Middle		Outer	
	Temperature	Salinity	Temperature	Salinity	Temperature	Salinity
Sept 1997	25.85 25.83	36.20 37.22	25.23 25.51	36.67 37.35	25.10 25.28	36.23 36.83
Oct	20.60 20.72	35.91 36.37	20.72 20.12	36.47 37.00	20.85 20.00	36.56 37.17
Nov	16.43 16.48	34.87 36.52	16.23 16.26	36.32 36.88	na na	na na
Dec	14.10 14.13	35.94 36–27	13.73 14.42	35.90 37.05	14.13 14.41	35.46 37.10
Jan 1998	12.27 12.26	33.95 36.12	12.04 12.68	35.68 36.99	11.75 12.74	35.86 37.00
Feb	13.89 13.33	34,61 36.21	13.53 12.87	35.85 37.06	13.33 12.72	36.42 37.24
Mar	16.90 16.36	36.24 36.91	16.87 14.42	36.48 37.24	16.98 13.91	36.84 37.34
Apr	23.93 12. 18	34.52 35.93	22.37 17.54	35.67 37.13	22.10 18.47	35.83 37.20
May	na	na	na	na	na	na
Jun	25.12 24.94	35–76 36.47	24.63 22.83	36.51 36.88	24.43 24.21	36.39 36.73
Jul	27.19 27.11	36.07 36.30	27.27 25.60	36.78 37.14	27.09 23.84	36.83 37.31
Aug	25.26 25.49	35.59 36.12	25.58 25.58	36.33 36.44	25.39 24.31	36.28 36,50

4°C. The following day the optical absorption was measured at the same wavelengths as those used for the determination of phytoplankton pigments, against 90% acetone. These tests showed that the filters used in this study did not change the optical properties of the acetone, having no effect on the pigment measurements.

Particulate organic carbon (POC) was determined using the wet oxidation method (Parsons et al. 1984a) of the material collected after filtration of a certain volume (0.7–1.5 l) of sea-water on precombusted (500°C, 4 h) Whatman GF/F filters.

To investigate the nutrient limitation of the phytoplankton cells, the physiological index of Heath et al. (1990) was applied to the data. This index is the ratio of absorbance at 480 nm to the absorbance at 664 nm – corrected for turbidity – of the samples used for the determination of chl *a* (see above).

All statistical analyses were performed with the Statistica (StatSoft Inc.) software package. Non-parametric tests were used for all the analyses (Zar 1984).

Results

Temperature (Table 1) showed the expected fluctuation, with the lowest values in January (11.75–12.74°C) and the highest (up to 27.27°C) in July. No thermocline was observed in the gulf; however, in stations M and O in March and April there was a difference of about 2.5–4.8°C between surface and bottom water. Salinity (Table 1) in the gulf fluctuated between 33.95 and 37.35 psu, with the lowest values in winter and/or spring and the highest in summer. The lowest values were found at station I. This station also showed the greatest variability between surface and bottom water salinity (approx. 2.2 psu in January).

Kruskal-Wallis tests showed no statistical differences between depth in each station for the nutrients and all the chl *a* fractions. Consequently, in this paper we present the trapezoid depth integrated values of these parameters.

Nutrient concentrations are shown in Fig. 2. Phosphate ranges were similar at all stations (I: 0.00–0.26 µM, M: 0.01–0.68 µM and O: 0.05–0.34 µM). Nitrate concentrations also showed similar ranges in the three stations; I (0.00–0.74 µM), M (0.00–0.84 µM) and O (0.00–0.88 µM). Ammonium reached higher concentrations at station I (0.00–0.20 µM) than in M (0.00–0.09 µM) and O (0.00–0.12 µM). On average, nitrate dominated (35–38%) over ammonium (10–14%) in the dissolved inorganic nitrogen (nitrate + nitrite + ammonium, DIN) pool in all stations (Fig. 3). The relative abundance of ammonium was higher during the warm months and February and/or March. Phosphate, nitrate and ammonium showed no clear temporal pattern. Silicate (Fig. 2) concentrations were below 10 µM, except in December and January (up to 16.03 µM in station I).

