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Particulate organic matter in the subsurface chlorophyll maximum layer of the Southeastern Mediterranean

Subsurface
Chlorophyll maximum
Particulate organic carbon
Biogenic silica
Southeastern Mediterranean

Couche subsuperficielle
Maximum de chlorophylle
Carbone organique particulaire
Silicium biogénique
Sud-Est Méditerranée

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ABSTRACT

A well-developed subsurface chlorophyll maximum layer (SCML) appeared during early summer 1986 in the offshore waters overlying the continental shelf of the southeastern Mediterranean basin off the Egyptian coast. The layer occupied the base of the euphotic zone. Maximum levels of particulate organic carbon (POC), particulate organic nitrogen (PON), particulate phosphorus (PP) and biogenic silica (BSi) were associated with the subsurface chlorophyll maximum. The ratios observed between the different particulate matter components investigated in the SCML (POC/PON 6.63 ± 0.89; POC/PP 107.7 ± 22.4 and PON/PP 16.2 ± 3.25) were very close to those published for phytoplankton. Regressions indicated that detrital components of organic matter constituted a small fraction in the SCML compared with other layers, particularly below the euphotic zone. POC/Chl *a* mass ratio *i.e.* 245 ± 63 and biogenic Si/POC ratio *i.e.* 0.36 ± 0.10 observed for the SCML suggested increased photosynthetic efficiency for diatoms and increased silica production relative to carbon. The flourishing of benthic diatoms in the SCML also contributed to increased biogenic silica levels. Maximum Chl *a*/protein ratio *i.e.* 1.10 ± 0.13 was recorded in the SCML, indicating that phytoplankton is the major biomass constituent. Phytoplankton accounted for between 40 and 65% of the protein in the SCML, while above and below this layer the percentage does not exceed 22%.

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RÉSUMÉ

Matière organique particulaire dans la couche subsuperficielle du maximum de chlorophylle au sud-est de la Méditerranée

La Couche Subsuperficielle du Maximum de Chlorophylle (SCML) se développe au début de l'été 1986 dans les eaux du large au-dessus du plateau continental bordant la côte égyptienne. Cette couche se trouve au bas de la zone euphotique. Des maxima de carbone organique particulaire (POC), azote organique particulaire (PON), phosphore particulaire (PP) et silicium biogénique (BSi) y sont associés au maximum subsuperficiel de chlorophylle. Les rapports mesurés entre les différents constituants de la matière particulaire (POC/PON 6,63 ± 0,89; POC/PP 107,7 ± 22,4 et PON/PP 16,2 ± 3,25) sont très proches des valeurs publiées pour le phytoplancton. Les régressions indiquent que les composants détritiques de la matière organique sont relativement peu abondants dans la SCML. Les valeurs du rapport de masse POC/Chl *a* (245 ± 63) et du rapport Si biogénique/POC (0,36 ± 0,10) indiquent une efficacité accrue de la photosynthèse pour les diatomées et une production de silicium supérieure à celle du carbone. La floraison des diatomées benthiques dans la SCML contribue aussi à l'augmentation du taux de silicium biogénique. Le rapport maximal Chl *a*/protéine (1,10 ± 0,13) indique que le phytoplancton est le constituant majeur de la biomasse. Dans la SCML, les protéines représentent entre 40 et 65 % du phytoplancton, tandis qu'au-dessus et au-dessous de cette couche, leur contribution ne dépasse pas 22%.

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INTRODUCTION

The subsurface chlorophyll maximum layer (SCML) constitutes one of the interesting characteristic features of most oceanic waters subject to stratification. The depth range and position of this layer depends mainly on a number of factors, including light, nutrients, seawater density and the behaviour of the various organisms. Association of the SCML with the pycnocline and nutricline, as well as the 1% surface irradiance depths, is a common phenomenon in tropical and subtropical waters (Cullen, 1982).

In the western Mediterranean, the SCML is usually found during summer below 70 m depth (Cruzado and Velasquez, 1986), while in the eastern Mediterranean phytoplankton maxima based on cell counts were observed at 80-100 m by Kimor and Wood (1975) who declared the ability of chlorophyll-containing organisms to divide below the euphotic zone. Off the coast of Israel, Berman *et al.* (1984) observed SCM at depths between 75-150 m. In the offshore waters of the Gulf of Naples, the SCML occurred below the thermocline in late summer and autumn (Marino *et al.*, 1984), while in the open waters of the central and southern Adriatic, Marasovic and Pucher-Petkovic (1988) showed that maximum chlorophyll *a* concentrations regularly occurred in the subsurface layer, most frequently between 50 and 75 m depth. Off the Egyptian Mediterranean coasts, the SCML was regularly observed by Dowidar (1984) and Moustafa (1985), showing a seasonal persistence in the area at depths varying between 70 and 150 m.

