



Phytoplankton Blooms in Black Sea and Mediterranean Coastal Ecosystems Subjected to Anthropogenic Eutrophication: Similarities and Differences

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The similarities and differences in phytoplankton response to anthropogenic nutrient enrichment were studied in coastal sites of the Western Black Sea and the Eastern Mediterranean (Aegean Sea). Although by physico-chemical parameters, two different environments have been compared, the two regions exhibited similar features: 14 common bloom species in the list of bloom producing algae, the highest rate of occurrence and variety of microalgae involved in summer, the highest average level of competitors-strategies species during the summer outbursts, the similar range of maximum bloom densities attained, and similar capacity to sustain critical biomass during all seasons. The low taxonomic similarity (Bray-Curtis index lower than 30%) between the different basins and among sites, could be attributed to both natural factors and dissimilarities and to the gradients in nutrient levels and their ratios, as affected by the different nature and severity of the anthropogenic pressures on the coastal ecosystems. The results of the PCA analysis indicate that temperature and salinity are factors contributing to the differences outlined between the Aegean Sea and the Black Sea ecosystems, but the differences among the selected sites give support to the importance of nutrients and their ratios. Although competitive outcomes in phytoplankton species selection and succession cannot yet be predicted, the analysis suggests that anthropogenic nutrient enrichment could play an important role in driving the phytoplankton bloom performance. The comparative studies between different basins could be a step forward to highlight common patterns and modes of ecosystem response to anthropogenic eutrophication and to suggest common indices to scale eutrophication impact.

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Introduction

Since the late 1970s, anthropogenic nutrient enrichment (eutrophication) has been identified as a key ecological problem for the Black Sea ecosystem, especially its north-western and western part, which is subjected most to the influence of freshwater nutrient inputs to the basin (Mee, 1992; Zaitzev, 1992; Aubrey *et al.*, 1995). According to previous authors, the input of nutrients and dissolved organic matter to the north-west shelf of the Black Sea by the Danube, the Dniepar and the Dniestar river flow for the period 1950–1980 increased about 10 times. During 1988–1992, the annual total inorganic nitrogen, phosphate and silicate loads draining into the Black Sea from the Danube river alone were $6-8 \times 10^5$ t, $0.23-0.32 \times 10^5$ t and $1.5-3 \times 10^5$ t, respectively (Cociasu *et al.* 1997).

An increase in phytoplankton blooms frequency, species involved, duration, timing and area are well

documented, provoking substantial perturbations of the entire food web structure and functioning (Bodeanu, 1995; Moncheva & Krastev, 1997). Changes in zooplankton communities structure and deterioration of benthic coenoses, culminating during the 1980s (period of intensive eutrophication in the Black Sea), were to a great extent associated with the dramatic alterations in phytoplankton communities and recurrent hypoxic conditions. Microalgal blooms were therefore identified as one of the key issues for the Black Sea's ecological health (Moncheva *et al.*, 1995; Velikova *et al.*, 1999; Shtereva *et al.*, 1999).

Despite the fact that the Eastern Mediterranean Sea is generally an oligotrophic region (Souvermezoglou *et al.*, 1992; Siokou-Frangou *et al.*, 1998; Gotsis-Skretas *et al.*, 1999), similar eutrophication problems have been recognized in a number of Aegean and Ionian coastal areas, affected by urban and industrial wastewaters and/or nutrient inputs from rivers and agricultural activities (Ignatiades *et al.*, 1986; Gotsis-Skretas

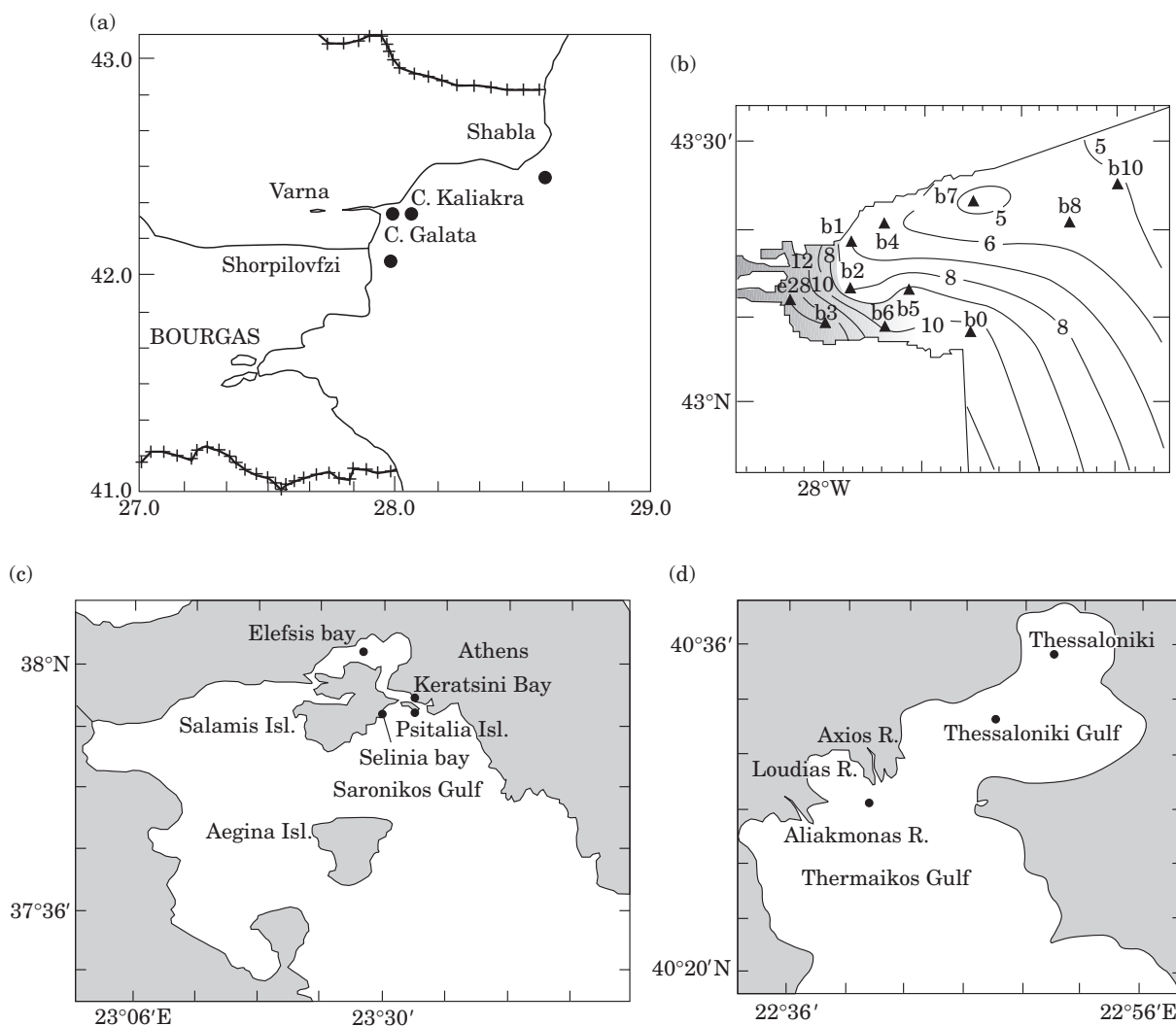


FIGURE 1. Maps of sampling areas. (a) Black Sea (Cape Kaliakra) (b) Black Sea (Varna Bay), (c) Saronikos Gulf (Central Aegean Sea), (d) Thermaikos Gulf (Northern Aegean Sea).

& Friligos, 1990; Pagou, 1990; Pagou & Ignatiades, 1988, 1990; Gotsis-Skretas, 1995; Pagou & Assimakopoulou, 1996). Phytoplankton, as primary producer, became the first target of the anthropogenic induced stress, resulting in dramatic alterations in species composition, abundance and biomass, seasonal dynamics and succession in the two basins (Frigilos & Gotsis-Skretas, 1989; Bodeanu, 1993; Moncheva, 1995; Bodeanu *et al.*, 2000).