Depth-integrated total chl *a* (Fig. 4) showed a decreasing gradient from station I (0.27–2.65 µg l^{-1}) to station O (0.14–1.20 µg l^{-1}). The highest values in stations I and M occurred in January, while in station O they occurred in February. The lowest values were measured in March, September and January for stations I, M and O, respectively. For most of the stations and sampling times, the ratio of chl a:(chl *a* + phaeo) was >50%.

Figure 5 shows the chl *a* concentrations of each studied size fraction and its relative abundance in total chl *a*. The contribution of the three largest fractions to total chl *a* showed very similar ranges in all stations. On average, net phytoplankton varied between 9.7–11.7%, mi-

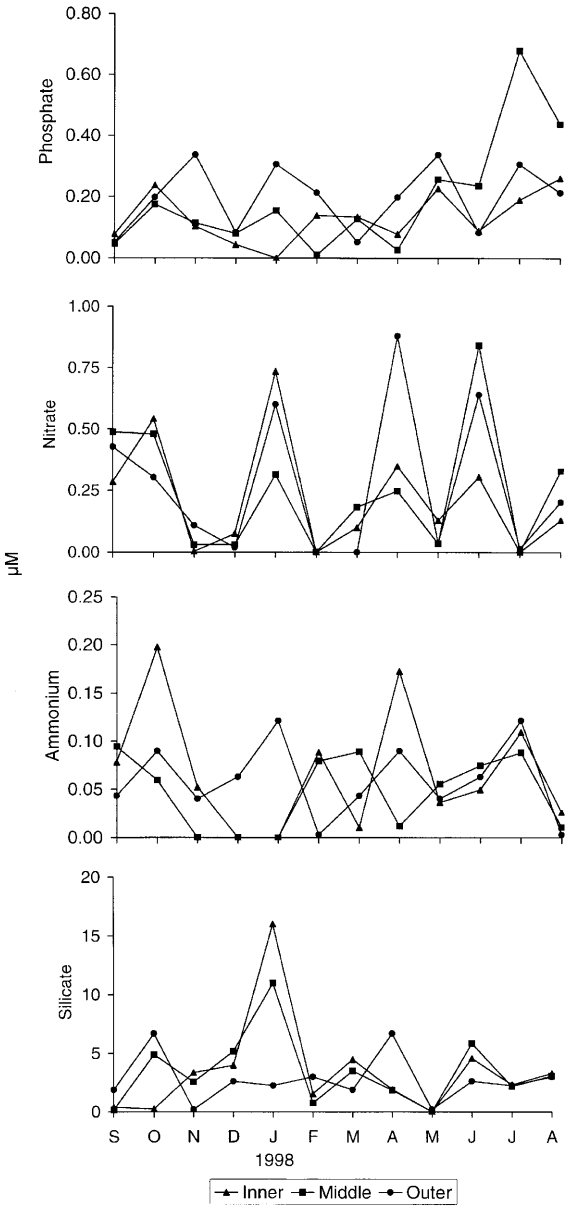

Fig. 2 Annual cycle of depth-integrated concentrations of nutrients in the inner, middle and outer Maliakos Gulf

