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Elemental composition of seston and nutrient dynamics in the Sea of Marmara

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Abstract

The Sea of Marmara, an intercontinental basin with shallow and narrow straits, connects the Black and Mediterranean Seas. Data obtained during 1991–1996 have permitted the determination of the elemental composition of seston in the euphotic zone and the N : P ratio of the subhalocline waters of the Marmara Sea. Since primary production is always limited to the less saline upper layer (15–20 m), of the Marmara Sea, the subhalocline waters of Mediteranean origin are always rich in nutrients ($NO_3 + NO_2 = 8$–$10\ \mu$m, $PO_4 = 0.8$–$1.2\ \mu$m) but depleted in dissolved oxygen (30–50 μm) throughout the basin, yielding an $-O_2 : N : P$ ratio of 178 : 9 : 1. Pollution of the surface waters since the 60s has modified the subhalocline nutrient chemistry slightly. In the euphotic zone, the N : P ratio of the seston changes from 5.9 to 9.5 between the less and more productive periods. Though the biology of the Marmara has changed significantly during the previous two decades, the close relationship observed between the elemental composition of the surface seston and the $NO_3 : PO_4$ ratio of the subhalocline waters strongly suggests that during the whole year primary production throughout the basin and POM export to the lower layer remain nitrogen-limited. This suggestion needs to be confirmed by bio-assays, biological studies and sediment trap data from the upper subhalocline depths. Nonetheless, the counterflows in the Marmara basin possess relatively low N : P ratios in both dissolved and particulate nutrients and extend as far as the adjacent seas.

Introduction

Particulate organic matter (POM) produced photosynthetically in surface waters of marine environments possesses carbon, nitrogen and phosphorus in the ‘Redfield ratio’ of C : N : P = 106 : 16 : 1. This conventional relationship represents the average chemical composition of ocean phytoplankton growing with maximum growth rates (Goldman et al., 1979). However, the C : N : P ratio is well known to vary markedly in marine, brackish and fresh waters, depending on the species composition and the nutrient composition of the productive surface waters (Vinogradov, 1953; from Redfield et al., 1963; Goldman et al., 1979; Sakshaug et al., 1983). POM in the surface waters, moreover, is not solely composed of phytoplankton; throughout most of the year, excluding the bloom period, bacteria, microzooplankton, protozoa and detrital material constitute a major fraction of the total POM inherent in the euphotic zone (Vostokov & Vedernikov, 1988). Furthermore, the total suspended matter in surface waters, the so-called seston, generally – and especially in coastal margins and enclosed seas – contains inorganic material (Vostokov, 1996). Thus, the chemical composition of seston collected from surface waters may differ from the conventional Redfield ratio. As Copin-Montegut & Copin-Montegut, 1983 clearly stated, the stoichiometric ratios of seston from the world ocean vary between 5.5–12.7 for C : N, 42–168 for C : P and 6.5–23.0 for N : P. The POM initially in the euphotic zone is either consumed by herbivores, decomposes in the productive zone, or it sinks to the oxygenated aphotic layer where it decays in the water column and in the sediment with the release of carbon dioxide and nutrients into the ambient water (Redfield et al., 1963; Richards, 1965; Brewer & Murray, 1973).

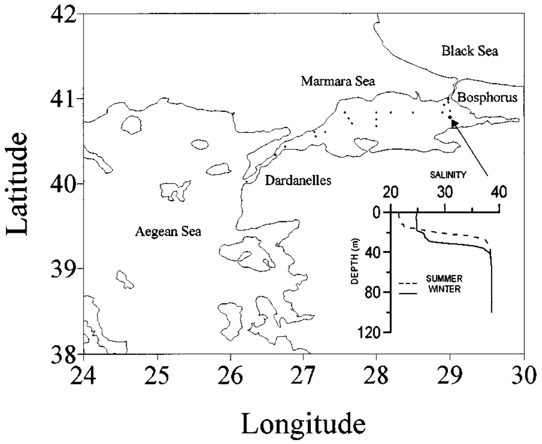

Figure 1. Sampling stations in the Sea of Marmara and typical summer, winter salinity profiles at a reference station with 1230 m depth.

In this paper, we present the elemental stoichiometry of seston collected in the surface waters of the Marmara Sea during 1991–1996. We then discuss the seasonal variation in the elemental ratios of seston and the possible reasons for deviations from the Redfield ratio (C : N : P = 106 : 16 : 1). We also discuss the relationship between the elemental composition of the surface seston and the mean N : P ratio of the subhalocline waters, based on long-term unpublished data obtained in the Sea of Marmara since 1990.

