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Vertical profiles of particulate organic matter and its relationship with chlorophyll-*a* in the upper layer of the NE Mediterranean Sea

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Abstract

Particulate organic matter (POM), nutrients, chlorophyll-*a* (CHL) and primary production measurements were performed in the upper layer of three different regions (cyclonic, anticyclonic and frontal+peripherial) of the NE Mediterranean Sea in 1991–1994. Depth profiles of bulk POM exhibited a subsurface maximum, coinciding with the deep chlorophyll maximum (DCM) established near the base of the euphotic zone of the Rhodes cyclone and its periphery, where the nutricline was situated just below the euphotic zone for most of the year. Moreover, the POM peaks were broader and situated at shallower depths in late winter–early spring as compared to its position in the summer–autumn period. Under prolonged winter conditions, as experienced in March 1992, the characteristic POM feature disappeared in the center of the Rhodes cyclone, where the upper layer was entirely occupied by nutrient-rich Levantine deep water. Deep convective processes in the cyclonic gyre led to the formation of vertically uniform POM profiles with low concentrations of particulate organic carbon (POC) (2.1 μM), nitrogen (0.21 μM), total particulate phosphorus (PP) (0.02 μM) and chlorophyll-*a* (0.5 μg/L) in the euphotic zone. Though the Levantine deep waters ascended up to the surface layer with the nitrate/phosphate molar ratios (28–29) in March 1992, the N/P molar ratio of bulk POM in the upper layer was low as 10–12, indicating luxury consumption of phosphate during algal production. Depth-integrated primary production in the euphotic zone ranged from 38.5 for oligotrophic autumn to 457 mg C m^{-2} day^{-1} for moderately mesotrophic cool winter conditions.

Keywords: NE Mediterranean; Particulate organic matter; Nutrients; C/N/P ratios; Chlorophyll-*a*; Primary production

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1. Introduction

The eastern Mediterranean is one of the well-known basins of low productivity among the world's seas due to limited nutrient supply to its surface layer from external and internal sources (Dugdale and Wilkerson, 1988). Its deep water is characterized by relatively high nitrate to phosphate molar ratios (27–28.5), suggesting that phosphorus is a potentially limiting factor for the algal production in the upper layer (Yılmaz and Tuğrul, 1998). The euphotic zone waters possess very low concentrations of phosphate

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(<0.02–0.03 μM) and nitrate (0.1–0.3 μM) for most of the year, excluding winter upwelling period in the cyclonic region (Yılmaz and Tuğrul, 1998). Therefore, the annual primary production in the eastern Mediterranean has been estimated to range regionally between 16 and 60 g C m^{-2} (Dugdale and Wilkerson, 1988; Salihoğlu et al., 1990; Psarra et al., 2000). The phytoplankton biomass, in terms of chlorophyll-*a*, is always greater in the Rhodes cyclone and its peripheries during winter–spring periods (Ediger and Yılmaz, 1996). Chlorophyll-*a* concentrations were as low as 0.19–0.45 μg/L in the anticyclonic regions, increasing to levels of 1.0–3.1 μg/L in the cyclonic gyre during the late winter–early spring bloom period. Moreover, a well-developed deep chlorophyll maximum (DCM) established near the base of the euphotic zone is a characteristic feature of the NE Mediterranean virtually throughout the year (Berman et al., 1984; Abdel-Moati, 1990; Salihoğlu et al., 1990; Krom et al., 1992; Yılmaz et al., 1994; Yacobi et al., 1995; Ediger and Yılmaz, 1996).

The abundance and chemical composition of particulate organic matter (POM) in marine environments are controlled by complex physical and biochemical processes interacting in the upper layer as well as nutrient supplies from various sources (Tselepides et al., 2000). Thus, particulate concentrations in the Mediterranean upper layer increase in more productive western regions and seasons (Rabitti et al., 1994; Socal et al., 1999). Concentrations of particulate organic carbon (POC) in the western Mediterranean generally range from 1.9–3.9 μM in less productive open sea to 1.4–9.2 μM in the more productive basins (Rabitti et al., 1994; Socal et al., 1999) receiving more nutrients from deep waters and land-based sources. Naturally, similar spatial and temporal trends appear in the nitrogen (PON) component of bulk POM in the euphotic zone of the western Mediterranean (Socal et al., 1999; Doval et al., 1999), with values ranging between 0.1 and 1.8 μM PON in the stratified period. Limited particulate data from the oligotrophic eastern Mediterranean indicate that the upper layer waters contain low concentrations of bulk POM (Abdel-Moati, 1990; Ediger et al., 1999). Moreover, particulate profiles exhibit coherent peaks within the deep chlorophyll maximum (DCM) zone, constituting a remarkable fraction of total POM in the upper layer (Abdel-Moati, 1990).

During 1991–1994, we carried out four scientific expeditions in the NE Mediterranean. The overall objective of the present work was to document the seasonal and spatial variability in the distribution of particulate organic matter, nutrients, chlorophyll-*a* and primary production related to the hydro-dynamical properties of the Levantine basin. Simultaneous measurements of these parameters are of vital importance for a sound understanding of marine ecosystems exhibiting different oceanographic properties and distinct features in their upper layer water column. In this context, the present study for the first time has provided seasonal and regional POM data and their relationship with the chlorophyll distribution, the formation of DCM and other biomass indices in the NE Mediterranean Sea.

2. Methodology

The study area and sampling stations are located between the longitudes 28°00′ –36°00′ E and latitudes 34°00′ –36°45′ N (Fig. 1). The oceanographic cruises detailed here took place between October 1991 and March 1994. The cruises of October 1991 and July 1993 represent stratified conditions. The March 1992 and 1994 cruises represent cooler and mild winter conditions, respectively. Biologically related measurements (POM, CHL and PP_T) did not always cover the entire basin (Fig. 1).

The 1% light penetration depth (euphotic zone) was calculated from a profile of photosynthetically active radiation (PAR) performed around noon using a biospheric instrument (LI-COR). Hydrographic measurements were performed using a Seabird Model 9 CTD probe. Seawater samples for nutrient measurements were collected from stations (Fig. 1) with 5l-Niskin bottles on a rosette attached to CTD probe down to 1000 m. Water samples for particulate organic carbon (POC), particulate organic nitrogen (PON), particulate phosphorus (PP), primary productivity (PP_T) and chlorophyll-*a* (CHL) measurements were collected from the surface to 150-m depth. Depending on particulate contents of water samples, at least from 2 to 10 L of seawater were filtered using pre-combusted GF/F glass-fibre filters, which were then kept frozen until processing on land. The filters for