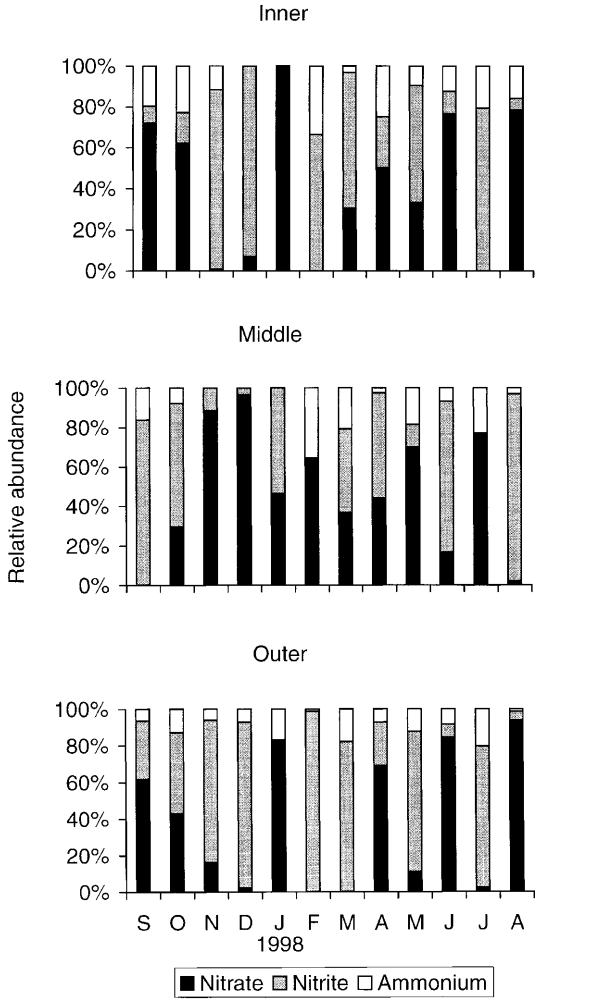

Fig. 3 Annual cycle of the relative contributions of nitrate, nitrite and ammonium to total dissolved inorganic nitrogen in the inner, middle and outer Maliakos Gulf

croplankton between 17.1–20.7% and nanoplankton varied between 37.6–45.2%. Picoplankton showed an increasing contribution to total chl *a* from station I (14.7%) to station O (22.2%). The fractions studied showed different temporal patterns (Fig. 5). Net phytoplankton was more significant during the cold months (December and March). Its lowest contribution occurred during the warm months (July, September, October). Microplankton had its minimal contribution in the winter while its maximal varied throughout the year in the gulf. Nanoplankton had its lowest contribution in autumn and its maximum in late winter/early spring. Picoplankton peaked in summer and beginning of autumn while its minimal contribution to total chl *a* occurred during cold months (November, December, March).

Kruskal-Wallis tests showed no statistical differences between stations for the nitrogen limitation index. For each phytoplankton size fraction a similar trend in nitrogen limitation (index >2) occurred throughout the gulf (Fig. 6). Net phytoplankton seemed never to be limited by nitrogen, while in picoplankton nitrogen limitation occurred occasionally.

Net phytoplankton (R=–0.296, n=85, P <0.001) and microplankton (R=–0.328, n=85, P <0.001) chl *a* values were negatively correlated with temperature. No significant correlations were found between chl *a* and nutrients.

POC (Fig. 7) reached 644–794 µg l^{-1} in August. However there were two more periods of increased concentrations, in December/January (234–599 µg l^{-1}) and April/May (355–562 µg l^{-1}). During the rest of the year, POC was below 200 µg l^{-1}. The average ratio of POC:chl *a* (Fig. 7) showed an increasing pattern from station I (250) to station O (928). Station O had higher ratios for most of the year. Increased ratios occurred in spring and late summer.

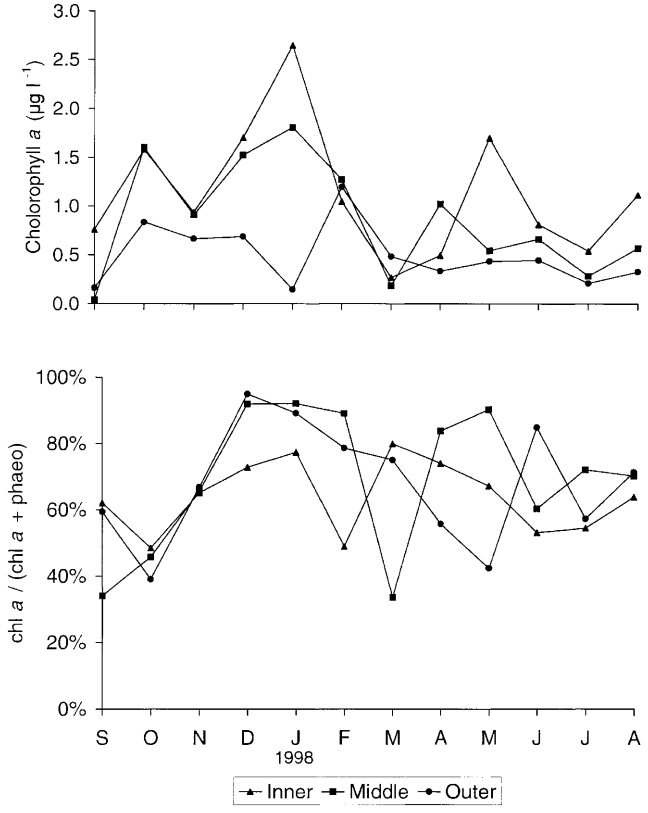

Fig. 4 Annual cycle of the concentrations of depth integrated total chlorophyll *a* and its ratio to total phytopigments [chl *a*:(chl *a* + phaeo)] in the inner, middle and outer Maliakos Gulf