Most of these studies link the mechanisms of SCML formation to environmental conditions, including phytoplankton biomass maximum, nutricline layer formation, variations in phytoplanktonic cell settling velocities as well as variations in grazing pressure between layers. Self-shading by phytoplanktonic cells was also considered by Cruzado and Velasques (1986) as a factor limiting SCM depth. A microscopic examination revealed that nanoplankton < 20 µm constitute the greater part of the chlorophyll biomass in this layer (Dowidar, 1984). However, Platt *et al.* (1983) showed that the SCML contains an important component of autotrophic picoplankton which is capable of growth under *in situ* conditions and may contribute about 60% of the total primary production of the SCML.

Apart from the work of Dortch (1987) on the biochemical composition of plankton in the subsurface chlorophyll maximum for an oceanic station off the Washington coast, using DNA, RNA and amino acids as biomass maximum indicators; and despite the establishment and crediting of this phenomenon in several oceanic regions, no attention has been paid to the quantification of the organic constituents specially those of particulate matter, in this layer. It was thus deemed necessary in the present work to throw some light on the different proportions of certain particulate organic constituents in the SCML by determining their variations in a densely phytoplankton-populated subsurface water layer, the aim being to evaluate the magnitude of this layer as a carrier of an important portion of the particulate organic load present in the whole water body. This research will also increase our overall understanding of the correspondence between chlorophyll maximum and other biomass indices in the SCML, and extend our ability to use the ratios of different particulate organic matter components and biomass indices as tracers for the SCML in the different Mediterranean regions.

MATERIAL AND METHODS

During a programme of regular seasonal cruises to the southeastern Mediterranean waters off the Egyptian coast, seawater samples were collected from eight stations overlying the edge of the continental shelf during June-July 1986. Stations are located between 20 and 65 miles from the shore (Fig. 1), beyond the influence of the Nile River plume which does not exceed 10 miles offshore during the flood period.

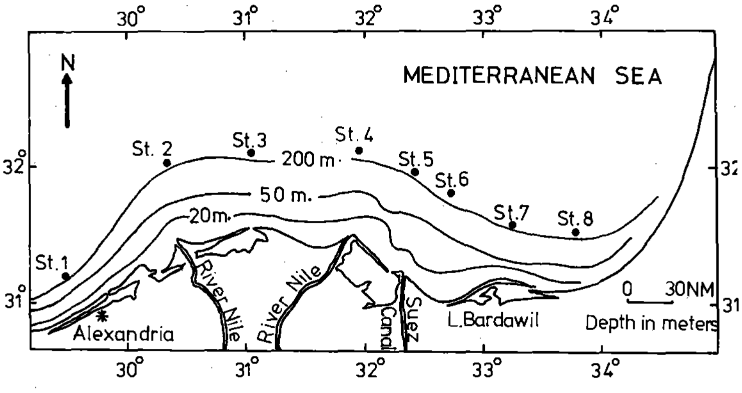

Figure 1
Study area showing sampling locations.

At each station, water samples were taken at selected depths between sea surface and about 200 m using Niskin 5-l non-metallic sampling bottles equipped with reversing thermometers. Collected water samples were drained into 20-l pre-cleaned polyethylene bottles. Vacuum filtration (50-60 mm Hg) was conducted immediately after sampling. About 3-5 l were filtered through 47 mm Whatman GF/C glass fibre filters precombusted overnight at 450°C in an electric furnace. Filters were then stored frozen at −20°C until later analysis at the shore laboratory.

Organic carbon (POC) was determined using the model 543D Carbon Analyzer according to the method of Menzel and Vaccaro (1964) as modified by Fredricks and Sackett (1970) (filter blank = 0.15 µmol/l, mean for triplicate sample analysis C.V. = 13%); a Hitachi 026 CHN Analyzer was used for organic nitrogen (PON) determination (filter blank = 0.05 µmol/l, C.V. for triplicates = 9%). For determination of particulate phosphorus (PP), filters were fused with carbonate in platinum crucibles, neutralized by HCl and analysed for phosphate using the method of Murphy and Riley, 1962 (filter blanks = 0.002 5 µmol/l, C.V. for triplicates = 8%). Suspended inorganic phosphorus was checked using the 1N HCl extraction of unignited dry suspended matter (Aspila *et al.*, 1976), and showed negligible values. The use of 2.2 N H_2SO_4 in the molybdate reagent supressed interferences by silica (Aspila *et al.*, 1976).

