ISSN 0001-4370, Oceanology, 2009, Vol. 49, No. 1, pp. 83–92. © Pleiades Publishing, Inc., 2009.
Original Russian Text © L.V. Stel'makh, I.I. Babich, S. Tugrul, S. Moncheva, K. Stefanova, 2009, published in Okeanologiya, 2009, Vol. 49, No. 1, pp. 90–100.

MARINE BIOLOGY

Phytoplankton Growth Rate and Zooplankton Grazing in the Western Part of the Black Sea in the Autumn Period

L. V. Stel'makh[a], I. I. Babich[a], S. Tugrul[b], S. Moncheva[c], and K. Stefanova[c]

[a] *Institute of Biology of the Southern Seas, National Academy of Sciences of Ukraine, Sevastopol', Ukraine*
[b] *Institute of Marine Sciences, Middle East Technical University, Erdemli, Turkey*
[c] *Institute of Oceanology, Bulgarian Academy of Sciences, Varna, Bulgaria*
E-mail: lstelm@ibss.iuf.net

Received July 7, 2007; in final form February 15, 2008

Abstract—The results of the studies within the framework of the international expedition onboard R/V *Vladimir Parshin* in September–October 2005 are presented. Intensive development of Bacillariophyceae and Dynophyceae was recorded in the coastal waters of Bulgaria, Turkey, and in the Danube River Delta during the period of the investigations. The increase in the algae population was accompanied by rising of the Chlorophyll *a* concentration up to 2.0–5.5 mg m^{-3}. In the deep water region, it did not exceed 0.54 mg m^{-3}. The phytoplankton growth rate in the surface water layer varied from 0.1 to 1.0 day^{-1}. The phytoplankton growth rate and NO_2+NO_3 concentration, as well as the silicon concentration, were correlative, as was described by the Michaelis–Menten equation. The phytoplankton growth was affected by the integral impact of basic nutrients. The zooplankton grazing varied from 0.10 to 0.69 day^{-1}, and the average values in different regions may vary by 1.5 times. The microalgae size range is one of the major factors of the grazing regulation. The rate of the phytoplankton consumption was decreasing according the increasing of the largest diatom *Pseudosolenia calcar-avis* impact on the total biomass of the nano- and microphytoplankton.

DOI: 10.1134/S000143700901010X

INTRODUCTION

A number of studies describing the phytoplankton growth rates in different areas of the Ocean were published in the last decade. The minimal values of the relative growth rate (0.1–0.2 day^{-1}) were found in the oligotrophic areas, while the maximal ones (1.0–2.0 day^{-1}) were observed in the coastal areas of high productivity and upwellings [15, 18, 22, 28, 29]. The data obtained allow one to conclude that the nitrate/nitrite concentrations in the areas of the photosynthesis are the major limiting factors of the primary production and the phytoplankton growth.

Few studies on the phytoplankton growth rates in the Black Sea are mainly targeted on the abundant algae species of nano- and microphytoplankton [2, 3, 12]. The growth rates of nano- and microphytoplankton may vary in order of magnitute of 10 in the coastal areas. The minimal values (0.1–0.3 day^{-1}) were observed in the spring diatom bloom. The maximal values of 0.90–1.68 day^{-1} were usual for the prebloom period [2, 12].

The present study was aimed to assess the bulk phytoplankton growth rate and the grazing impact of the zooplankton, as well as to reveal the major factors governing these processes in the surface waters of the Black Sea in the autumn period.

MATERIALS AND METHODS

The investigations were conducted during the international GEF/UNDP Black Sea Ecosystem Recovery Project during the scientific cruise of R/V *Vladimir Parshin* to the Western Part of the Black Sea. The studies were carried out from September 20 to October, 15, 2005, at 20 stations, both in the coastal and deep-water regions (Fig. 1).

Assessing the phytopankton growth rate and the zooplankton grazing impact. The assessing of the phytopankton growth rate and zooplankton grazing impact were carried out with dilution method [26], which is widely used in such kinds of hydrobiological investigations. The major advantage of this method is the possibility of assessing the bulk phutoplankton growth rate and the grazing impact of zooplankton, mainly microzooplankton. The application of the method involves three major assumptions. First, the phytoplankton growth rate does not depend on the sample dilution factor. Second, the grazing rate of the zooplankton decreases accordingly to the dilution factor. Lastly, the grazing rate is constant and is not affected by the zooplankton abundance in the experimental vial [27].

The water samples (15–20 L) were taken in the morning (6.00–7.00) or in the late afternoon (14.00–16.00) from the surface. A water volume of 6–8 L was sieved through a glass fiber filter (Whatman GF/F;

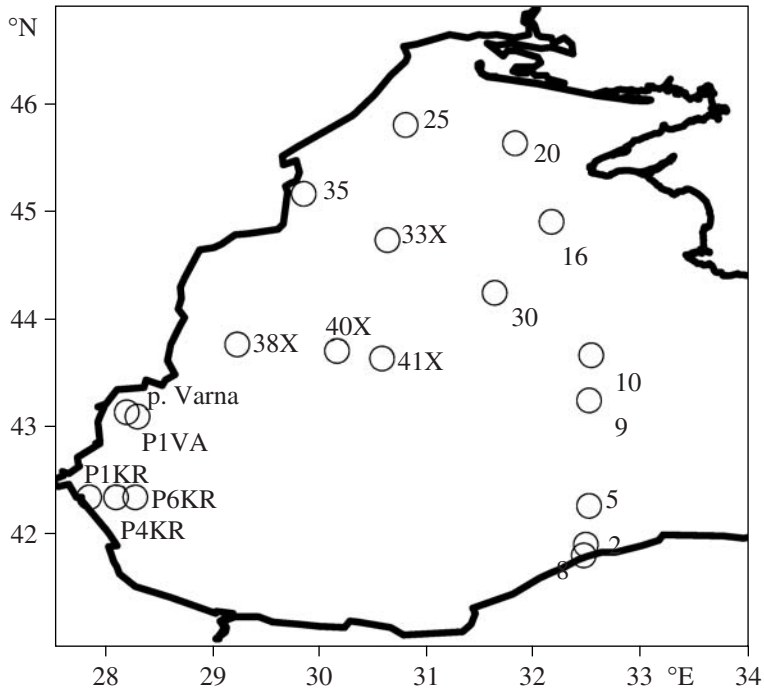

Fig. 1. The investigation sites.