Discussion

For most of the year, no thermo- or halocline was observed in Maliakos Gulf. This seems to be a permanent characteristic of the gulf and might be due to the rapid mixing of the water column (Christou et al. 1995; Kormas 1998). However, intrusion of saline cold water from the open Aegean Sea seemed to have occurred in March and April, especially at stations O and M. This minor stratification was rather episodic and caused no vertical differences in nutrient and chl *a* concentrations in any of the size fractions studied.

Nutrient concentrations were rather low but higher than those reported for open Greek seas (reviewed in Stergiou et al. 1997). No clear temporal patterns for most of the nutrients measured were found, resulting in the lack of correlations with chl *a*, which showed a distinct temporal pattern. This is another consequence of the strong mixing of the Maliakos water column. Another possible reason for the uncoupling of nutrient concentrations and chl *a* could be grazing control (e.g. Mura et al. 1996), which was not studied here. However, some temporal trends of nutrient concentrations that are related to phytoplankton biomass dynamics can be observed. The lowest phosphate concentrations were more frequent in early winter/end of spring, and the highest in late spring/summer. Although nitrate was the dominant form of inorganic nitrogen throughout the year, the relative abundance of ammonium was increased during spring and the warm months.

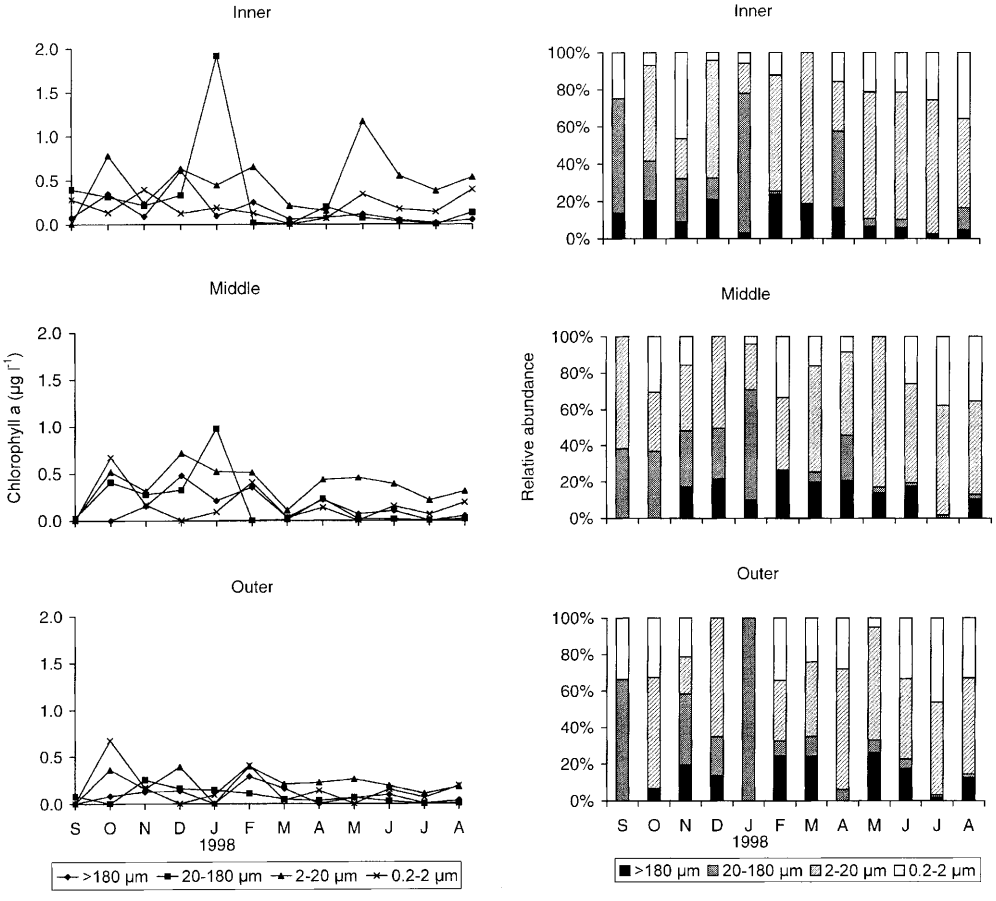

Fig. 5 Annual cycle of the concentrations of depth-integrated chlorophyll *a* of >180, 20–180, 2–20 and 0.2–2 µm size fractions (*left panel*) and the relative contributions of these fractions to total chlorophyll *a* (*right panel*) in the inner, middle and outer Maliakos Gulf

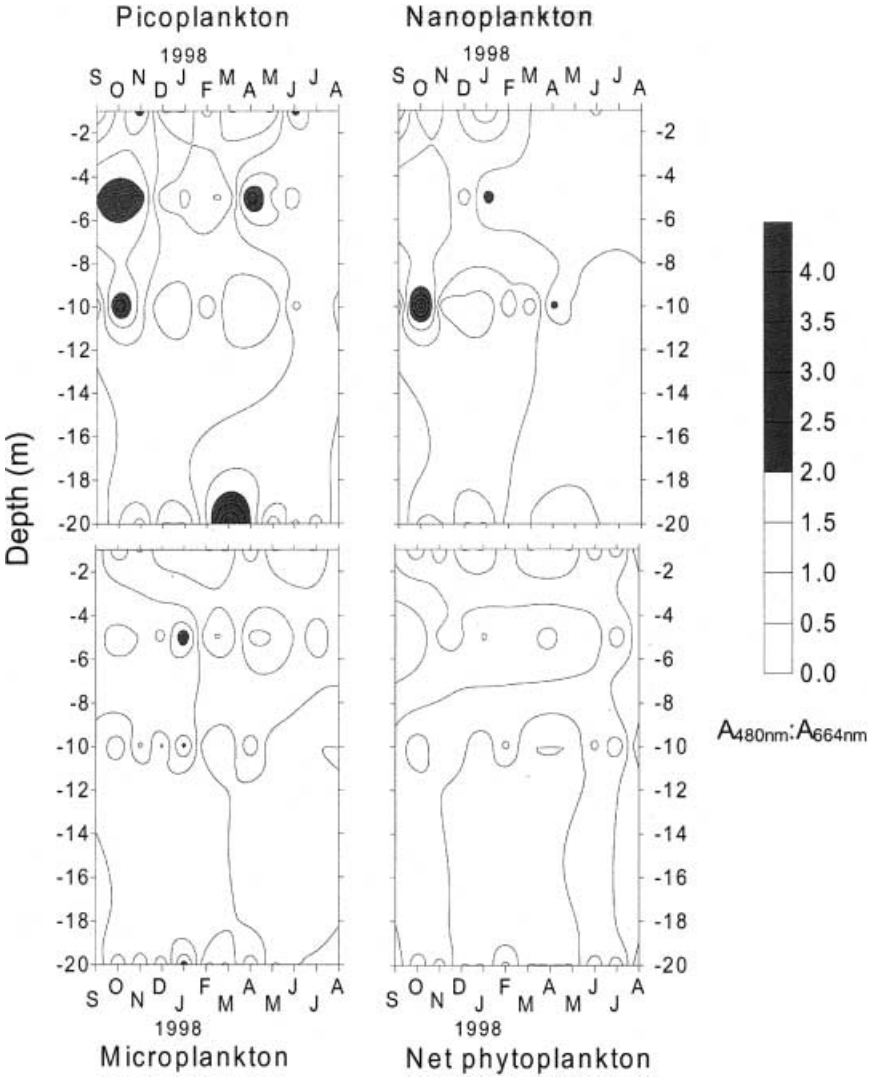

Fig. 6 Contour plots of the A_{480}:A_{664} ratio of each fraction for all studied stations and sampling times in the inner, middle and outer Maliakos Gulf (see text for details)

In terms of nutrient limitation, as revealed by the physiological index of Heath et al. (1990), nitrogen does not seem to be the limiting nutrient throughout the gulf and for most of the year, which was also found in older studies (Kormas 1998). This seems to follow the general rule that phosphorus instead of nitrogen is the most probable limiting nutrient in the Aegean Sea (Stergiou et al. 1997).