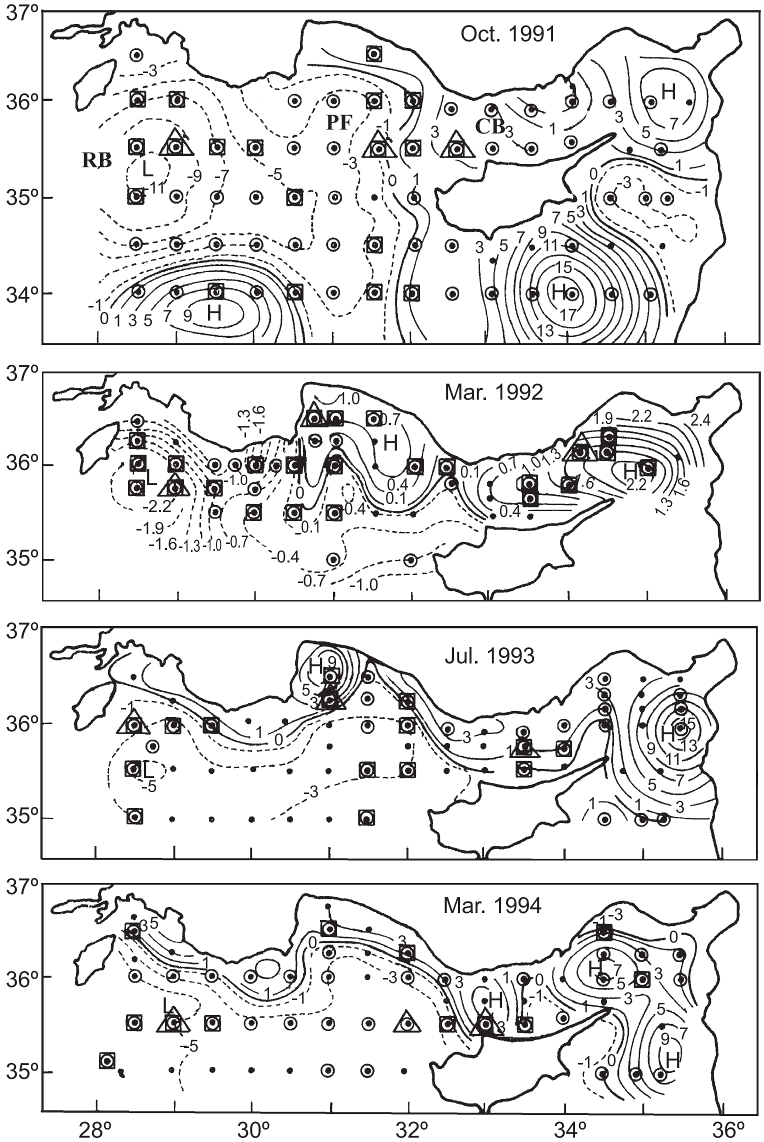

Fig. 1. Locations of stations and geopotential height anomalies during Oct. 1991, Mar. 1992, Jul. 1993 and Mar. 1994 in the NE Mediterranean Sea. (●) for hydrographic stations, (○) for nutrients, (□) for chlorophyll and (△) for POM and Primary Production. Dynamic topography contours are given in centimetre units. L and H show Low (cyclonic) and High (anticyclonic) pressure areas. RB: Rhodes Basin, P+F: Peripherial, Frontal area, CB: Cilician Basin.

POC and PON analysis were dried at 50–60 °C overnight and then exposed to concentrated HCL fumes to remove inorganic carbonates. The filters were dried again and kept in a vacuum desiccator until analysis by the dry combustion technique, using a Carlo Erba model 1108 CHN analyzer. The analytical precision was 3% for both POC and PON and detection limits were 0.2 μg-atom-C and 0.07 μg-atom-N for the method followed in this study whereas the POC and PON contents of filter samples were in the range of 1.5–15 μg-atom-C and 0.2–3.2 μg-atom-N levels.

The filters for PP analysis were first exposed to dry combustion at 500 °C for 2 h and then treated with 10 ml of 2 N HCL for 10 h and filtered (Karl et al., 1991). After the adjustment of pH to 8, the oxidized phosphorus contents of the sample solutions were determined colorimetrically by the routine ortho-phosphate method using a 10-cm cell (analytical precision: 5% and detection limit: 0.02 μM). The rates of carbon fixation by phytoplankton in the samples taken from 75%, 50%, 25%, 10% and 1% surface light depths were determined by tracing the conversion of dissolved inorganic radioactive carbon (^{14}C) into particulate organic carbon. The original methodology (Steemann Nielsen, 1952) was followed with slight modifications (Gargas et al., 1976). Incubator experiments were performed in 50-ml glass bottles under artificial growth conditions. Light conditions within the incubator were controlled with neutral density filters to simulate the light intensity at the depths from which the samples were drawn. The water samples were filtered using 0.2-μm membrane filters immediately after the incubation period (4 h) under dimmed light conditions. ^{14}C activities of filter samples dissolved in a cocktail (Ultima Gold Packard LSC-cocktail) were measured by the Packard Tri-Carb 1550 Model liquid scintillation counter. Seawater samples (1–3 L) for CHL analysis were filtered using GF/F glass-fibre filters. These filters were homogenized and extracted in 90% acetone solutions. The CHL contents of particle-free solutions were measured by the fluorometric method (Holm-Hansen et al., 1965), using a Hitachi F-3000 Model fluorometer (analytical precision: 8% and detection limit: 0.01 μg/L) and a commercially available CHL standard from Sigma. Sub-samples for nutrient analysis were taken in 100-ml acid-washed plastic bottles and kept frozen until measurements by using a Technicon Model, multi-channel autoanalyzer. The analytical methods followed were very similar to those described in Strickland and Parsons (1972) and Grasshof et al. (1983). The detection limits achieved for low concentration samples were 0.02 and 0.05 μM for phosphate and nitrate, respectively. Nitrite concentrations measured at selected locations were very close to the detection limits (0.01 μM) or below it. The nitrate+nitrite data, therefore, presented here are effectively all nitrate. The reliability of the nutrient measurements has been confirmed by the results obtained from an international inter-comparison exercise (ICES, 1995).

3. Results

3.1. Hydrographic properties

The hydrodynamics and hydrochemistry of the NE Mediterranean Sea display three regions of distinct behavior; namely, the cyclonic Rhodes basin (CYC), the anticyclonic Cilician basin (ACYC) and the transitional area (periphery and frontal regions) (P+F) (Fig. 1). Depth profiles of temperature, salinity and density in these three regions, therefore, display distinctly different features from the surface to at least 500–600 m (Fig. 2).

In the Rhodes cyclonic gyre, when the surface layer is seasonally stratified during the summer (July 1993) and autumn (October 1991) period, the less saline and cooler Levantine deep water (LDW) ascends up to 150–200 m; it is separated from the saltier and warmer upper layer by a well-defined pycnocline (Fig. 2). During the prolonged period of cooling in winter, denser surface waters lead to occur deep convective mixing processes in the gyre; thus a well-mixed (isohaline and isothermal) water mass can be formed from the surface to at least down to 1000-m depth as experienced in March 1992 (see Fig. 2; temperature: ~13.8 °C and salinity: ~38.8). Provided winter condition is insufficient to make surface waters as dense as the LDW, the saltier surface water is mixed thoroughly with the intermediate layer and the LDW can not rise up to the surface. A similar feature appeared in March 1994 and the LDW was topped by saltier and warmer waters at about 150 m (Fig. 2).