Study area

The Sea of Marmara, a small intercontinental basin with a surface area of about 11500 km^2 and a total volume of 3378 km^3, connects the less saline Black Sea (S = 17–18 ppt) to the more saline Mediterranean (S = 39 ppt) via the Turkish Straits, the Bosphorus and Dardanelles (Figure 1). Because of the large salinity difference between the adjacent seas, two-layer exchange flows are established in the two straits, resulting in the formation of a permanent two-layered stratification of the entire basin of the Marmara Sea. The basin consists of three topographic depressions (the max. depth being 1390 m) in the north and a wide shallow area (shelving to 100 m) in the southern margin. Summer and winter salinity profiles (Figure 1) show the brackish water of Black Sea origin to occupy merely the upper 20–25 m with a renewal time of about 5–6 months (Besiktepe et al., 1994). This upper layer, whose salinity and temperature vary seasonally between 22–26 ppt and 7–24 °C respectively, is separated throughout the year from the underlying saline Mediterranean water by a steep halocline at 25–30 m. The subhalocline waters of the Marmara basin which possess nearly constant salinity and temperature ($\sim$ 38.5–38.6 ppt and 14.5–15.0 °C) throughout the basin are renewed on avearge in 6–7 years by the Mediterranean inflow via the Dardanelles undercurrent (Besiktepe et al., 1994). In the Sea of Marmara, primary production occurs only in the upper layer, extending down to the halocline during summer–autumn when the surface nutrient concentrations are low (Ediger & Yilmaz, 1996). The total annual primary production, derived from chlorophyll-a measurements, is of the order of 100 gC m^{-2} for the entire basin (Ergin et al., 1993). Morkoc (1995) estimated an annual production of 170–190 gC m^{-2} y^{-1} for a coastal embayment, based on long-term measurements of carbon assimilation.

During the last three decades dramatic changes have occurred in the Black Sea ecosystem as a result of both human and natural pressures (Mee, 1992; Kideys, 1994; Bologa et al., 1995). Since the Marmara upper layer water is renewed at least twice a year by the Black Sea inflow, similar modifications have been observed in the Marmara ecosystem (Kocatas et al., 1993). Its recent state has been studied by Sorokin et al. (1995) and Shiganova et al. (1995), who have emphasized the contributions of microheterotrophs, carnivorous organisms, and of the chetonopore *Mnemiopsis leidyi* to the lower trophic levels of the marine ecosystem. Unfortunately, as emphasized by Uysal (1996) in his study of some of the planktonic species, there exists a lack of long-term biological data.

Although biological studies are still very limited, a national programme has been investigating the chemical oceanography of the Marmara Sea and Turkish straits since 1986. From the data collected in the two straits, Polat & Tuğrul (1995, 1996) and Tuğrul & Polat (1995) evaluated the exchange of nutrients and organic carbon between the adjacent seas via the Bosphorus and Dardanelles. They showed that the nutrient budget of the Marmara upper layer (and thus the primary production in the sea) is dominated by inputs both from natural and land-based sources; these being the Black Sea inflow, the input from the subhalocline waters by vertical mixing and the domestic/industrial waste discharged directly into the coastal surface waters, especially by the city of Istanbul (Orhon et al., 1994). The inputs from these sources vary seasonally and regionally. In winter, the Black Sea inflow is enriched with dissolved inorganic nutrients whereas its particulate nutrients are depleted. The nitrate + nitrite concentrations increase from 0.1–0.2 μm in spring–autumn to 4.5–7.5 μm in winter but the seasonal change in particulate nutrients is less pronounced due to the background of seston in the inflow. Similar winter increases observed in Romanian coastal waters (Bologa, 1985) suggest that the inorganic nutrient-enriched northwestern shelf waters of the Black Sea reach as far as the Bosphorus region via alongshore currents and may enter the Sea of Marmara through the Bosphorus (Sur et al., 1994). In late spring-summer, when the Danube discharge to the northwestern Black Sea is maximal, the Black Sea inflow occasionally contains high nitrate concentrations (Tolmazin, 1985; Serpoianu et al., 1992; Cociasu et al., 1997). The POM content of the inflow increases markedly during the late winter–spring bloom in the southwestern Black Sea (Oguz et al., 1996). Accordingly, the POC concentration ranges from background levels of 12–17 μm in the less productive period to 25–40 μm during the bloom. Similarly, the PON varies seasonally between 1.0 and 5.5 μm, whereas the seasonality in PP is less pronounced, ranging merely between 0.1–0.2 μm between 1991 and 1994 (Polat & Tuğrul, 1995).

Before they enter the deep Marmara Sea, the saline Mediterranean waters possess relatively low nutrient and organic carbon concentrations but saturated levels of dissolved oxygen (DO) as clearly demonstrated at the Dardanelles-Aegean Sea junction (Polat & Tuğrul, 1996). The phosphate concentration ranged seasonally between < 0.02 and 0.1 μm, with an annual mean of about 0.05 μm; nitrate + nitrite concentrations varied between < 0.1 and 2.4 μm (annual mean: 1.0 μm), the highest values always occurring in winter. Average annual particulate concentrations (POC = 1.2–7.0 μm, PON = 0.04–0.7 μm, PP = 0.01–0.04 μm) are comparable to dissolved nutrient values Polat & Tuğrul (1996). Both old and new chemical data from the deep Marmara basin (Figure 2) demonstrate that during its stay of 6–7 years (on average) in the basin, the inorganic nutrient content of the Mediterranean inflow increases nearly ten-fold whereas its DO content declines from saturated levels to 30–50 μm since only limited ventilation of the subhalocline waters is possible through the permanent halocline (Besiktepe et al., 1993). The TOC content of the Mediterranean inflow (68 μm), some 3 times lower than that of the Black Sea inflow (210 μm), changes little in the Marmara basin, because POM sinking from the surface waters becomes oxidized in the subhalocline waters and makes only a small contribution to the DOC pool of the system (Tuğrul, 1993; Polat & Tuğrul, 1995).