The phytoplankton bloom of the gulf occurred in winter, as was expected, although total chl *a* was lower than the values reported in older studies (Kormas 1998). The bloom in the outer gulf occurred one month later than in the middle and inner gulf. This is an indication that, although no expected gradient in salinity and nutrients from the inner to the outer part of the gulf was found (Kormas 1998), the phytoplankton bloom was more intense close to the Sperhios River mouth.

During the bloom, most of the chl *a* was attributed to the larger fractions (i.e. >20 µm). The dominant group was diatoms (K. Kormas, unpublished data). This is a common feature of many marine systems (Malone and Chervin 1979; González et al. 1989; Tamigneaux et al. 1995; Vant and Safi 1996; Del Amo et al. 1997; Pagou and Assimakopoulou 1997; Nincevic and Maracovic 1998; Sin et al. 2000) and a rather interannually consistent phenomenon (e.g. Mozetic et al. 1998). This bloom could explain the dramatic decrease in nitrate observed as a consequence of uptake by phytoplankton. There are several possible reasons for the dominance of large, mostly diatom, cells in nitrate abundant waters and/or during the winter/spring phytoplankton bloom: (1) large phytoplankton cells are better competitors for nitrate (Stolte et al. 1994; but see Dauchez et al. 1996) because of their larger specific storage volume (Stolte and Riegman 1995), while smaller cells take up ammonium more efficiently (Le Corre et al. 1996); (2) in addition, a novel hypothesis has been introduced recently by Lomas and Glibert (1999) explaining the rapid nitrate uptake by diatom-dominated populations during periods of low temperature. They found that, at low temperatures, nitrate uptake by diatoms is higher than ammonium uptake and in excess of nutritional requirements. The excess ni-

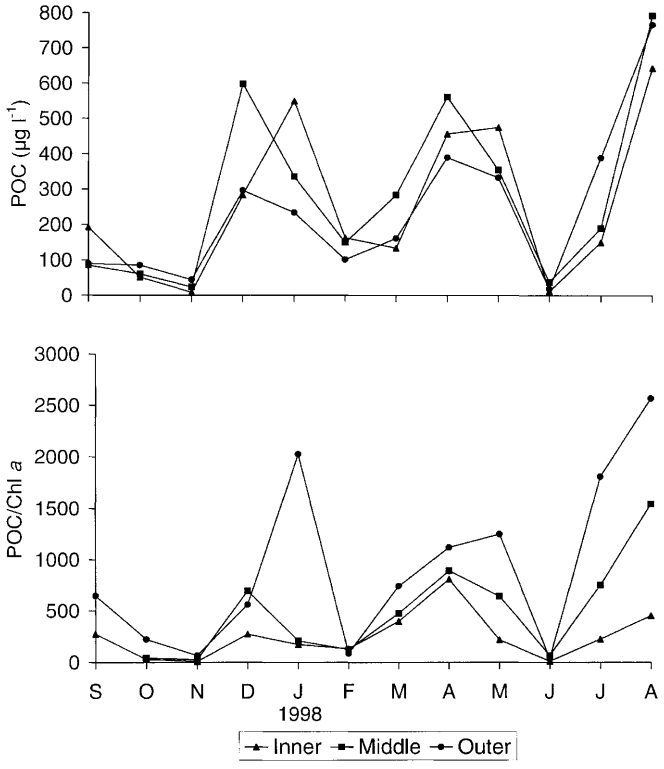

Fig. 7 Annual cycle of the concentrations of particulate organic carbon (*POC*) and the ratio of POC to chlorophyll *a* (POC:chl *a*) in the inner, middle and outer Maliakos Gulf

trate stored in the cell can be reduced, serving as a sink for electrons during transient periods of imbalance between light energy harvesting and utilisation; (3) the increase in phosphate in Maliakos Gulf in winter compared with the preceding months (Fig. 2) could be another reason for a shift to larger cells, as small cells have been shown to have higher phosphate uptake rates than large cells in low concentrations (Wang et al. 1997); and (4) silicate levels in Maliakos Gulf during December and January are favourable for diatom growth as the half-saturation constant for silicate uptake by diatoms is 0.8–3.4 µM (Parsons et al. 1984b), far below the winter silicate concentrations in the gulf (Fig. 2).

