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EXPERIMENTAL ARTICLES

Bacterioplankton of the Gdansk Basin, Baltic Sea

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Abstract—The numbers, biomass, and production of bacterioplankton were determined in the Russian Sector of the Gdansk Basin (Baltic Sea) in 2007–2009. Significant spatial and temporal variations were determined. During the year, bacterial activity increased with increasing water temperature and higher availability of organic substrates. The lowest bacterial production (0.01–31.63 mg C m^{-3} day^{-1}) was observed in late winter and late autumn, while the highest (0.17–341.70 mg C m^{-3} day^{-1}) occurred in spring and summer. Since bacterial numbers and biomass were found to depend on the weather conditions and the terrigenous inflow, significant variations were observed from year to year. The highest and lowest numbers and biomass of bacterioplankton determined in summer were 0.09–1.10 × 10^6 cells mL^{-1} and 2–22 mg C m^{-3} for July 2007 and 1.96–11.23 × 10^6 cells mL^{-1} and 23–123 mg C m^{-3} for July 2009. The values of these parameters were the highest along the coast and decreased towards the open sea.

Keywords: bacterioplankton, numbers, biomass, production, Gdansk Basin, Baltic Sea.

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The data on bacterioplankton of the Baltic Sea have mostly been obtained in the 1970s–1980s [1–10]. Intensified microbiological investigation during that period was associated with significant advances in the methods of investigating bacteria. In marine ecology, epifluorescence microscopy was originally used for determination of the numbers and biomass of bacterioplankton in 1973 [11]. Two major techniques were proposed for assessment of bacterial growth and production, namely dark $^{14}CO_2$ fixation [12] and the thymidine method [13]. Russian researchers used mostly the first approach, while the second was used in a number of laboratories worldwide.

The numbers of bacterioplankton in the Baltic Sea were found to vary from 0.1 to 6.4 × 10^6 cells mL^{-1} [8], while the upper value for microbial numbers observed in some eutrophic estuaries of the World Ocean exceeds 20 × 10^6 cells mL^{-1} [14]. Bacterial production in the Baltic Sea varied from 0.06–0.1 mg C m^{-3} day^{-1} in winter [6] to 50–165 mg C m^{-3} day^{-1} in summer [3, 15]. In other regions of the World Ocean, primary production varied from 0.4 to 153 mg C m^{-3} day^{-1} [16].

The Gdansk Basin is located in the southeastern part of the Baltic Sea, washing the shores of Poland in the south and Russia and Lithuania in the east (Fig. 1). Its water area is 22000 km^2. In the center of the basin, a 114-m depression is located, separated from the nearby Gotland depression to the north-west by the Gdansk–Gotland rift with the maximal depth of 86 m. Similar to the sea as a whole, the Gdansk Basin is subject to unfavorable effects of environmental factors, including the limited water exchange with the North Sea and the salinity and temperature barriers between the surface and near-bottom water. The latter hinder the water circulation and, in combination with significant production, facilitate development of extensive zones of anoxia in the near-bottom horizons of the depression. To a significant extent, the hydrological regime of the coastal part of the Gdansk Basin is determined by the flow of the rivers Vistula and Neman at the southern and northeastern parts of the basin, respectively [17]. Under favorable conditions, the discharge of the Vistula Lagoon and of the Pregola estuary via the Strait of Baltiysk may also be significant. Location of the water mass fronts in the estuaries and their effect on the biochemical processes in the upper seawater are variable. The penetration of the relatively fresh water along the eastern shore of the Gdansk Basin depends significantly on the wind force and direction.

The seasonal and spatial distribution of the parameters of bacterioplankton in the Russian part of the Gdansk Basin has been very poorly studied. Some measurements of bacterial numbers using erythrosine staining have been carried out [1, 2]. The goal of the present work was therefore to obtain reliable quantitative characterization of the numbers, biomass, and