In the Cilician basin, quasi-permanent and small-scale anticyclonic eddies are generally observed (Özsoy et al., 1991, 1993). Its surface waters are always warmer and saltier as compared to those of the Rhodes cyclone and its peripheries (Fig. 2). Convective winter mixing in 1992 homogenized the upper layer of the basin down to 650–700 m, leading to the formation of the Levantine intermediate water (LIW) with vertically almost isohaline (39.1) and isothermal (15.5 °C) properties. The LIW is known to be much ticker in the core of the anticyclonic eddies (Hecht et al., 1988; Özsoy et al., 1993). However, its thickness varies both in space and time; in winter, the LIW is mixed thoroughly with the saltier surface waters to form a vertically homogenous upper layer down to the LDW (Fig. 2). When a seasonal thermocline is

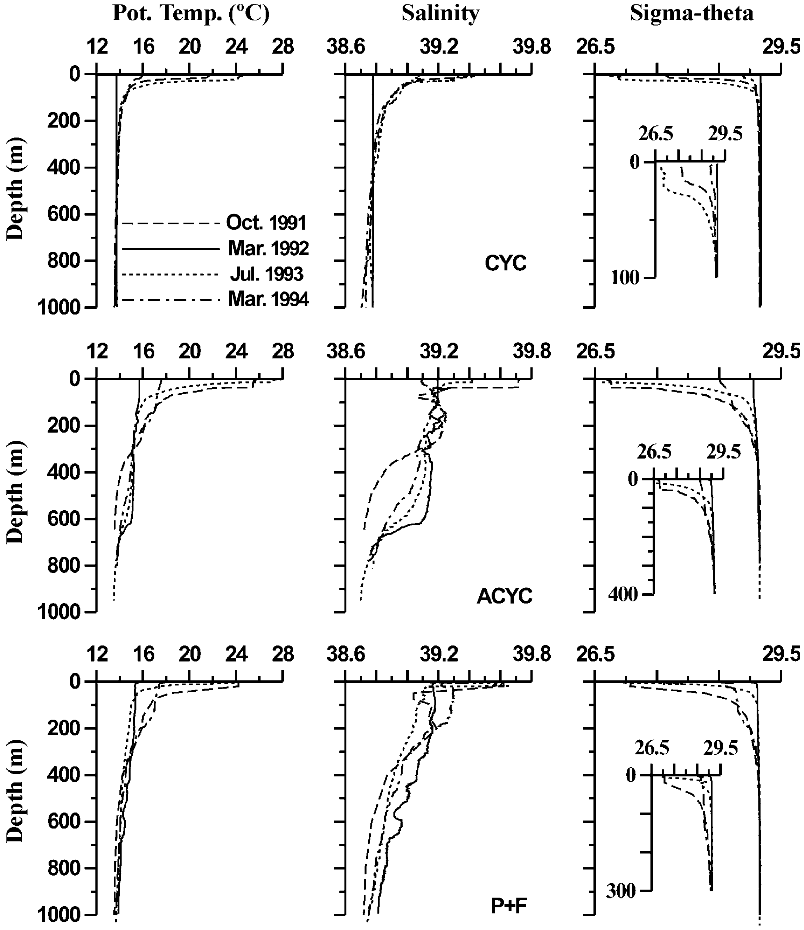

Fig. 2. Vertical profiles of hydrographic parameters (after Sur et al., 1993 and unpublished data of the Institute of Marine Sciences, Physical Oceanography Section) for selected stations in the Rhodes Gyre (CYC), Cilician Basin (ACYC) and Peripherial and Frontal area (P+F) for Oct. 1991–Mar. 1994.

established in the surface layer, the LIW becomes a characteristic feature of the intermediate depth until the next winter mixing period. The LDW appears at much greater depths in the basin as compared to its position in the Rhodes cyclone. It appeared at about 500 m in October 1991 and further deepened to 650–700 m in March 1992.

In the frontal and peripherial region off Antalya Bay, the water layer characteristics displayed remarkable variations between 1991 and 1994. In October 1991, when a seasonal pycnocline was formed below the surface mixed layer, the LIW was relatively thin (125 m). Below this zone, salinity and temperature declined to the lowest values down to at least 1000 m in October 1991, indicating the presence of slightly diluted LDW (Fig. 2) as compared to its properties in 1992 and 1993. Intensive convective winter mixing in 1992, however, led to the formation of a relatively thick mixed layer of about 400 m in the upper layer. Moreover, in March 1992, intermediate depth waters down to at least 1000 m had greater salinity than in October 1991, indicating the dimension of convective mixing that weakened with the increasing depths (Fig. 2). In June 1993, the LIW became thinner (50 m) and the intermediate layer down to 1000 m was occupied with the LDW less diluted (less saline) than in 1992. The March-94 profiles show that the upper mixed layer was relatively thin (100 m) and possesses higher salinity and temperature values than in March 1992.

3.2. Nutrients

Nutrient profiles in Fig. 3 exhibit different vertical features in the hydro-dynamically different regions of the NE Mediterranean, depending on the thickness and depths of both the LIW and LDW layers. The euphotic zone waters (~80 m) (Table 1) are very poor in both phosphate and nitrate for most of the year, excluding the winter upwelling period in the Rhodes cyclone. The layer-averaged concentrations