Biogenic silica (BSi), retained on 47 mm diameter Gelman membranes (0.45 µm) rinsed with isotonic NaCl solution and dried for 12 hours at 60°C, was digested in 5% Na_2CO_3 solution for 100 minutes at 100°C in a water-bath following the procedure described by Kamatani and Takano (1984). Correction for non-biogenic silica (clay minerals) was performed using particulate Al concentration in the final solution and the conversion factor (2.42 ± 0.2) mentioned by Kamatani and Takano (1984) and Abdel-Moati (1990). Blanks for biogenic silica do not exceed 0.015 µmol/l, while the C.V. for triplicate determinations of the same sample was 6%. Protein (Pr) concentrations were determined accoridng to the method described by Lowry *et al.* (1951) and modified by Dortch *et al.*, 1984 (blanks = 0.010 µmol/l, C.V. for triplicates = 10%).

For chlorophyll *a* estimation, 2 l of water samples were filtered through 0.45 µm Millipore filters 47 mm diameter and chlorophyll *a* was determined spectrophotometrically using the acetone extraction technique according to Strickland and Parsons, 1972 (blank = 0.0, C.V. for triplicates = 8%).

The accuracy of the methods was tested against prepared standards, and the deviations from real standard values expressed as coefficients of variation (C.V.%) were 10% for POC, 5% for PON, 3% for PP, 6.5% for biogenic silica and 8% for protein.

Routine hydrographic observations including temperature, salinity and dissolved oxygen were carried out simultaneously on board during sampling. Statistical calculations including regression slopes and intercepts of chemical composition data were performed using the SPSS/PC$^+$ IBM Statistical Package taking into account statistical and biological problems associated with data grouping (Banse, 1977).

RESULTS AND DISCUSSION

Hydrographic structure of the study area

Before dealing with the organic composition of particulate matter, a short account must be given of the hydrological features of the studied area during this time of the year (June-July). The vertical profiles of temperature and salinity indicate the presence of three well-defined water masses. A surface water mass (0-25 m) of maximum salinity (38.9-39.22) and high temperature (> 26°C) is succeeded by a subsurface layer (75-100 m) of minimum salinity (38.66-38.82), maximum oxygen (> 5.4 ml/l) and temperature (17.0-22.0°C). This layer is mainly of Atlantic origin, spreading over a density gradient between 27.4 and 28.0 kg/m^3. Morcos and Hassan (1976) observed this layer in summer between 50 and 75 m, with a main axis between two 38.6 isohalines enclosing water of less than 38.6 flowing eastward parallel to the coast.

Below this layer lies a second layer of maximum salinity (> 39) with a temperature ranging between 15.8 and 17.2°C and density in excess of 28.8 kg/m^3. This layer was identified as Levantine Intermediate Water formed in certain regions of the eastern Mediterranean, and spreads to occupy depths of more than 200 m (Abdel-Moati and Said, 1987).

POM composition in the SCML

The depth profiles for chlorophyll *a* values (Fig. 2) showed a conspicuous subsurface chlorophyll maximum layer in association with the subsurface water mass occupying the depth range between 75 and 100 m in all sampled stations. The chlorophyll *a* concentration of this layer fluctuated between 0.15 and 0.35 µg/l with an average of 0.22 ± 0.05 µg/l.

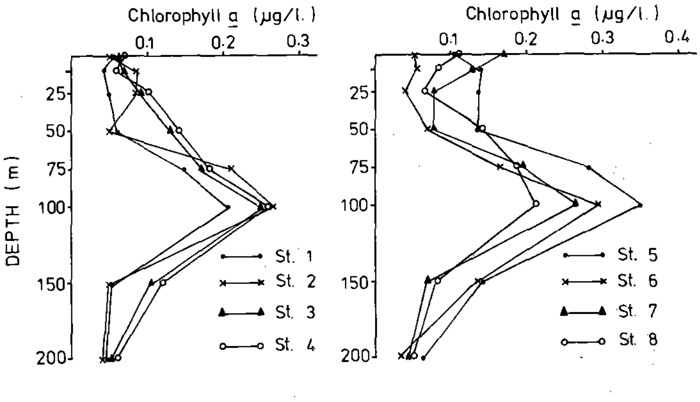

Figure 2
Vertical profiles of chlorophyll a.

During this season, the SCML occurred at the lower boundary of the euphotic zone (indicated by the depth of 1% surface irradiance) which varied between 93 and 124 m in different stations (Tab. 1).

Despite the resemblance between the chlorophyll concentration range in the SCML observed for the present study and those previously mentioned by Moustafa (1985) in the offshore area for August 1982 samples (range 0.16-0.34 µg/l), the depth of occurrence of his maximum values *i.e.* 120-150 m was much deeper, mainly due to the different sampling period (early and late summer).