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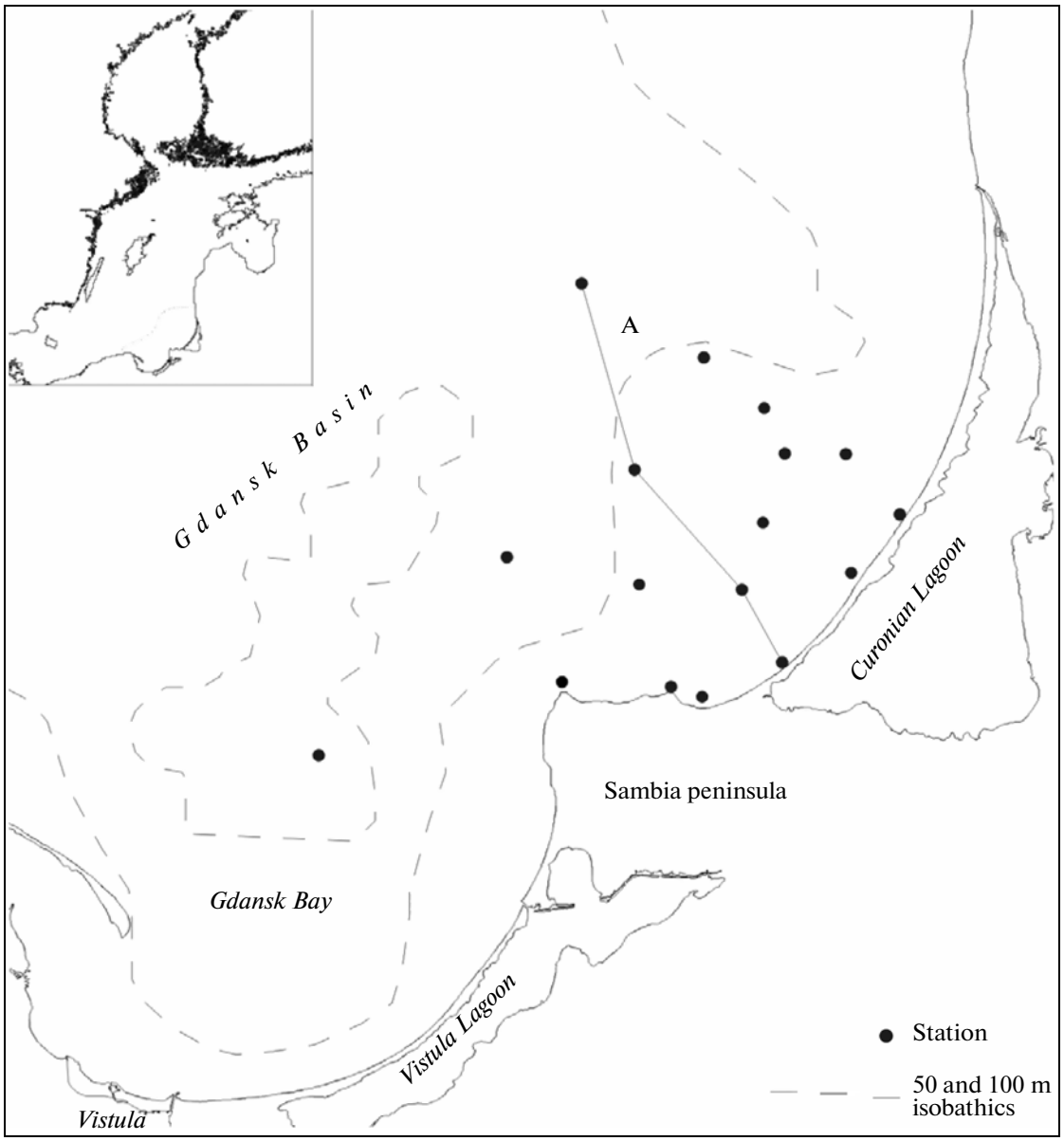

Fig. 1. Region of investigation and location of the stations. The section used for constructing the profiles of the vertical distribution of investigated parameters is marked as "A".

production of bacterioplankton in the Russian sector of the Gdansk Basin in different seasons using the standardized procedures.

MATERIALS AND METHODS

The material for investigation was obtained in the cruises of research vessels *Professor Shtokman* and *Shelf* in March (2007–2008), July (2007–2009), October 2007, and November 2008. In April–October 2010, monthly sampling was carried out along the northern shore of the Sambia peninsula and along the shore of the Curonian Spit.

The water was sampled with Rosette-mounted 5-L bathometers from the standard horizons of 0, 10, 30, 50–65 m (depending on the halocline depth), and from the near-bottom horizon. The samples for determination of bacterial numbers and biomass were fixed with formalin (4% final concentration). The fixed samples (0.8–5 mL) were filtered through black polycarbonate membranes (GE Water&Progress Technologies) with 0.22 μm pore diameter. Bacterial cells were enumerated and measured under an Axio Imager D-1 microscope (Carl Zeiss, Germany) at 1000× magnification. The filers were stained with acridine orange [11]. Cell volumes were calculated from their measurements as volumes of cylinders or spheres. The cor-

rection factor of 1.6 was used for the biomass calculation. For the calculation of biomass carbon from the wet weight values, 10% carbon content of wet biomass was assumed.

The rate of dark CO_2 fixation was determined by the radiocarbon method [12]. One hour after sampling, 0.1 mL of ^{14}C-labeled bicarbonate (1–5 μCi) was added into the vials. The samples were incubated for 24 h at close to in situ temperatures in an on-deck flow incubator or in a refrigerator at 4–8°C (for the samples collected from the depths with similar water temperature). The samples were filter through nylon filters (Katehol Khrom, Russia, 0.22 μm pore diameter). Radioactivity was measured in a Rackbeta scintillation counter (Sweden). The values of dark $^{14}CO_2$ assimilation were accepted for 6% of bacterioplankton production. The primary production of phytoplankton was determined by the radiocarbon method as described in [18].

The hydrochemical analyses were carried out using the standard methods [19]. Mineral nitrogen was determined as a sum of the individual forms of inorganic nitrogen: $N_{min} = NO_3^- + NO_2^- + NH_4^+$. Since 2008, organic forms of nitrogen and phosphorus were determined as the differences between the bulk concentrations and the concentrations of the mineral forms: $N_{org} = N_{bulk} - N_{min}$ and $P_{org} = P_{bulk} - PO_4^{3-}$. Oxygen concentrations were determined by the Winkler method [19]. Chlorophyll concentration was measured according to the standard procedure [20].