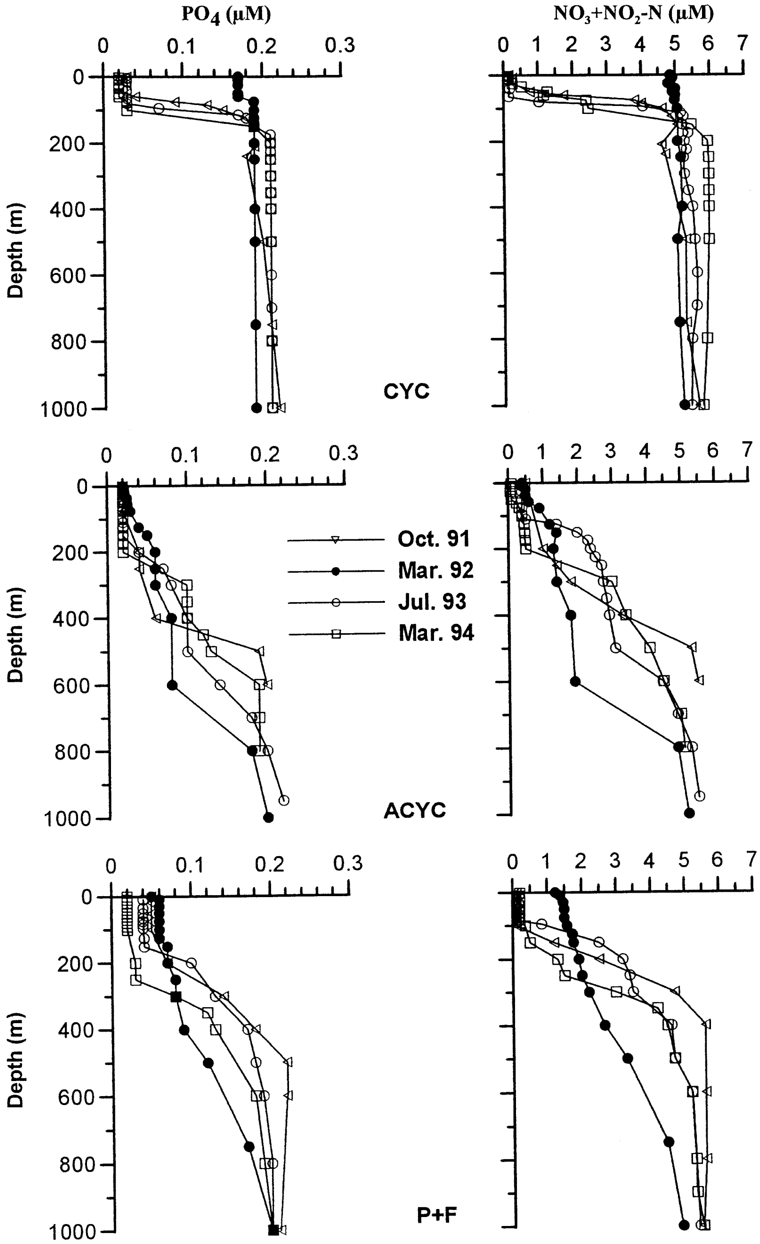

Fig. 3. Vertical profiles of dissolved nutrients for selected stations in the Rhodes Gyre (CYC), Cilician Basin (ACYC) and Peripherial and Frontal area (P+F) for Oct. 1991–Mar. 1994.

Table 1
Thickness of the Euphotic Zone (EZ; 1% light depth) in the Northeastern Mediterranean concerning the eddy fields

Region	Oct. 91 (m)	Mar. 92 (m)	July 93 (m)	Mar. 94 (m)
Rhodes Basin (CYC)	80	59	70	70
Periphery+Front (P+F)	78	45	80	–
Cilician Basin (ACYC)	90	70	100	80

for the euphotic zone are as low as 0.02 μM for phosphate and 0.11 μM for nitrate over the entire basin during the late spring–autumn period when the surface layer is seasonally stratified (Table 2). The tabulated values also demonstrate that the largest seasonality in the euphotic zone nutrient concentrations appears in the Rhodes cyclonic gyre. For instance, in March 1992, the nutrient-rich LDW occupied the surface layer, with the nitrate and phosphate concentrations of 4.7 and 0.17 μM, respectively. However, in March 1994, the LDW could not ascended up to the surface; the euphotic zone nitrate values, therefore, increased merely to 0.36 μM while the phosphate content of the euphotic zone remained almost constant at summer–autumn value of 0.02 μM (Table 2).

In the anticyclonic Cilician basin, nutrient enrichment of the euphotic zone was much less pronounced during intense winter mixing. Average concentrations of nitrate increased from 0.15 μM in summer–autumn period to 0.76 μM in March 1992, while the seasonality in phosphate was almost less than 0.02 μM (Table 2). In other words, the nutrients in the euphotic zone display less seasonal variations in the anticyclonic eddies due to insufficient input from intermediate depths via convective mixing in winter (Fig. 3 and Table 2). The LIW layer situated in the anticyclonic Cilician basin is relatively poor in nutrients as compared to the concentrations measured at similar depth ranges of the frontal regions and peripheries.

The nutricline, closely correlated with the main pycnocline, is situated at much shallower depths (50–125 m) in the Rhodes cyclone as compared to its position (300–600 m) in the anticyclonic region (Figs. 2 and 3). As emphasized in recent studies (Kress and Herut, 2001), the nutrient profiles display a small maximum at the base of the nutricline and then vary slightly in the LDW sampled down to 1000-m depth (5.5±0.5 μM for nitrate and 0.2±0.05 μM for phosphate).

3.3. Production, abundance and composition of particulate organic matter

3.3.1. Rhodes cyclonic region

POC, PON, PP and CHL concentrations of the euphotic zone waters (thickness of the EZ of the region was given in Table 1) are generally higher in the cyclonic gyre throughout most of the year (Figs. 4a, 5 and Table 3). However, POM content of the euphotic zone was unexpectedly low and almost uniformly distributed down to at least 80 m in March 1992 (Fig. 4a and Table 3). In summer–autumn period, POM concentrations increased from the surface mixed layer to the base of the euphotic zone (70–100 m), exhibiting a prominent maximum at about 60 m where deep chlorophyll-*a* maximum (DCM) was consistently formed (Figs. 4a, 5 and

Table 2
The average concentrations of dissolved nutrient elements and N/P molar ratios for the Euphotic Zone (EZ) and Deep Water (DW) in the Cyclonic (CYC), Peripherial and Frontal (P+F) and Anticyclonic (ACYC) areas in the NE Mediterranean

Date			PO4-P (μM)	NO3+NO2 (μM)	N/P
October 1991	CYC	EZ	0.03±0.004	0.28±0.27	9.3
		DW	0.20±0.03	4.99±0.41	24.9
	P+F	EZ	0.02±0.0	0.11±0.0	5.5
		DW	0.20±0.03	5.16±0.43	25.8
	ACYC	EZ	0.02±0.0	0.15±0.02	7.5
		DW	0.20±0.03	5.84 ± 0.57	29.2
March 1992	CYC	EZ	0.16±0.02	4.66±0.41	29
		DW	0.17±0.03	4.71±0.56	27.7
	P+F	EZ	0.06±0.02	1.70±0.88	28.3
		DW	0.16±0.05	4.60±0.96	28.7
	ACYC	EZ	0.03±0.01	0.76±0.26	25.3
		DW	0.17±0.03	4.78±0.70	28
July 1993	CYC	EZ	0.03±0.0	0.15±0.01	5
		DW	0.21±0.004	5.50±0.01	26.2
	P+F	EZ	0.02±0.0	0.18±0.0	9
		DW	0.18±0.03	4.79±0.62	26.6
	ACYC	EZ	0.02±0.0	0.13±0.02	6.5
		DW	0.17±0.02	5.66±0.43	33.3
March 1994	CYC	EZ	0.02±0.0	0.25±0.19	12.5
		DW	0.22±0.005	5.80±0.22	26.4
	P+F	EZ	0.02±0.0	0.36±0.13	18
		DW	0.22±0.01	5.25±0.20	23.9
	ACYC	EZ	0.02±0.0	0.16±0.13	8
		DW	0.18±0.03	4.90±0.50	27.2