Table 1. Cruise dates of R/V Bilim in the Sea of Marmara during 1991–1996.

	1991	1992	1993	1994	1995	1996
Jan.	10–13					
Feb.			11–17			
Mar.	1–13	15–21				
Apr.	30.3–1.4			11–14	28–30	6
May						
June	19–23					
July			4–10			
Aug.						
Sep.					23–25	
Oct.	1–7	17–19				
Nov.						
Dec.			5–16			

For a better understanding of the nutrient chemistry of the Marmara Sea, typical depth profiles have been displayed in Figure 2, based on unpublished data collected with R/V Bilim and on measurements reported previously by Miller (1970; R/V Chain), Sen Gupta (1971; R/V Phillsbury), Anderson & Charmack (1974; R/V Thompson), Friederich et al. (1990; R/V Knorr). Figure 2 shows nutrient concentrations to be relatively low in the brackish upper layer throughout the year; the ranges estimated from the unpublished measurements of 1990–1996 are 0.2–1.5 μm for nitrate + nitrite and 0.04–0.25 μm for phosphate, with atomic N : P ratios commonly of < 2–4. The indicated seasonalities are much less pronounced than those reported for the Black Sea inflow (Polat & Tuğrul, 1995). Since primary production only occurs in the upper layer, subhalocline nutrient concentrations are as high as 8–10 μm for nitrate and 0.8–1.2 μm for phosphate, changing little with either depth or season. Thus, on an annual time scale, the lower layer system approximates to a steady state. Comparison of the old and new profiles also reveals that long-term changes are more pronounced in the upper subhalocline; the nutricline, which in the past extended below the halocline, is now established within the halocline. Although nutrient concentrations in the deep water have increased slightly since 1965, the atomic N : P ratio has remained almost constant at 8–10. This strongly suggests that, although the biology of the Marmara upper layer has changed since 1960s, the biogenic POM exported from the euphotic zone has retained its chemical composition.