The objective of the present paper is a comparative study of phytoplankton blooms in the Western Black Sea and the Eastern Mediterranean (Aegean Sea) coastal ecosystems, which are characterized by different physico-chemical features. It aims to assess similarities and differences in phytoplankton responses to anthropogenic nutrient enrichment. This is the first time that such a comparative study, for these two

marine basins which have different environmental profiles, has been performed.

Material and methods

Areas of investigation

Data from two coastal regions along the Bulgarian Black Sea coast were analysed: (a) Cape Kaliakra, influenced by the Danube freshwater plume [Figure 1(a)]; (b) the coastal zone of Cape Galata, including Varna bay, which is influenced by industrial, agricultural and sewage loads [Figure 1(b)]. The corresponding regions in Aegean Sea were: (a) Saronikos Gulf (Elefsis Bay and Keratsini-Selinia Bay) impacted by untreated sewage discharge from the metropolitan Athens [Figure 1(c)]; (b) Thermaikos Gulf subjected

to the urban and industrial pollution of the major Thessaloniki area (Thessaloniki Bay) and affected by the Axios, Aliakmon and Loudias rivers' discharges (NW Thermaikos Gulf) [Figure 1(d)].

Variables

Sea water samples for the investigation of phytoplankton communities (taxonomic structure, numerical abundance and biomass) and physico-chemical parameters were collected monthly to seasonally. The stations located along the Bulgarian Black Sea coast were as follows: at Cape Kaliakra (30 m depth) during 1983–1986 and 1995–1998; at Cape Galata (3 miles offshore, 20 m depth) during 1990–1997; at Varna Bay (maximum depth 18 m) a long-term data set (1983–1997) was analysed. The samples were collected from three standard depths of the water column (0 m, 10 m, and above the bottom). Additional samples were processed during phytoplankton blooms. In Saronikos Gulf (Central Aegean Sea) samples were collected monthly or bimonthly during the period 1983–85 and 1995 from 0, 10, 20 and 30 m (maximum station depth: 32 m). In Thermaikos Gulf, sampling was performed seasonally during 1984–85 and 1995 (maximum station depth: 35 m). Additional sampling (monthly or bimonthly) was performed to monitor phytoplankton blooms during the period 1982–1996.

Phytoplankton samples from the Black Sea area were fixed with glutaraldehyde–Lugol solution and concentrated according to Utermohl (1958). Species identification and cell counting were done under light microscope (Olympus CH 30) in a Palmer-Maloney chamber after Sournia (1978). Chlorophyll *a* was measured spectrophotometrically in acetone extract, applying the equations of Jeffrey and Humphrey (1975) and Lorentzen (1967). Phytoplankton samples from the Aegean Sea, were fixed with Lugol's solution (without acetic acid), concentrated according to Utermohl (1958) and quantitatively and qualitatively examined under a NIKON Diaphot inverted microscope. Chlorophyll *a* was determined by fluorometric measurements of acetone extracts (Yentsch & Menzel, 1963) in a TURNER AU-10 fluorometer, calibrated against a spectrophotometric measurement of pure chlorophyll *a* standard solution.

Temperature and salinity data were collected by Sea Bird SBE 911 Plus CTD-Rosette System casts in the two basins. In the Aegean Sea, samples for the determination of nutrients were collected in 100-ml polyethylene bottles and kept continuously under deep freeze (-20°C) until their analysis in the laboratory. Phosphate and ammonium were measured

by a Perkin Elmer Lambda 2S UV/VIS spectrometer, according to the methods of Murphy and Riley (1962) and Koroleff (1969), respectively.

Silicate, nitrite and nitrate, prior to 1995, were determined using a Technicon CSM6 auto-analyser, according to the methods described by Armstrong *et al.* (1967). After 1995, nutrients were determined by ALP-KEM automatic analyser. Nutrient supply from the Black Sea was analysed by standard methods (Grasshoff *et al.*, 1983). The determination of dissolved oxygen was carried out *in situ* (on board) using the Winkler method according to Carritt and Carpenter (1960).

To target the problem of similarities and differences of phytoplankton blooms in the coastal areas of the Black and Aegean seas, in addition to the classical taxonomic approach (list of species, taxonomic ratios, abundance, seasonal patterns), the recent tropho-species concept of Turner and Roff (1993) and that of Reynolds and Smayda (1998) were applied for identifying functional groups. As a functional compromise, retaining taxonomy-based information and reducing the number of compartments, the species were subdivided into: (a) autotrophs and mixo/heterotrophs (Turner & Roff, 1993); (b) C (=competitors), R (=disturbance tolerant) and S (=stress tolerant) strategy species (Reynolds & Smayda, 1998).

Environmental factors (temperature, salinity, nutrients and their ratios) are discussed in order to differentiate between the specific natural peculiarities of the two basins and the effects induced by the anthropogenic pressures. The Trophic State Index (TRIX), as proposed by Vollenweider *et al.* (1998) based on chlorophyll *a*, oxygen saturation, inorganic nitrogen and inorganic phosphorous, was calculated in order to scale the eutrophication level of the investigated areas.

Indices to measure the response of biota to eutrophication, as recommended by GESAMP (1995) were used in the interpretation of the results. A statistical analysis (Cluster and PCA, PRIMER, 1996, Statistics for Windows) was applied to score and narrow down the selection of parameters, in testing similarities and differences between sites and between the two basins.

Results

(a) Phytoplankton blooms

The analysis of species taxonomic list reveals that, during the 1980s–90s, the number of blooming microalgae in the western Black Sea (44 species) was about

TABLE 1. Taxonomic list of blooming phytoplankton species and maximum densities attained (1×10^6 cells l^{-1}) in the Black and the Aegean Sea