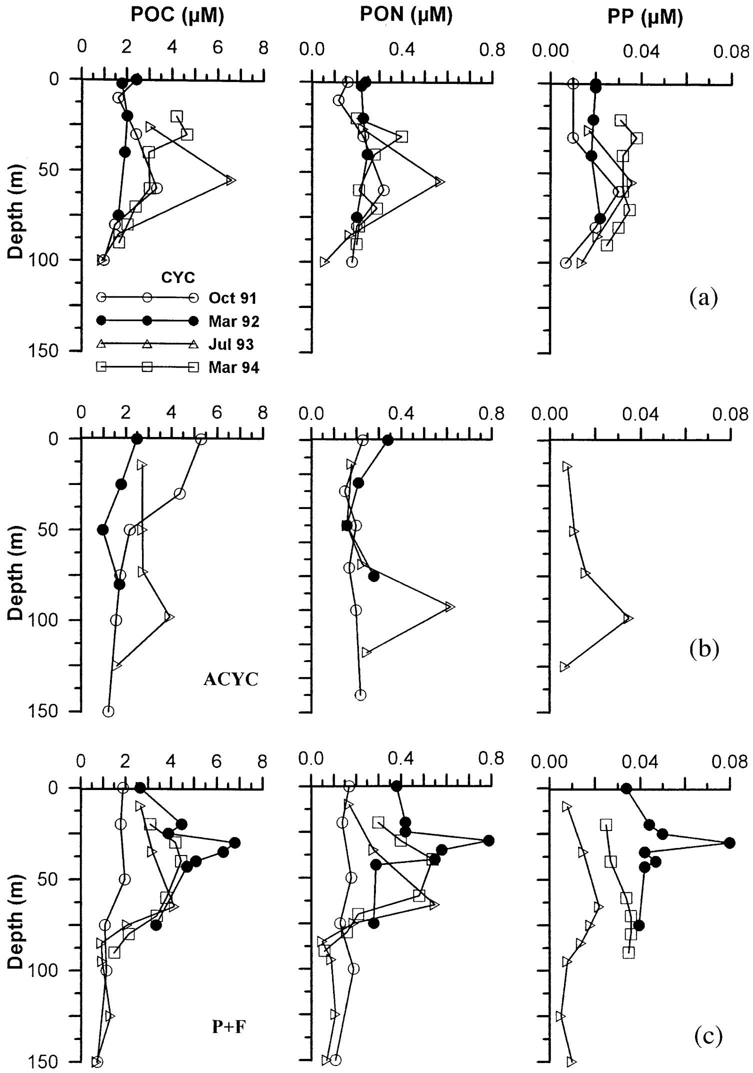

Fig. 4. Vertical profiles of POC, PON and PP for selected stations in the (a) Rhodes Gyre (CYC), (b) Cilician Basin (ACYC), (c) Peripherial and Frontal area (P+F) for Oct. 1991–Mar. 1994.

Table 1). Concentrations at the particulate maximum depths were recorded as 3.32 µM for POC, 0.32 µM for PON and 0.03 µM for PP in October 1991, which are much lower than the peak values of the July-93 POM profiles. In March 1994, the particulate maximum was less pronounced and situated at shallower depths (~30 m). CHL concentrations measured in the euphotic zone varied markedly with depth and season, ranging from 0.02 to 1.0 µg/L, exhibiting a subsurface maximum at about 40–60 m during the year, excluding the period of the LDW upwelling to the surface in late winter (Fig. 5). This unusual case occurred in March 1992, and vertically uniform CHL and POM profiles were observed in the euphotic zone (Figs. 4a and 5). Carbon uptake data from October 1991 and March 1992 indicate higher primary production rates in the near-surface waters, decreasing markedly with depth (Fig. 6). The depth-integrated primary productivity was as low as estimated as 38.5 mg C m^{-2} day^{-1} for October 1991, increasing markedly to a level of 286 mg C m^{-2} day^{-1} in March 1992.

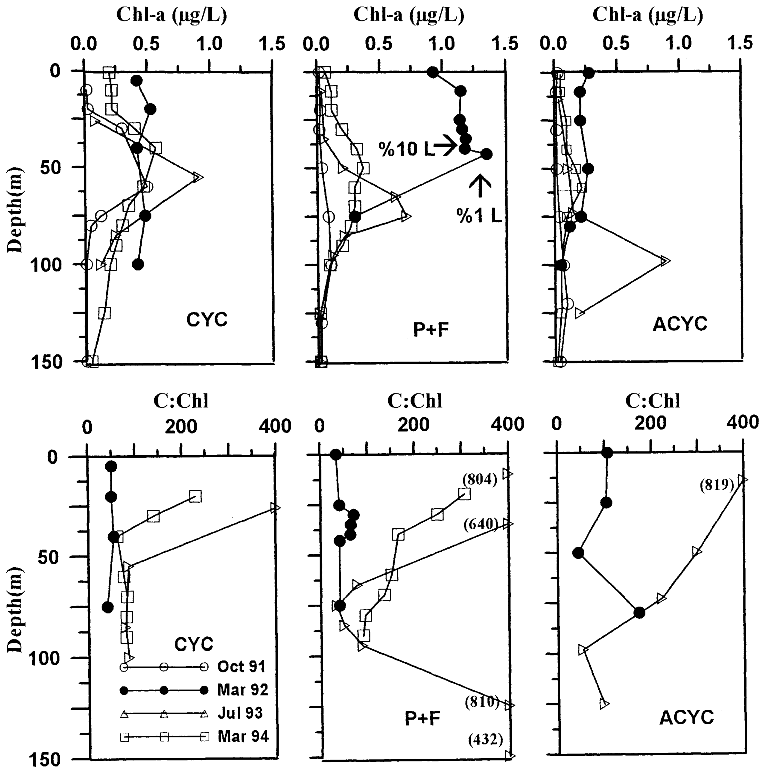

Fig. 5. Vertical profiles of CHL-*a* and POC/CHL ratios for selected stations in the Rhodes Gyre (CYC), Cilician Basin (ACYC) and Peripherial and Frontal area (P+F) for Oct. 1991–Mar. 1994.

3.3.2. Anticyclonic region (Cilician basin)

Particulate and chlorophyll data depicted in Figs. 4b and 5 clearly show that POC concentrations for October 1991 were unexpectedly high (5.3 μM) in the surface mixed layer whereas PON (0.15–0.23 μM) and CHL (0.02–0.5 μg/L) values being relatively low and also remained almost constant in the entire euphotic zone. In March 1992 when the euphotic zone waters were mixed thoroughly, POM and CHL profiles displayed nearly similar depth distributions; particulate values decreased slightly from 2.5 μM for POC and 0.34 μM for PON in the surface water to 1.0 and 0.16 μM levels, respectively, between 30 and 50 m. The CHL minimum, however, was situated at shallower depths (20–30 m). In July 1993, POM profiles displayed a coherent maximum at about 100 m, coinciding with the DCM at the base of the euphotic zone (Figs. 4b and 5). The chlorophyll-*a* content of the surface waters increased markedly from levels of 0.02 μg/L in October 1991 to 0.27 μg/L in March 1992; then it declined to typical summer values of 0.03 μg/L in July 1993 (Fig. 5). Carbon uptake

Table 3
The average values of POM concentrations (μM) in the Rhodes Cyclonic Region (CYC), Anticyclonic Cilician Basin (ACYC) and Peripherial and Frontal region (P+F) in the NE Mediterranean