47 mm diameter). The filtration was performed under low presuure (<0.1 atm) to avoid the breakage factor of the phytoplankton cells and thus to minimize their intrusion into the filtrate. The native sample was then diluted with the filtrate freshly obtained by a factor of dilution of 1.0, 0.75, 0.50, 0.25 and 0.10 in duplicates. The factor 1.0 means an undiluted sample, while the factor of 0.10 means the sample was diluted ten times with filtrate. The prepared solutions were then placed into polycarbonate bottles of 1–2 L volume, which were prewashed with 10% HCl and then with distilled water. The bottles were incubated for 24 hours on board, opened for the solar impact, and cooled down to 20°C by running pumped surface water of the same temperature. If the solar impact was more than 800 μE m^{-2} s, the bottles were shadowed to decrease the solar impact by 2–3 times. After the experiment ended, the water was filtered through GF/F filters and stored in liquid nitrogen until the measurement. The concentration of Chlorophyll *a* was determined by the fluorometric method described by standard international protocol [19]. The fluorometer calibration was performed using a Sigma Chemical Co Chlorophyll stock solution.

The phytoplankton growth rate was calculated under the daily increase of Chl *a* in the experimental bottles. The initial concentration of Chl *a* (Chl_0) was determined only for the undiluted samples, while, for the diluted samples, it was recalculated according to the dilution factor (DF) using the equation

$$Chl_0^D = Chl_0 \ DF. \quad (1)$$

The Chlorophyll concentration after the experiment (Chl_t) was determined for all the samples. However, one has to take into account that the final concenration of Chlorophyll in the bottles with diluted samples might be overestimated due to the pigment penetration to the filtrate used for the dilution. Small algae may penetrate through the filter ($Chl_{filtrate}$). However, this value did not exceed 1% in the pure filtrate after 24 hours of incubation under the same conditions during the present investigation. This value was taken into account in the final recalculations:

$$Chl_t^D = Chl_t - (1 - DF)Chl_{filtrate}. \quad (2)$$

The observed phytoplankton growth rate (μ_v) for each of the 5 dilution treatments was recalculated as

$$\mu_v = \ln(Chl_t^D/Chl_0^D). \quad (3)$$

The linear regression equations were recalculated to estimate the interrelations between the observed phytoplankton growth rate (μ_v), the recalculated (true) phytoplankton growth rate (μ) and the zooplankton grazing rate (g), as:

$$\mu_v = -gKP + \mu. \quad (4)$$

The taxonomic analysis of the nano- and microphytoplankton and the determination of its abundance and biomass. Water samples of 3–4 L volume were taken from the surface. The method of reverse filtration with nucleopore filters (pore diameter 2.5 μm) was used at most of the stations. The condenced samples were then fixed using a 1% formaldehyde solution

and were stored in darkness at 17–18°C for 20–30 days prior to the analysis. The abundance and linear size of the phytoplankton were determined for a subsample volume of 0.1 mL in 3–5 replicates under a light microscope (MBI-3).

The sampling of the phytoplankton along the Bulgarian coast was conducted by means of the down flux method. The samples were immediately fixed with a 4% formaldehyde solution and were stored in darkness in a cool place for 20 days prior to the analysis. The sunken particles were then concentrated to a 50 mL volume. The taxonomic analysis and linear size of the particles were then determined using a Sedjwick–Rafter camera under a light microscope (Olympus-40). The volume of the phytoplankton cells was recalculated according to their geometry. The taxonomic analysis was conducted according to [16, 33].

The mesozooplankton analysis. The zooplankton samples were taken using a Juday net (mouth opening diameter 36 cm; mouth opening square 0.1 m^2) on the Bulgarian coast. The total sampling was performed from the bottom to the surface. The freshly taken samples were fixed with a 4% formaldehyde solution. The zooplankton was sorted by the species and developmental stages using Bogorov's camera. The abundance of each species was later used to recalculate the biomass units using Chislenko nomograms [9, 13]. The taxonomic analysis was performed using [4, 5, 6].

The hydrochemical analyses and light intensity measurements. The standard methods were used to determine the concentrations of nitrates, nitrites, nitrogen, phosphates, and silicates in the sea water [19]. The bulk daily light intensity was recalculated after every hour of measurements of the solar intensity in the daylight period by means of a luxmeter (U-116). The transition coefficient of 10^4 = 200 μE m^{-2} sec [7] was used to transform the Lux units into the solar radiation intensity (PAR).

RESULTS

The phytoplankton biodiversity and Chl *a* concentration. The dominant species of phytoplankton observed during the priod of the investigations belonged to the diatoms (*Bacillariophyceae*). The Northwestern shelf diatoms contributed from 71.7 to 92% of the total nano- and microphytoplankton abundance, which was 83.7% on average. In the biomass units, they formed from 42 to 71% of the total biomass and 56.5% on average (Table 1). The dominant species were *Proboscia alata* (Brightw.) Sundström, *Pseudonitzschia seriata* (Cl.) H. Perg., and *Pseudosolenia calcar-avis* (M. Schultze) Sundstrom. This region was characterized by a relatively low concentration of Chl *a*: from 0.51 to 1.70 mg m^{-3}, 0.87 mg m^{-3} on average (Table 1). The only exception was found for station 35, which was situated in the Danube River Delta, where the diatoms were dominant by abundance (91.59%), but most of the biomass (64.9%) was formed by *Dinophyceae* species such as *Prorocentrum micans* Ehrenberg, *Protoperidinium* sp., and *Gymnodinium* sp., and the Chl *a* concentration reached up to 5.50 mg m^{-3}.