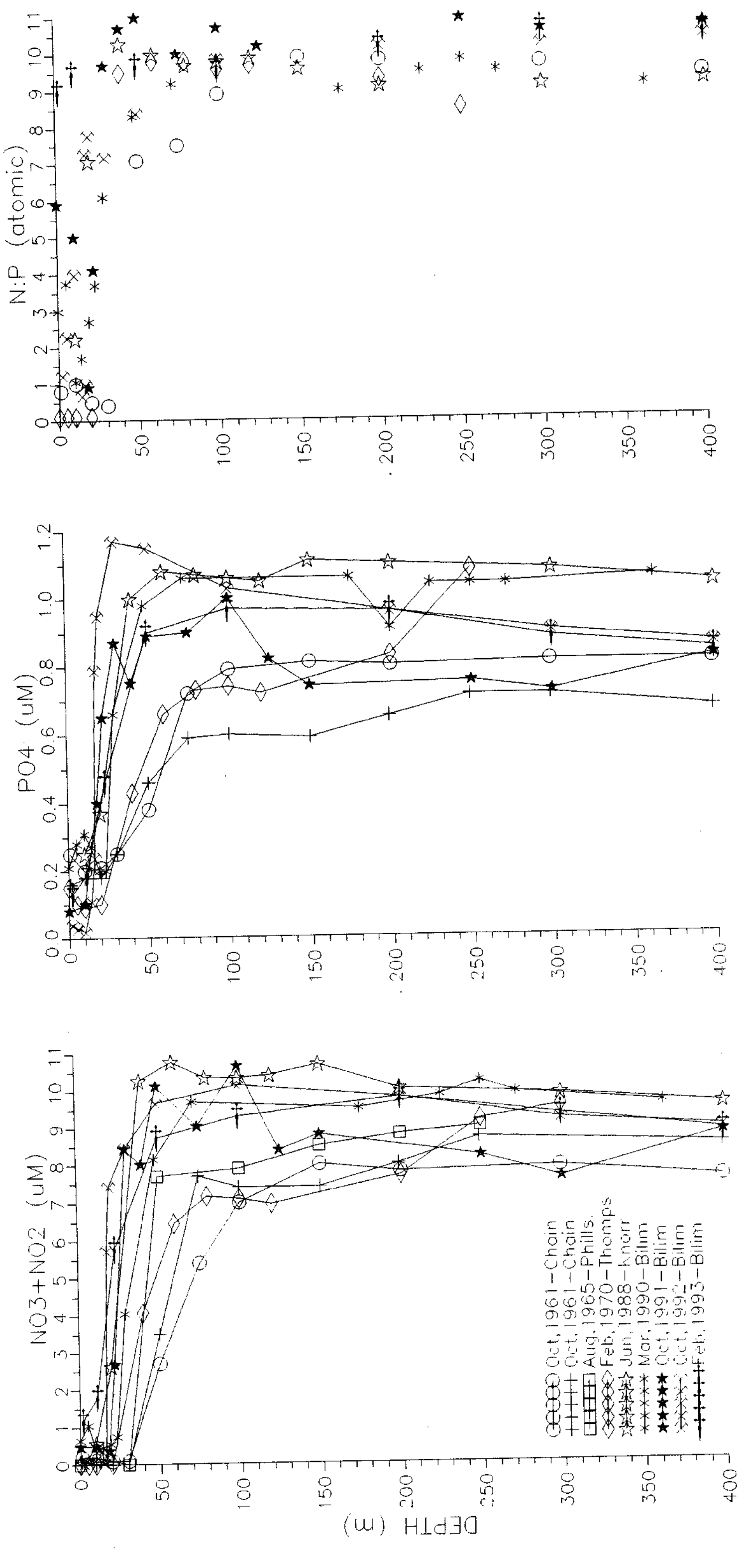

Figure 2. Vertical profiles of $NO_3 + NO_2$, PO_4 and N : P of the upper 400 m at the eastern deep basin of the Sea of Marmara.

Material and method

During 1986–1996, a series of oceanographic cruises covered the Sea of Marmara and the two straits, at the station network being given by Besiktepe et al. (1994). The locations of the chemical stations visited during the 1991–1996 surveys (see Table 1) are illustrated in Figure 1. CTD data were obtained by a Sea-Bird model probe attached to a remote-controlled, 12-bottle (5 l capacity) rosette system. At selected stations at least 6–7 samples for chlorophyll-*a* (Chl-*a*) analysis were collected down to the depth where the light was 0.1% as intense as at the surface; these samples were filtered immediately through Whatman GF/F filters and kept frozen. Nutrient and dissolved oxygen samples (nitrate + nitrite, phosphate) were collected using the 12-bottle rosette. DO samples were taken into a 50 or 150 ml glass bottle; DO fixing chemicals were then added and the bottle was kept in the dark for 1–2 hr. Nutrient subsamples in high density polyethylene bottles were kept frozen; depth intervals of nutrient samples can be realized from the profiles depicted in Figure 2. POM was sampled discretely from at least 5–6 depths from the surface to just below the halocline using 5 l Niskin bottles attached to the rosette. Approximately 2–5 l of subsamples were filtered through 47 (or 25) mm GF/F filters (pre-combusted at 450–500 ˚C for 3 h). Subsamples were prefiltered through 200 μm nylon mesh placed in a funnel, in order to remove the larger particles (e.g. meso-zooplankton) which would otherwise have caused errors. Occasionally, this step was skipped and forceps were used to remove visible particulates retained on filters. Filters for POM analysis were kept frozen until processed on land. Before analysis, they were dried at low temperature (40–50 ˚C) and fumed with concentrated hydrochloric acid to remove any carbonate retained on the filters. About 20 mg of each filter was placed in a pre-cleaned tin capsule and the POC and PON content of the samples were determined quantitatively using a Carlo Erba 1108 model CHN analyzer. For particulate phosphorus (PP) analysis, the dry combustion + weak acid dissolution method given by Karl et al. (1991) was followed; the concentrations of the oxidized phosphorus in the samples were then measured colorimetrically as for reactive phosphate. Nutrient (nitrate + nitrite, phosphate) analyses were carried out using a two-channel Technicon autoanalyzer; the methods were similar to those given by Strickland & Parsons (1972). Chl-a samples were first extracted with 90% acetone and then determined fluorometrically (Holm-Hansen et al., 1965). Dissolved oxygen was measured by the automated Winkler titration method.

Results

Surface water

Particulate and chlorophyll-*a* (Chl-*a*) data displayed in Figures 3 and 4 represent euphotic zone concentrations of POC, PON or PP and Chl-a at different stations in the deepest western, central and eastern basins of the Marmara Sea (Figure 1). These stations were visited 14 times at different months between 1991 and 1996 (see Table 1 for cruise dates). The layer-averaged (upper 25 m) data from the three sub-basins for each cruise illustrate the spatial variations in POM. The restricted number of data sets (only 14) prevents reliable deductions of the seasonal trends in POM for 1991–1996. Nevertheless, the basic feature of Figure 3 exhibits coherent increases of POC, PON and PP concentrations of the euphotic zone during late winter-early spring, as a result of the pronounced biomass increases (in terms of chl-a data) during the early spring bloom (Figure 4). The highest particulate concentrations, ranging between 15 and 45 μm for POC, 1.8 and 4.5 μm for PON and between 0.20 and 0.45 μm for PP, were obtained in the February–April period of 1991–1996. During the June–January period variable background concentrations of POM were always observed; for example, in June 1991 and July 1993, unexpectedly high POM values were recorded in the surface waters, accompanied by apparent decreases in the water transparency. In fact, in summer, the surface mixed layer is separated by a well defined thermocline which inhibits the input of nutrients from the nutricline and it was unfortunate that the species responsible for the episodic backgrounds were not identified. The autumn-winter period generally corresponds to the POM-poor seasons in the Marmara upper layer; however, slight increases were recorded in October, when the seasonal thermocline was weak enough to permit wind-induced nutrient input from the nutricline.