Class/Species	Black Sea			Aegean Sea		
	Varna Bay	Cape Galata	Cape Kaliakra	Elefsis Bay	Keratsini Bay	Thermaikos Gulf
Bacillariophyceae						
<i>Cerataulina pelagica</i> (Cleve) Hendey-R*	11.2	1.1	6.4			1.8
<i>Chaetoceros insignis</i> Pr.Lavrenko-C			1.4			
<i>Chaetoceros affinis</i> Lauder-C	4.2					
<i>Chaetoceros curvicaetus</i> Cleve-C	1.1				1	
<i>Chaetoceros rigidus</i> Ostenfeld-C			2.3			
<i>Chaetoceros similis</i> Cleve-C	7.7		1.02			
<i>Chaetoceros simplex</i> Ostenfeld-C	1.1					
<i>Chaetoceros socialis</i> Lauder-C	3.5		1.9			0.43
<i>Cyclotella caspia</i> Grunow-C	9.9	3.6	2.5			
<i>Cylindrotheca closterium</i> (Ehrenb) Reiman and Lewin-R	3.2	5				2.8
<i>Detonula confervaceae</i> (Cleve) Gran-R	8.7	0	1.01			
<i>Detonula pumila</i> (Castracane) Gran-R	10.4	4.8				
<i>Dytilum brightwellii</i> (West) Grunow-R	1.1	0.8	0.06			
<i>Leptocylindrus danicus</i> Cleve-R		0.9		0.42	0.25	
<i>Leptocylindrus minimus</i> Gran-R	5					25
<i>Lithodesmium undulatum</i> Ehrenberg-R						2
<i>Nitzschia tenuirostris</i> Mereschkowsky-R	20.2					
<i>Porosira glacialis</i> (Grunow) Jorgensen-R	1.85	0.5	0.7			
<i>Pseudo-nitzschia seriata</i> (Cleve) H. Peragallo-R	5.3	0.5				
<i>Pseudo-nitzschia delicatissima</i> (Cleve) Heiden-R	4.2	1.1				
<i>Pseudosolenia calcar-avis</i> (Schultze) Sundstrom-S	0.2	0.3	0.48			
<i>Guinardia delicatula</i> (Cleve) Hasle = <i>Rhizosolenia delicatula</i> -R						8.1
<i>Dactyliosolen fragilissimus</i> (Berg.) Hasle = <i>Rhizosolenia fragilissima</i> -R	8.4	4	0.7	2.51		1.8
<i>Rhizosolenia setigera</i> Brightwell-S	0.2					
<i>Skeletonema costatum</i> (Grev) Cleve-C	61.06	10	15.3		14	2
<i>Thalassionema nitzschioides</i> (Grun.) Mereschkowsky-R				2.1	1.9	
<i>Thalassiosira parva</i> Pr.-Lavrenko-R	6.3					
<i>Thalassiosira rotula</i> Meunier-R				0.63		2
<i>Thalassiosira</i> sp.-R					0.75	3
<i>Thalassiosira subsalina</i> Pr.-Lavrenko-R	2.7					
Dinophyceae						
<i>Alexandrium monilatum</i> (Howell) Taylor-R	1.7		2.7			
<i>Ceratium furca</i> (Ehrenb) Claparede & Lachmann-S	1.2					
<i>Gymnodinium breve</i> Davis-C					27	
<i>Gymnodinium najadeum</i> Schiller-C			2.16			
<i>Gymnodinium</i> sp.-C				0.52		0.21
<i>Gymnodinium sanguineum</i> Hirasaka = <i>Gymnodinium splendens</i> -R	0.2		0.2			
<i>Gymnodinium uberium</i> Schiller-C	5.39		1.4			
<i>Gyrodinium aureolum</i> Hulburt-R				1.9		
<i>Heterocapsa triquetra</i> (Ehrenb.) Stein-R	39.5	2.1	7.02			
<i>Lingulodinium polyedrum</i> (Stein) Dodge-S	2.2					
<i>Oxyphhis oxytoxoides</i> Kofoid-S	1.4					
<i>Prorocentrum balticum</i> (Lohm) Loeblich-R					1.1	
<i>Prorocentrum dentatum</i> Stein-R				120	0.6	24
<i>Prorocentrum micans</i> Ehrenberg-R	2.98				1.1	
<i>Prorocentrum minimum</i> (Pav.) Schiller-C	481.3	2.2	42.3			12
<i>Prorocentrum rostratum</i> Stein-R						1
<i>Scrippsiella trochoidea</i> (Stein) Loeblich-R	1.9			29		

TABLE 1. *Continued*

Class/Species	Black Sea			Aegean Sea		
	Varna Bay	Cape Galata	Cape Kaliakra	Elefsis Bay	Keratsini Bay	Thermaikos Gulf
Chlorophyceae						
<i>Chlorophyte</i> sp.-R					16.8	
<i>Monoraphidium convolutus</i> -R	6.1					
<i>Pavlova</i> sp.-R					5	
Chrysophyceae						
<i>Emilliana huxleyi</i> (Lohman) Hay & Mohler-C	52.9	5	17.4	3.1		
<i>Coccolithus</i> sp.-C				0.42		
Prymnesiophyceae						
<i>Phaeocystis pouchettii</i> (Hariot) Lagerheim-C	90	8.9		2.5	35	
<i>Phaeocystis</i> sp.-C						14
Cryptophyceae						
<i>Cryptomonas</i> sp.-C	1.1	0.9		23	10.8	0.68
Euglenophyceae						
<i>Astasia</i> sp.-R	3.3					
<i>Eutreptia viridis</i> Perry-R	20		1.2			
<i>Eutreptiella</i> sp.-R					3.9	
Flagellates						
<i>Cyclotrichium meunieri</i> -R				2.3		
<i>Microflagellate</i> sp.-C	42.84					
Prasinophyceae						
Prasinophyte sp.-C					68	
Cyanophyceae						
<i>Oscillatoria</i> sp.-R	5					
Total number of species	40	17	20	13	15	16

The common species for the two basins are given in shaded rows; *-C, -R, S-strategy species.

30% higher than that in the Aegean Sea (30 species), among which 14 species were common for the two basins (Table 1).

Taxonomically, both areas were dominated by diatoms (25 species in the Black Sea, 12 species in the Aegean Sea), out of which 8 were common. Dinoflagellates are ranked second (11 and 9 species, respectively—3 common species). Six other classes were represented by one or two species only (with the exception of Chrysophyceae—four species in Aegean Sea). Diatom species common to the two areas were: *Chaetoceros socialis*, *Chaetoceros curvisetus*, *Cerataulina pelagica*, *Skeletonema costatum*, *Dactyliosolen fragilissimus* (= *Rhizosolenia fragilissima*), *Cylindrotheca closterium*, *Leptocylindrus minimus*, *Leptocylindrus danicus*. Common dinoflagellates included: *Prorocentrum minimum*, *Prorocentrum micans*, *Scrippsiella trochoidea*; common Chrysophyceae species were: *Phaeocystis pouchettii*, *Emilliana huxleyi*.

With the exception of Varna Bay, where the number of blooming species was much higher (40), the total

number for the other locations does not differ substantially (Table 1). Consequently, the Bray-Curtis similarity index based on taxonomic composition/abundance matrix between the Black and the Aegean Sea coastal areas is very low (20%), and the two regions are definitely separated into two clusters [Figure 2(a)]. The similarity between the sites among the regions is also not high [Figure 2(a)]. It increases to 30–40% when only the presence/absence of the species is taken into consideration [Figure 2(b)] and when the matrix is based on functional groups (auto/heterotrophs) [Figure 2(c,d)], illustrating that the differences in the critical densities also account for the dissimilarities. In the case of auto/heterotrophs matrix, the clusters are restructured and the similarity index between Thermaikos Gulf and Varna Bay increases to 40–55%, advocating the advantage of the functional groups approach in the comparative study [Figure 2(c,d)].

In general, the range of maximum densities sustained in the two regions is comparable, varying from

