

VERTICAL DISTRIBUTION OF SUMMER PHYTOPLANKTON IN THE WESTERN BLACK SEA DURING 1991-1995 WITH RESPECT TO SOME ENVIRONMENTAL FACTORS

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Abstract. The present paper deals with the vertical distribution of summer phytoplankton in different layers (SHL, TCL and CIL) at selected subregions of the western Black Sea. A comparison between the north-western, western and southern Black Sea is also presented. A special statistical software package was used to display the core species along the vertical axis and to select environmental variables explaining the community distribution. Despite the subregional differences the results reveal that about 50% of the total biomass was maintained in the SHL, about 40% in the TCL and from 10% to 20% in the CIL depending on the position and depth of each layer. The environmental factors, especially nutrients have more important implications for algal species composition and abundance in the SHL, while for the deep flora the formation of CIL waters and the mechanisms of biological control may be the more significant processes.

1. Introduction

During the last two decades changes in species composition and abundance of phytoplankton in the Black Sea related to increased anthropogenic pressure over the basin have been well documented. Evidence for long-term fluctuations during spring-summer in the north-western and western regions of the Black Sea has been found [4, 5, 19, 20, 24, 25].

The overproduction of autochthonous organic matter [35], has substantially altered the bio-optical properties of the water domain [40] as well as the composition and vertical distribution of C_{org} . Phytoplankton account for about 30-45% of the vital C_{org} especially in the deep C_{org} maximum located in the Cold Intermediate Layer (CIL) [41]. Recent investigations reveal that among the natural factors contributing to the ecological

status of the Black Sea the biotic properties and the pattern of distribution of the CIL waters may play a significant role [1, 21, 36].

The summer phytoplankton distribution in the Black Sea has been studied from different aspects and in different regions. Based on data collected during 1978-1989 Georgieva [10] discussed the phytoplankton vertical distribution basically in terms of size class distribution. Vedernikov & Mikaelyan [38] studied the vertical distribution in terms of the productive characteristics of phytoplankton during the summer period of 1987. A comprehensive discussion on the vertical distribution pattern of phytoplankton off the Turkish Economic Exclusive Zone with respect to taxonomy and numerical abundance during July 1992 is presented by Bayrakdar et al. [3]. Despite the numerous investigations on phytoplankton in the north-western and western Black Sea, recent data on its vertical distribution are rather scarce [11]. Furthermore, as the physical, biological and chemical properties of the Black Sea vary greatly on a spatial and temporal scale, observed data must be interpreted bearing this in mind. Only in this context can data provide information regarding interactions between the abiotic and biotic components of the environment relevant for modeling studies, which are the main goal of the NATO TU-Black Sea Project.

The present paper is aimed at evaluating the main trends in the summer vertical distribution of phytoplankton for the recent period (1991-1995) in terms of taxonomic structure, species composition, abundance and biomass in different layers as defined by the density gradients (Surface Homogeneous Layer (SHL), Thermocline (TCL) and Cold Intermediate Layer (CIL)) in selected subregions of the western Black Sea with special attention given to the biotic properties of the CIL. An attempt is made to relate the pattern of vertical distribution to some environmental factors, such as nutrients (NO_3^- , O_4^{3-} , Si and their ratios), temperature and salinity. A comparison between phytoplankton vertical distribution in the north-western, western and southern part of Black sea is also presented.

Materials and Methods

The study is based on data collected during the interdisciplinary and multinational CoMSBlack and TU-Black Sea summer cruises in the period 1991-1995 (September'91, June'92, July'92, August'95). Sampling stations were selected from the CoMSBlack sampling network (R/V Akademik sampling grid; Fig. 1) at inshore (<200 m depth) and offshore (>200 m depth) transects for the comparison of coastal and open sea areas and 4 identified subregions within the area under investigation. In the present paper, the subdivision of the north-western and the western Black Sea was based on circulation represented by the dynamic height anomalies using data obtained during cruises in the period 1986-1995 [7] and on chl.a data [42]. The following regions were classified: Aliakra Gyre Region (KG), Danube Region (DR), RIM Current Region (RCR) and

Deep Cyclonic Region (DCR). In summer, the presence of five distinct vertical layers (SHL, THC, CIL, halocline and anoxic deep water) is a prominent characteristic of the Black Sea. Although the depth of each layer changes temporally and spatially, this can be expressed by consistent density values. Analyses of the physical and chemical data for the Black Sea in September'91 and July'92 [2, 22, 36] and August'95 [17] are already published.

Physical parameters such as salinity, density and depth were obtained using a CTD probe (Sea Bird Electronics - 1991, 1995 and Vostok- 1992) and the phytoplankton were sampled- by GO FLO bottles attached to the CTD probe. In addition, the Secchi disk depth (SDD), chl.a concentrations, nutrients (phosphate, nitrate, nitrite and silicate) were also measured at the selected stations.

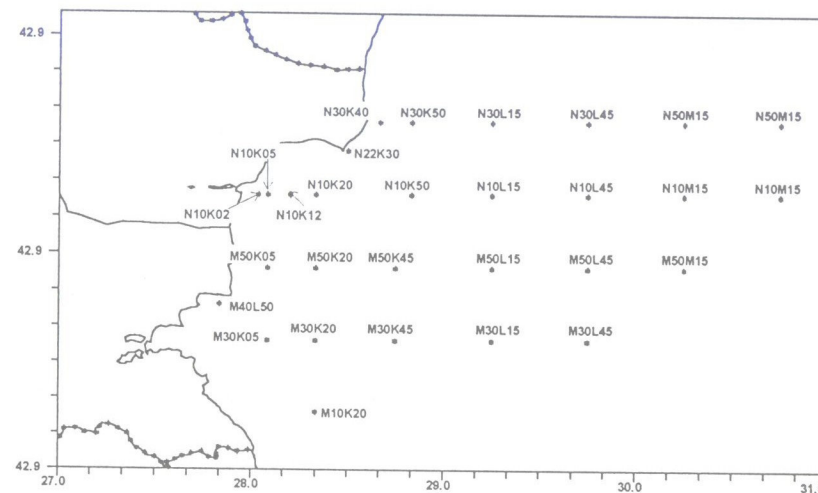


Figure 1. Map of R/V Akademik sampling grid.

Data from a total of 40 stations have been analyzed from depths corresponding to the thermohaline vertical profile of the water column down to 100 m depth. Information on sampling depths and the ranges of variability of the different physical and chemical parameters is presented in Table 1.

TABLE 1. Ranges of variability of basic physical and chemical parameters for each layer.