Date	CYC			ACYC			P+F		
	POC	PON	PP	POC	PON	PP	POC	PON	PP
October 1991	2.1±0.8	0.21±0.06	0.02±0.01	2.7±1.61	0.20±0.03	–	1.45±0.50	0.16±0.03	–
March 1992	2.0±1.30	0.22±0.06	0.02±0.002	1.8±0.61	0.25±0.08	–	4.66±1.40	0.46±0.10	0.047±0.014
July 1993	3.07±2.52	0.26±0.21	0.020±0.01	2.7±0.82	0.29±0.21	0.015±0.01	2.40±1.0	0.21±0.13	0.011±0.004
March 1994	2.95±1.02	0.28±0.09	0.033±0.01	–	–	–	3.45±1.1	0.35±0.16	0.034±0.005

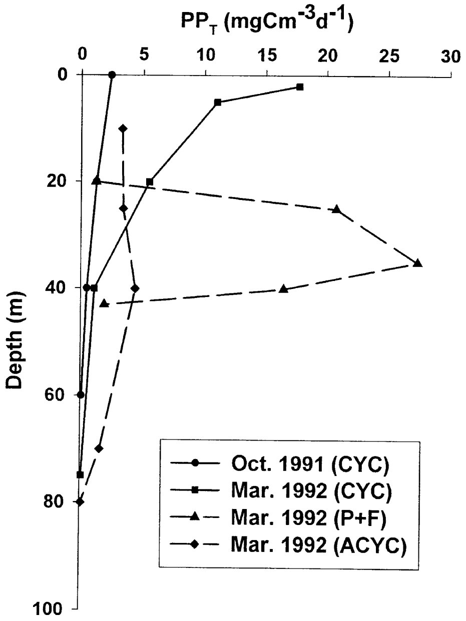

Fig. 6. Vertical profiles of Primary Production (PP$_T$) in the Rhodes Gyre (CYC), Peripherial and Frontal Area (P+F) and Cilician Basin (ACYC) for Oct. 1991 and Mar. 1992 in the NE Mediterranean.

rates measured in March 1992 were nearly constant in the euphotic zone, vanishing at about 80-m depth (Fig. 6), yielding a depth-integrated rate of about 250 mg C m^{-2} day^{-1} for this location.

3.3.3. Peripheries and frontal area

Depth profiles of bulk POM in Fig. 4c demonstrate that in October 1991, POC and PON concentrations vary only slightly with depth in the upper 150 m, while the CHL profile displays a weak maximum between 70 and 120 m of the same water column (Figs. 4c and 5). The most striking vertical POM profiles appeared in March 1992, exhibiting a coherent subsurface maximum between 30 and 40 m (Fig. 4c), whereas the chlorophyll-*a* distribution was nearly uniform with a small increase at about 40 m (Fig. 5). In July 1993, the expected vertical features of bulk POM and CHL profiles were observed again in the euphotic zone. The particulate concentrations were relatively low in the surface mixed layer, increasing apparently in the light-limited zone to form a well-defined maximum at about 65 m, which was slightly shallower than the broad deep chlorophyll-*a* maximum (DCM) established between 70 and 80 m at the same location (Figs. 4c and 5). In March 1994, the POC and PON profiles displayed subsurface maxima within the DCM zone formed between 40 and 80 m (Figs. 4c and 5). Interestingly, the PP profile (Fig. 4c) had a slightly different feature, the increasing trend commenced hardly below 50 m and then concentrations remained almost constant down to 90-m depth. Primary productivity data from March 1992 show that the maximum carbon uptake rate occurred at 35 m, which nearly coincided with the POM maximum where the light intensity dropped to 10% of its surface value (Figs. 4c and 6). Depth-integrated production rate in March 1992 was as high as 457 mg C m^{-2} day^{-1}.

4. Discussion and conclusions

The eastern Mediterranean upper layer waters receive limited nutrient supplies from both intermediate depths and external sources including atmospheric input, riverine and waste discharges (Dugdale and Wilkerson, 1988). The input from the deep waters during winter–early spring dominates the new production in the open sea, with much greater contribution to primary productivity the cyclonic gyre and its peripheries (Yılmaz and Tuğrul, 1998). However, dry+wet deposition from the atmosphere seems to dominate the new production in the open sea during spring–autumn period when the surface layer is thermally stratified (Markaki et al., 2003). Therefore, phytoplankton production rate and abundance of bulk POM are relatively low in the euphotic zone of the oligotrophic sea and show coherent variations with region and season (Berman et al., 1984; Abdel-Moati, 1990; Çoban-Yıldız et al., 2000). Nevertheless, relative importance of nutrient sources, complicated physical and biogeochemical processes on nutrient cycling and POM pools in the upper layer of the eastern Mediterranean is still poorly understood.

Layer-averaged particulate concentrations in Table 3 for the euphotic zone of NE Mediterranean reveal that the greatest temporal variations in both abundance and composition of bulk POM occurred in the Rhodes cyclone and its peripheries due to large fluctuations in nutrient input to the upper layer from intermediate depths. For instance, the layer-averaged POC concentrations in the periphery of the gyre ranged from 1.45 μM in October 1991 to 4.66 μM in March 1992 (Table 3). Such coherent POM increases in the periphery was the result of the upwelling of the nutrient-rich deep waters up to the surface in the Rhodes cyclone and subsequent horizontal flows towards peripheries in the upper layer. This nutrient supply most probably promoted the successive growth of algae and thus the accumulation of living and non-living POM in the euphotic zone of the peripheries. Thus, these POM concentrations are comparable with the results from the more productive NW Mediterranean basin (Doval et al., 1999; Socal et al., 1999).

POM results in Table 3 also demonstrate that in March 1992, the euphotic zone of the Rhodes cyclone contained unexpectedly low concentrations of bulk POM though the surface layer of the Rhodes cyclone was occupied by the upwelling nutrient-rich LDW. It appears that the strong convective mixing processes down to at least 1000 m in the core of the Rhodes gyre highly limited the accumulation of living and non-living POM in the Rhodes euphotic zone. Simply put, in March 1992, the Rhodes euphotic zone was relatively enriched in both nitrate (4.66 μM) and phosphate (0.16 μM) but possessed low concentrations of both algal biomass (in terms of chlorophyll-*a*: <0.5 μg/L) and bulk POM (see Tables 2 and 3). Intense deep convective mixing processes in winter, leading to the appearance of high nutrient but low chlorophyll (HNLC) condition in the euphotic zone of the Rhodes cyclone, also prevented the establishment of subsurface maximum in both Chlorophyll-*a* and POM profiles (Figs. 4a and 5) though the rate of inorganic carbon uptake by algae was markedly high in the cyclonic surface water (Fig. 6). It should be noted that incubation was carried out in incubator on board. Krom et al. (1993) previously observed a similar situation in the anticyclonic gyre of the SE Mediterranean, where the deep convective mixing in February 1989 was strong enough to mix the nutrient-poor water column thoroughly down to 500–600 m, resulting in vertically uniform and relatively low chlorophyll-*a* concentrations extending far below the euphotic zone. These findings also indicate that deep convective mixing processes in winter have additional contribution to POM export from the euphotic zone to intermediate depths, which can not be captured by sediment traps. On the other hand, the importance of convective mixing on the dilution of POM in the upper layer can be realized from the March-1994 particulate data in the Rhodes cyclone (Table 3), when the LDW could not ascended up to the surface but nutrients supply by vertical mixing was sufficient to sustain enhancement of bulk POM in the euphotic zone of the cyclone.