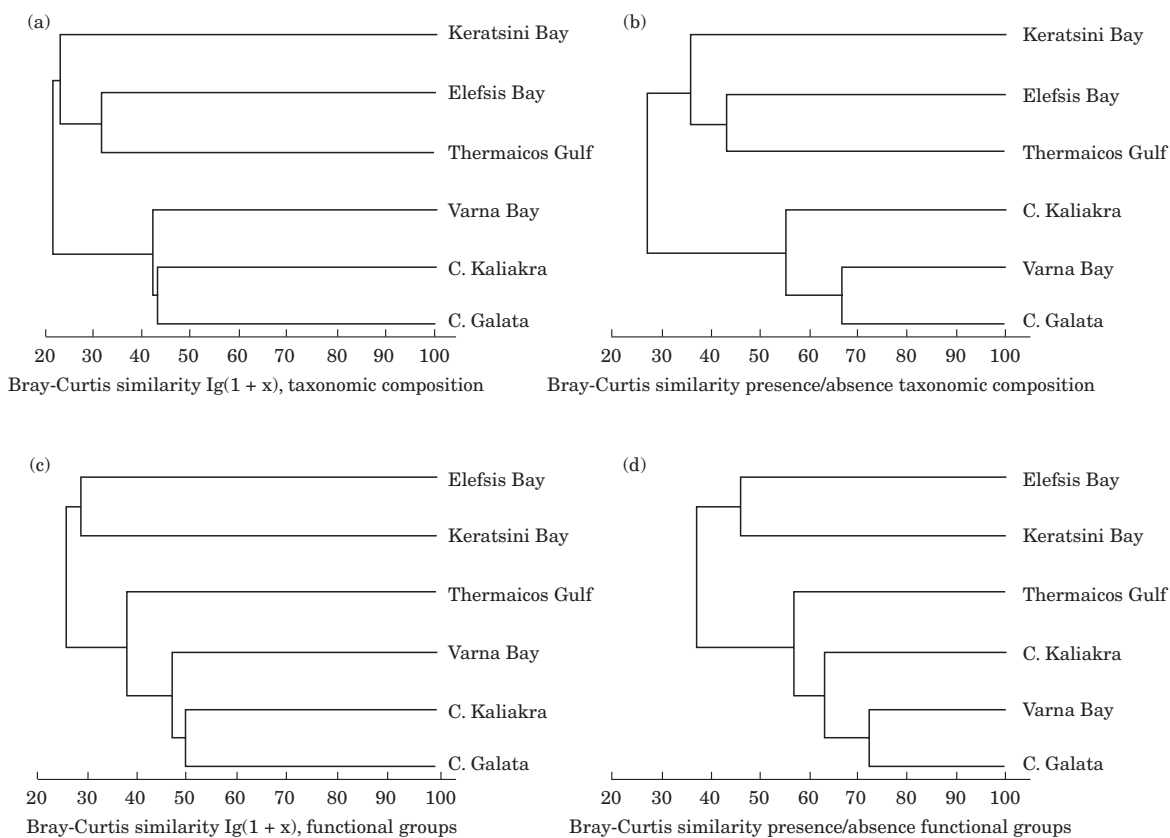


FIGURE 2. Bray-Curtis similarity cluster dendrogram based on (a) species taxonomic composition and (b) presence/absence of species. Bray-Curtis similarity cluster dendrogram based on (c) species functional groups (auto/mixotrophs), and (d) presence/absence of functional groups.

1×10^6 cells l^{-1} to 1×10^8 cells l^{-1} . However, the number of species reported to reach very high levels and the frequency of these episodes was higher in Black Sea (Varna Bay) (Table 1). The record of numerical densities, $>1 \times 10^7$ cells l^{-1} in Varna bay; exceeded 35, the recurrent species being *Prorocentrum minimum*, *Skeletonema costatum*, *Emilliana huxleyi*; the corresponding cases in Aegean Sea were 14.

The comparative analysis of the seasonal dynamics in the two basins reveals substantial differences in the taxonomic dominance, number of species involved, average seasonal abundance attained and sequence of episodes, no matter how close the values were of the average annual abundance (9.9×10^6 cells l^{-1} and 7.9×10^6 cells l^{-1}). In winter, Black Sea phytoplankton communities were basically composed of diatoms, the recurrent species recorded in bloom densities being *S. costatum*, *C. caspia* *Chaetoceros* spp. In spring, diatoms shared dominance with dinoflagellates (*H. triquetra*, *P. minimum*), the latter often dominating over the diatoms. Occasionally, *Eutreptia viridis* was involved in a bloom episode as a co-dominant species. In summer, the microalgae that usually proliferated

were *P. minimum*, *S. trochoidea*, *D. fragilissimus*, *C. pelagica*, *E. huxleyi*, *E. viridis*. The autumn assemblage was habitually composed of the diatoms *C. pelagica*, *D. confervaceae*, *L. minimus*, *S. costatum* and of the dinoflagellates (*P. minimum*, *Alexandrium monniliatum*, *Gymnodinium uberium*) as more or less sporadic species. In contrast, as a general trend, diatoms were less common in the Aegean Sea in comparison to the Black Sea region, with the exception of Thermaikos Gulf. In this Gulf, in winter, diatoms (*Ch. socialis*, *Th. rotula*) co-occurred with *Cryptomonas* sp. and *P. pouchettii*. In spring, the phytoplankton outbursts were due to a diatom assemblage (*Guinardia delicatula*, *C. pelagica*, *Thalassiosira* sp., *L. minimus*). During summer, together with the diatoms *D. fragilissimus*, *S. costatum*, *Thalassiosira* sp., several dinoflagellates proliferated such as, *P. rostratum*, *P. minimum*, *Gymnodinium* sp. In Saronikos Gulf, Dinophyceae, Chrysophyceae and Chlorophyceae species frequently outcompeted the diatoms.

These peculiarities are well illustrated by the pattern of dynamics of average seasonal densities of phytoplankton groups (Figure 3). As evident from

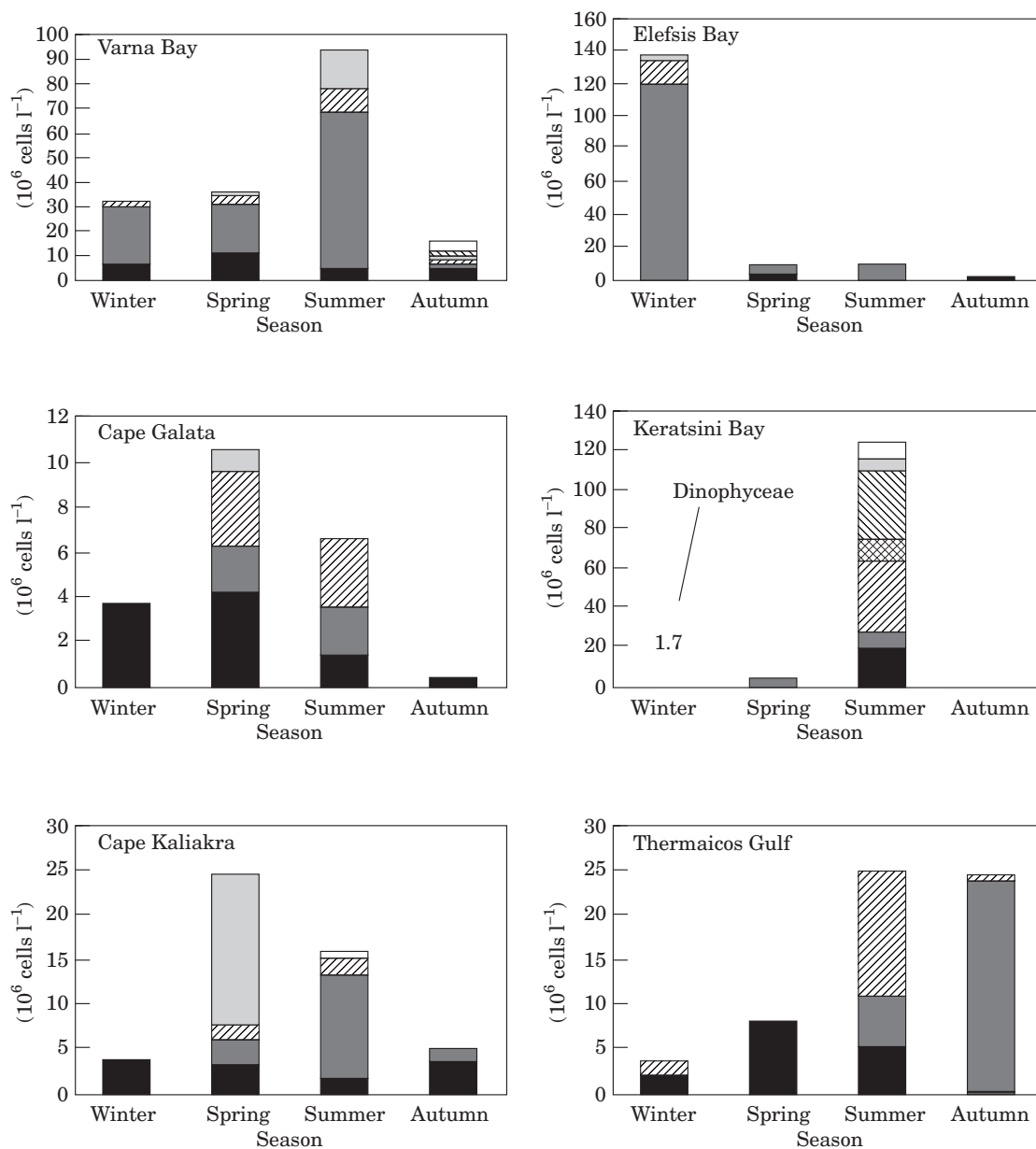


FIGURE 3. Seasonal distribution of cumulative bloom densities ($\times 10^6$ cells l^{-1}) by classes at three sites in the Black Sea (left hand) and at three sites in the Aegean Sea (right hand). ■ Bacillariophyceae; ■ Chrysophyceae; ▨ Dinophyceae; □ Euglenophyceae; □ Chlorophyceae.