Layer	Cruise	Depth	Density	PO ₄ ³⁻	NO ₃ ⁻	Si
		m	σ _θ	μM.l ⁻¹	μM.l ⁻¹	μM.l ⁻¹
SHL	sep-91	0-20	9.8-12.4	0.0-0.49	0.30-9.70	nd
	jun-92	0-10	-	0.0-0.32	1.07-2.29	nd
	jul-92	0-10	10.4-11.68	0.0-0.31	0.0-0.99	1.56-6.26
	aug-95	0-15	9.44-11.49	0.0-1.28	6.24-22.76	nd
TCL	sep-91	15-30	10.87-12.87	0.0-0.08	0.30-2.90	nd
	jun-92	5-10	-	0.0-0.5	0.95-5.27	nd
	jul-92	9-25	10.37-13.68	0.0-0.04	0.07-0.59	4.32-5.00
	aug-95	13-35	10.75-14.50	0.0-0.91	4.55-22.0	nd
CIL	sep-91	30-100	14.12-15.74	0.0-1.34	0.3-0.31	nd
	jun-92	25-100	-	0.0-1.37	0.58-7.13	nd
	jul-92	25-100	14.11-15.58	0.0-1.56	0.0-9.49	3.63-45.12
	aug-95	30-100	13.96-16.0	0.01-1.53	4.2-29.7	nd

The phytoplankton samples, preserved in formaldehyde to 4% final concentration were analyzed by the combined method [33, 37] using a light microscope. The biomass was calculated using the standard individual weight of each species. In the present study nano- and microphytoplankton are discussed.

Cluster analysis, based on the Bray-Curtis similarity index was performed and results presented as a dendrogram, to display the species distribution pattern along the vertical axis (the transition from shallow to deep flora) and to select the core species in each gradient layer. Ordination by non-metric Multidimensional Scaling (MDS) was performed on the phytoplankton data and the environmental data, the respective similarity matrices being used to select environmental variables explaining the community pattern of distribution. Multilinear correlation coefficients were calculated to detect dissimilarities between the SHL and CIL. the statistical analyses [6]. The comparison with the north-western region is restricted to the HydroBlack'91 cruise (Romanian data, R/V Akademik sampling grid), and with the southern region to CoMSBlack'92 data (Turkish data, R/V Bilim sampling grid), as discussed in [3].

3. Results

During the summer period of 1991-1995 a total of 153 phytoplankton species were identified ranked by the main taxonomic divisions. The Dinophyta division was the most diverse (89 species), accounting for more than 58% of the total species listed, followed by the Bacillariophyta- 27% of total species (42 species). The remaining groups were represented by several species only (Chrysophyta- 11 species, Chlorophyta- 4, Cyanophyta- 3,

Cryptophyta- 2 and Euglenophyta- 2). The total number of species found during the study period varied between 71 and 100 species. Same proportions in the taxonomic vertical structure of phytoplankton communities were found, irrespective of the variability of total species present. As expected, species richness decreased along the vertical axis in all selected regions (Table 2).

TABLE 2. Vertical distribution of the number of phytoplankton species by taxonomic groups.

Taxonomic group	Bulgarian area			Romanian area			Turkish area		
	SHL	TCL	CIL	SHL	TCL	CIL	SHL	TCL	CIL
Bacillariophyta	10-11	4-14	6-9	13	16	18	32	25	19
Dinophyta	50-54	38-48	23-44	27	25	20	64	59	43
Chrysophyta	1-4	1-2	1-2	2	2	4	1	1	1
Other groups	1-4	1-4	1-4	6	6	6	4	3	4
Total	71	66	57	48	49	48	101	88	67

The distribution of surface phytoplankton exhibited a high heterogeneity in terms of species composition, taxonomic groups dominance, abundance and biomass- Fig. 2. In September 1991 the community was dominated at the inshore stations by diatoms in which the highest abundance was attained by *Cerataulina pelagica* in the periphery of the KG (5.7×10^6 cells.l⁻¹ at st. N30K50 and 2.7×10^6 cells.l⁻¹ at station N30K40) and in the north-eastern coastal zone (1.5×10^6 cells.l⁻¹ in st. P10L15). A bloom density of the dinophyte *Gessnerium mochimaensis* (2.6×10^6 cells.l⁻¹) was also recorded at the Kaliakra region. This is a new species for the Black Sea, found recently in the Aegean Sea too- Ignatiades, personal communication. The cyanophyte *Phormidium* sp. attained the highest abundance (10.6×10^6 cells.l⁻¹) in the north-western Black Sea. At the offshore stations, the abundance of the latter two species fell by an order of magnitude, the chrysophyte *Emiliania huxleyi* being dominant (3.3×10^6 cells.l⁻¹ at st. N30N45 and 2.2×10^6 cells.l⁻¹ at st. N30M45), co-dominating the coastal stations with the dinoflagellate species (*Prorocentrum minimum*- 2.2×10^6 cells.l⁻¹ at st. N10K05). Regarding biomass however the diatoms were the dominant group both in coastal and open waters. In June'92 among the diatoms (much less abundant than in September'91) the core species was again *C. pelagica* (0.5×10^6 cells.l⁻¹) with the coccolith *E. huxleyi* dominating phytoplankton numerical abundance both inshore (max. density $1.7 \div 3.2 \times 10^6$ cells.l⁻¹) and offshore (max. density 4.5×10^6 cells.l⁻¹ at st. N10K20), but in general, the biomass was dominated by dinoflagellate species (60-70% of the total biomass). In July'92 the blooming species were *P. minimum* (1.2×10^6 cells.l⁻¹) inshore and *E. huxleyi* (highest density 5.1×10^6 cells.l⁻¹) offshore.

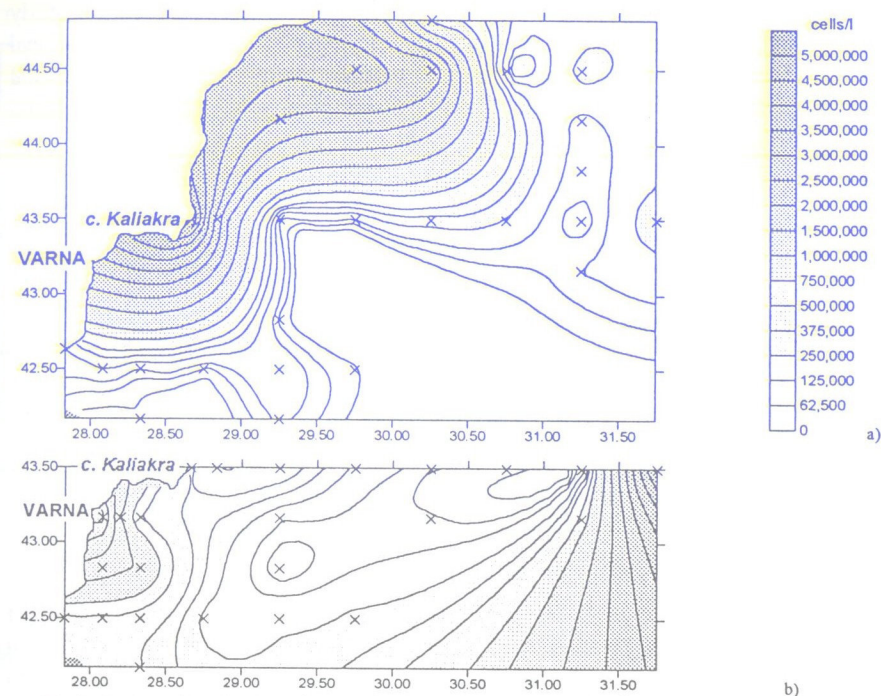


Fig 2. Surface distribution of phytoplankton abundance [cells.l⁻¹]: a) September, 1991; b) July, 1992

In August'95 the general trend was maintained whereby diatoms (*C. pelagica*, *Rh. calcar-avis*, *N. delicatula*, *Ch. lorenzianus* etc.) were seen to dominate inshore waters whereas dinoflagellates displayed a higher diversity and biomass and the coccolith *E. huxleyi* increased in abundance towards offshore waters. In comparison to 1991-1992 a decrease in total numbers and biomass (by a factor of 2) is evident on the account of an increase in species richness and diversity in all taxonomic groups, including Chrysophyta (*Apedinella spinifera*), Chlorophyta (*Carteria*, *Schroderia*) and Cryptophyta (*Chroomonas caudata*, *Hillea fusiformis*).