RESULTS

Hydrophysical conditions during the sampling period. In early March 2007, the surface temperature varied within a relatively broad range from 1.4 to 3.6°C. The coldest surface water spread from the northeast along the Curonian Spit. In March 2008, the temperature and salinity in the upper layer (to 68–80 m) were highly uniform throughout the sampling region. In the upper layers of the open sea, the temperature was high for that season (4.2–4.3°C), probably as a result of the unusually warm winter. The least saline waters were found close to the northern shore of the Sambia peninsula.

During spring–summer (April–May), the upper homogeneous and cold intermediate layers were formed. In June 2007, the temperature of the upper layer (to 10 m) was the lowest during the period of observation (14–16°C). In 2008, the upper quasi-homogeneous layer (~17°C) spread to the depth of ~15 m. Unlike 2007, in 2008, according to the geophysical data, desalination of the coastal waters resulted from withdrawal from the Vistula Lagoon under the favorable effect of the southwestern winds. In July 2009, the temperature of the surface water was the highest (18–21°C), with the thermocline at 18–20 m. Extensive rain showers preceding the investigation contributed to desalination of the coastal wasters (5.95–6.5 psu).

By the sampling time in October–November 2007–2008, autumnal stratification developed, with the upper mixed layer to the depths of 50–70 m. The autumn of 2008 was warmer, so that the water temperature was relatively high (9.5–10°C). Northeastern wind prevailed in October 2007, while the western one was predominant in November 2008.

Numbers and biomass of bacterioplankton. Under different hydrometeorological conditions, the numbers and biomass of bacterioplankton varied significantly.

Both the highest and lowest values were obtained in summer. In July 2007 (Tables 1, 2), the number and biomass were $0.09–1.10 \times 10^6$ cells mL^{-1} and 2–22 mg C m^{-3}, while in July 2009 the values were as high as $1.96–11.23 \times 10^6$ cells mL^{-1} and 23–123 mg C m^{-3}, respectively.

In the seasonal dynamics, these parameters increased gradually from winter to summer and then decreased again. Bacterial numbers and biomass were usually higher along the shores of the Sambia peninsula and Curonian Spit and decreased towards the open sea (Fig. 2). In July 2007 and 2008, as well as in October 2007, the distribution of bacterioplankton number and biomass was different. The values lower than those for the open sea surface waters were found along the Curonian Spit and adjoining part of the Sambia peninsula.

The vertical distribution of bacterial numbers and biomass within the upper mixed layer down to the thermocline (in summer) or halocline (in autumn and winter) was in general similar to their distribution at the surface. During summer, in the cold intermediate layer between the thermocline and halocline, bacterial number and biomass were lower than in the upper and lower water layers (Fig. 3). In the near-bottom horizon, both the number and the biomass were higher than in the upper horizon. The measurement made in June 2007 in the near-bottom layer of the deepest part of the water area yielded an exceptional result: it was the lowest value of bacterial numbers throughout the period of observation (0.09×10^6 cells/mL).

Three morphological forms of bacteria prevailed in all samples: mainly cocci and rods, with vibrios in a slightly lesser number. Filaments, closed and open rings, and other curved forms occurred very rarely. For bacterioplankton in the studied sector of the Baltic Sea, cell volumes varied from 0.05 to 0.47 μm^3, with the average values for different stations and depths varied from 0.09 to 0. 24 μm^3 (Tables 1, 2). The cells from the surface horizon of the open sea were usually somewhat larger than in the coastal area and deeper water layers. In the near-bottom horizons of the deep stations (over 60–70 m) of the Gdansk Basin, where hydrochemical analysis revealed a drastic decrease in

Table 1. Seasonal variations of the average values of bacterioplankton parameters and environmental factors for the coastal stations with depths less than 20 m

Date	Layer	T	S	BN	BB	V_{cell}	DF	P/B	O_2	PO_4^{3-}	P_{org}	N_{min}	N_{org}	PP	Chl *a*
3–5 March 2007	0-bottom	2.1	7.3	6.30	132	0.21	0.1	0.02	13.6	22	–	132	–	10	1.0
13–15 March 2008	0-bottom	4.3	6.9	1.65	34	0.21	–	–	13.2	18	27	140	284	80	13.3
21–22 April 2009	0-bottom	4.9	7.3	4.35	38	0.09	–	–	13.9	2	27	51	610	–	9.7
20–21 May 2009	0-bottom	11.0	7.2	5.35	48	0.09	1.1	0.42	10.6	2	23	34	444	52	2.8
17–18 June 2009	0-bottom	13.8	7.0	5.63	61	0.11	1.6	0.45	10.5	3	26	17	452	153	4.5
2–5 July 2007	0-bottom	15.6	7.1	0.64	13	0.20	3.8	5.50	8.9	12	–	39	–	129	3.5
7–9 July 2008	0-bottom	17.5	7.0	2.74	48	0.16	2.4	1.05	10.4	6	19	18	378	161	5.7
12–14 July 2009	0-bottom	19.0	6.1	8.72	79	0.09	4.5	1.01	10.5	5	26	35	512	204	7.4
25–26 August 2009	0-bottom	18.9	7	3.62	35	0.10	1.3	0.66	9.3	6	24	48	412	87	3.0
7–8 October 2009	0-bottom	12.8	6.8	4.00	41	0.10	0.2	0.09	10.2	13	27	55	394	105	6.8
27–30 October 2009	0-bottom	10.2	7.1	4.64	46	0.10	0.3	0.23	11.2	11	23	81	380	10	2.9
10–15 November 2008	0-bottom	8.4	7.2	2.24	27	0.12	0.3	0.16	11.8	20	21	72	300	25	5.7