The chlorophyll *a* concentration at the SCML is much higher than the corresponding surface values. At most stations, the chlorophyll content at the SCML is nearly 3.7 times that observed for surface samples. This reflects the extent of oligotrophy of the surface south-eastern Mediterranean waters during the summer season. The ratios between the chlorophyll values observed in the SCML and those above and below were 2.6 : 1 and 3.2 : 1, respectively. Variation in the integrated chlorophyll *a* values (mg/m^2) calculated for the SCML and below the euphotic zone were not significant (Tab. 1). However, integrated values for SCML showed that chlorophyll *a* in the base of the euphotic zone constituted on the average more than 42 ± 6% of the total integrated content of the upper 100 m.

Due to high temperature and nutrient depletion in the surface waters, phytoplankton would sink and accumulate in the nutrient rich water at the base of the

Table 1

Integrated values of chlorophyll a *biomass (mg/m^2) in the euphotic zone, the SCML and below the euphotic zone.*

Sampling date	Sampling time	Station	Maximum depth (m)	Depth* 1% light	Chl *a* euphotic** zone ($n=4$)	Chl*a* SCML** ($n=2$)	Chl *a* below** euphotic zone ($n=2$)
15/7/86	10 : 55 am	1	220	124	9.54	4.43 (46)	2.55
14/7/86	15 : 00 pm	2	210	104	11.07	5.89 (53)	2.48
20/6/86	11 : 00 am	3	205	106	13.73	5.25 (38)	3.83
21/6/86	12 : 45 pm	4	220	104	14.49	5.55 (38)	4.55
22/6/86	15 : 39 pm	5	230	96	19.74	7.88 (40)	5.08
23/6/86	12 : 30 pm	6	245	114	11.37	5.74 (50)	4.25
23/6/86	15 : 45 pm	7	210	93	13.85	5.63 (41)	2.80
24/6/86	13 : 00 pm	8	220	108	13.83	5.06 (37)	3.30

* Calculated using the formula: depth 1% light = 1.78 + 2.61 Z (SD) (Moustafa, 1985) where SD = Secchi disk readings.
** Euphotic zone (100-1% light), SCML (33-1% light), sub-euphotic zone (< 1% light).
N. B.: Values between parenthesis indicate (Chl *a* in SCML/Chl *a* in euphotic zone %) (average 42 ± 6%).

euphotic zone. Shade adapted cells inhabiting the subsurface layer could benefit from elevated nutrient concentrations due to their ability to increase their chlorophyll *a* content in response to low light availability. The increase of chlorophyll content per cell with decreasing light intensity was previously reported by Jorgensen (1964), Steeman-Nielsen and Jorgensen (1968), Takahashi and Nakamoto (1972) and Cullen (1982).

The data indicate some compositional variations in the concentrations of the organic fraction of suspended matter. POC, PON and PP maxima were mainly associated with the SCML (Fig. 3). The average concentrations of POC, PON and PP in the SCML were 4.653 ± 1.263 µmol/l, 0.701 ± 0.190 µmol/l and $433 \times 10^{-4} \pm 117 \times 10^{-4}$ µmol/l, respectively, which are nearly three orders of magnitude higher than the average values above and below the SCML (Tab. 2). For POC, PON and PP the minimum concentrations in the whole water column were always observed at the 200 m depth (Fig. 3).

The POC/PON ratio increased significantly in the euphotic zone ($p < 0.05$) and slightly below the SCML (Tab. 3). The mean POC/PON ratio in the SCML, *i.e.* 6.63 ± 0.89 is very close to that observed by Redfield *et al.* (1963). Among analysts there is disagreement on the C/N ratio in detrital material below the euphotic zone. In phytoplankton the C/N ratio is about 6 while sediments have relatively higher ratios reaching 10 or more (Seki *et al.*, 1968; Degens, 1970). The south-eastern Mediterranean sediments maintained ratios up