Comparative analysis of the phytoplankton distribution pattern for the 4 selected subregions was based on analysis of the following parameters: total phytoplankton biomass (Bt), Bacillariophyta biomass (Bb), Dinophyta biomass (Db) and their ratio (Bb:Db) and the average size of the communities (biomass:abundance ratio— B:A) (Fig. 3). The corresponding values for temperature, nutrients and nutrient ratios are presented in Table 3.

TABLE 3. Average nutrient concentrations in 1991 and 1992. KG=Kaliakra Region, DCR=Deep Cyclonic Region, DR=Danube Region, SHL=Surface Homogeneous Layer, CIL=Cold Intermediate Layer..

Cruise	SHL						CIL					
	T	P	N	Si	N:P	N:Si	T	P	N	Si	N:P	N:Si
	°C	μM	μM	μM	-	-	°C	μM	μM	μM	-	-
KG												
1991	22.32	0.13	0.87	-	6.7	-	7.09	0.19	0.9	-	-	-
Jul-1992	21.11	0.05	1.69	5.59	33.8	0.3	6.68	0.29	3.68	9.7	12.7	0.38
DCR												
1991	21.12	0.29	1.85	-	6.4	-	7.27	0.86	2.75	-	3.2	-
Jul-1992	21.66	0.13	0.34	5.53	2.6	0.06	7.42	1.08	2.14	17.48	1.98	0.12
DR												
1991	20.77	0.088	3.26	-	36.2	-	6.82	0.12	3.20	-	26.7	-
Jul-1992	21.86	0.19	0.28	2.98	1.47	0.09	5.85	0.22	5.89	9.39	26.7	0.63

While in the KG and DR regions the vertical profile of the biomass is characterized with a maximum in the SHL (average biomass being within the range 59.806-29.509 mg l⁻¹ in 1991) and 2.424 mg l⁻¹ in 1992), for the RCR and DCR the maximum values were found in the thermocline (1.359 mg l⁻¹ for the RCR and 1.307-1.989 mg l⁻¹ for the DCR). As depicted in Fig. 3a second peak in the vertical distribution of total biomass in the DCR is apparent at a depth of about 50 m (e.g. in the CIL) mainly due to the species *Ceratium fusus* (max. density 113×10³ cells l⁻¹), *C. furca* and *C. tripos*, accounting for more than 80% of the total phytoplankton biomass there.

The data sets for September 1991 and July 1992 manifest several differences: while during 1991 the biomass is highest in KG (average 18.758 mg l⁻¹), about twice that in the DR (10.908 mg l⁻¹) and more than 30 times higher than the DCR (0.589 mg l⁻¹). During 1992 the trend is reversed unexpectedly, the highest average biomass being recorded in the DCR (1.037 mg l⁻¹) about 1.4 fold greater than in the KG (0.753 mg l⁻¹) and more than 3 fold higher than in the RCR (0.315 mg l⁻¹). The same is seen for the average integrated biomasses (g m⁻²) with the following values; 1519.458 g m⁻², 650.857 g m⁻² and 56.538 g m⁻² for the KG, DR, and DCR respectively, in 1991 and 49.722 g m⁻², 31.437 g m⁻² and 67.016 g m⁻² for the KG, RCR and DCR respectively, in 1992. As for biomass distribution in the different layers, the same trend for the two data sets is apparent only for the DCR where about 40% of total phytoplankton were maintained in the TCL and rather close values for the SHL and CIL occur, within the following ranges; 34-24% (SHL), 37-47% (TCL) and 29% (CIL). For the KG region, a decreasing trend from the SHL down to the CIL was seen (from 78 to 49% in the SHL, from 19 to 15% in the TCL) but the percentage share of CIL differed (1.6% in 1991 versus 36% in 1992). The vertical distribution pattern in terms of percentage share of each layer in the

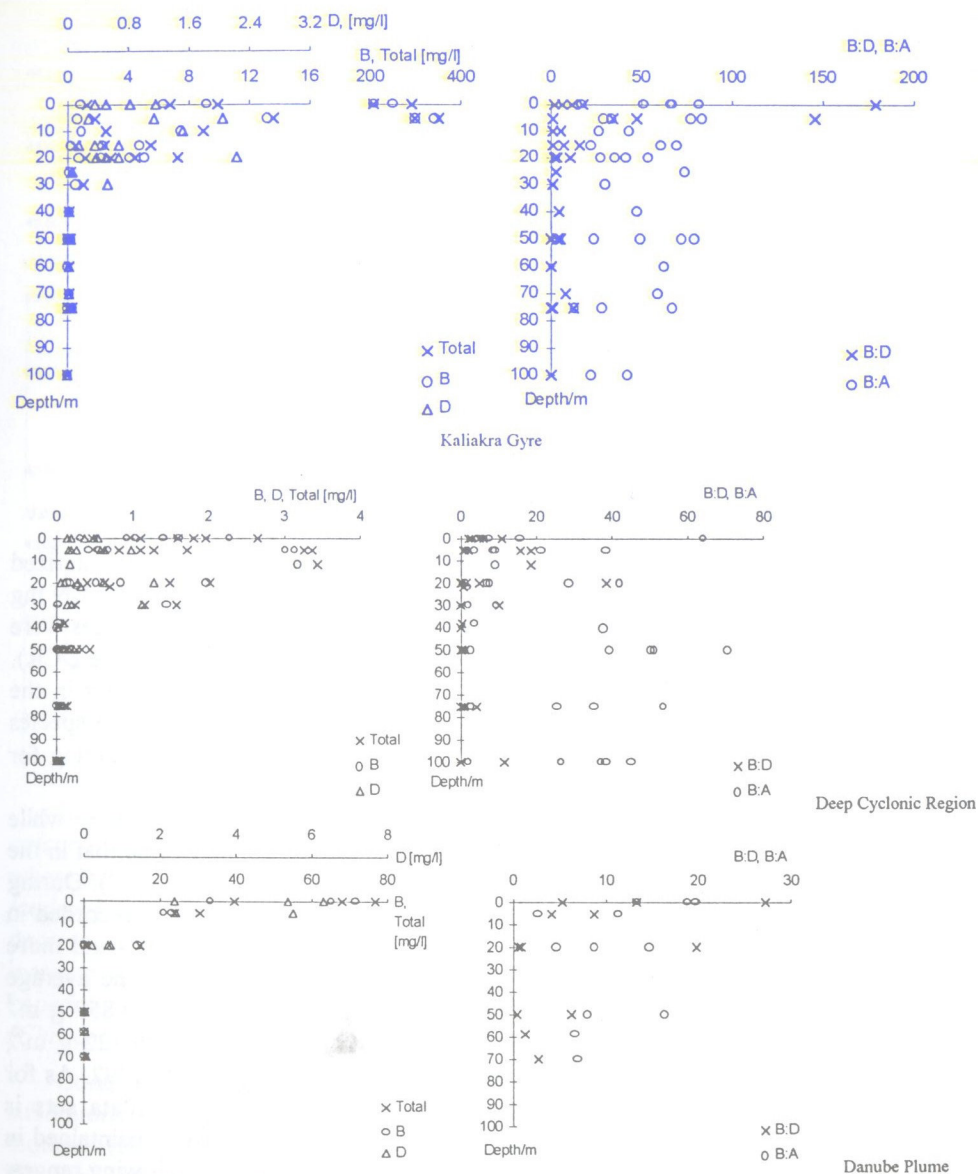


Figure 3a. Vertical distribution of phytoplankton biomasses [mg/l] with respect to depth: B–Bacillariophyta; D–Dinophyta; B:D ratio and mean population size (B:A) at selected stations in three different regions of the north-western Black Sea (1991).