The general trend of the euphotic POM data depicted in Figure 3 for 1991–1996 enables one to divide all the data into two subgroups corresponding to high (February to April) and low (June to January) periods of production, irrespective of the sampling locations. The validity of this classification is corroborated by the similar seasonality observed in the chl-a data sets for 1991–1996 (Figure 4). The elemental stochiometry of

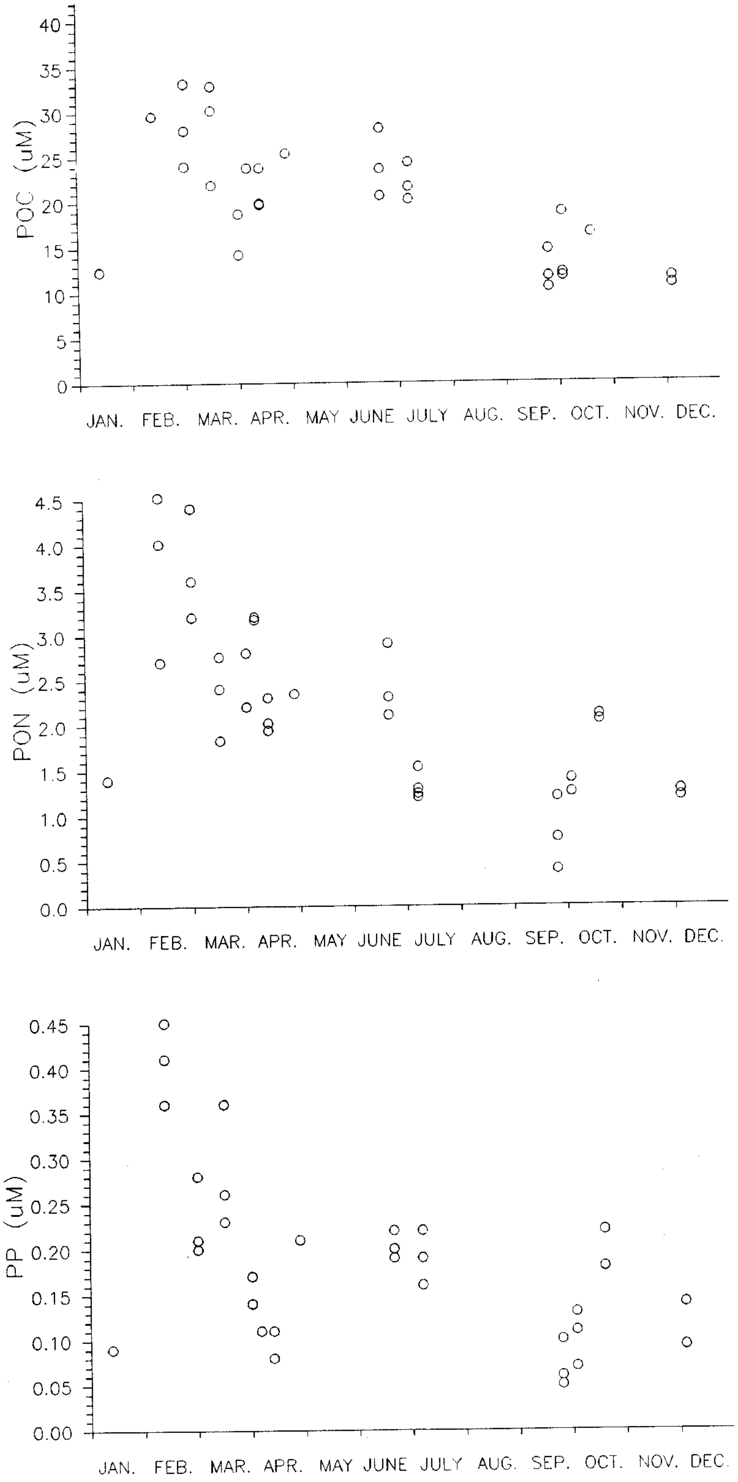

Figure 3. Variation of POC, PON and PP between 1991 and 1996 obtained from depth averaged data of the upper 20–30 m of the Sea of Marmara.