The most intensive development of the phytoplankton community was observed on the Bulgarian coast, where the Chl *a* concentration varied from 0.92 to 4.33 mg m^{-3} (2.09 mg m^{-3} on average) (Table 1). The diatom species abundance, which was mostly formed by *Cerataulina pelagica* (Cl.) Hend and *P. calcar-avis*, was on average 79.9% (57.4–88.7%) of the total nano- and microphytoplankton abundance. However, these species dominated by biomass only at single stations (PIVA, 38X). The *Dinophyceae* species were dominating at the other stations. These species were mostly represented by *P. micans*, *Dinophysis caudata* Kent, and *Lingulodinium polyedrum* (Stein) Dodge (Table 1). Their impact on the total phytoplankton biomass varied from 15 to 88% (56.7% on average).

In the Southern part of the investigation area on the Turkish coast, the impact of diatom species on the total phytoplankton abundance and biomass was maximal. The diatom abundance varied from 89.3 to 95.2% (92.4% on average); the biomass varied from 55 to 94% (80% on average). Only one species of *C. pelagica* was dominant at all of the stations, and the concentration of Chl *a* reached on average 4.19 mg m^{-3} and varied from 2.48 to 5.40 mg m^{-3}.

The deep-water region was also characterized by diatom species dominating (*C. pelagica, P. alata, P. calcar-avis*). Their impact on the total abundance varied from 41.1 to 86.7% (68.7% on average), and the impact on the total biomass was 72.6% on average (63–91%, Table 1). However, the Chl *a* concentration in this area was the lowest; it varied from 0.39 to 0.57 mg m^{-3} (0.49 mg m^{-3} on average) (Table 1).

The phytoplankton growth rate. The results concerning the phytoplankton growth rates and the zooplankton grazing rates obtained in the dilution experiments are presented in the Table 2. For each of the experiments, the linear regression equations were recalculated. These equations contain the observed phytoplankton growth rate (μ_B), which coordinates with the dilution factor (DF). The coefficient r^2 varied in the same value span of 0.50 to 0.96 for both the coastal and deep water regions, and the average values for these regions differed insignificantly.

The maximal phytoplankton growth rates were observed close to the Bulgarian coast and varied from 0.17 to 1.00 day^{-1} (0.53 day^{-1} on average (Table 1)). This region was characterized by relatively high concentrations of nitrites and silicates, and the average concentrations were 1.41 and 5.28 μM, respectively (Table 3).

The phytoplankton growth rates on the western shelf were approximately two times lower compared to those on the Bulgarian coast (on average 0.29 day^{-1}). The same values were observed for the deep water regions,

Table 1. The true phytoplankton growth rate (μ), zooplankton grazing rate (*g*), Chl *a* concentration (Chl), phytoplankton abundance (A, % of total) and biomass (B, % of total). The data are given for major phytoplankton groups

$\frac{A_{diatom}}{B_{diatom}}$	$\frac{A_{dinophyta}}{B_{dinophyta}}$	$\frac{A_{others}}{B_{others}}$	μ, day^{-1}	*g*, day^{-1}	Chl, mg m^{-3}	Dominant species
The Bulgarian coast (st. Varna, PIVA, PIKR, P4KR, P6KR, 38X)						
79.9 ± 10.9 $\frac{(57.4 – 88.7)}{48.5 ± 21.5}$ (35.0 – 84.0)	17.0 ± 14.5 $\frac{(11.0 – 41.5)}{50.8 ± 20.5}$ (15.0 – 65.0)	3.1 ± 2.7 $\frac{(0.6 – 8.1)}{0.8 ± 0.7}$ (0.0 – 2.0)	0.52 ± 0.37 (0.17 – 1.00)	0.32 ± 0.20 (0.10 – 0.60)	2.09 ± 1.29 (0.92 – 4.33)	*P. micans, D. caudata, L. polyedrym, P. calcar-avis, C. pelagica*
The North-Western Part (st. 16, 20, 25, 33X)						
83.7 ± 8.6 $\frac{(71.7 – 92.0)}{56.5 ± 13.0}$ (42.0 – 71.0)	14.0 ± 6.4 $\frac{(8.0 – 24.6)}{43.4 ± 12.9}$ (28.9 – 57.9)	2.3 ± 2.2 $\frac{(0 – 4.9)}{0.1 ± 0.2}$ (0.0 – 0.4)	0.29 ± 0.15 (0.03 – 0.42)	0.38 ± 0.2I (0.14 – 0.69)	0.90 ± 0.56 (0.51 – 1.70)	*P. alata, P. seriata, P. calcar-avis*
The Danube River Delta (st. 35)						
$\frac{91.6}{35.0}$	$\frac{8.3}{64.9}$	$\frac{0.1}{0.1}$	0.33	0.49	5.50	*P. micans, Gimnodinium* sp.*, Prototoperidinium* sp.*, P. seriata*
The Turkish coast (st. 0, 0, 2, 5)						
92.4 ± 2.9 $\frac{(89.3 – 95.2)}{80.0 ± 17.3}$ (55.0–94.0)	7.3 ± 4.1 $\frac{(4.8 – 11.1)}{19.9 ± 17.3}$ (5.8–44.9)	0.3 ± 0.2 $\frac{(0 – 0.6)}{0.1 ± 0.1}$ (0.0–0.2)	0.18 ± 0.12 (0.01 – 0.28)	0.41 ± 0.20 (0.15 – 0.61)	4.19 ± 1.24 (2.48 – 5.40)	*C. pelagica, Gymnodinium* sp.
The deep sea part (st. 9, 10, 30, 40X, 41X)						
68.7 ± 17.9 $\frac{(41.1 – 86.7)}{72.6 ± 15.3}$ (63.0 – 91.0)	30.0 ± 12.2 $\frac{(12.6 – 53.5)}{27.3 ± 15.3}$ (9.0 – 42.5)	1.3 ± 2.9 $\frac{(0 – 6.4)}{0.1 ± 0.2}$ (0.0 – 0.5)	0.29 ± 0.07 (0.10 – 0.60)	0.28 ± 0.19 (0.11 – 0.49)	0.49 ± 0.08 (0.39 – 0.57)	*P. alata, P. calcar-avis, C. pelagica*

Note: The numbers in brackets are the min-max values.

and the low nitrate concentration may be named as a major reason for such phenomenon. The nitrate concentration varied from 0.05 to 0.18 μM and was on average 0.11 μM in the Northwestern part and 0.13 μM in the deep-water area (Table 3).