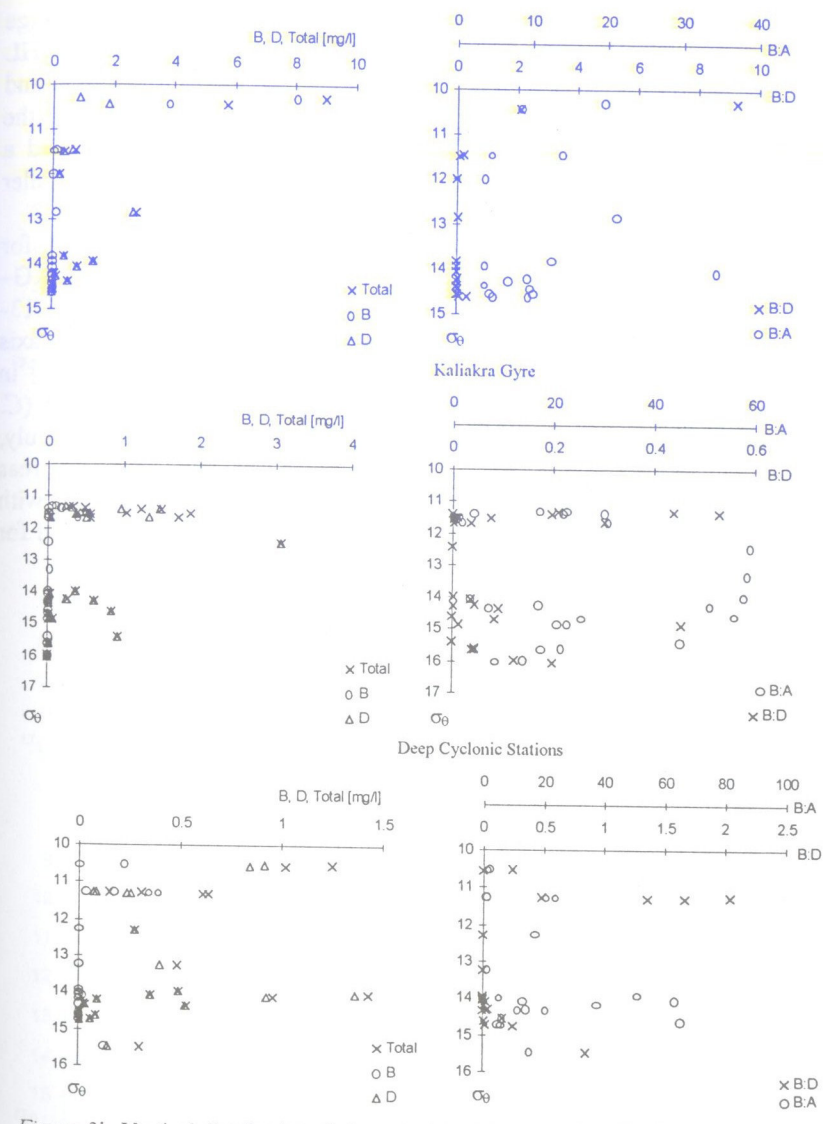


Figure 3b. Vertical distribution of phytoplankton biomasses [mg/l] with respect to density (σ_θ): B – Bacillariophyta; D–Dinophyta; B:D ratio and mean population size (B:A) at selected stations in three different regions of the north-western Black Sea (July, 1992).

DR was found to be very close to that of the KG (53%:39%:8%) and likewise, values for the RCR were very close to those for the DCR (18%:47%:35%).

Despite the heterogeneity in the distribution of the communities in terms of average size, in general the mean size (i.e. B:A ratio) was found to be smaller in the SHL especially for the RCR ($8.6 \cdot 10^{-6}$) and DCR ($7 \cdot 10^{-6}$) than for the TCL ($25\text{--}32 \cdot 10^{-6}$) and CIL ($21\text{--}24 \cdot 10^{-6}$), which obviously dependant upon the dominant species in the corresponding layer. Interannual comparison between the different regions revealed a clear trend only for the 1991 data set; larger average size in the KG ($48 \cdot 10^{-6}$) and smaller in the DR ($11 \cdot 10^{-6}$) and DCR ($14 \cdot 10^{-6}$) (Fig. 3).

On the contrary the B:D biomass ratio decreased from the SHL down to the CIL for the selected regions despite the differences in the values between the data sets (KG–20.3–2:5.1–0.3; 2.2–0.1; DR–14:7:3; RCR–0.96:0.01:0.15; DCR–7–0.07:2.0–0.02:0.13–0.05). The same stands for the average ratio along the inshore-offshore axis (KG:DR(RCR):DCR–9.8:3 and 0.8:0.4:0.05 respectively). However whilst in September the Bacillariophyta species were dominant in the phytoplankton biomass (*C. pelagica*, *C. caspia* in the KG and DR and mainly *Rh. calcar-avis* in the DCR), in July, this was the case only for the SHL in KG (again *C. pelagica*). For the other areas Chrysophyta (*E. huxleyi*) and Dinophyta (*P. minimum*) were the dominant groups, with the Chrysophyta accounting for 17–30% of the biomass in the SHL of the RCR and for about 33–68% in the SHL of the DCR.

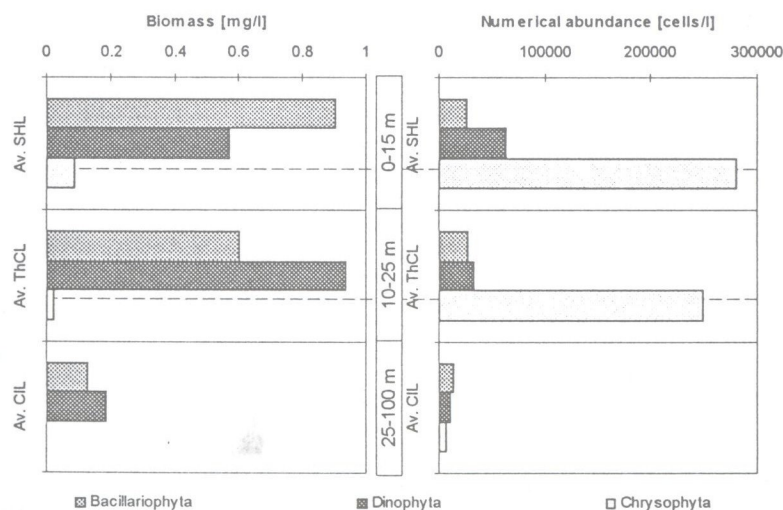


Figure 4. General pattern of phytoplankton vertical distribution by abundance and biomass. (average data for the four data sets)