the figure, the average cell density of diatoms and their relative distribution along the Bulgarian Black Sea coast were higher especially in winter and autumn (Figure 3). In spring, phytoplankton cell density was shared between diatoms, dinoflagellates and chrysophytes, the latter being more abundant in summer, when dinoflagellates reached the highest abundance. In contrast, in the Aegean Sea, the contribution of diatoms was relatively small (with the exception of Thermaikos Gulf in spring). The contribution of dinoflagellates was highest in Elefsis

bay (winter, spring and summer) and in Thermaikos Gulf in autumn. In the Black Sea, cumulative average cell numbers in spring–summer usually exceeded those of winter–autumn by a factor of 3 to 5, while in the Aegean Sea there was no apparent trend in the seasonal maxima sequence (Figure 3).

Clearer patterns could be outlined when the comparative study was based on functional groups (Figure 4). The dominance of C-R-species was almost inverse in the two regions.

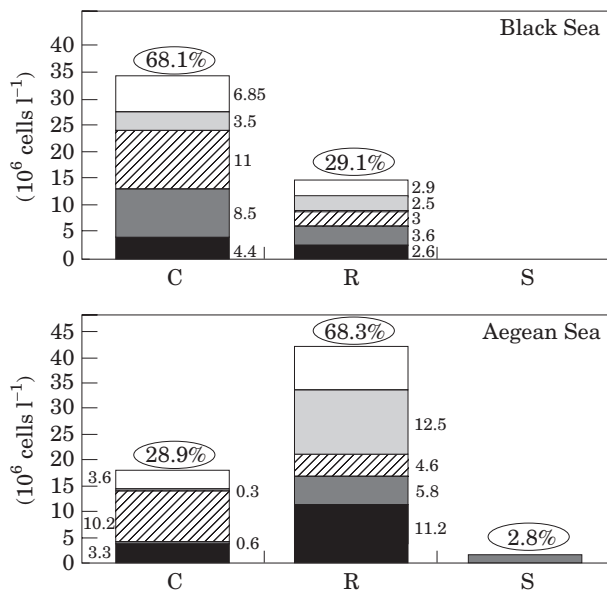


FIGURE 4. Seasonal distribution of average seasonal blooming cell densities by functional groups in the Black Sea and Aegean Sea. C=competitors, R=disturbance tolerant, S=stress tolerant species. ■ winter, ■ spring, ▨ summer, □ autumn, □ av.

The percentage contribution (in terms of the average annual numerical abundance) of C-strategy species was 68% in the Black Sea, exactly equal to the share of R-strategy species in the Aegean Sea. While in the Black Sea the R-strategy species were almost evenly distributed (as seasonal average density), in the Aegean Sea their portion was largest in winter and autumn. The highest average abundance of C-species in summer (11×10^6 cells l^{-1} in the Black Sea, 10.2×10^6 cells l^{-1} in the Aegean Sea) was a common feature for the two regions which is noteworthy as it might have some bearing on the impact of nutrient enrichment on phytoplankton succession.

Overall, the abundance of mixotrophs was higher in the Aegean Sea in comparison to the Black Sea, with the exception of Varna Bay, where the average density of mixotrophs was comparable to that of Elefsis Bay [Figure 5(a)]. Accordingly, the ratio of Autotrophs/Mixotrophs at these sites was the lowest [Figure 5(a)]. This ratio was highest in Cape Kaliakra and Cape Galata, and about two times lower in Keratsini and Thermaikos Gulf.

As expected, the total number of autotrophs blooms is higher in Black sea (170 versus 73 cases), while in Aegean Sea the frequency of autotrophs/mixotrophs blooms was similar (25/23 cases) [Figure 5(b)].

The ratio of auto/mixotroph rate of occurrence was steady during all seasons in the Aegean Sea, irrespective of the differences between sites. In the Black Sea,

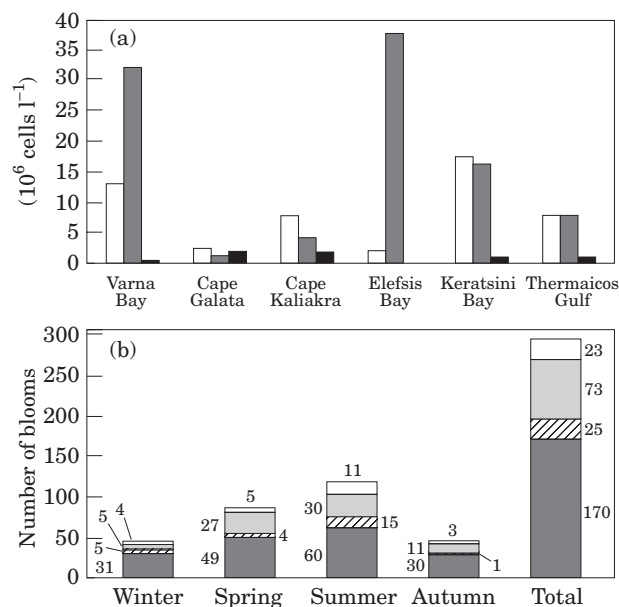


FIGURE 5. Average cell densities (a), and ratios of Autotrophs (A) and Mixotrophs (M) and number of blooms: □ A, □ M, ■ A:M; (b) in the Black Sea and the Aegean Sea: ■ Black Sea A, ▨ Aegean Sea A, □ Black Sea M, □ Aegean Sea M.

this ratio was variable, despite the fact that the number of autotrophs blooms was always higher (six and three times in winter and autumn, respectively, and about twice in spring–summer). On average, the number of bloom events in the Black Sea coastal area exceeded that in the Aegean Sea by a factor of 5, but to some extent this could be attributed to the different frequency of sampling and the long-term data set discussed from Varna Bay. The seasonal variety of blooming species in the Black Sea (within the range 1–17 species per site) was higher than that in the Aegean Sea (1–8, respectively), often several species proliferating in a single episode.

(b) Physico-chemical parameters, nutrient ratios and Trophic State Index

The comparison of the environmental factors (temperature, salinity, nutrients and their ratios) reveals clear differences between the coastal areas of the Black Sea and the Aegean Sea (Figure 6, Table 2).

Temperature and salinity were higher (more than 2 times) in the Aegean Sea than in the Black Sea (Figure 6, Table 2). The difference of these two parameters was negligible among the Black Sea sites, whereas it was more evident between Saronikos and Thermaikos Gulf in the Aegean Sea.

In contrast to temperature and salinity, the concentrations of nutrients, irrespective of the strong

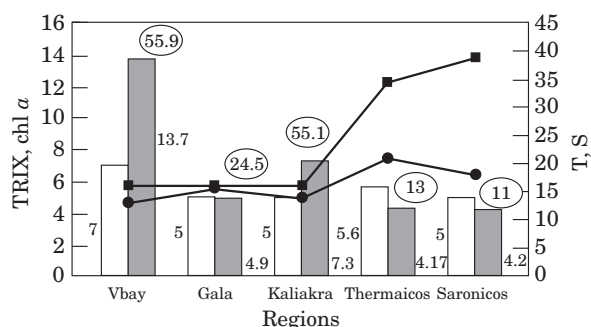


FIGURE 6. Average annual values of TRIX, chlorophyll *a*, temperature and salinity, by sites. (Maximum chlorophyll *a* values are shown in the circles) ● T, ■ S.

seasonal variability, were higher in the Black Sea region. Thus, the average concentrations of Si-SiO₄ exceeded that in the Aegean Sea by a factor of 2. Total N values were about 10 times higher, while P-PO₄ concentrations were rather similar, consequently resulting in different nutrient ratios (Table 2).