The Turkish coast was characterized by both low nitrate and silicate concentrations and minimal phytoplankton growth rates: from 0.01 to 0.28 day^{-1} (0.18 day^{-1} on average).

The phytoplankton growth rates did not depend either on the phosphate concentration or on the nitrogen/phosphate ratio (Fig. 2c, 2f). In the meantime, the Michaelis–Menten equation nicely describes the relationship between the phytoplankton growth rate and the sum concentration of nitrates and nitrites (Fig. 2a, 2b). According to the recalculations, the coefficient of 50% saturation (K_s) for the nitrogen was 0.33 μM for the coastal areas and 0.30 μM for all the investigation area. The most part of the investigation area was characterized by lower values of K_s for nitrogen, and only for some stations along the Bulgarian coast and the Danube River Delta did they reach or even exceed K_s (Table 3).

The Michaelis–Menten equation was also applicable to describe the interrelationships between the phy-

toplankton growth rate and the dissolved silicon concentration (Fig. 2d, 2e). The K_s for the silicon in the coastal waters was 1.79 μM, whereas, for the whole western part, it was only 0.92 μM. The dissolved silicon concentration in the water reached or even exceed K_s only at several stations situated on the Northwestern shelf and along the Bulgarian coast (Table 3).

To assess the combined effect of the three main nutritive element concentrations (nitrogen, silicon, and phosphorus) on the phytoplankton growth rate, the multiple regression method was applied. The following equation was then obtained:

$$\mu = 0.430 Si^{0.297} N^{0.133} P^{0.026} \quad (r^2 = 0.70). \qquad (5)$$

As could be clearly observed, nitrogen and phosphorus were the major limiting factors in September–October 2005.

There was no evidence of any effect of solar radiation impact (14–34 μE m^{-2} day) on the phytoplankton growth rate for the whole period of the investigations (Fig. 3).

The zooplankton grazing rates. The zooplankton grazing rates varied from 0.10 to 0.69 day^{-1}; the average values differed by approximately 1.5 times for the different areas investigated (Table 1). The absolute values of the total biomass of the nano- and microzooplankton were mostly governed by the abundance of the large diatom *P. calcar-avis* (V = 60000–30000 μm^3). The increase in abundance of this algae significantly deceased the zooplankton grazing rate (Fig. 4).

The comparison of the average phytoplankton growth rates and the zooplankton grazing rates clearly indicates that only on the Bulgarian coast did the algae grow faster (μ_{mean} = 0.52 day^{-1}) than they were consumed by the zooplankton (g_{mean} = 0.32 day^{-1}). The deep water area was characterized by nearly the same values of these two parameters, 0.29 and 0.28 day^{-1}, respectively.

The zooplankton grazing rate (0.38 day^{-1}, on average) exceeded the phytoplankton growth rate (0.29 day^{-1},

Table 2. The experimental data on phytoplankton growth rates and zooplankton grazing rates in the surface waters of the Black Sea in September–October, 2005

Station	The linear regression equation	r^2
The Bulgarian coast		
pVrn	$\mu_B = -0.10$ DF + 0.29	0.50
P1V	$\mu_B = -0.20$ DF + 0.53	0.55
P1KR	$\mu_B = -0.60$ DF + 1.00	0.83
P4KR	$\mu_B = -0.55$ DF + 0.93	0.78
P6KR	$\mu_B = -0.18$ DF + 0.17	0.90
38X	$\mu_B = -0.30$ DF + 0.18	0.70
Mean		0.71 ± 0.16
The North-Western Part		
16	$\mu_B = -0.39$ DF + 0.35	0.64
20	$\mu_B = -0.69$ DF + 0.03	0.96
25	$\mu_B = -0.14$ DF + 0.42	0.77
33 X	$\mu_B = -0.28$ DF + 0.35	0.79
35	$\mu_B = -0.49$ DF + 0.33	0.77
Mean		0.77 ± 0.11
The Turkish coast		
0	$\mu_B = -0.39$ DF + 0.22	0.93
0	$\mu_B = -0.61$ DF + 0.28	0.69
2	$\mu_B = -0.49$ DF + 0.01	0.71
5	$\mu_B = -0.15$ X + 0.22	0.56
Mean		0.72 ± 0.15
The deep sea part		
9	$\mu_B = -0.49$ DF + 0.60	0.94
10	$\mu_B = -0.38$ DF + 0.10	0.57
30	$\mu_B = -0.11$ DF + 0.23	0.57
41X	$\mu_B = -0.12$ DF + 0.24	0.53
Mean		0.65 ± 0.19

Note: The linear regression equation appears as $-\mu_B = -g$ DF + μ, where μ_B observed growth rate, day^{-1}; g—zooplankton grazing rate, day^{-1}; DF—dilution factor; μ—true phytoplankton growth rate, day^{-1}.