The phytoplankton vertical distribution (>200 m depth – average data from the four data sets) reveals quite a different distribution pattern with respect to abundance and biomass (Fig. 4). The diatoms constituted more than half of the biomass in the SHL

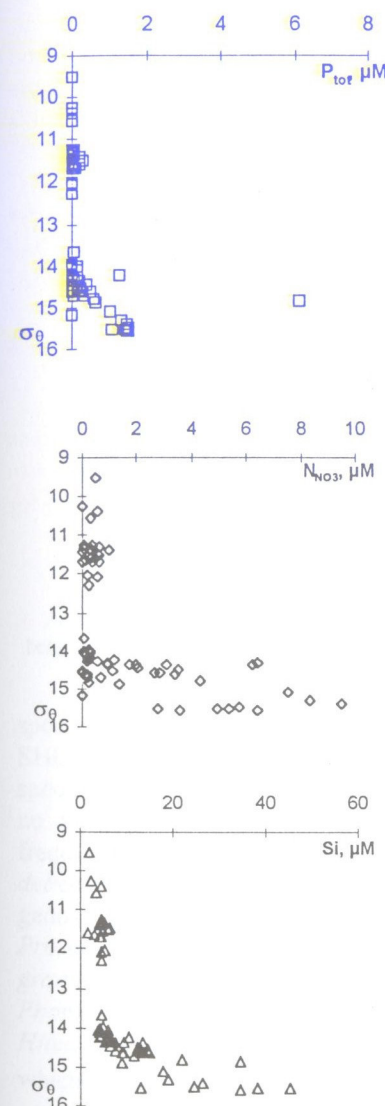


Fig 5. Chemical parameters vertical distribution against σ_t (July 1992). stations and sampling depths is presented in Annex I). The similarity index is significant only between cluster B and C (higher than 65% at a stress value 0.19). The heterogeneity in

(57.8%) with an almost equal share in the TCL and CIL (38.7% and 39.8%), while dinoflagellates were the dominant group numerically in the TCL and CIL (about 60%) with a significant share of total phytoplankton biomass in the SHL (36.7%). All the other groups were merely represented. Regarding abundance the chrysophytes constituted the overwhelming majority their numbers being greater in the SHL and TCL (76% and 80%, respectively), with the dinoflagellates taking second place (17% and 11%, respectively), while in the CIL the diatoms and the dinophytes shared the dominance (41% and 36%, respectively). The biomass ratio Bacillariophyta: nonBacillariophyta varied from 1.52 in the SHL to 0.65 in the THC and 0.68 in the CIL. Spatial analysis during different sampling periods revealed that proportions between the different taxonomic groups remain much more stable in the CIL than in the SHL. For the upper 100 m, as expected, an increase in nutrient content was evident towards the CIL with NO_3^- maximum located at σ_t 15.30–15.66 (70–75 m; Fig. 5).

A dendrogram of the Bray-Curtis similarity index based on phytoplankton species composition and abundance comparing stations and depths sampled at each station manifest a high heterogeneity in the horizontal and vertical phytoplankton distribution. However, comparison of different layers in the selected subregions gave more homogeneous results. As apparent in Fig. 6a main clusters were identified in July 1992: cluster A– the CIL in the RCR and DCR (with very low similarity index), cluster B– surface inshore stations, cluster C– the SHL and TCL in the RCR and inshore stations and cluster D– the TCL, the CIL and SHL in the RCR and DCR (a list of the

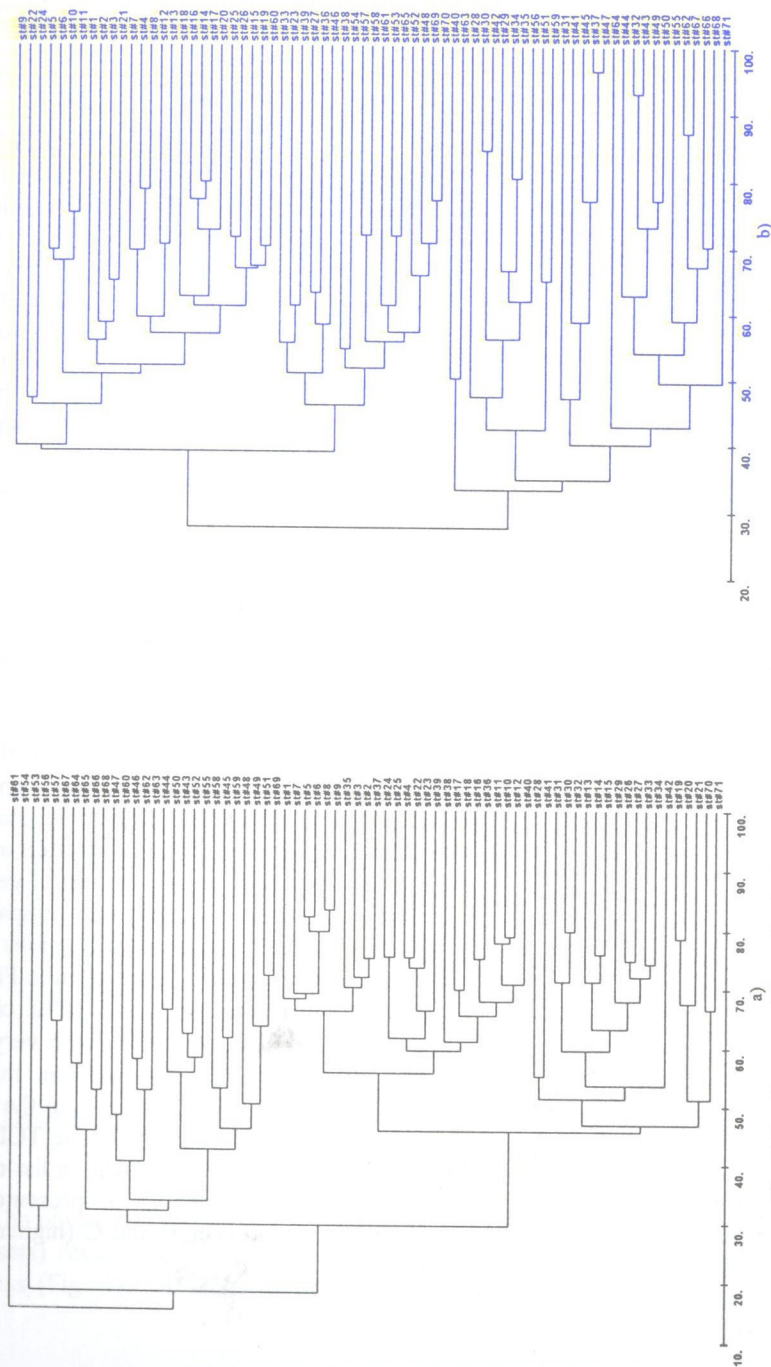


Fig. 6. Dendrogram of Bray-Curtis similarity index between stations based on phytoplankton species composition and abundance: a) July, 1992; b) September, 1991.