Note: T is temperature, °C; S is salinity, ‰; BN stands for bacterial number, 10^6 cells mL^{-1}; BB is bacterial biomass, mg C m^{-3}; V_{cell} is the average cell volume, μm^3; DF is dark CO_2 fixation mg C m^{-3} day^{-1}; P/B is a coefficient, day^{-1}; PP is primary production, mg C m^{-3} day^{-1}; O_2, PO_4^{3-}, P_{org}, N_{min}, N_{org}, and Chl are the concentrations of oxygen, mineral and organic phosphorus, mineral and organic nitrogen, and chlorophyll *a*, mg/L.

Table 2. Seasonal variations of the average values of bacterioplankton parameters and environmental factors for the open sea stations

Date	Layer	T	S	BN	V_{cell}	BB	DF	P/B	O_2	PO_4^{3-}	P_{org}	N_{min}	N_{org}	PP	Chl *a*
3–5 March 2007	0–10 30–80	2.9 4.2	7.4 8.6	1.74 1.46	0.22 0.22	37 32	0.1 0.1	0.04 0.05	13.4 10.1	16 30	–	95 87	–	10	0.6 0.4
13–15 March 2008	0–10 30–80	4.2 4.3	7.5 7.7	0.80 0.76	0.24 0.24	21 21	–	–	12.8 11.4	20 27	9 9	64 93	183 236	24 –	2.1 1.4
2–5 July 2007	0–10 30–80	15.1 8.1	7.3 7.7	0.78 0.58	0.20 0.20	16 7	2.4 0.5	2.87 1.48	10.2 8.9	6 17	–	20 32	–	152	3.8 0.8
7–9 July 2008	0–10 30–75	17.5 7.4	7.0 7.6	2.74 1.22	0.19 0.15	48 18	2.9 1.0	1.05 1.09	10.4 9.4	6 19	19 11	18 45	378 284	172	7.1 0.6
12–14 July 2009	0–20 30–65	16.5 9.0	7.1 7.3	5.13 3.03	0.13 0.12	65 36	5.2 1.4	1.25 0.72	10.5 9.0	4 17	16 9	25 45	379 281	117	3.3 1.3
21–27 October 2007	0–10 30–75	13.3 12.0	7.4 7.8	1.08 1.06	0.20 0.20	22 21	0.5 0.7	0.42 0.63	9.9 8.7	10.8 17	–	37 74	–	16	1.4 1.0
15–10 November 2008	0–10 30–65	9.8 9.3	7.4 7.5	0.98 0.99	0.13 0.16	13 10	0.2 0.2	0.28 0.43	11.4 10.9	12 16	10 9	47 63	294 267	16	2.5 2.1

Note: Designations are as in Table 1.