Values lower than the theoretical for the open sea (16:1) were found mainly in Thermaikos Gulf (average ratio: 4-6), and Elefsis Bay (in the area near

the sewage outfall in Saronikos Gulf) in winter and autumn, indicating inorganic nitrogen as the most likely limiting nutrient for primary production. N:P values higher (16-50) than the Redfield ratio were observed in the outer Saronikos Gulf during spring and summer, suggesting inorganic P to be the limiting factor for primary production in this area.

The average N:P ratio for the Aegean Sea coastal areas studied was below the Redfield ratio (average: 10.8; seasonal range: 2-30). On the contrary, in the Black Sea, in the three sites studied, the N:P ratio exceeded classical 16:1 (seasonal average within the range 25-144) (Table 2). The Si:N ratio was below 1 in the Black Sea and around 1 in the Aegean Sea coastal area. The Si:P ratio, on average, was larger than three times in the Black (25) than in the Aegean Sea (8), of a rather high seasonal and spatial variability (Table 2).

The average TRIX index (Vollenweider *et al.*, 1998), as an integrated measure of the eutrophication level, displayed similar values in the two regions; 5.7 in the Black Sea and 5.3 in the Aegean Sea coastal ecosystems (Figures 6 and 7, Table 2). Among sites, the levels were also close (about 5) except at Varna

TABLE 2. Seasonal values of some environmental parameters

Region/Parameter	T C	S	P (PO ₄) (μm l ⁻¹)	N _{tot} (μm l ⁻¹)	SI (OH ₄) (μm l ⁻¹)	N:P	SI:N	SI:P	TRIX
Varna Bay									
winter	8.63	15.86	5.530	266.303	13.297	56.6	0.1	2.7	8.6
spring	15.43	16.35	2.087	153.653	17.333	45.9	0.2	24.6	8.2
summer	22.73	15.31	2.070	117.300	8.207	65.8	0.1	5.3	6.7
autumn	14.10	16.84	2.555	100.900	52.450	42.3	0.5	20.1	5.9
Cape Galata									
winter	3.27	16.34	0.383	36.882	5.220	77.7	0.2	25.7	6.2
spring	11.77	16.67	0.243	70.657	4.870	144.4	0.1	21.1	6.6
summer	24.10	15.47	0.108	4.045	4.893	55.6	1.8	42.4	3.8
autumn	15.60	17.21	0.250	9.039	5.687	34.3	1.2	28.5	4.6
Cape Kaliakra									
winter	3.88	15.94	0.358	38.547	7.763	101.0	0.2	16.3	5.8
spring	12.08	16.56	0.190	19.473	1.710	89.0	0.1	7.6	5.2
summer	23.58	15.30	0.128	6.857	3.563	62.2	0.6	36.0	4.0
autumn	13.73	16.51	0.310	6.680	7.900	25.1	1.5	27.1	5.2
Thermaikos Gulf									
winter	13.45	35.60	0.690	3.540	4.300	5.1	1.2	6.2	5.6
spring	19.07	36.35	0.518	0.595	0.998	2.0	1.7	1.9	5.7
summer	26.68	35.54	0.444	1.408	2.314	3.5	1.6	5.2	5.1
autumn	13.02	36.32	0.594	4.632	4.470	8.0	1.0	7.5	6.0
Saronikos Gulf									
winter	12.44	38.68	0.196	1.966	0.484	10.6	0.2	2.5	5.3
spring	13.87	38.05	0.135	3.763	1.893	30.0	0.5	15.3	5.0
summer	26.17	38.96	0.118	1.868	1.320	16.3	0.7	11.2	3.7
autumn	14.19	38.60	0.400	4.340	5.310	11.0	1.2	13.3	6.2

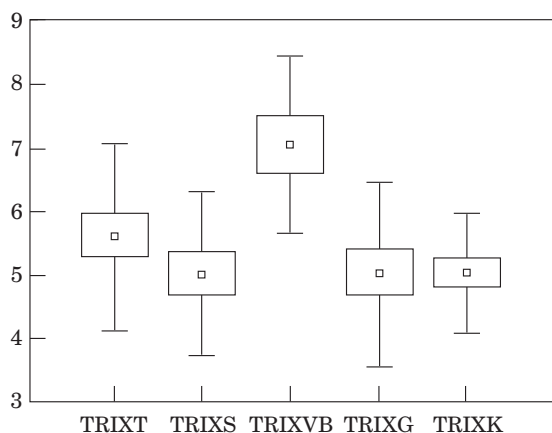


FIGURE 7. Box-Whisker Plot for TRIX by sites. TRIX=Trophic State Index (Vollenweider *et al.*, 1998). (T-Thermaikos Gulf, S-Saronikos Gulf, VB-Varna Bay, G-Cape Galata, K-Cape Kaliakra)

bay, where it was much higher (7). At all the sites, the seasonal variability of TRIX was substantial. In the Black Sea, it varied from 5.9 to 8.6 in Varna bay, from 3.7 to 6.6 in Cape Galata and from 4.0 to 5.8 in Cape Kaliakra. In the Aegean Sea, TRIX index values varied from 5.0 to 6.0 in Thermaikos Gulf and from 3.7 to 6.2 in Saronikos Gulf. In all sites studied, the lowest values were recorded in summer (Table 2).

Average annual chlorophyll *a* concentration, as an approximate of total phytoplankton biomass, did not differ significantly between Saronikos and Thermaikos Gulf and between Cape Galata and Cape Kaliakra, whereas the mean chlorophyll *a* concentration in Varna Bay was more than 3 times higher (Figure 6). The very high maximum chlorophyll concentrations, varying from $11 \mu\text{g l}^{-1}$ in Saronikos Gulf to $55.9 \mu\text{g l}^{-1}$ in Varna Bay (the numbers in circles, Figure 6), show that all the sites have the potential to sustain very high phytoplankton levels coinciding with the occurrence of phytoplankton blooms.

(c) PCA analysis

Principal Component Analysis (PCA) was applied in order to assess the similarities and differences between the two basins and the relevant parameters responsible for the differentiation [Figures 8(a, b) and 9]. Variables included in the matrix were temperature, salinity, nutrients and their ratios, TRIX and auto/mixotrophs or C-, R-, S-strategies, thus two different approaches were applied. The combination of nutrients, their ratios and TRIX is referred as eutrophication component.