Particulate data in Table 3 also show that temporal variations are less pronounced in the Cilician basin of NE Mediterranean, where quasi-permanent anticyclonic eddies are formed during the year and the nutricline is always established much below the euphotic zone. Therefore, POM pool in the upper layer is principally sustained by regenerated production, partial nutrient inputs from the atmosphere and land during the spring–autumn period when the surface layer is seasonally stratified over the basin. As previously suggested by Krom et al. (1991, 1992, 1993) for the SE Mediterranean, the euphotic zone of the anticyclonic regions receives limited nutrients from especially phosphate-depleted intermediate depths during winter period. This supply is insufficient to raise suspended POM content of the euphotic zone to remarkable levels (Table 3). POC concentrations, for instance, ranged from 2.7 μM in October 1991 and July 1993 to 1.8 μM in March 1992 when nutrients were supplied from intermediate depths by vertical mixing.

In addition to temporal changes, POM content of the upper layer also displayed remarkable variations with region. In October 1991, for example, the POC content of the surface mixed layer in the Cilician basin was unexpectedly greater than in the Rhodes cyclone (Fig. 4a–c and Table 3) even though the Cilician surface waters were dramatically poor in algal biomass (in terms of CHL) (Fig. 5). Accordingly, POC/CHL (~1000) and C/N (14) ratios were anomalously high in the surface mixed layer (Table 4), bulk POM in this layer may have been dominated by detritus of regenerative origin and heterotrophic activities and mainly bacteria and atmospheric origin. According to the results of Robarts et al. (1996), bacterial biomass constitutes on average about 50% of phytoplankton biomass in the SE Mediterranean Sea and, with a production rate of around 24 mg C m^{-2} day^{-1} for October–November 1991. Rabitti et al. (1994) and recently Socal et al. (1999) have obtained similar results and suggested that bacteria, protozoo-

Table 4
The average values of ratios for the euphotic zone in Cyclonic (CYC), Anticyclonic (ACYC) and Peripherial and Frontal (P+F) areas of the NE Mediterranean Sea

	POC/PON (molar)	POC/PP (molar)	PON/PP (molar)	POC/CHL (w/w)
CYC				
October 1991	10.3±3.0	157±72	15±5	~400
March 1992	8.5±0.95	105±16	11.8±1.6	51±8
July 1993	12.5±2.5	127±63	10.4±5.2	163±157
March 1994	10±1.7	93±27	7.9±2.4	107±58
ACYC				
October 1991	14±8.0	–	–	~1000
March 1992	7.0±1.2	–	–	109±53
July 1993	11.4±4.8	222±85	21±9	214±142
March 1994	–	–	–	–
P+F				
October 1991	9.2±2.5	–	–	~500
March 1992	10±2.7	102±30	9.8±2.3	65±33
July 1993	12.2±3.6	162±96	13.8±7.8	222±142
March 1994	11±2.6	107±47	10.9±6.4	171±80

plankton and organic detritus contribution to POM pool may be significant in the upper layer of Adriatic and Ionian Seas in summer–autumn period.

Depth distributions of bulk POM and CHL in the NE Mediterranean display a close relationship in the light-limited depths below the surface mixed layer for most of the year (Figs. 4 and 5). In the Rhodes cyclonic gyre, where the nutricline is mostly established just below the euphotic zone, the subsurface POM maxima almost coincided with the broad DCM situated near the base of the euphotic zone during the October 1991 and July 1993 sampling period (Figs. 3, 4a and 5). The coincidence of these features is dominated by the production of shade-adapted algae fueled by nutrient intrusion from the nutricline into the light-limited depths of the euphotic zone. It is known that algae produced in this zone synthesize more chlorophyll pigment per cellular carbon, markedly lowering POC/CHL ratio in the DCM zone. Since POM pool in the euphotic zone possessed both living and non-living organic matter, POM profiles displayed a less pronounced subsurface peak as compared to increases in CHL within the DCM zone in October, 1991 (Figs. 4a and 5). Nevertheless, relatively low ratios of both C/N and C/CHL in bulk POM sampled from the DCM zone (Table 5) imply that algal biomass has a remarkable contribution to POM pool in this zone. However, in October 1991, primary productivity and CHL profiles did not match in cyclonic region (Figs. 5 and 6), suggesting that shade-adapted biomass production was dominated by small size phytoplankton with very low sinking rate and thus fueled by regenerated nutrients (Kimor, 1990; Li et al., 1993; Yacobi et al., 1995; Vidussi et al., 2001). On the other hand, in July 1993, POM and CHL concentrations both increased coherently near the base of the euphotic zone in all regions of NE Mediterranean (Figs. 4a–c and 5), indicating greater biomass production and consequent accumulation of living biomass within the light-limited zone than those in the surface waters.

Temporal and spatial changes in CHL content of nutrient-depleted surface waters are much more pronounced than in abundance of bulk POM in the same water masses. The surface mixed layer waters of NE Mediterranean are mostly poor in CHL but always possess background levels of bulk POM due to regenerative production. POC/CHL ratios, therefore, display a remarkable decrease from the near-surface water to the DCM zone near the base of the euphotic zone. For instance, the surface layer ratio was as high as 1000 in October and 800 in July 1993 in the Cilician basin; however, it appeared to be as low as 35–100 in more productive regions and seasons, when more nutrients were supplied to the near surface waters (Fig. 5). Depth-averaged values of the POC/CHL ratio for the whole euphotic zone of October 1991, July 1993 and March 1994 were in the range of 100–1000, markedly greater than the DCM ratios of 64–129 (Tables 4 and 5). The relatively low ratios of POC/PON (~9) and POC/CHL (~65) in the DCM

Table 5
The average values of ratios for the DCM layer of the NE Mediterranean Sea

DCM	POC/PON (molar)	POC/PP (molar)	PON/PP (molar)	POC/CHL (w/w)
October 1991	10	105	10.8	75
March 1992[a]	9.05±2.4	100±19	10±2.2	66±36
July 1993	9.1±2.5	150±41	17±6	64±18
March 1994	9.25±1.9	102±13	11.4±3.7	129±45

[a] DCM was not observed in March 1992 thus water column averages were taken into account.

zone, together with concomitant increases in POC concentrations, indicate that in July 1993, the shade-adapted phytoplankton biomass has a remarkable contribution to bulk POM pool in DCM zone as observed in the Adriatic Sea (Socal et al., 1999). In March 1992, when the upper layer became vertically well mixed, the POM and CHL concentrations were almost uniformly distributed in the euphotic zone of the cyclone, leading to small variations in their ratios, ranging between 51 and 109 in the upper layer. Thus, the March-92 POC/CHL ratios (66) for the euphotic zone were very similar to the DCM ratios of both July-1993 (64) and October-1991 (75), suggesting that phytoplankton populations were dynamic and healthy during the extraordinary conditions of 1992.