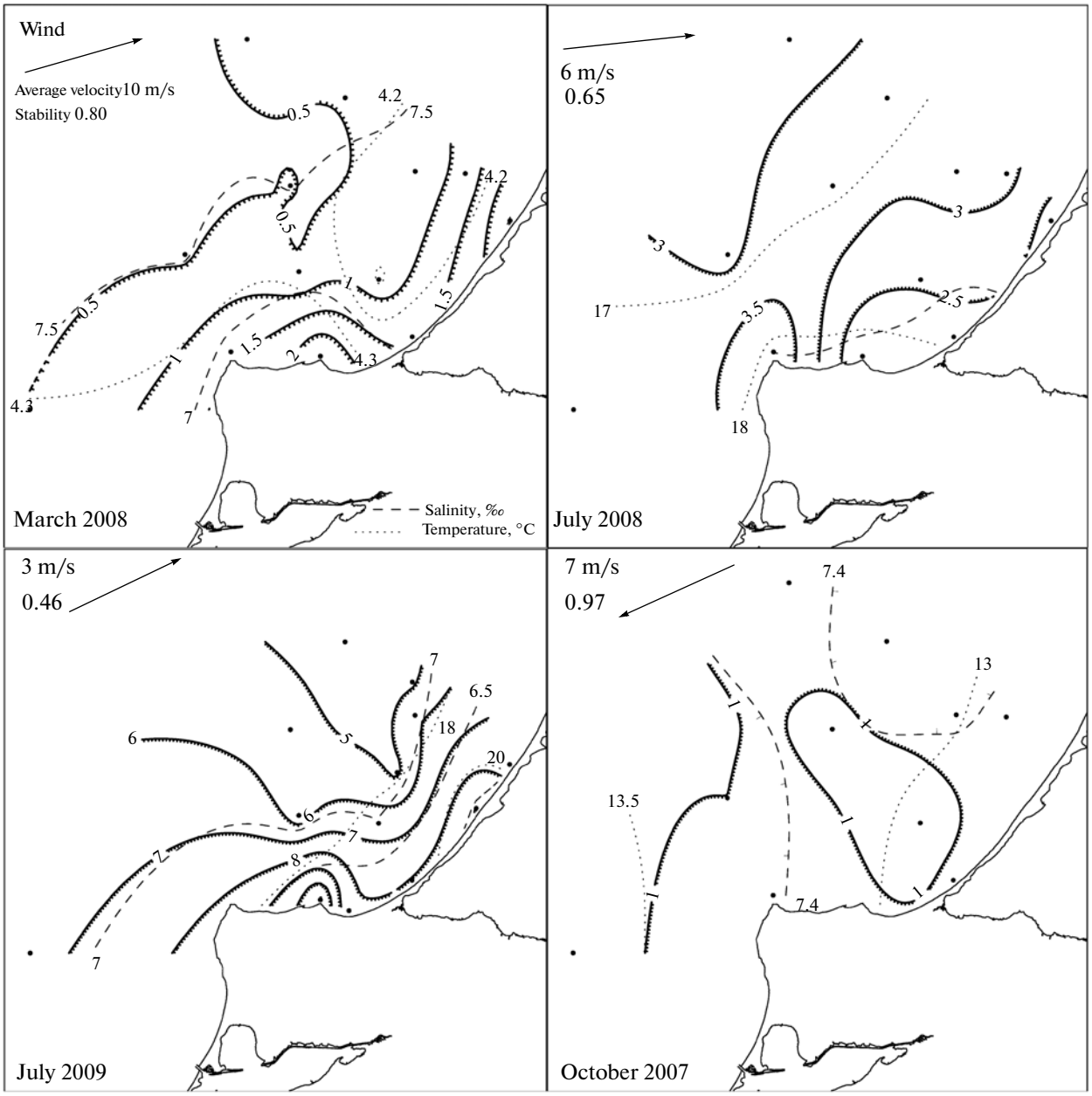

Fig. 2. Bacterioplankton number (10^6 cells/mL) in the surface layer and the distribution of salinity and temperature. The arrow marks the progressive vector (wind).

oxygen concentrations, a certain increase in abundance of the filamentous forms was observed.

The rates of dark CO_2 fixation (DF) in the photic layer varied from the level at the threshold sensitivity of the method to very high values, sometimes up to 11.8 and 20.6 mg C m^{-3} day^{-1}. In summer, DF values in the layer below the photic zone and above the halocline (65–80 m) were lower than at the surface, varying from 0.01 to 2.5 mg C m^{-3} day^{-1}. Elevated DF values were more often observed along the Curonian Spit shore, rather than in the open sea.

Similar to bacterial production calculated from the DF values, specific productivity of bacterioplankton (P/B coefficient, day^{-1}) increased from winter to summer and then decreased again. By the end of winter, the P/B ratios were the lowest throughout the period of investigation (0.01 to 0.09). Their vertical distribution within the well-mixed upper layer was uniform, as was the spatial distribution. A tendency for an increase of

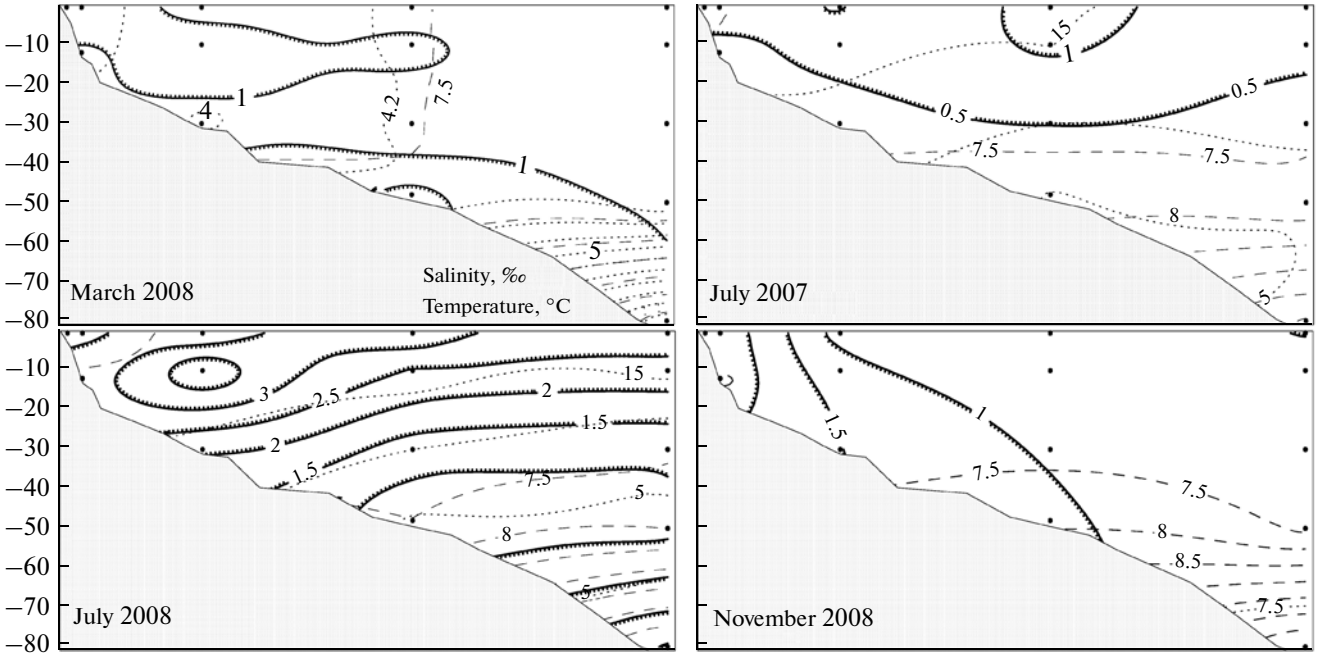

Fig. 3. Bacterioplankton number (10^6 cells/mL) along the section "A" and the distribution of salinity and temperature.