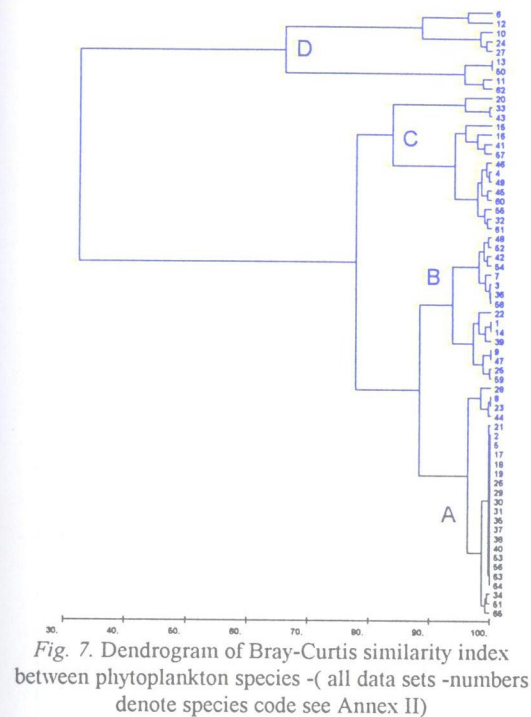


Fig. 7. Dendrogram of Bray-Curtis similarity index between phytoplankton species - (all data sets - numbers denote species code see Annex II)

the phytoplankton taxonomic structure and abundance was even higher in September '91 (Fig. 6b).

Despite the heterogeneity in species composition both for the different layers and time periods, the data revealed the bulk of phytoplankton abundance and biomass to be formed by several species only. The dendrogram presented in Fig. 7 (based on the average density of each species from all the data sets for the respective vertical layer) revealed four main clusters (A, B, C, D; a similarity index >0.80 denotes species with the similar pattern of distribution [39]). Group D species could be considered rare species (low similarity coefficient). Cluster C contains the

species representing the CIL community, cluster B species were equally represented in SHL and CIL and cluster A— the highly represented species in the SHL (the list of species is presented in Annex II). The high similarity index between the clusters suggests no abrupt difference between the CIL and the SHL. Among the species of higher frequency distribution in the CIL were the diatoms *Cerataulina pelagica*, *Nitzschia delicatissima*, *Nitzschia closterium*, *Rhizosolenia calcar-avis*, the dinophytes from the genus *Ceratium*, the species *Gyrodinium fusiforme*, *Gymnodinium najadeum*, *Prorocentrum minimum*, *Prorocentrum micans*, *Protoceratium reticulatum*, *Peridinium granii* and only at some stations species from other taxonomic divisions, Cyanophyta— *Phormidium sp.*, *Mycrocystis aeruginosa* and Cryptophyta— *Chroomonas caudata*, *Hilea fusiformis*. No specific species complex was identified related to the NO_3^- maxima, which in general conforms with the results of other investigations.

A comparison between the similarity matrices of the phytoplankton data by species abundance performed separately for the SHL and CIL (for the stations deeper than 200 m) and the environmental data (temperature, salinity and nutrients— phosphates, nitrates and silica) revealed only subtle evidence of a correlation for the SHL and no correlation for the CIL, which suggest that the selected variable does not control the phytoplankton species communities in the CIL (Fig. 8, Table 4). When correlated in terms of taxonomic groups however, the environmental control in the SHL is more evident ($r^2=71.65\%$ for Dinophyta and $r^2=63.7\%$ for Bacillariophyta) (Table 4). As apparent from the table

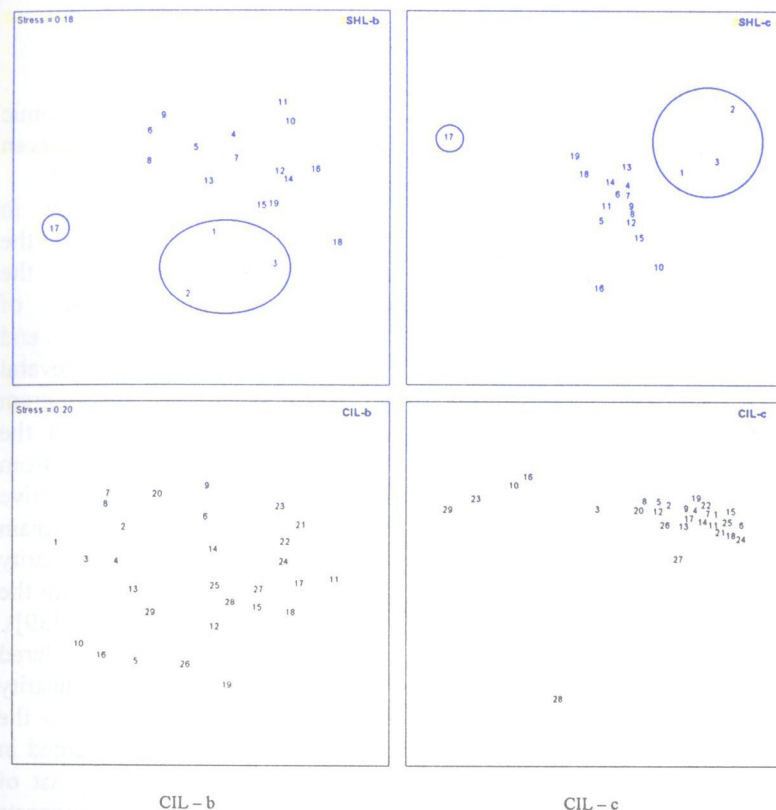


Fig. 8. Similarity matrices of phytoplankton data (species abundance)– b and environmental data (temperature, salinity and nutrients (phosphates, nitrates and silica))– c in SHL and CIL (September, 1991 and July, 1992).

among the selected variables the contributions of salinity, Si (negative correlation) and temperature are the most important.

TABLE 4.1. Multilinear correlation coefficient between phytoplankton abundance and environmental parameters in the SHL (September, 1991 and July, 1992).

Parameter	P	P, N	P, N, Si	P, N, Si, T	P, N, Si, T, S
<i>Dinophyta</i>					
a	44897	49269	95006	179360.4	583857.1
b	-99223.1	-89819.9	-78852.98	-74787.4	-1968.1
c		-13624.34	-3227.98	1644.9	-14816.8
d			-12407.55	-13486.7	-1256.7
e				12761.6	4402.3
f					-35535.94
r	0.256	0.277	0.552	0.598	0.846
r ²	6.55	7.7	30.54	35.83	71.65
<i>Bacillariophyta</i>					
a	2386.3	784.1	12542.2	48297.9	44356.1
b	-7543.49	-10989.5	-9507.4	-8688.5	1123.3
c		4992.9	6398.1	7379.5	7056.1
d			-1676.9	-1894.2	-2342.9
e				2570.5	1629.36
f					-4000.7
r	0.137	0.31	0.551	0.641	0.798
r ²	1.88	9.63	30.41	41.1	63.7

TABLE 4.2. Multilinear correlation coefficient phytoplankton abundance and environmental parameters in the CIL (September, 1991 and July, 1992).