The upward diffusion of nutrients, possibly combined with the accumulation of sinking phytoplankton in the lower part of the euphotic zone, results in the establishment and maintenance of the DCM with relatively high chlorophyll-*a* concentrations. It can be concluded that the rates of nutrient supply from lower layer waters and regenerative production are the primary factors for the formation and coincidence of the DCM and POM maximum in the light-limited zone of the NE Mediterranean for most of the year.

In March 1992, though the upper layer was well mixed in the peripheries of the Rhodes gyre, the POM profile displayed a coherent peak, perfectly coinciding with the depth of the maximum primary production between 30–40 m (Figs. 4c and 6) which corresponded to 10% light penetration depth. Interestingly, the CHL distribution was almost vertically uniform, exhibiting a small peak near the base of the well-mixed euphotic zone (Fig. 5). The primary production and POM peaks observed in the periphery waters may have originated in local processes. A similar mechanism was suggested previously by Raimbault et al. (1993) and Claustre et al. (1994) in the frontal regions of the Western Mediterranean Sea.

In the NE Mediterranean Sea, primary production above the DCM zone always occurs under light saturated but nutrient limited conditions, leading to higher organic carbon/CHL ratios in living cells as experienced in NW Mediterranean (Socal et al., 1999). Therefore, an estimate of phytoplankton biomass from the seasonally and vertically variable POC/CHL ratios (Fig. 5 and Tables 4 and 5) should be used cautiously in determining the contribution of algal carbon to the POC pool in the euphotic zone of the NE Mediterranean.

Depth-averaged C/N ratios of bulk POM suspended in the euphotic zone are mostly greater than the Redfield ratio (Table 4), indicating that POM in the nutrient-depleted euphotic zone was dominated by carbonaceous compounds. It is most probably the result of selective decay of nitrogenous constituents of POM as experienced in fast and slowly sinking particulate matter in the marine environments (Libes, 1991; Çoban-Yıldız et al., 2000). On the other hand, the N/P ratios of bulk POM were unexpectedly lower than the Redfield ratio especially during the bloom period of March 1992. Primary production in the Mediterranean Sea is known to be potentially limited by reactive phosphate because nutrient supplies from intermediate depths, rivers and atmospheric sources always occurs with high NO_3/PO_4 molar ratios (Yılmaz and Tuğrul, 1998; Krom et al., 1992; Markaki et al., 2003). The low N/P ratios of phosphate of bulk POM (9.8–11.8) for the March-92 bloom period strongly suggests luxury uptake by algae in P-limited waters when nutrient-rich deep waters are supplied to the upper layer. Moreover, the appearance of relatively low PON/PP ratios in Table 4 for the less productive seasons strongly suggests that some fraction of phosphorus in bulk POM might be of non-biogenic origin via adsorption of inorganic phosphates on particles. Our phosphate data in Table 2 for the euphotic zone mostly were very close to the detection limit of the method (20 nM), leading to some uncertainty in lower nitrate: phosphate ratios (5–18). These estimated ratios are inconsistent both with higher nitrate/phosphate ratios (24–33) of deep waters (Table 2) and P-limited algal growth in the euphotic zone (Moutin et al., 2002; Krom et al., 1991, 1992; Yılmaz and Tuğrul, 1998; Kress and Herut, 2001). A similar conclusion has been reached by Moutin et al. (2002) suggesting that the concentrations of biologically available phosphate, determined from turnover rate of P in the Mediterranean, are lower than the values obtained by classical chemical methods including the magnesium-induced co-precipitation. Therefore, nitrate/phosphate ratios in the nutricline may be a more reliable indicator for assessing potential limiting in the euphotic zone. The nitrate/phosphate ratios have been observed to reach the peak values in the upper nutricline zone of the eastern Mediterranean due to the shift of phosphacline to greater depths. A similar situation has been observed in the western and eastern Mediterranean (Moutin and Raimbault, 2002) and attributed to faster consumption of phosphate supplied by diffusion and advection.

POC/PP and POC/PON ratios are greater than the classical Redfield ratio (106:16:1) during summer–autumn period (October, 1991 and July 1993), indicating selective accumulation of carbonaceous compounds in bulk POM of nutrient depleted euphotic zone (Table 4). Not unexpectedly, these particulate ratios appear to decline in the DCM zone, though bulk POM still possesses less nitrogenous compounds, especially in October 1991. In addition to possibility of analytical artifact, some fraction of particulate phosphorus determined in the filtered particles might be inorganic phosphates captured by small size organisms which dominate primary productivity in the light-limited zone (Moutin et al., 2002; Moutin and Raimbault, 2002).

In conclusion, the Levantine basin of NE Mediterranean Sea is characterized by its large seasonal and regional variability in hydro-dynamical and biochemical properties, extending from the surface layer down to at least 1000-m depth. Bulk POM from the nutrient-depleted surface mixed layer possess relatively high C/N and C/CHL ratios, indicating that POM pool is dominated by detritus, bacteria and zooplankton as experienced in other oligotrophic seas (Rabitti et al., 1994). However, the contribution of algal biomass to POM pool increases in the DCM zone of the Rhodes cyclone and its peripheries, where a close relationship appears between the POM and chlorophyll profiles and the nutricline remains situated near the base of the euphotic zone of these regions throughout most of the year.

Very low primary production rates in summer–autumn period (as low as 40–50 mg C m^{-2} day^{-1}) indicate oligotrophy in the NE Mediterranean Sea. However, the upwelling of nutrient-rich LDW but with high N/P molar ratios (about 28–29) in winter fuel the algal production coherently to level of 457 mg C m^{-2} day^{-1} in the peripheries of the cyclone. It appears to become as fertile as the western Mediterranean (330–600 mg C m^{-2} day^{-1}) (Estrada et al., 1993) when deep convective mixing processes significantly supply nutrients to the surface waters. On the other hand, deep convective winter mixing in the core of the Rhodes cyclone generates a typical example of the high nutrient low chlorophyll (HNLC) condition, most probably due to dilution of biomass in the well-mixed upper layer.

Relatively low N/P (10) and C/CHL (66) ratios of bulk POM for March 1992 strongly suggest luxury consumption of the upwelled phosphate by algae and thus export of selectively P-enriched POM to the phosphorus depleted LDW. In other words, P-rich particle snow during the bloom period does not help the establishment of high nitrate/phosphate ratios (28–29) in the LDW. There should be other natural processes in the eastern Mediterranean upper layer waters and atmosphere, which predominantly sustain such high nitrate/phosphate ratios in the LDW. These sources could be slow recycling of nitrogen in the euphotic zone (Yılmaz and Tuğrul, 1998) and atmospheric deposition (wet+dry) with very high N/P ratios (Markaki et al., 2003) during late winter, which lead to selective enrichment of biologically labile DON, suspended POM and dissolved inorganic nitrogen in the eastern Mediterranean upper layer which sinks at selected sites (Adriatic and Aegean Seas) to the Levantine deep basin.

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