P/B coefficients with depth and in the direction from the coast into the open sea was observed in October–November. Such distribution is in agreement with the patterns of decrease in water temperatures throughout autumn [21]. The range of P/B values was from 0.01 to 3.08 (at the depth of 75 m).

The distribution of the P/B coefficients within the water column in summer was uneven, with the higher values usually observed at the surface, in the thermocline zone, and in the near-bottom horizon of the medium-deep stations (60–70 m). In June 2007, specific productivity along the Curonian Spit shore was as high as 5, the value considered the uppermost limit for eutrophic waters [12]. At the remainder of the sea area, P/B coefficients were generally close to the values measured in July 2008 and 2009 (0.13–3.79).

Bacterial growth is usually considered to depend primarily on the temperature and the presence of available organic substrates. Linear equations of the rates of DF by bacterioplankton depending on temperature ($R_2 = 0.45$) and the rate of photosynthesis ($R_2 = 0.56$) were obtained for the Gdansk Bay during the vegetation period. The highest relation between the activity of bacterioplankton and temperature ($R^2 = 0.74$), primary production ($R^2 = 0.73$), and chlorophyll concentration ($R^2 = 0.71$) was observed for the data collected during the period from March to July (Fig. 4). Weak relation was found between DF and the levels of mineral nitrogen ($R^2 = 0.36$) and phosphorus ($R^2 = 0.20$), while DF was found not to depend on the concentrations of their organic forms. However, bacterioplankton numbers were found to depend moderately from the concentrations of organic nitrogen ($R^2 = 0.49$) and phosphorus ($R^2 = 0.51$) (Fig. 5).

DISCUSSION

Our data on bacterioplankton numbers in the Russian part of the Gdansk Basin were comparable to those available on its Polish part (Table 3) [22–24] and somewhat lower than the results for other regions of the Baltic Sea [1–10, 25]. Although the differences from the earlier works in bacterioplankton numbers may be explained by annual variations, they may be primarily due to the changed procedure of enumeration of bacterial cells. Fluorochrome-stained, brightly fluorescent cells against the dark background and less brilliant detritus particles are easier discernable than erythrosine-stained cells counted under a light microscope.

Our values of the maximal bacterioplankton production (197–341 mg C m^{-3} day^{-1}) were higher than the results of the measurements of bacterial production by the radiocarbon method carried out in the central Baltic Sea in summer 1987 (91–165 mg C m^{-3} day^{-1}) [1, 3].

Our data may be compared with the few available literature sources on bacterial production in the Gdansk Bay and other Baltic sites. Bacterial production at 500–800 m from the Gdynia and Sopot shores was measured in February, April, May, August, and October 1997 [23]. The highest rate determined by the thymidine method was observed in May (78 mg C m^{-3} day^{-1}). This is twice the value for bacterial