Parameter	P	P, N	P, N, T	P, N, T, Si	P, N, Si, T, S
<i>Dinophyta</i>					
a	6483.2	8141.5	17538.2	-32074.5	-30239.8
b	-917.4	-369.4	-1275.5	796.1	778.6
c		-838.6	-1120.3	-569.6	-581.8
d			5675.7	6217.2	6264.6
e				-374.5	-364.9
f					-121.6
r	0.103	0.257	0.44	0.504	0.505
r ²	1.07	6.62	19.41	25.43	25.45
<i>Bacillariophyta</i>					
a	70	31.7	-401.7	-188.5	-1021.8
b	67.7	18.5	8.2	106.1	36.4
c		13.9	10.7	-98.83	20.7
d			64.9	70.8	55.2
e				-4.1	-7.22
f					40.1
r	0.085	0.173	0.176	0.191	0.222
r ²	0.73	1.87	3.12	3.65	4.96

As expected, the comparison between the different Black Sea regions revealed that inshore waters in the north-western and western Black Sea are the most productive due to the Danube river influence (Rumanian area) and its interaction with the RIM current (Bulgarian area; Table 5). Phytoplankton abundance for the Turkish area is underestimated as only phytoplankton species $>55 \mu$ have been taken into consideration [3].

TABLE 5. Phytoplankton average abundance in different regions and density gradients (cells.l⁻¹).

Layer	Bulgarian area, 1991		Bulgarian area, July, 1992		Romanian area, 1991		Turkish area, July, 1992	
	inshore	offshore	inshore	offshore	inshore	offshore	western	eastern
SHL	1370446	274517	584995	137645	2773182	168837	16401	19069
TCL	77641	199633	740488	72800	302986	246690	27595	10694
CIL	4513	22095	47346	8471	31921	188508	9877	1857

4. Discussion

Despite the heterogeneity observed in the summer phytoplankton distribution (both horizontally and vertically) in terms of taxonomic composition, abundance and biomass, the data presented underlined some general trends.

The average phytoplankton biomasses found were 9.755 g m⁻³ for the KG region, 10.908 g m⁻³ for the DR and 0.630 g m⁻³ for DCR. These values are about 10 times higher than those reported by Sorokin [32] for the coastal waters of the north-western Black Sea (200-700 mg m⁻³) and about three times higher than values given for the deep region, but are within the range reported in recent investigations, the differences being related mainly to the increased anthropogenic pressure over the basin [4, 20, 30, 11]. The average biomass value for July'92 (1.037 g m⁻³) given in this study is only half of that (2.3 g m⁻³) reported for the central Black Sea [11]. Such a discrepancy between different summer data sets could not solely be related to the anthropogenic factor. The unexpected trend of an increase in phytoplankton biomass towards offshore in July'92 (reported also for the north-western Black Sea, [11]) could hardly be related to the chemical parameters of the environment. The observed decrease in nitrate concentration offshore and the comparable values of Si (Table 3) disprove that nutrient limitation occurred inshore. The high zooplankton biomass inshore (706 mg m⁻³, about 6 times higher than the offshore value— 114 mg m⁻³) and notably the extremely high percentage share of *Noctiluca scintillans* and Copepoda, comprising 82% of the total zooplankton biomass [17] suggests high grazing pressure inshore especially in the SHL. A possible reason also for the high phytoplankton abundance offshore could be the low winter temperatures in 1992 and the related hydrodynamic processes in the Black Sea [18].

The relatively higher similarity between the same layers in the different subregions (Fig. 6) suggests an inshore-offshore interaction [23, 36] despite the prominent vertical stratification and different controlling mechanisms of phytoplankton distribution and maintenance in the different strata. The latter is well supported by the correlation coefficients between the biological and physicochemical parameters in the CIL and SHL (Table 4) and the deviations in the MDS graph plots between the biological and environmental matrix (Fig. 8). As apparent from the B:D ratio the dominance of the diatoms only in KG and DR (June-July – B:D in the range 14-20) especially in the SHL could be related to the higher inorganic nutrient supply due to the Danube river input, while the N:Si ratio far below 1 [26] and the recorded increase of the organic matter [11] facilitate development of the non-diatom phytoplankton community (B:D ratio close to or below 1). This is in conformity with the general concept that anthropogenically induced changes in the nutrient ratios and the increase of the organic matter are the main factors responsible for the shift in the late-spring– summer phytoplankton in the Black Sea to a non-diatom community (dinoflagellates and chrysophytes) which has already been discussed in several papers [3, 14, 20]. The significant negative correlation with Si presented in this paper is also in support of the latter statement. The impact of Sahara

dust as suggested by Saydam [28], could also contribute to the shift to *E. huxleyi* dominance offshore.

One of the most conflicting subjects facing marine ecologists is that of development and maintenance of the deep sea flora. Among the possible mechanisms reported are sinking from the upper layers, different grazing pressure, or different adaptive physiological mechanisms for survival at depth (mixotrophy, shade flora, physiological shift to light limitation, resting stages etc.– [39]). The deep phytoplankton maximum is a typical feature of the phytoplankton vertical profile in the deep regions in the Black Sea from late-spring to autumn [27, 29, 34]. Senichkina [29] has found diatoms (in June 1985) dominating at depths 20–40 m and 60–100 m. Ratkova et al. [27] has reported a deep maximum of *Nitzschia* species, coexisting with picophytoplankton and cryptomonads, and Sukhanova [34]– of *Rhizosolenia alata* and *Rh. calcar-avis*. The species composition of the CIL, independent of their taxonomic relationships as well as the lack of a sharp transition between the shallow and deep flora (Fig. 7) ultimately suggest different strategies involved. Dinoflagellates are considered a characteristic group that achieves dominance in strata with insufficient light due to their mixotrophy, which could be a good explanation for their dominance in deeper layers. For *Ceratium fusus* (one of the dominant species in the CIL– up to 80% of the biomass) it is established that they do not form resting cysts [12] and may behave either as a mixotroph or heterotroph (Mikaelyan, personal communication), resulting in a high biomass being achieved during summer.

Smetacek [31] has suggested that rapid sinking of diatoms through aggregation (usually occurring after a bloom– “spring cleaning of the water”) is a survival strategy whereby cells switch from a growth phase when nutrients and light are both available to a resting dark stage and also to obtain shelter from grazing when the nutrient supply is exhausted; in this scenario cells do not only avoid environmental stress, but also act as the seed population. So the deep association may represent a stage in the life-cycle of the species and the major period of growth may occur only when winter mixing returns the cells to the euphotic zone. Alternatively the lower association (namely autotrophic species like diatoms) may represent a physiologically transitional population [9], adapted to suboptimal light but receiving some new nutrients from the nutricline, located, as the chemical data reveal, in the CIL. The relatively good correlation between the SHL biomass and the CIL biomass inshore (Fig. 9) and the species composition discussed is in favor of sinking as the possible mechanism. The mechanisms for the formation CIL waters in this part of the basin [1, 8, 23] could also contribute to the survival strategy of the deep flora. There is evidence that the deep association could be utilized more through the detrital food chain (coexisting high abundance of bacterioplankton, nanoheterotrophs and infusoria), rather than being directly grazed by zooplankton, which at certain times of the year may be crucial for the functioning of the open sea ecosystem [13, 27].