The dominance of large diatoms during the winter phytoplankton bloom in Maliakos Gulf has implications for the trophic web. It is known that large diatoms sink quickly through the water column (Smetacek 1985). Kormas (1998) found rapid sedimentation rates of approximately 10 m day^{-1} of chl *a* during the winter phytoplankton bloom in Maliakos Gulf, thus confirming the dominance of large phytoplankton cells. Assuming a carbon:chl *a* ratio of 44 and 80 for the 0.2–20 µm and >20 µm fractions, respectively (Malone and Chervin 1979), phytoplankton contributes more than 50% to the POC pool during the winter phytoplankton bloom. Regarding the increased POC:chl *a* ratio in the outer gulf due to low chl a concentrations, this implies that the contribution of phytoplankton carbon as we move from the inner to the outer gulf increases, thus providing better food quality for grazers. This may be related to the increasing biomass of mesozooplankton from the inner to the outer gulf found by Kormas (1998), which is affected by the turbidity of the gulf (Christou et al. 1995). For the benthic community of Maliakos Gulf, the sedimentation of POC during the winter phytoplankton bloom has been found to support benthic carbon demands (Kormas and Papaspyrou 2001). During the rest of the year, increased POC concentrations in April–May could be attributed to mesozooplankton faecal pellets and the summer increase to microzooplankton faecal pellets. It is known that mesozooplankton peaks in biomass and abundance in May (Kormas 1998) and that microzooplanktonic groups are more abundant in summer (Kormas et al. 1998).

After the end of the winter phytoplankton bloom, the pico- and nanoplankton contribute largely to total chl *a*. Their maximum contribution occurs in summer, when the gulf has a typical open sea oligotrophic character (see this paper; Kormas 1998). In addition, cyanobacteria are known to be much more abundant in the gulf during the summer (2.1–7.6×10^3 cells ml^{-1}) than in the winter (0.3–1.7×10^3 cells ml^{-1}) (unpublished data). This situation is typical for oligotrophic waters, where production is largely based on regenerated nutrients, such as ammonium, and rapid cycling of matter is driving the whole system (Eppley and Peterson 1979). The dominance of smaller cells during periods of low nutrient concentrations is related to their ability to take up nutrients more efficiently than bigger cells (Raven 1986). Indeed, in Maliakos Gulf during summer, nutrient levels are very low and reach analytical zero (Fig. 2). Also, the relative contribution of ammonium to total inorganic nitrogen increases, possibly as a result of regeneration processes, through a microbial-dominated trophic web. Such evidence was provided by Kormas et al. (1998), who suggested that the microbial loop in Maliakos Gulf is more functional during the warm months than during the rest of the year. Moreover, Ikeya et al. (1997) have shown that even nanomolar phosphorus concentrations can support high cell growth of cyanobacteria. This also explains the increased abundance of picophytoplankton in Maliakos Gulf during the warm months when phosphate levels are at their lowest levels of the year. Finally, it is known that dissolved organic carbon (DOC) excretion is higher in smaller autotrophs than in larger ones (Malinsky-Rushansky and Legrand 1996), and since phytoplankton-excreted DOC is highly labile for bacteria (Baines and Pace 1991), summer dominance of small-sized phytoplankton can fuel bacterial activity and therefore contributes to the onset of the microbial loop, as suggested by Kormas et al. (1998).

In conclusion, this paper shows that the typical succession in the dominant phytoplankton cells, from large algal cells during the winter phytoplankton bloom to small ones during the summer, occurs in Maliakos Gulf. This oscillation of the system between a eutrophic and an oligotrophic situation, allows the onset of a microbial-

dominated food web in the summer that makes feasible the transfer of energy to higher trophic levels. This might be reflected in the high fish production of Maliakos Gulf. The picoplankton dominance and the microbial-dominated food web have been related to productive fishing grounds (Wehr et al. 1994; Wang et al. 1997). Studies of size-fractionated primary productivity are recommended, as it has recently been reported, contrary to the conventional belief, that in some coastal systems new production can also be attributed to small phytoplankton cells (Dauchez et al. 1996).

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