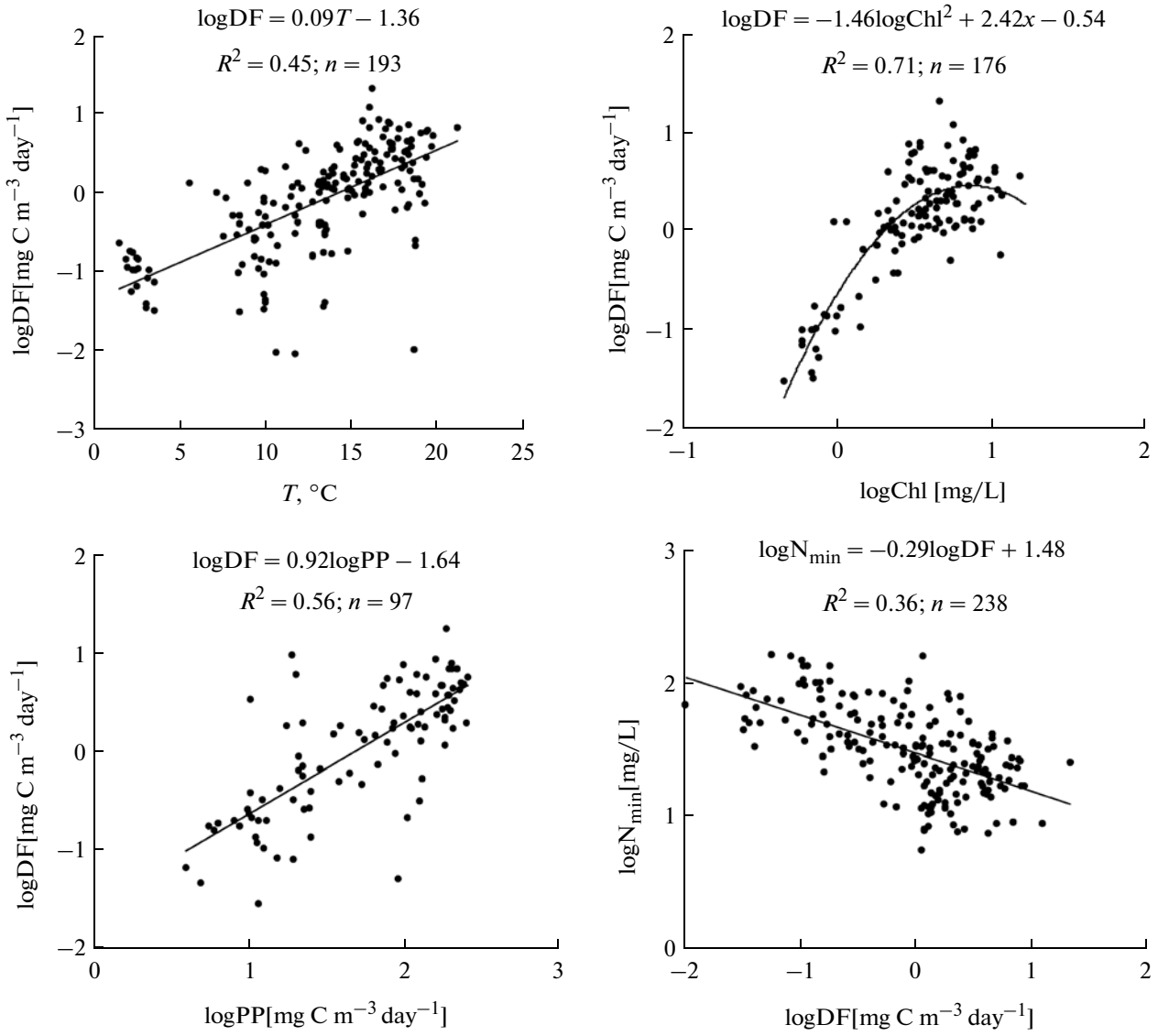

Fig. 4. Dark CO_2 assimilation (DF) depending on temperature (T), average weighted primary production (PP), and chlorophyll *a* concentration (Chl), as well as correlation with the concentration of mineral nitrogen (N_{min}).

production in this month close to the shore (34.3 mg C m^{-3} day^{-1}). The levels of bacterial production determined by the Polish researchers in February and October 1997 were similar to those found in the present work for March 2007, early October 2009, and November 2008 (~1–10 mg C m^{-3} day^{-1}). In August and late October 2009, however, we observed higher values (up to 37.6 mg C m^{-3} day^{-1}). In the cited work, the levels of bacterial production and growth efficiency were found to be very low for the highly trophic water body. Elevated bacterial production was revealed in December and August. In another publication on the Gdansk Bay [26], materials of five expeditions (1996–2001) were used for analysis and the highest weighted average value of bacterial production for the photic layer was revealed (40 mg C m^{-3} day^{-1}).

In other parts of the Baltic Sea, both bacterial numbers and production (as determined by the thymidine method) were lower than in the Gdansk Bay. For example, in the Bay of Pomerania located in the southern part of the sea, opposite to the Oder estuary, bacterial production at the depth of 2 m measured in May 1997 and July 1996 varied from 0.8 to 26.7 mg C m^{-3} day^{-1}. Bacterial production in the central Baltic Sea and the Gulf of Finland was 1.7–15.3 mg C m^{-3} day^{-1} in late summer 1987 and 1988 [6] and 17.8–24.6 mg C m^{-3} day^{-1} in 1992 [10], while the summer maximum in the Kiel Bay did not exceed 7.2 mg C m^{-3} day^{-1} [7]. Moreover, bacterial production in the hypereutrophic Gulf of Riga in summer was reported to be equal to the primary production [15], with the average values of bacterial production for the

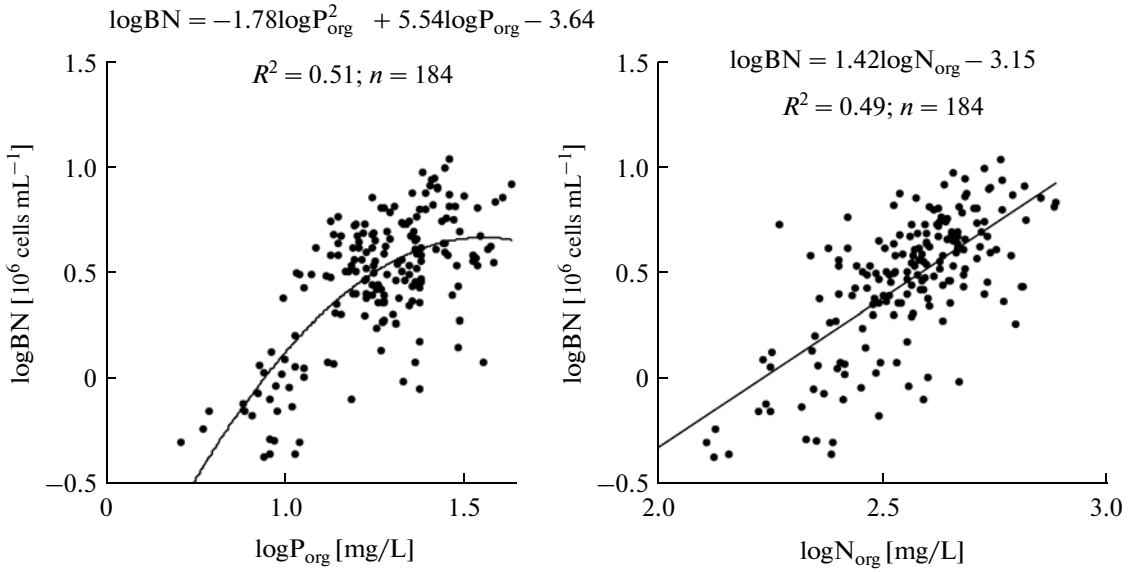

Fig. 5. Bacterial number (BN) depending on organic forms of phosphorus (P_{org}) and nitrogen (N_{org}).