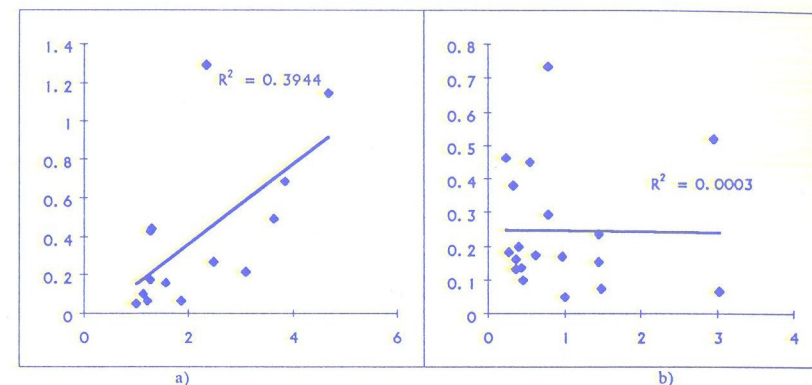


Figure 9. Relationship between the SHL biomass (x-axis):CIL biomass (y-axis) (inshore– a and offshore– b)

According to the SDD measurements, which at the inshore stations varied in the range 2.0–5.2 m (2.5–3.0 m the most frequent depth) and at the offshore stations in the range 3.4–7.4 m (average about 5.5–6 m) the thickness of the euphotic zone was about 7.5–20 m supporting about 45% of the total biomass in the water column. If the thickness of the different layers is taken into consideration in summer, about 50% of the total biomass was maintained in the SHL, about 40% in the TCL and from 10% to 20% in the CIL depending on its position and depth. This does not hold for the near inshore stations, where more than 70% of the total biomass and abundance were maintained in the SHL.

The results discussed give ground to state that the environmental factors, especially nutrients have more important implications for algal species composition and abundance in the SHL, while for the deep flora the formation of CIL waters and the mechanisms of biological control may be the more significant dimensions, which invoke the necessity of discussing phytoplankton in terms of functional groups. Although not by themselves conclusive enough, the results suggest that the CIL may play a significant functional role in the productive processes of the euphotic zone, for which further process oriented studies will be of extreme importance.

Annex I

Stations number for Fig. 5a.

Station, Depth

1 m10k20.....0	16 n10n15.....0	31 m30k05....50	46 n10l15.....50	61 n30n15.....20
2 m30k05.....0	17 n10n15.....10	32 m30k05....62	47 n10l15.....70	62 n30n15.....50
3 m30-k20.....0	18 n30l45.....0	33 m30-k20...25	48 n10m15....50	63 n30n15.....75
4 m30k45.....0	19 n30m45....0	34 m30-k20...50	49 n10m15....75	64 n30n15....100
5 m30k45....10	20 n30n45.....0	35 m30-k20...75	50 n10m15....100	65 n30m45....25
6 m30l15.....0	21 m30k05....9	36 m30k45....50	51 n10n15....21	66 n30m45....50
7 m30l15....10	22 m30k20....11	37 m30k45....78	52 n10n15....50	67 n30m45....75
8 m30l45.....0	23 m50l15....25	38 m30l15....25	53 n10n15....78	68 n30m45....100
9 m30l45....10	24 n30l15....10	39 m30l15....50	54 n30l15....25	69 n30n45....25
10 m50l15.....0	25 n30n15....10	40 m30l15....75	55 n30l15....50	70 n30n45....50
11 m50l15....10	26 n30m45....10	41 m30l45....50	56 n30l15....75	71 n30n45....75
12 n10l15.....0	27 m10k20....23	42 m30l45....64	57 n30l45....20	
13 n10l15....10	28 m10k20....50	43 m30l45....72	58 n30l45....50	
14 n10m15.....0	29 m10k20....75	44 m50l15....50	59 n30l45....75	
15 n10m15....10	30 m10k20....97	45 m50l15....69	60 n30l45....100	

Stations number for Fig. 5b.

Station, Depth

1 m10k20.....0	16 m30l45.....0	31 n30n45.....5	46 n10l15.....50	61 n30l15.....75
2 m10k20.....5	17 m30l45.....5	32 n30n45....22	47 n10l15.....75	62 n30l45.....50
3 m10k20....20	18 m30l45....20	33 n10n15.....0	48 m30k05....63	63 n30l45.....75
4 n10l15.....0	19 m50l15.....0	34 n10n15.....5	49 m30k20....50	64 n30m45....50
5 m30k05.....0	20 m50l15.....0	35 m10k20....30	50 m30k20....75	65 n30m45....75
6 m30k05.....5	21 m10l15....20	36 n10l15....20	51 m30k20....95	66 n30n15.....50
7 m30k05....20	22 n30l15.....0	37 m30k20....20	52 m30k45....50	67 n30n15....75
8 m30k20.....0	23 n30l15.....5	38 m30k45....30	53 m30k45....75	68 n30n45....50
9 m30k20.....5	24 n30l45.....0	39 n30l15....20	54 m30l15....75	69 n30n45....75
10 m30k45.....0	25 n30l45.....5	40 n30l45....15	55 m30l45....50	70 n10n15.....50
11 m30k45.....5	26 n30m45.....0	41 n30n15....20	56 m30l45....75	71 n10n15.....75
12 m30k45....20	27 n30m45.....5	42 n10n15....20	57 m30l45....100	
13 m30l15.....0	28 n30n15.....0	43 m10k20....50	58 m50l15....50	
14 m30l15.....5	29 n30n15.....5	44 m10k20....75	59 m50l15....75	
15 m30l15....20	30 n30n45.....0	45 m10k20....100	60 n30l15.....50	

Annex II

Species numbers for Fig. 4.

# Species	# Species	# Species	# Species
1 Cerataulina pelagica	18 Dinophysis sacculus	35 Goniodina polyedraum	52 Peridinium steinii
2 Chaetoceros affinis	19 Dinophysis ovum	36 Gymnodinium najadeum	53 Peridinium subinermis
3 Chaetoceros curvisetus	20 Dinophysis acuta	37 G. uberimum	54 Peridinium sp.
4 Coscinodiscus sp.	21 Gessnerium mochimaense	38 G. rotundum	55 Phalacroma rotundatum
5 Coscinosira oestrupii	22 Glenodinium danicum	39 G. wulfii	56 Polykricos schwarzii
6 Cyclotella caspia	23 Glenodinium lenticula	40 G. galcaeforme	57 Prorocentrum compressum
7 Nitzschia closterium	24 Gl. lenticula f. minor	41 G. splendens	58 Prorocentrum micans
8 Nitzschia delicatissima	25 Glenodinium paululum	42 Gyrodinium fusiforme	59 Prorocentrum minimum
9 Rhizosolenia calcar-avis	26 Glenodinium rotundum	43 Gyrodinium lachryma	60 Protoceratium reticulatum
10 Skeletonema costatum	27 Goniaulax digitale	44 Gyrodinium nasutum	61 Scripsiella trochoidea
11 Thalassiosira meneghiniana	28 Goniaulax polyedra	45 Heterocapsa triquetra	62 Phormidium sp.
12 Thalassiosira subalina	29 Goniaulax apiculata	46 Peridinee (cysts)	63 Dictyocha speculum
13 Thalassionema nitzschioides	30 Goniaulax cochlea	47 Peridinium divergens	64 Ebria tripartita
14 Ceratium furca	31 Goniaulax minima	48 Peridinium granii	65 Emiliana huxleyi
15 Ceratium fusus	32 Goniaulax orientalis	49 Peridinium cuspidess	
16 Ceratium tripos	33 Goniaulax polygranum	50 Peridinium palidum	
17 Dinophysis caudata	34 Goniaulax spinifera	51 Peridinium pellucidum	

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