Table 3. The concentration of major micronutrients (μM) in the investigated area

Area	PO_4	NO_3	NO_2	NH_4	Si	N
The Bulgarian coast	0.08 ± 0.07	1.41 ± 1.08	0.11 ± 0.09		5.28 ± 3.55	6
	(0.03 – 0.23)	(0.04 – 2.55)	(0.01 – 0.23)		(0.05 – 8.55)	
The North-Western Part	0.06 ± 0.05	0.11 ± 0.05	0.04 ± 0.04	0.13 ± 0.10	1.38 ± 2.03	4
	(0.02 – 0.14)	(0.05 – 0.18)	(0.01 – 0.09)	(0.04 – 0.26)	(0.30 – 4.43)	
The Danube River Delta (st. 35)	0.39	3.22	0.27	0.19	7.30	1
The Turkish coast	0.03 ± 0.02	0.14 ± 0.04	0.05 ± 0.01	0.28 ± 0.15	0.63 ± 0.39	4
	(0.02 – 0.05)	(0.09 – 0.18)	(0.04 – 0.06)	(0.08 – 0.43)	(0.45 – 1.09)	
The deep sea part	0.08 ± 0.08	0.13 ± 0.06	0.03 ± 0.02	0.12 ± 0.11	0.21 ± 0.16	5
	(0.02 – 0.18)	(0.06 – 0.18)	(0.01 – 0.05)	(0.05 – 0.30)	(0.09 – 0.40)	

Note: The numbers in brackets are the min-max values.

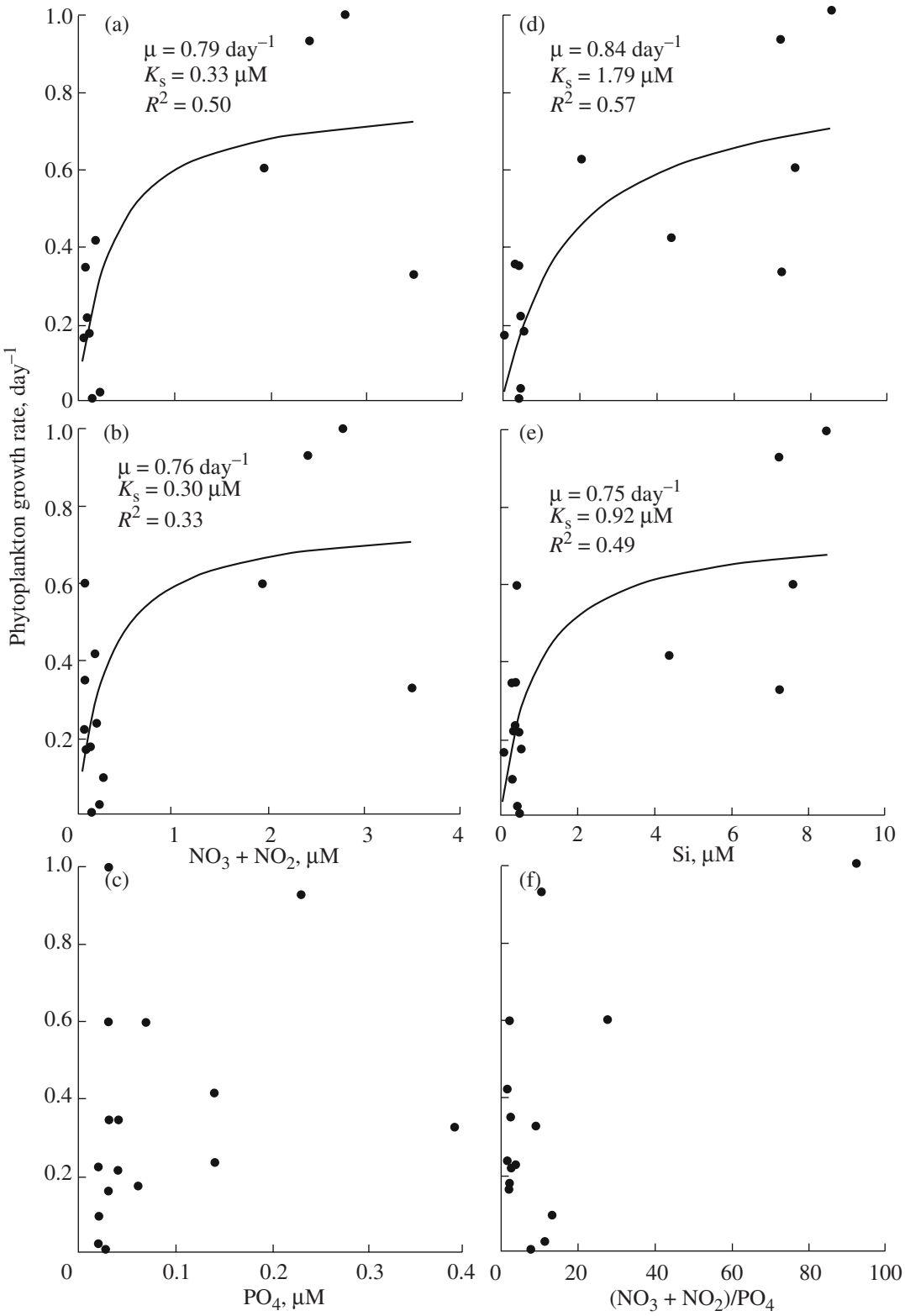

Fig. 2. The interrelationships between the phytoplankton growth rate and major micronutrients concentrations in the Black Sea: (a) and (d) ñ data for coastal waters; (b), (c), (e), (f) ñ data for all the investigated area.

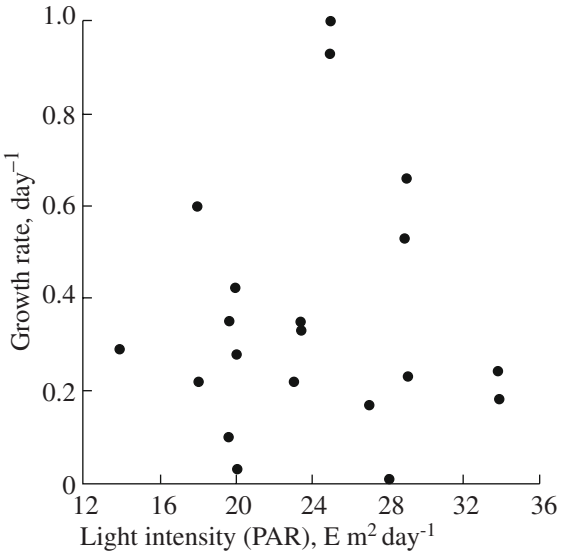

Fig. 3. The solar radiation impact to the phytoplankton growth rate.