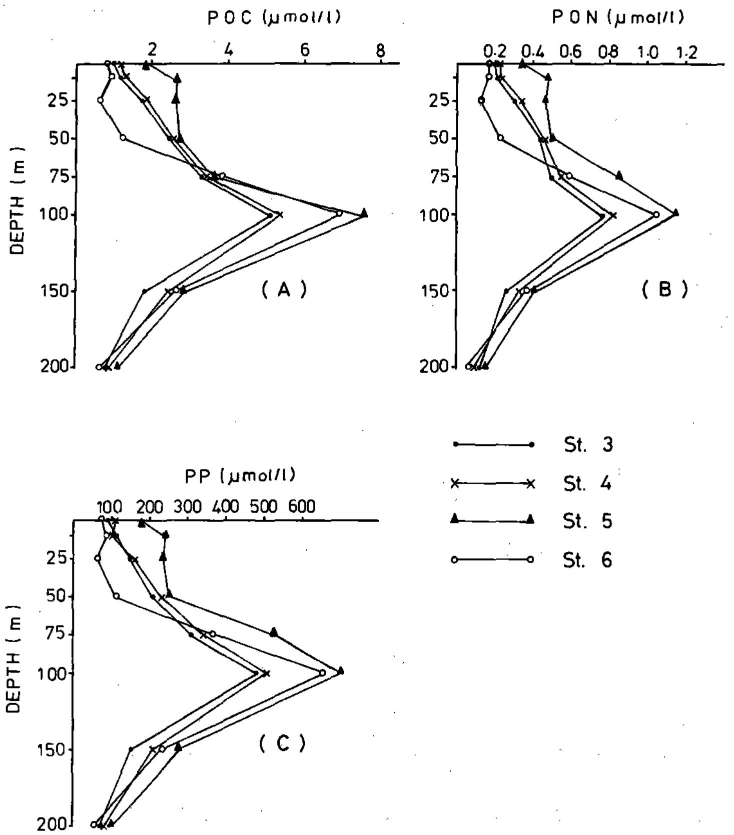

Figure 3

Vertical profiles of POC (A), PON (B) and PP (C).

Table 2

Mean chemical composition of particulate matter in the different water layers of the offshore Southeastern Mediterranean waters (±standard deviation).

Water layer	Chl *a* (µg/l)	POC (µmol/l)	PON (µmol/l)	PP (µmol/l)*	Biogenic Si (µmol/l)	Protein-N (µmol/l)
Above SCML 0-50 m ($n=32$)	0.087	1.513	0.272	134	0.31	0.140
	±0.035	±0.651	±0.114	±58	±0.14	±0.056
SCML 75-100 m ($n=16$)	0.227	4.653	0.701	433	1.35	0.184
	±0.054	±1.263	±0.190	±117	±0.49	±0.048
Below SCML 150-200 m ($n=16$)	0.072	1.281	0.203	111	0.21	0.188
	±0.034	±0.709	±0.111	±63	±0.11	±0.074

* Values are multiplied by 0.0001.

Table 3

Mean mole ratios of particulate organic components in different water layers of the offshore Southeastern Mediterranean waters (ratios derived from linear regression slope).

Water layers	POC/PON	POC/PP	PON/PP	POC/Chl *a**	B.Si/POC	Chl *a*/Pr**	Pr/PON
Above SCML ($n=32$)	5.68	111.85	19.65	206	0.20	0.61	0.55
	±1.43	± 24.20	± 4.36	± 46	±0.04	±0.19	±0.07
SCML ($n=16$)	6.63	107.65	16.22	245	0.36	1.10	0.26
	±0.89	± 22.40	± 3.25	± 63	±0.10	±0.13	±0.02
Below SCML ($n=16$)	7.07	113.10	17.70	207	0.16	0.44	0.77
	±1.65	± 36.80	± 4.31	± 35	±0.03	±0.09	±0.09

* Mass ratios.
** µg Chl *a*/µmol Pr-N/L.
± = Standard deviation.

to 7.3, especially in the outer shelf region (El-Sammak, 1987).

However, particles below the SCML are expected to have ratios between those of phytoplankton and sediments. On the other hand, Copin-Montegut and Copin-Montegut (1983) found agreement between investigators that the C/N ratio in the surface layer ranges between 5 and 8, and that variability is greater in deep waters. They also suggested that the increase of ratio with depth is due to more rapid utilization of proteins than carbohydrates.

The mean POC/PP ratio in the whole water column, *i.e.* 110.9 exceeds the value of 106 mentioned by Redfield *et al.* (1963) while the POC/PP ratio in the SCML is a little closer (Tab. 3). Likewise, observed for nitrogen the average POC/PP ratio was significantly (2 tailed *t*-test, $p < 0.05$) higher (average 113.1 ± 36.8) below the euphotic layer. The work of Copin-Montegut and Copin-Montegut (1983) in the western Mediterranean showed mean C/N ratios between 5.06-12.70 in surface (upper 75 m) and 6.10-6.75 in deep waters (> 150 m depth) and mean C/P ratios between 89-168 in surface and 95-125 in deep waters for samples collected during May and August 1975, respectively. Variabilities observed between oligotrophic Mediterranean basins could be related to phytoplankton blooming periods as well as the timing of the onset of stratification in both basins.

On the other hand, the PON/PP ratio of particulate matter in the salinity minimum layer approximates those recorded for phytoplankton *i.e.* 16 (Redfield *et al.*, 1963). Due to the difference in degradation resistivities above and below the SCML, the PON/PP ratio below the euphotic zone showed a slight increase lying between that recorded for the SCML and surface waters.