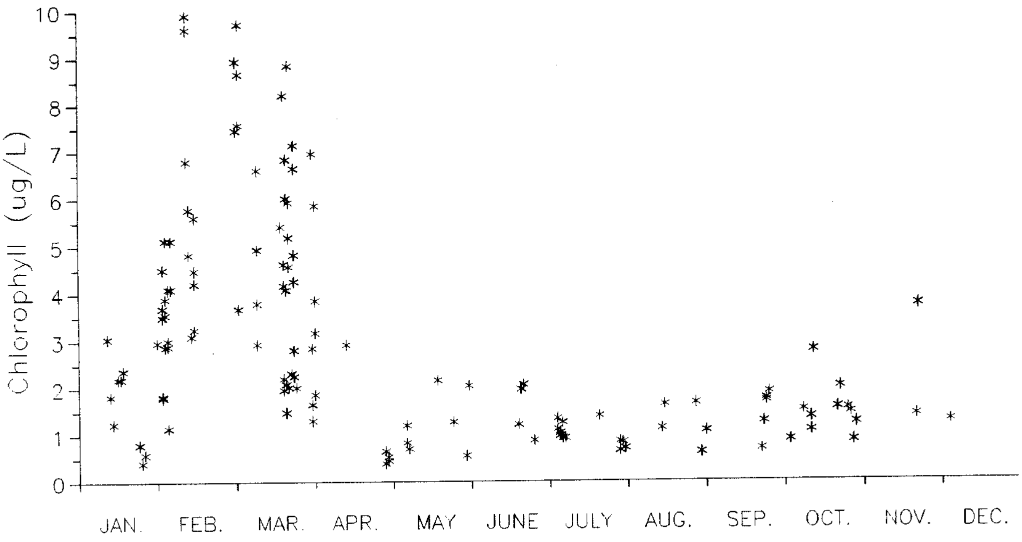

Figure 4. Variation of chlorophyll-a in the surface waters of the eastern Marmara basin from the discerete depths in the euphotic zone (upper 30 m).

Table 2. Elemental (atomic) and POM vs. Chl-a ratios achieved with linear regression equations for the surface waters of the Marmara Sea.

	High				Low			
	b	a	*r*	*n*	b	a	*r*	*n*
POC : PON	7.4 ± 1.16	5 ± 13.0	0.87	54	8.3± 1.68	3.5± 10.3	0.80	62
POC : PP	98 ± 24.5	6 ± 17.7	0.75	53	78 ± 18.6	5 ± 11.4	0.73	63
PON : PP	9.5 ± 3.43	0.85± 2.48	0.62	53	5.9± 2.02	0.7± 1.27	0.60	62
POC : Chl	38.4 ± 7.30	172 ± 210	0.81	60	37.5*	174*	0.28*	62
PON : Chl	4.7 ± 1.35	21 ± 38.9	0.67	61	8.0± 3.18	14 ± 18.4	0.54	63
PP : Chl	0.8 ± 0.24	4.4 ± 5.39	0.71	43	2.8± 1.23	2.2± 5.35	0.59	41

* Insignificant correlation at $p = 0.05$.

POM and POM to Chl-a ratios, derived from regression analyses of the sub-grouped 1991–1996 data sets are summarized in Table 2. The high correlation coefficients of the reported linear regressions indicate that the bulk of the seston consisted principally of organic material composed of living phytoplankton, heterotrophs and detritus. The estimated POC : PON ratio of the high production period was 7.4, slightly lower than the ratio of 8.3 for the low production period (Table 1). The POC vs PON intercept values are high and variable, suggesting throughout the year the presence of background concentrations of carbonaceous compounds (low in organic nitrogen) in the seston of the Marmara upper layer.

During the period of high production the estimated N : P ratio of the seston, 9.5, was lower than the Redfield ratio of 16 for ocean phytoplankton whereas the C : P and C : N ratios were 98 and 7.4, respectively (Table 2). The estimated POC : Chl-*a* ratio (w/w) for the same period is 38.4. The intercept of the regression line, found to be as high as 172, indicates a relatively high detrital carbon content of seston pool as the Chl-*a* decreases to low levels. The organic carbon pool, except the photosynthetically produced organic material, possibly covers the microzooplankton which may be dominating the heterotrophic community in the period of high production. The estimates from the linear regression equation in Table 2 strongly suggest that the seston was composed of significant amounts (as high as 50%) of living phytoplankton during the period of high production. The living phytoplankton carbon concentration, estimated from the POC : Chl ratio (38.4) and the total POC values, is in the range of 60–370 μg l^{-1} (mean = 193 μg l^{-1}) in the period of high production. This is 25–100% (mean = 50%) of POC pool in the surface waters. Moreover, the bulk of the seston was enriched in phosphorus relative to nitrogen. The ratios of N : Chl-*a* and P : Chl-*a* derived from the regressions of data sets, are 4.7 and 0.8 for the period of high productivity, yielding a C : N : P ratio of 124 : 13 : 1 for living particulate matter. The relatively low N : P ratios of both seston and living phytoplankton, accompanied with the low molar ratios of nitrate to phosphate observed in the surface waters for most the year, suggest primary production in the whole of the basin to be nitrogen limited.

During the period of low productivity, the PON : PP was as low as 5.9 though the estimated POC : PP ratio was 78 (Table 2). The seasonal difference observed between the PON : PP ratios of the high and low productivity periods is significant (two tailed *t*-test, $p = 0.1$). The difference becomes highly significant ($p = 0.01$) if the April data of the last two years (see Table 1) are excluded from the regressions. On the other hand, there is no significant correlation between POC and chlorophyll during these years; this finding suggests low carbon synthesis in the surface waters, low algal biomass as seen in Figure 4. The heterotrophic community developed during this period may also provide a low phytoplankton biomass and enhance regenerated production. On the other hand, PON : Chl and PP : Chl correlations are still significant in the period of low production, and the estimated PON : PP from chlorophyll relations is around 6.3 and close to the value (5.9) given in Table 2.