PCA analysis demonstrates that when the matrix is based on temperature, salinity, auto/mixotrophs,

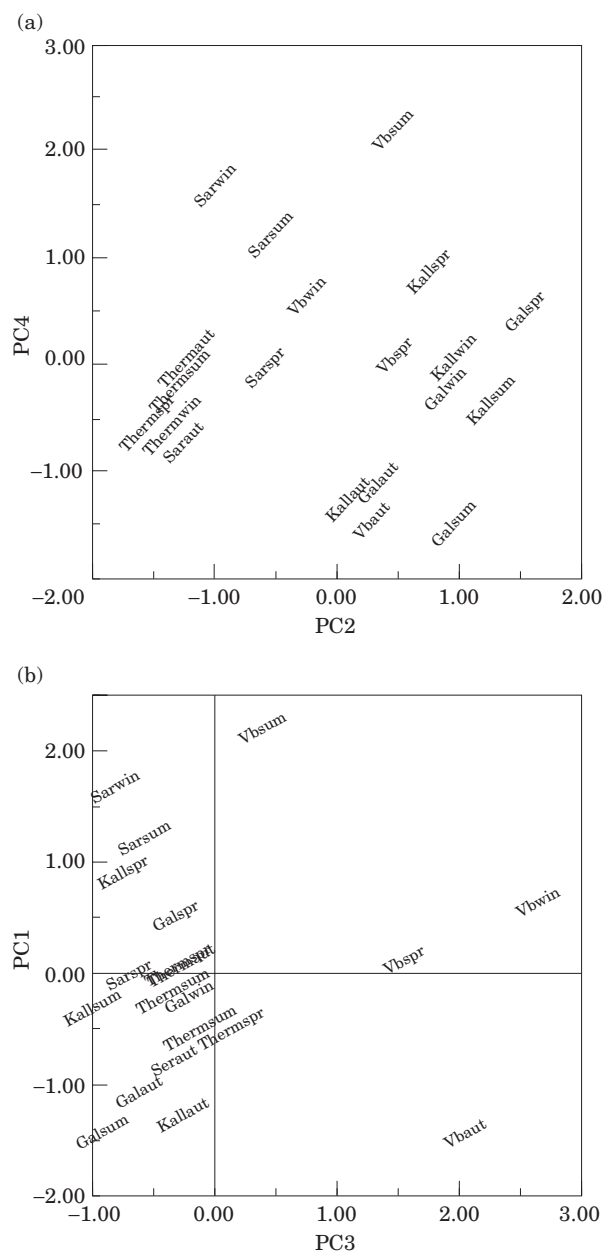


FIGURE 8. PCA plot of matrix based on (a) salinity and nutrient ratios, and (b) TRIX, and nutrients, and auto mixotrophs.

nutrients, nutrient ratios, and TRIX (first approach), temperature alone (represented by PC1 axis) accounts for 37% of the total variance; salinity and N:P ratio (PC2 axis) for 21%; nutrients and TRIX (PC3 axis) for 13.8%, and mixotrophs (PC4 axis) for 11.8% [Figure 8(a)]. On the PCA plot of eutrophication component/mixotrophs (PC3/PC4) the differentiation between the two basins is not clear [Figure 8(b)]. Varna Bay only stands separate as a site of both high nutrients and TRIX, as well as, high mixotrophs in

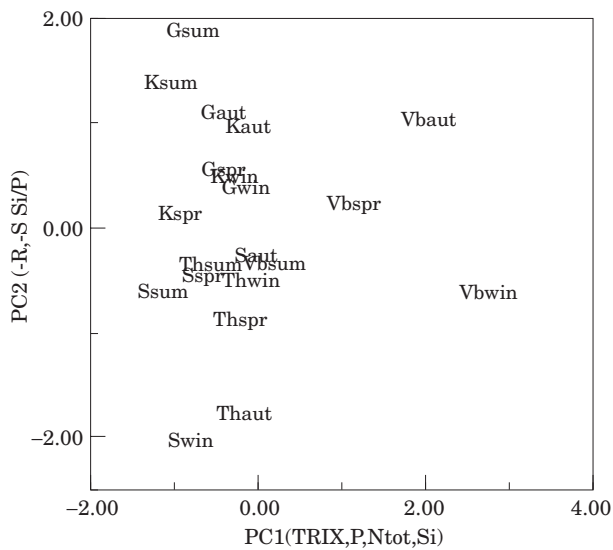


FIGURE 9. PCA plot of matrix based on temperature, salinity, nutrients and their ratios, TRIX and C-R-S-strategies.

summer, spring and winter, and low mixotrophs in autumn. For all the other sites the differentiation is more apparent along the PC4 axis (mixotrophs), than along the eutrophication axis. Saronikos Gulf in winter and summer, and Cape Galata and Cape Kaliakra in spring, are projected at the coordinate of high mixotrophic phytoplankton component. In general, Thermaikos Gulf is characterized by low mixotrophs and higher nutrients than Saronikos Gulf. The PCA plot of PC2/PC4 (S; N:P/mixotrophs) demonstrates a distinct polarity between the two basins [Figure 8(a)], an indication of the pertinent role of salinity and N:P ratio for the dissimilarities. Thermaikos Gulf is projected at coordinates corresponding to lower N:P ratio and low mixotrophs as compared to Saronikos Gulf, which could well be related to the differences in the source and nature of the eutrophication input. Obviously, the seasonal differences among the Black Sea sites are stronger and mask the site differentiation with mixotrophs dominating in spring.

According to the second approach, when the matrix is based on temperature, salinity, nutrients, their ratios, TRIX and C-R-S-strategies, the eutrophication component (PC1) has the highest loading (34.6%) in the total variance, followed by salinity, Si:P ratio and R-strategies (PC2=20.3%), C-S-strategies (PC3=15.9%) and N:P and Si:N ratio (PC4=10%), as a total the four PCs explaining 81% of the variance. The PC1/PC2 plot distinguishes well the basins with apparent differentiation along the PC2 axis, and clear separation of Varna bay along the eutrophication axis (Figure 9). The Black Sea sites are projected at

coordinates of high salinity and Si:P ratio and low R-strategies, in contrast to the Aegean Sea, suggesting the significance of salinity, R-species and the Si:P ratio. As apparent from the PCA plots, salinity and nutrients ratios count substantially for the differentiation no matter if autotrophs/mixotroph component or C-R-S-strategy component have been considered.

Discussion

A phytoplankton bloom has regional, seasonal and species-specific aspects (Sournia, 1995; Smayda, 1997). Blooming species are originally considered as 'keystone species' or 'ecological engineers' that strongly influence and shape ecosystem processes and resilience (Carpenter & Cottingham, 1997). A growing body of laboratory, field and theoretical work suggests that the episodes and dynamics of algal blooms are frequently controlled by many factors—not only by physiological responses to local environmental conditions but also by a series of interactions between biological and physical processes (e.g. advective losses, grazing, sinking, and cell death, top down versus bottom up control, light regime etc.), including global climatic changes—(Petrova-Karadjova & Apostolov, 1988; Garet & Moum, 1995; Donaghay & Osborn, 1997; Hopkins, 1997; Franks & Walstad, 1997; Jones & Gowen, 1990; Peperzak *et al.*, 1998). Collectively, all these arguments emphasize the complexity of the phenomenon phytoplankton bloom and the difficulty in relating blooms to a single parameter only and identifying common scenarios. Alternatively, certain control processes are repeated in coastal regions, so one can look for general structures and mechanisms to explain broad patterns (GESAMP, 1995).

The comparison between the Black Sea and the Aegean Sea coastal ecosystems reveals both differences and similarities in phytoplankton bloom performance. The main differences, at regional level as inferred from this study are the following. The taxonomic composition and number of blooms producing microalgae are more diverse in the Black Sea coastal area (44 species), compared to the Aegean Sea (30 species). Diatoms were less common blooming species in the Aegean Sea, with the exception of Thermaikos Gulf. Consequently, the contribution of dinoflagellates, chlorophytes and chrysophytes, in the average seasonal cumulative density, was higher in the Aegean Sea. Overall, mixotrophs were more abundant in the Aegean Sea, with the exception of Varna bay where the average density was comparable to that of Elefsis bay. Alternatively, the dominance of C- (competitors) and R- (disturbance tolerant) strategy species was almost inverse, the C-species being more

successful in the Black Sea. Traditionally, the frequency of episodes and the total number of autotrophs blooms is higher in the Black sea (170 versus 73), while in the Aegean Sea the number of autotrophs/mixotrophs blooms is almost equal.

Although by physico-chemical parameters, two different environments have been compared (higher temperature and higher salinity in the Aegean Sea, contrasting to higher nutrient levels and different nutrient ratios in the Black Sea ecosystem), the two regions exhibited similar features: 14 common bloom species, the highest bloom rate of occurrence, the variety of species and average level of C-strategies in summer, the similar range of maximum bloom densities attained, and similar capacity to sustain critical biomass during all seasons. The average annual Trophic State Index (TRIX) and its range of variability was very similar among the Thermaikos and Elefsis Gulfs and Cape Galata and Cape Kaliakra sites. Only Varna bay site differed substantially (average TRIX index: 7).