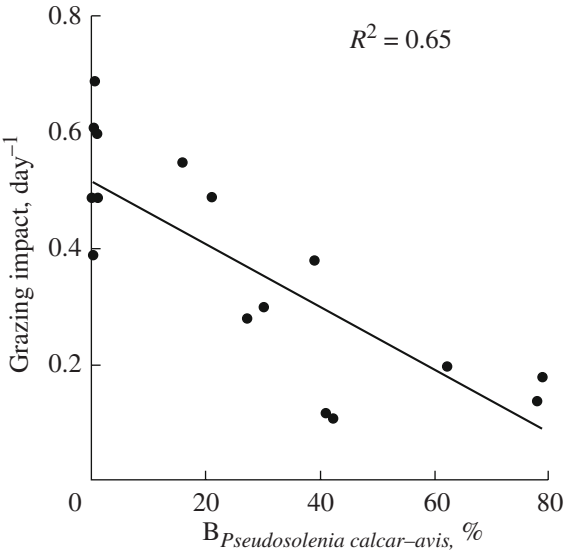

Fig. 4. The impact of relative biomass of *Pseudosolenia calcar-avis* to the zooplankton grazing rate on nano- and microphytoplankton.

on average) on the Northwestern shelf. Station 35 situated in the Danube River Delta was characterized by a high zooplankton grazing rate (0.49 day^{-1}), which exceeded the phytoplankton growth rate by 1.5 times.

Finally, on the Turkish coast, the zooplankton grazing rate (0.41 day^{-1}) exceeded the phytoplankton growth rate by 2.3 times (Table 1).

The zooplankton abundance and biomass. *Copepoda, Chaetognatha*, and *Meroplankton* were the dominating groups in the zooplankton along the Bulgarian coast. The maximum mesozooplankton abundance of 7564 ind m^{-3} was observed at the most shallow station (P3VA). The mimimal values of 2625 ind m^{-3} were obtained for the most distant station from the shore (P6KR, Table 4). The other stations were characterized by similar values from 4378 to 4893 ind m^{-3}. *Copepoda* had the greatest impact of more than 50% on the total abundance at every station.

As was observed for the abundance, the maximum biomass was also found at the shallow station P3VA (262.72 mg m^{-3}); however, the minimal one, which was 4 times less, was recalculated for the closest station (PIVA) (Table 4). *Chaetognatha* (18.12–74.63%, 51.14% on average) and *Copepoda* (17.10–76.83%,

Table 4. The mesozoolpankton abundance (A_{zoo}, ind m^{-3}) and biomass (B_{zoo}, mg m^{-3}) and relative impact of key zooplankton groups (%) along the Bulgarian coast

Station	Depth, m	Layer, m	$\frac{A_{zoo}}{B_{zoo}}$	$\frac{A_{copepoda},\ \%}{B_{copepoda},\ \%}$	$\frac{A_{chaetognatha},\ \%}{B_{chaetognatha},\ \%}$	$\frac{A_{meroplankton},\ \%}{B_{meroplankton},\ \%}$	$\frac{A_{other},\ \%}{B_{other},\ \%}$
P1VA	37	0–25	4752 / 88.69	52.88 / 38.64	2.17 / 34.84	36.98 / 19.28	8.06 / 7.24
P3VA	24	0–22	7564 / 262.72	58.47 / 24.45	7.09 / 62.58	32.18 / 10.94	12.03 / 22.97
P4VA	70	0–40	4723 / 217.48	67.14 / 17.10	11.22 / 74.63	7.58 / 4.71	3.56 / 8.27
P1KR	48	0–30	4983 / 114.87	73.62 / 31.24	3.92 / 55.11	15.88 / 5.26	6.58 / 8.39
P4KR	60	0–30	4378 / 144.77	53.79 / 20.46	6.35 / 61.55	23.92 / 11.16	15.94 / 6.83
P6KR	90	0–80	2627 / 225.17	78.45 / 76.83	5.18 / 18.12	9.90 / 1.81	6.47 / 3.24

34.79% on average) had the greatest impact on the total biomass.

DISCUSSION

The investigations were conducted in the period of the autumn phytoplankton bloom in the coastal waters of the Western part of the Black Sea. The bloom was found at most of the stations along the Bulgarian coast and at some stations of the Northwestern shelf and at the southern part of the Turkish coast. The diatoms were the mostly represented bloom algae. Their maximum impact on the total abundance (92.4%) and biomass (80%) of the phytoplankton was found along the Turkish coast. In the meantime, in the Danube River Delta and along the Bulgarian coast, some Dinophyta species also increased their presence.

The changes in the phytoplankton biomass over the time period are governed, on the one hand, by the difference between the phytoplankton growth rate and the zooplankton grazing rate and, on the other hand, by the rate of passive sinking of the phytoplankton particles [23]. Obviously, the incresing of the phytoplankton biomass is possible when the phytoplankton growth rate exceeds the zooplankton grazing rate. In September–October, 2005, this was observed only for the station along the Bulgarian coast. Additionally, higher nitrite/nitrate and phosphate concentrations were also determined for this area. These values exceeded the same obtained for the Turkish coast by 10 times. These high nutrient concentrations were the main reason for the increasing of the phytoplankton biomass. In contrast, the Turkish coast was characterized by high zooplankton grazing rates, which exceeded the phytoplankton growth rate by two times, and by extremely low concentrations of the most important nutrients (phosphates, nitrates, and silicates). The last could be treated as a sign of the final stage of the autumn phytoplankton bloom.