Subhalocline water

The ratio (nitrate + nitrite) : phosphate in the subhalocline waters of the Marmara Sea has been estimated from the linear regression of the long-term, basin-wide data. All the unpublished data obtained in the deep subhalocline waters of the entire basin from the Dardanelles to the Marmara-Bosphorus exit in 1990–1994 have been combined (see Figure 1), excluding nutrient data from heavily polluted coastal areas. This regression analysis is based on the following assumptions:

(a) nutrient increases in the subhalocline waters are principally the result of aerobic oxidation of labile biogenic particles exported from the productive upper layer; nitrate loss via denitrification is insignificant;

(b) the Mediterranean water enters the basin with low and seasonally constant nutrient concentrations (the so-called preformed values).

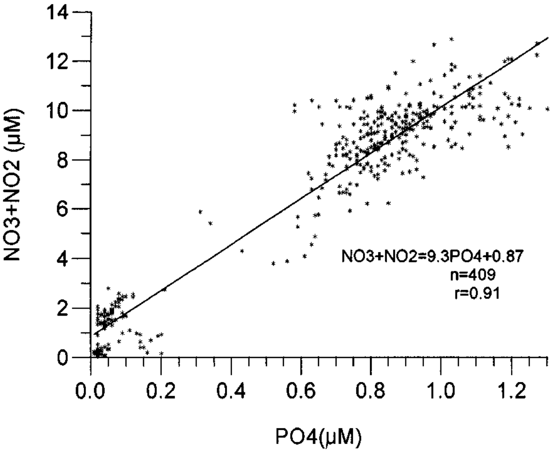

Figure 5. The regressions between $NO_3 + NO_2$ and PO_4 concentrations ($n = 409$, $r = 0.91$) from the subhalocline waters of the Marmara Sea between 1990 and 1994.

In fact, as described in the 'Study Area' section, the latter assumption is weakened by the data at the Dardanelles-Aegean Sea Junction where the subhalocline water has low nutrient concentrations which increase noticeably in winter. The $NO_3 + NO_2$ vs. PO_4 regression for the subhalocline water mass yields a N : P ratio of 9.3 (Figure 5). Data with low concentrations ($PO_4 < 0.2$ μm and $NO_3 + NO_2 < 2.5$ μm) represent the slightly diluted Mediteranean inflow in the Dardanelles near its exit to the Marmara Sea; the second group of data having higher concentrations represents the aged Marmara subhalocline waters including the Bosphorus-Marmara Junction where the fresh Mediterranean inflow is diluted rapidly with aged subhalocline waters having modified chemical properties. Data from moderately diluted or less aged inflow is scarce. The DO vs. $NO_3 + NO_2$ and DO vs. PO_4 regressions demonstrate that the measured nutrient concentrations increased linearly with decreasing DO concentrations in the subhalocline waters; the molar ratios derived from the regression lines are 178 for $-O_2 : PO_4$ ($n = 668$, $r = 0.89$) and 19.7 for $-O_2 : NO_3{+}NO_2$ ($n = 664$, $r = 0.90$), yielding an atomic N : P ratio of nearly 9.0 for the entire subhalocline water. This ratio is very similar to that, 9.3, derived from the $NO_3 + NO_2 : PO_4$ regression.

Discussion

The atomic ratio of nitrate to phosphate (9.0–9.3) in the subhalocline waters of the Marmara Sea is very close to the mean elemental ratio of 9.5 estimated for the total seston – about 50% of which, especially during the high productivity period (February–April), is composed of phytoplankton living in the euphotic zone. Unfortunately no data from sediment traps exist which would corroborate this close relationship between the mean N : P ratios of the surface seston and the subhalocline nutrient concentrations. The C : N : P ratio obtained from seston during the period of high production is 98 : 9.5 : 1, which is less than that (124 : 13 : 1) estimated from the slopes of particulate data vs. Chl-a concentrations for the same period; the living particulate ratio being similar to those of diatoms (Tett et al., 1975; Epply et al., 1977; Oguz et al., 1996). This finding suggests that the majority of the fast sinking POM (diatom) produced during the late winter-spring period and exported from the euphotic zone possesses an N : P ratio comparable to that of the surface seston but less than the Redfield ratio of 16 for ocean phytoplankton. In the adjacent Black Sea, POM produced during the spring and autumn bloom dominates the particle flux to the lower layer (Izdar et al., 1987). Uysal (1996) has found that during spring in the Marmara Sea the centric diatom species (*Skeletonema costatum, Thalassiosira spp. and Coscinosira spp.*) dominate the phytoplankton population. Diatoms generally have high sedimentation rates; their important role in the vernal export flux has been discussed previously by Smetacek (1985) and several scientists have studied the physical and biological mechanisms controlling the vertical fluxes of POM (Alldredge & Gotschalk, 1989; Rieseball, 1991a and 1991b). On the other hand, grazing may also play an important role during spring blooms of phytoplankton (Banse, 1994) which is usually known to be terminated by nutrient exhaustion.