There exists a widespread belief that the outbreaks of red-tides are now becoming more frequent as a consequence of increasing eutrophication in coastal waters (nutrient supply and nutrient ratio hypothesis, Anderson, 1989; Smayda, 1990; Hallegraeff, 1993). The use of Redfield ratio and the nutrient ratios in general are subjected to a number of limitations (e.g. high variability, difficulties in the interpretation when the nutrients approach their detection limits (Hecky & Kilham, 1998). Similar restrictions exist for the ambient nutrients in evaluating the level of eutrophication, (different cycling of N and P in the ecosystem, large capacity of phytoplankton to store P versus its limited capacity to store N, the strong dependence on input/consumption/regeneration processes and dual nutrient feedback control in the seasonal changes of phytoplankton community (Smith, 1984; Nixon, 1988; Jenkinson & Wyatt, 1995; Ulanowicz & Baird, 1999). Nonetheless, numerical displacement of diatoms with dinoflagellates, chrysophytes, prymnesiophytes and picoplanktonic cyanobacteria, in geographically diverse regions experiencing decreased Si:N and Si:P ratio due to the decreased availability of Si relative to N and P, has been well documented (Boalch, 1987; Lancelot *et al.*, 1987; Riegman *et al.*, 1990; Schollhorn & Graneli, 1993). Long-term monitoring of phytoplankton community composition in coastal Helgoland (German Bight) waters shows a 10-fold increase in flagellates (relative to other major bloom-forming groups) as Si:N loading ratios have decreased (Radach *et al.*, 1990).

The analysis of the main nutrient ratios and ambient Si levels in this study suggests that in the

Black Sea, during late spring, Si could be the limiting factor for diatom growth since the reported growth optimum Si:N and Si:P ratios are 20:16 and 20:1, respectively, while concentrations of Si-SiO₄ below 5 µg l⁻¹ are considered limiting for the diatom growth, with a high range of species specific differences (Platt, 1981). After an intensive winter diatom bloom, the Si stripping from the environment in spring is reported as a possible scenario triggering the intense proliferation of dinoflagellates at still high concentrations of the other nutrients in the Black Sea replacing the diatoms (Moncheva & Krastev, 1997). For example, this scenario has been documented to occur in spring 1996 at Cape Galata site too, when analytical zero values of Si-SiO₄ were measured (Shtereva *et al.*, 1999). The model results of Van Eeckhout and Lancelot (1997), demonstrating a 10 times decrease of Si input relatively to N and P input in the north-western Black Sea, are in a good agreement with the reported shift in the taxonomic composition of phytoplankton towards non-diatoms during the 1980s in comparison to the 1960s (Moncheva & Krastev, 1997; Bodeanu *et al.*, 1999; Shtereva *et al.*, 1999).

Therefore, the differences in the nature of nutrient loads to the environment, imposing differences in the nutrient ratios, may lie behind the higher dominance of diatoms for example, in Thermaikos Gulf, compared to Saronikos Gulf. In Thermaikos Gulf, the Si demanding diatoms are more efficient in utilizing high nutrient levels (especially of Si) as mainly supplied by the three rivers' run-offs. On the contrary, the sewage outfalls, rich in dissolved organic matter (a major source of eutrophication in Saronikos Gulf) stimulate the growth of mixotrophic microalgae (Hickel *et al.*, 1993). Flagellates taxa diverge from diatoms in their vulnerability to turbulence, low nutrient affinity, considerable nutritional diversity involving mixotrophy, generally lower growth rates and different phytoplanktonic life mode (Riemann *et al.*, 1995; Smayda, 1997), a fact which imposes differences in the degree of internal versus external control of bloom dynamics. In addition, dinoflagellates and chrysophytes are thermophilic species in contrast to diatoms. Thus the low taxonomic similarity (Bray-Curtis index lower than 30%) between the different regions and among sites, could be attributed to both natural factors and dissimilarities (temperature, salinity, hydrodynamics) and the gradients in nutrient levels and their ratios, as affected by the different nature and severity of the anthropogenic pressure over the coastal ecosystems. According to the PCA analysis, the differences in salinity and nutrients ratios explain about 21% of the total variance no matter if autotroph/mixotroph

component or C-R-S-strategy component have been considered. The temperature alone (PC1) is responsible for 34% in the total variance, so thus the eutrophication component (PC1)—34.6%, depending on weather auto/mixotrophs or C-R-S-strategies, has been included in the matrix.

In the present study, the Trophic State Index is used as an integration of both ambient nutrients and their portion trapped in phytoplankton biomass (chlorophyll *a*) which to a certain extent overcomes the limitations of ratios and ambient nutrients concentrations. Irrespective of the differences in the nutrient levels, the TRIX index manifests similar values in both regions with the exception of Varna bay where the nutrients were much higher, emphasizing the importance of the degree of alteration and the departure from the natural background, induced by external inputs (anthropogenic stress). According to the TRIX index, the coastal ecosystems of the two basins are classified as eutrophicated and the Varna bay site as highly eutrophicated (according to Vollenveider *et al.* (1998) scale of eutrophication).

Since the nutrient availability sets the biomass carrying capacity, the higher nutrients concentrations in the Black Sea could to a certain extent explain the higher frequency of the number of blooms and maximum densities attained in comparison to the Aegean Sea. The striking differences between Varna bay and the other two sites in the Black Sea (substantial differences in TRIX values, too) provide further evidence that the gradient in the level of eutrophication is a pertinent factor for the differences in phytoplankton blooms response.

One of the suppositions advanced in this study is that taxonomically different species could function in a similar mode (functional groups), e.g. to play similar role in the energy flow and ecosystem metabolism (Turner & Roff, 1993; Reynolds & Smayda, 1998). This approach has proved useful in identifying common modes that are difficult to detect by analysis of the taxonomic composition only. As evident from the analysis, the Bray-Curtis similarity index between the two regions increased to more than 50% when the matrix is based on functional groups. In the PCA analysis they appear as an important factor of differentiation.

The results also reveal that the high share of C-strategies species is a common feature of the summer dynamics in both basins. By definition, the C-strategies species are equivalent to R-strategies of Margalef's classification (Margalef, 1978). From the viewpoint of the classical phytoplankton succession in the basins of temperate latitudes, the dominance of C-strategies species in summer reported in this study

could be considered a succession perturbation. It is deduced that increasing nutrient levels of coastal waters, especially those subjected to anthropogenic eutrophication, causes the deviation of the trajectory of 'main sequency' towards selection preferentially of fast growing small microalgae (preferably dinoflagellates and haptophytes [Reynolds & Smayda, 1998]). Besides the common phytoplankton species, the coastal ecosystems of the two basins manifest comparable range of maximum levels attained and similar capacity to produce critical biomass during all seasons. This could be well attributed to the eutrophication, as the increase in nutrient concentration results in an alteration in the annual cycle of the species and acceleration of the succession stages in comparison to the natural pattern (Miheeva, 1983; Moncheva & Krastev, 1997; Bodeanu *et al.*, 2000).

In conclusion, the results indicate that temperature and salinity are factors contributing to the outlined differences between the Aegean Sea and the Black sea ecosystems, but the differences among the selected sites give support to the importance of nutrients and their ratios. Although competitive outcomes in phytoplankton species selection and succession are too complicated to be predicted, as the relative effects of natural versus anthropogenic factors are resolved, the forgoing analysis suggests that anthropogenic nutrient enrichment could play an important role in driving phytoplankton bloom performance. Thus, the comparative studies between different basins could be a step forward to highlight common patterns and modes of ecosystem response to the anthropogenic eutrophication and to suggest common indices to scale eutrophication impact.

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