It is well-known that the light, temperature, and nutrient concentrations are the major factors governing the phytoplankton growth. The water temperature was optimal for the phytoplankton growth (about 20°C) in the period of the investigations. The values of the daily solar radiation were 3–6 times higher than the limit values for the phytoplankton growth (I_k) that were found for this area earlier [12]. Therefore, we assume the light was not the limiting factor. Also, the phytoplankton growth rate did not depend on the solar radiation during the investigation period. Besides that, the I_k values for the autumn period are about 10% of the solar radiation, and the same light intensity could be found at the depths from 10 to 25 m. Therefore, we assume the same growth rates for the phytoplankton inhabiting this water layer as for the surface algae.

The equations that describes the nutrient impact on the phytoplankton growth rates allow one to conclude that the last ones were mostly limited by nitrites/nitrates and silicates concentrations. The only exception was the stations along the Bulgarian coast, where the concentrations of these nutrients were higher than the coefficient of 50% saturation (K_s) and the phytoplankton growth was not limited. The low number of observation in the deep water area did not allow us to obtain the K_s for nitrogen and silicon for this region. However, a value of 0.18 μM for the nitrates was found for the same region and season in the previous studies [21]. The nitrates concentrations were lower than this value during the period of the present studies and so were the phytoplankton growth rates. The observed average values of K_s for the phosphates were sufficient or even exceeded the values obtained earlier [8].

Station 35 (the Danube River Delta) was characterized by the highest concentrations of phosphates (0.39 μM), nitrates (3.22 μM), and silicon (7.30 μM). However, the phytoplankton growth rate was quite low: about 0.33 day^{-1}, which is three times less than maximum values obtained. We tend to link this fact with the biomass dominating of some of the dinophyta species, such as *Gymnodinium* sp., *Protoperidinium* sp. and *P. micans*. These species are all characterized as mixotrophic ones; they use both organic and inorganic compounds to grow [31, 32]. In addition, it was proved experimentally that dinophyta species store ammonia in their cells, while diatoms tend to store nitrates [25]. The concentration of ammonia at station 35 was four times less than the K_s values obtained for the warm season for the Black Sea region close to Sevastopol [12]. This limitation, in addition to the organic compounds being limited, may negatively impact the phytoplankton growth rate.

It is widely accepted that the zooplankton grazing rate highly depends on the phytoplankton biodiversity, as well as on both the qualitative and quantitative food content. During the investigation period, the phytoplankton was represented mostly by microphytoplankton (>15 μm) and less by nanophytoplankton (2–15 μm). The impact of picophytoplankton (<2 μm), which is the main food source for the microzooplankton, was minor, about 10% of the total phytoplankton biomass [14]. The copepods are major consumers of microphytoplankton and "large" nanophytoplankton cells [1, 10, 24, 30]. The copepods dominated by abundance, and copepods and chaetognaths dominated by biomass along the Bulgarian coast in the period of the investigations. The chaetognaths are the major secondary consumers in marine ecosystems and feed mostly on copepods [20].

The copepods prefer the phytoplankton cells with an optimal linear size range of 10–40 μm [1, 10, 17, 24]. The colonial diatoms are the main food source for the copepods in the Black Sea during the spring phytoplankton bloom [10]. We argue for the regression between the zooplankton grazing rate and the total cell volume of the dominating phytoplankton species, even though the analysis of the data obtained did not allow

revealing such a relationship. However, the linear regression was significant for the relative abundance of the largest diatom *Pseudosolenia calcar-avis* (linear cell size up to 300 μm) and the zooplankton grazing rate. The increase of the relative abundance of this species negatively impacted the zooplankton grazing rate. As was shown by T.S. Petipa [10], this phytoplankton species is the only one that is not consumed by all the copepodit stages of *Calanus helgolandicus*.

Summarizing the results of the present investigation, we conclude that the phytoplankton growth rate was governed by the concentration of the essential nutriens, and the zooplankton grazing rate depended on the relative biomass of *P. calcar-avis* in the phytoplankton.