Regressions between POC, PON and PP (Tab. 3 and 4) calculated for SCML samples ($n = 16$) showed significantly high correlations ($r \leqq 0.99$, $p < 0.001$). Great care is needed when interpreting regression intercepts, especially that of the PON-PP relation which is not significantly different from zero. On average, the non-nitrogenous and non-phosphorus components constituted a small fraction not exceeding 1% of the average POC. Substituting the nitrogen and phosphorus by zero, the intercept may represent other carbon compounds which do not correlate with phosphorus and nitrogen. The magnitude of such compounds in the SCML was highly reduced compared with those above and below this layer (Tab. 4). The appearance of minute amounts of such carbonaceous compounds in the absence of phosphorus and nitrogen could indicate rapid mineralization of phosphorus and nitrogen from detrital material as well as the presence of excess carbonaceous in comparison with nitrogenous and phosphoric detritus. Below the SCML, regression intercepts of POC with PON and PP showed much higher values: 0.04 ± 0.013 and 0.3 ± 0.09, indicating the presence of

Table 4

Regression intercept for POC, PON and PP for the different water layers of the southeastern Mediterranean waters.

		POC		PON
PON	A	0.0113 ± 0.0028	–	
	S	0.0020 ± 0.0080	–	
	B	0.0400 ± 0.0130	–	
PP	A	0.0215 ± 0.0046	A	0.00016 ± 0.00006
	S	0.0039 ± 0.0012	S	0.00035 ± 0.00019
	B	0.3000 ± 0.0900	B	0.00025 ± 0.00008

A = Above SCML ($n=32$), S = SCML ($n=16$) and B = Below SCML ($n=16$).
± Standard deviation.

appreciable amounts of resistive carbonaceous compounds. Such compounds are of non-nutritive value, mainly consisting of crude fibre (Copin-Montegut and Copin-Montegut, 1983) which sometimes exists as non-degradable particles (Parsons and Strickland, 1962; Gordon, 1970).

In the case of PON/PP regression, the intercept for the SCML regression is close to the origin, suggesting the occurrence of both elements in the same proportions in particulate matter in this layer, similarity between their ratio in living and non-living fractions, and their dissolution in equivalent rates.

The mean POC/chlorophyll *a* ratio in the SCML was significantly ($p \leqq 0.02$) higher (mass ratio 245) than those observed for the over- and underlying water layers. Compared with the ratio normally used for phytoplankton, *i.e.* 35, the increase in the POC/chlorophyll *a* in the SCML indicates efficient photosynthetic activities for cells inhabiting this layer. The data of Mostafa (1985) showed that carbon assimilation in the SCML may reach more than twice that observed on the surface and more than four times those of the water column in some offshore southeastern Mediterranean stations. Furthermore, Nelson and Smith (1986) and Treguer *et al.* (1988) calculated a mean POC/chlorophyll *a* ratio of 138 for the Ross Sea and > 400 for the Indian sector of the Southern Ocean and anticipated high photosynthetic efficiency for the Southern Ocean ecosystem.

However, vertical profiles of total phaeophytin (measured according to Strickland and Parsons, 1972) for two locations off the Nile delta (stations 2 and 4) showed concentrations between 0.019 and 0.025 µg/l in the SCML (unpublished data).

These values indicate that the contribution of phaeophytin relative to chlorophyll *a* does not exceed 11% in the SCML. Surface phaeophytin concentrations (0-50 m) do not exceed 0.007 µg/l while subsurface phaeophytin maximum concentrations were slightly deeper than the SCML. Phaeophytin origin is mainly related to grazing of phytoplankton cells by microzooplankton and other copepods and their lysation by bacteria (Gieskes *et al.*, 1978). Such distribution indicates impoverishment of the SCML with respect to detrital material opposed by the considerably high POC/Chl *a* ratios observed in this layer.

Biogenic silica vertical profiles showed maximum concentrations in the SCML (Fig. 4) with an average of 1.35 ± 0.49 µmol/l (Tab. 2). In the upper 50 m, biogenic silica showed some variabilities with a mode matching that of chlorophyll *a* (Fig. 2 and 4), while in the lower 50 m biogenic silica concentrations in all sampled stations decreased with depth between 150 and 200 m. Regression lines between biogenic silica and chlorophyll *a* biomass, represented in figure 5, not only indicate the close covariation between chlorophyll *a* and siliceous organisms, but may also be used to evaluate the magnitude of non-siliceous organisms in the SCML relative to the layers above and below.