In the upper layer, during the period of low production, the elemental composition of seston appears to become modified, yielding low ratios of both N : P (5.9) and C : P (78). The former ratio is very similar to the low N : P ratio (6.3) derived from the slope of the particulate data vs. Chl-a concentrations (see Table 2). This strongly suggests that during the period of low productivity, the low concentrations of P-enriched seston found in the nutrient-depleted euphotic zone comprised living and dead phytoplankton of regenerative origin. Although the mechanism by which P-enriched seston was produced in the surface waters is still unclear, the PP observed during the low productive period was readily soluble in weak acid (Polat, 1995). During the period of low productivity when the Marmara surface waters are relatively warm and infertile, primary production is probably sustained by small phytoplankton species – not diatoms – utilizing nutrients regenerated in the surface layer. Thus, the temporary milky green color and the low transparency of the Marmara upper layer in summer is an indicator of *Emiliana huxleyi* production (Holligan et al., 1993). The contribution of the substantially increased ctenophere populations to the nutrient pool of the Marmara Sea and their possible effects on the other grazers is still understood poorly (Sorokin et al., 1995). However, ctenopheres also play a key role in the trophic structure of the Black Sea, especially in summer and autumn (Vinogradov, 1992).

The high intercepts values of the regression lines of POC vs particulate nutrients (Table 2) indicate the existence of measureable quantities of carbonaceous compounds (especially low in organic nitrogen) in the surface waters of the Marmara Sea throughout the year. In the two-layered ecosystem of the Marmara Sea, nitrogen and phosphorus deficiency of the surface seston relative to the conventional Redfield ratio (C : N : P = 106 : 16 : 1) may have originated from the slow decay of carbonaceous compounds in the productive zone. Selective accumulation of carbonaceous seston in surface waters from different seas was also reported by Copin-Montegut & Copin-Montegut (1983).

Nutrient concentrations in the subhalocline waters are determined both by the biogenic particle influx from the surface layer and the age (renewal time) of the Mediterranean waters in the basin. The molar -$O_2 : PO_4$ ratio, calculated from the regression analysis, was nearly 178, very similar to that estimated by Takahashi et al. (1985) for various deep ocean waters. Takahashi et al. (1985) therefore corrected the measured nutrient and DO concentrations using the initial concentrations of chemicals before they had left the ocean surface. This strongly suggests that the phosphate enrichment of the Marmara subhalocline waters is the result of the oxidation of biogenic particles by biomediated processes, rather than the sedimentation of phosphorus-attached lithogenic and/or biogenic particles and the subsequent release of phosphorus in the lower layer. On the other hand, the mean $-O_2 : NO_3 + NO_2$ ratio is 19.7, much larger than the mean ratio of 10.5 estimated by Takahashi et al. (1985) for the deep oceans. The contribution of denitrification to the anomalous $-O_2 : NO_3 : PO_4$ ratio (178 : 9.0 : 1) of the Marmara subhalocline waters is probably insignificant. According to Polat's (1995) estimate, the annual NO_3 loss by denitrification at the sediment/water interface is only a small fraction ($< 5\%$) of the annual PON influx from the surface layer to the subhalocline waters. Nevertheless, this process is evident in the polluted coastal areas where high concentrations of NO_2 and PO_4 were detected, the DO being $< 10\ \mu$m in the shallow bottom water. The sediment surfaces were not rich in organic carbon, ranging between 1–1.5% (Ergin et al., 1993). These points strongly suggest that during the high production period, the POM exported from the surface layer has a relatively low N : P ratio. This is consistent with the low N : P ratio found in the seston in the euphotic zone. Nonetheless, the subhalocline water leaves the Marmara basin with relatively low $NO_3 + NO_2 : PO_4$ ratios and is entrained in the surface counterflow, especially at the Bosphorus Maramara Junction, and flows out towards the Black Sea through the Bosphorus undercurrent.

Conclusions

The Sea of Marmara is occupied with the two distintly different water masses thoroughout the year. Since primary production is always restricted to the upper layer, the more saline water of Mediterranean origin is always enriched markedly with inorganic nutrients in 6–7 years but depleted in dissolved oxygen. The N : P ratio of seston in the Marmara euphotic zone, derived from the regression analysis, ranges from 5.9 to 9.5 between the periods of low and high production, which are lower than the Redfield ratio. Thus, the euphotic layer seston of biogenic origin must contain phosphorus-enriched particles which need to be identified. This fact, together with the consistently low ratios of $NO_3 : PO_4$ in the subhalocline waters throughout the basin since the 60's, suggests that during the whole year primary production in the Marmara Sea remains nitrogen-limited, even though the biology of the sea has been modified drastically during the last two decades. The suggestions that primary production is nitrogen limited and the POM exported from the surface is deficient in nitrogen still need to be confirmed by detailed bio-assays and biological studies together with sediment trap data from the subhalocline. Such efforts are essential for a better understanding of the nutrient cycling in the landlocked, two-layer Marmara Sea ecosystem which is now receiving substantial wastes from land-based sources, facilitating primary production and modifing community structure.

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