REFERENCES

1. E. G. Arashkevich and A. V. Drits, "Vliyanie razmera pishchevykh chastits na parametry zavisimosti skorosti potrebleniya ot kontsentratsii pishchi u kopepod - fitofagov roda Calanus," Okeanologiya **24** (4), 677–683 (1984).
2. T. M. Kondrat'eva, "Opredelenie sutochnoi produktsii fitoplanktona v Sevastopol'skoi bukhte," in *Pervichnaya produktsiya morei i vnutrennikh vod* (Izdatel'stvo Ministerstva vysshego i srednego obrazovaniya BSSR, Minsk, 1961), pp. 77–82 [in Russian].
3. A. S. Mikaelyan, D. A. Nesterova, and L. V. Georgieva, *Zimnee "tsvetenie" Nitzschia delisatula v otkrytykh vodakh Chernogo morya // Zimnee sostoyanie ekosistemy otkrytoi chasti Chernogo morya* (IO RAN, Moscow) [in Russian].
4. F. D. Mordukhai-Boltovskoi *Opredelitel' fauny Chernogo i Azovskogo morei (Protozoa, Porifera, Coelenterata, Ctenorhora, Nemertini, Nemathelminthes, Annelida, Tentaculata)* (Naukova dumka, Kiev, 1968), Vol. I, p. 423 [in Russian].
5. F. D. Mordukhai-Boltovskoi, *Opredelitel' fauny Chernogo i Azovskogo Morei (Arthropoda: Cladocera, Calanoida, Cyclopoida, Monstrilloida, Harpacticoida, Ostracoda, Cirriredia, Malacostraca, Decapoda)* (Naukova dumka, Kiev, 1969) [in Russian].
6. F. D. Mordukhai-Boltovskoi, *Opredelitel' fauny Chernogo i Azovskogo Morei (Arthropoda, Mollusca, Echinodermata, Chaetognatha, Chordata: Tunicata, Ascidiacea, Appendicularia)* (Naukova dumka, Kiev, 1972) [in Russian].
7. T. S. Parsons, M. Takahashi, and V. Hargrave, *Biological Oceanographical Processes* (Pergamon, New York, 1973)
8. A. V. Parkhomenko. *Pogloshchenie fosfatov mikroplanktonom v evfoticheskoi zone Chernogo i Sredizemnogo morei: Avtoref. dis. kand. biologicheskikh nauk: 03.00.18* (Sevastopol, 1988), Candidate's Dissertation in Biology, p. 17 [in Russian].
9. T. S. Petipa, "O srednem vese osnovnykh form zooplanktona Chernogo morya," Tr Sevastop. Biol. Stan **9**, 39–57 (1957) [in Russian].
10. T. S. Petipa, *Trofodinamika kopepod v morskikh planktonnykh soobshchestvakh* (Naukova dumka, Kiev, 1981) [in Russian].
11. Yu. I. Sorokin, I. N. Sukhanova, G. V. Konovalova, and E. V. Pavel'eva, "Pervichnaya produktsiya i fitoplankton raiona ekvatorial'noi divergentsii v vostochnoi chasti Tikhogo okeana," Tr IO AN SSSR **102**, 108–122 (1975) [in Russian].
12. L. V. Stel'makh, V. P. Gubanov, and I. I. Babich, "Sezonnye izmeneniya skorosti rosta i limitirovanie fitoplanktona pitatel'nymi veshchestvami v pribrezhnykh vodakh Chernogo morya v raione Sevastopolya," Morskoi Ekologicheskii Zhurnal **3** (4), 55–73 (2004) [in Russian].
13. L. L. Chislenko *Nomogramy dlya otsenki vesa vodnykh organizmov ispol'zuya razmer i formu tela* (Nauka, Leningrad, 1968), p. 107 [in Russian].
14. T. N. Churilova, Z. Z. Finenko, S. Moncheva, *et al.*, "Pogloshchenie sveta i maksimal'nyi kvantovyi vykhod fotosinteza v period osennego tsveteniya vodoroslei v zapadnoi chasti Chernogo morya," in *Problemy biologicheskoi okeanografii XXI veka: tezisy dokladov mezhdunarodnoi nauchnoi konferentsii (19-21 sentyabrya 2006 g., Sevastopol')* (EKOSI-Gidrofizika, Sevastopol, 2006), p. 135 [in Russian].
15. A. Calbet and M. R. Landry, "Phytoplankton Growth, Microzooplankton Grazing, and Carbon Cycling in Marine Systems," Limnol. Oceanogr. **49** (1), 51–57 (2004).
16. T. R. Carmelo, *Identifying Marine Phytoplankton* (USA: Academic Press, 1997) 858 p.
17. I. Gismervik, "Top-Down Impact by Copepods on Ciliate Numbers and Persistence Depends on Copepod and Ciliate Species Composition," J. Plankton Res. **28** (5), 499–508 (2006).
18. R. Goericke, "Top-Down Control of Phytoplankton Biomass and Community Structure in the Monsoonal Arabian Sea," Limnol. Oceanogr. **47** (5), 1307–1323 (2002).
19. JGOFS Protocols. Protocols for the Joint Global Ocean Flux Study (JGOFS) Core Measurements. Manual and Guides, 1994. V. 29. 100 p.
20. G. Kehayias, E. Michalondi, and K. Koutrakis, "Feeding and Predation Impact of Chaetognaths in the North Aegean Sea (Strymonikos and Lerissos Gulfs)," Mar. Biol. (Berlin) **85**, 1525–1532 (2005).
21. O. V. Krivenko, Z. P. Burlakova, and L. Y. Eremeeva, "Basic Characteristics of Biotic Nitrogen Cycle in the Open Western Part of the Black Sea," Ecosystem Modeling as a Management Tool for the Black Sea. Kluwer Academic Publishers, 121–136 (1998).
22. M. Latasa, M. Landry, L. Schlüter, and R. R. Bidigare, "Pigment Specific Growth and Grazing Rates of Phytoplankton in the Central Equatorial Pacific," Limnol. Oceanogr. **42** (2), 51–57 (1997).
23. L. Legendre, "The Significance of Microaigal Blooms for Fisheries and for the Export of Particulate Organic Carbon in Oceans," J. Plankton Res. **12**, 681–699 (1990).
24. P. V. Lehman, *Phytoplankton Biomass, Cell Diameter and Species Composition in the Low Salinity Zone of Northern* (Bay Estuary // Estuaries, San Francisco, 2000), Vol. 23.
25. M. W. Lomas and P. Glibert, "Comparisons of Nitrate Uptake, Storage, and Reduction in Marine Diatoms and Flagellates," J. Phycol **36**, 903–913 (2000).

26. M. R. Landry and R. P. Hassett, "Estimating the Grazing Impact of Marine Micro-Zooplankton," Mar. Biol. **67**, 283–288 (1982).

27. M. R. Landry, J. Kirshtein and J. Konstantinou, "A Refined Dilution Technique for Measuring the Community Grazing Impact of Microzooplankton, with Experimental Tests in the Central Equatorial Pacific," Mar. Ecol. **120** (1), 53–63 (1995).

28. E. Maraňón, "Phytoplankton Growth Rates in the Atlantic Subtropical Gyres," Limnol. Oceanogr. **50** (1), 299–310 (2005).

29. E. Maraňón and P. M. Holligan, "El Al. Basin-Scale Variability of Phytoplankton Biomass, Production and Growth in the Atlantic Ocean," Deep-Sea Res. **47** Part I, 825–857 (2000).

30. S. Schultes, P. G. Verity, and U. Bathmann, "Copepoda Grazing During An Iron-Induced Diatom Bloom in the Antarctic Circumpolar Current," J. exp. Mar. Biol. Ecol **338**, 16–34 (2006).

31. T. J. Smayda, "Harmful Algal Blooms: Their Ecophysiology and General Relevance To Phytoplankton Blooms in the Sea," Limnol. Oceanogr. **42** (5), 1137–1153 (1997).

32. D. K. Stoescer, "Mixotrophy Among Dinoflagellates," J. Eukaryotic Microbiology **46** (4), 397–401 (1999).

33. C. R. Tomas, *Identifying Marine Diatoms and Dinoflagellates* (Academic, New York, 1997).