Biogenic silica and POC were significantly correlated ($r = 0.9376$, $p < 0.001$) in the SCML with a regression line Biogenic $\mathrm{Si} = 0.36 \pm 0.10\ \mathrm{POC} - 0.326 \pm 0.094$. The BSi/POC ratio in this layer greatly exceeds the typical diatom ratio 0.13 mentioned by Brezinski

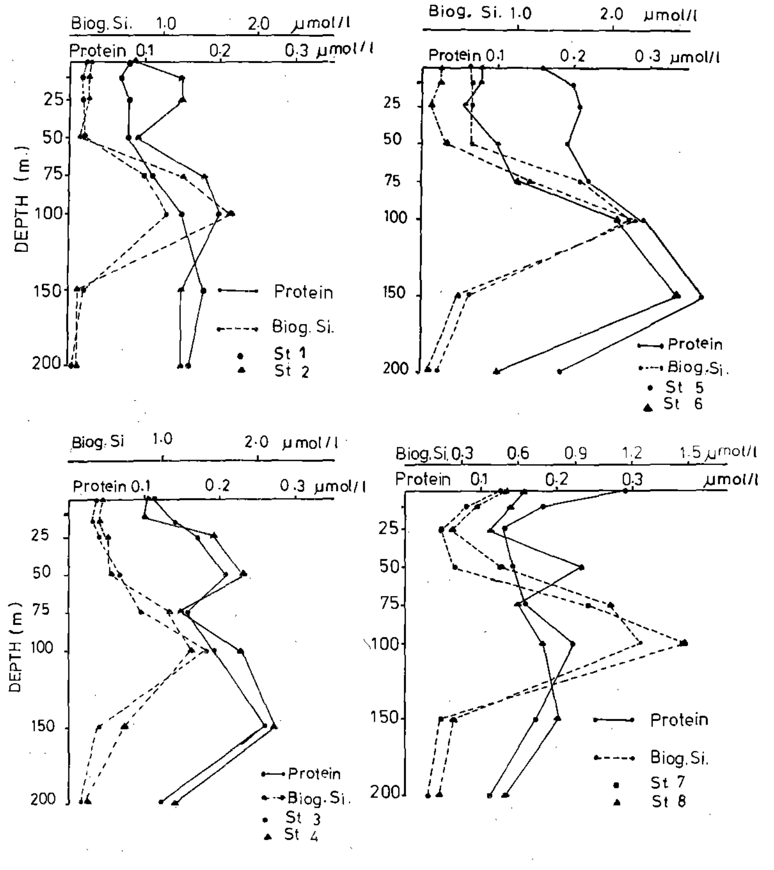

Figure 4

Biogenic silica and particulate protein vertical profiles.

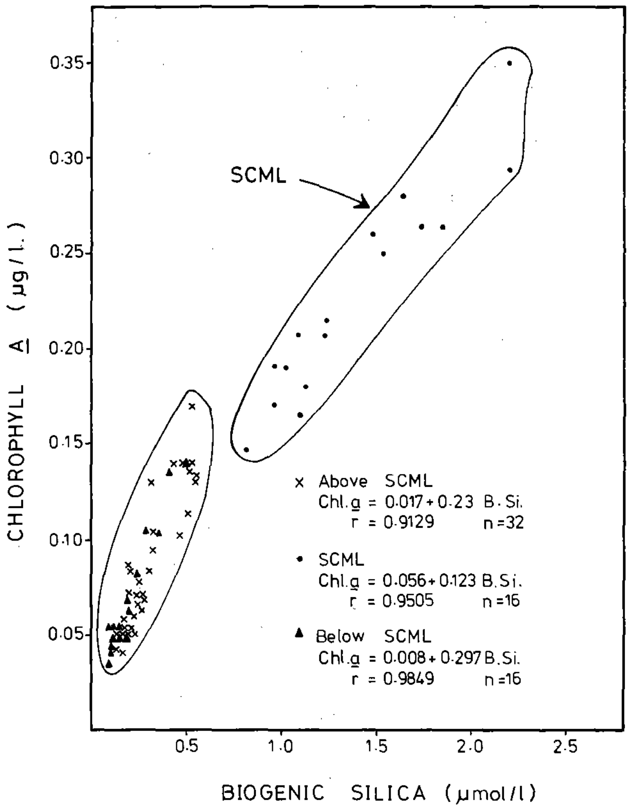

Figure 5

Biogenic silica (μ*mol/l*) vs. *chlorophyll* a (μg/*l*) *for all sampled stations.*

(1985), and may be regarded as increased silica production by diatoms relative to carbon. Similar anomalous ratios (0.3-0.5) were interpreted by Treguer *et al.* (1988) as related to excessive silica production by diatoms per unit carbon which may be two- or even fourfold. However, Nelson and Gordon (1982) and Nelson and Smith (1986) extended the interpretation of the elevated BSi/POC ratio to include the importance of differences in regenerative parts of the silicon and carbon cycles.

Moreover, a typical decrease in the dissolved silica in the subsurface water in summer profiles < 1.0 μmol/l (Abdel-Moati, unpublished data) was correlated with the high biogenic silica content. This may relate to unsuccessful regeneration of silica in bottom waters and a limited vertical transport during the summer stratification period as reflected in the lower ratios (average 0.16 ± 0.03) below the SCML (Tab. 3). Benthic diatoms (example: *Rhizosolenia robusta*, *R. castracanei*, *Hemiaulus membranaceum*) enriched at the SCML (Mostafa, pers. comm.) may contribute to biogenic Si enrichment and consequently enhance biogenic Si/POC ratios. Diatom skeletons enclosed in zooplankton fecal pellets were expected by Kamatani and Riley (1979) to release silica, especially when seawater is undersaturated with respect to biogenic silica.

In a dissimilar pattern to the above-mentioned components of particulate organic material, particulate protein concentrations in southeastern Mediterranean waters showed no correspondance with chlorophyll *a* maximum values (Fig. 2 and 4).

The average concentration below the SCML, *i.e.* 0.188 ± 0.074 μmol/l Pr–N, is close to that observed for the SCML (0.184 ± 0.048 μmol/l) but significantly different (1 tailed *t*-test, P < 0.05) from that observed for the surface (0.140 ± 0.056 μmol/l; Tab. 2).

The absence of a subsurface Pr maximum layer was usually observed in the oligotrophic waters of the central North Atlantic and central Pacific (Packard and Dortch, 1975; Siezen and Mague, 1978). On the contrary, the Chl *a*/Pr ratio observed in the SCML *i.e.* 1.10 (Tab. 3), was on the average twice that calculated for the over-and underlying layers (0.61 and 0.44, respectively), suggesting that phytoplankton comprise the major biomass constituent in the SCML. Chl *a*/Pr ratios in the upper and lower 50 m of the water column are similar to those recorded for the oligotrophic waters off the Washington coast, *i.e.* 0.42 ± 0.084 (Dortch, 1987), and in the central North Atlantic, *i.e.* 0.52 ± 0.079 (Packard and Dortch, 1975).

The amplitude of difference between the Chl *a*/Pr ratios recorded for phytoplankton cultures and that observed for different water layers reflect the extent of presence of non-plant protein in the water column, in the form of detritus, zooplankton and bacteria. The presence of certain dinoflagellate species (mainly *Ceratium* spp.) inhabiting the base of the euphotic zone in the Southeastern Mediterranean waters may lower the Chl/Pr ratios of the SCML. Dortch and Packard (1989) pointed out that dinoflagellates have a lower Chl/Pr ratio than other phytoplankton groups. Nour El-Din (1987) in a study of the vertical distribution of Southeastern Mediterranean copepods (> 90% of zooplankton community) mentioned that the depth of maximum density was positioned about 25 m below that of the SCML.

Based on the average Chl *a*/Pr ratio of phytoplankton cultures, *i.e.* 2.88 (Dortch and Packard, 1989), protein in the SCML represents between 40 and 65% of phytoplankton while above and below this layer the percentage does not exceed 22%. In the offshore waters of the Washington coast, between 10-20% of the protein content for corresponding layers comprised phytoplankton, while in the SCML the figure was between 50 and 90% (Dortch, 1987). However, apart from these findings, in another article, Dortch *et al.* (1984) pointed out that great care must be taken in interpreting these ratios in terms of phytoplankton, and that it must be kept in mind that such calculated ratios are based on particulate matter data.

On the other hand, Pr/PON ratio (indicating the fraction of PON made up of protein-N) was significantly low ($p < 0.05$) in the SCML (Tab. 3) and could be interpreted by the presence of N-sufficient phytoplankton in the SCML. The intercept of the regression line relating protein and PON in the SCML, *i.e.* 0.013, is more than 4-6 times that calculated for the under and overlying layers, suggesting the presence of other nitrogenous components incorporated with protein during formation. However, the presence of adequate light and nitrogen sufficiency is thought to have paved and established phytoplankton survival and bloom in the SCML.

Where the Pr/PON ratio is maximum below the euphotic zone, light limitation is more likely to influence N-deficiency, *i.e.* highest ratios in low light. Above the SCML adequate light encountered by inadequate nitrogen supply possibly limits phytoplankton growth. The degree of N-deficiency and phytoplankton growth rate in N-depleted layers was discussed by Goldman *et al.* (1979), who observed that despite N abundance below the SCML, phytoplankton growth may still be light-limited.

The foregoing results indicate that the SCML constitutes a store for the patriculate fraction of organic matter in the southeastern Mediterranean waters during summer stratification periods. About 45% of the organic carbon, 42% of the organic nitrogen, 47% of the organic phosphorus and 56% of the biogenic silica present in the whole water column appeared suspended in the SCML. During the following overturn (autumn season), when stratification breaks down, the SCML may act as an important source providing the over- and underlying waters with the necessary nutritive salts.

Furthermore, the ratios for different particulate organic fractions recorded in the present study could be easily used to trace the presence of the SCML in the continental shelf waters of the eastern Mediterranean, while biogenic silica in the SCML (average 1.35 ± 0.49 µmol/l) could be used together with chlorophyll *a* as biomass maximum indices for the Mediterranean waters.

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