28-m layer from 7 (in spring) to 80 mg C m^{-3} day^{-1} (in midsummer).

Importantly, these works, apart from the monthly measurements in the Kiel Bay during 1.5 years [7] and in the Gulf of Finland [10], were short-term ones, with the seasonal dynamics of bacterioplankton discussed using the data of the previous years. From this point of view, our data exhibit higher variation, since they were obtained by regular sampling during three years.

Comparative experiments for determination of bacterial primary production by dark CO_2 assimilation and the thymidine and leucine methods have been

Table 3. Total bacterial numbers in the upper layer of the Gdansk Basin in different years and seasons according to various authors

Region	Sampling time	Number, 10^6 cells mL^{-1}	Horizon	Source
Coastal part of the Gdansk Bay	July–August 1983, June 1984	1–4.2*	0–10 m	[2]
Gdansk Bay	May 1991–October 1993	0.30–8.40	Surface	[22]
	April–October 1993	1.20–3.80	Surface	[23]
	March–December 1997	1.54–4.25	Surface	[22]
Coastal part of the Gdansk Bay	July–August 1983, June 1984	0.5–4*	0–10 m	[2]
Gdansk Basin	December 1999–January 2000	0.1–0.15*	0–20 m	[1]
	March 2007–October 2009	0.42–11.23	0–20 m	Our data
Gdansk Basin	July–August 1983	0.3–4.5*	0–10 m	[2]
	March 1987–June 1988	3.36–5.15	0–15 m	[22]
	March–November 1989	2.56–6.11	0–10 m	[22]
	October 2002	1.90; 4.08	Surface	[24]
	March 2007–October 2009	0.45–7.3	0–20 m	Our data
Gdansk Basin	July–August 1983	0.5–3.0*	0–10 m	[2]
	September 1987	3.69	Surface	[6]
	March–November 1993	1.2–7.7	Surface	[22]
	March 2007–October 2009	0.38–6.6	0–20 m	Our data

Note: Erythrosine staining was used for enumeration of bacterial cells on the filters.

carried out only for the water of Lake Baikal [27]. In the uppermost layer, the production determined by dark CO_2 fixation was twice as high as the values obtained by two other methods. On the contrary, for deeper layers (10–100 m), the production determined by the leucine method was 1.5–2.5 times higher than that determined by two other methods. The thymidine method yielded the lowest values of bacterial production. Importantly, contradictory evidence exists in the literature on the comparison of the leucine and thymidine methods, both of which (as well as the radiocarbon one) involve conversion factors, which vary within significantly wide ranges [13, 27, 28]. Many researchers agree that additional investigation on the calibration of the major methods of assessment of bacterial production is required. We therefore consider the radiocarbon method useful for comparison of the values obtained by different methods, which increases the overall reliability of analysis.

It can be seen from the regression equation that bacterial production generally increased with increasing water temperature. A somewhat decreased effect of temperature on bacterial production at elevated water temperatures is probably associated with an increase in available organic substrates [26]. Inclusion of the results obtained during autumn resulted in a somewhat less pronounced dependence.

In marine ecosystems, heterotrophic bacteria have two sources of organic matter, excreta and remains of the phyto- and zooplankton and organic matter of terrigenous origin. The role of the autochthonous source is confirmed by the correlation between DF and the concentration of chlorophyll *a*. The equations obtained in the present work are characterized by a higher coefficient of determination (1), especially when using the data for the first half of the year (2), than a similar equation for the Polish part of the Gdansk Basin (3) [26]. In these equations, the variables are almost the same, while the difference between the free terms is almost twofold. This may result from higher scattering of observed values due to a larger database (especially for autumn) and/or from the more variable conditions in the Russian sector of the basin. Decreased dependence of bacterial production from temperature, chlorophyll content, and photosynthesis rate in the analysis involving the data from the autumn period may be explained by the fact that during the second part of the year the planktonic community relies significantly on the previously accumulated energy.

$$\log DF = 0.92 \log PP - 1.64 \ (R^2 = 0.56; n = 97), \quad (1)$$

$$\log DF = 0.94 \log PP - 1.62 \ (R^2 = 0.73; n = 70), \quad (2)$$

$$\log BP = 0.91 \log PP - 0.90 \ (R^2 = 0.56; n = 69), \quad (3)$$

where PP and BP stand for the primary production and bacterial production, respectively.

Unlike the Polish part of the Gdansk Basin, bacterial production in the Russian sector was not found to depend on the content of organic nitrogen and phosphorus species. High correlation in the Polish sector [26] resulted from the discharge of Vistula, the second largest river flowing in the Baltic Sea. Its yearly water flow is ~30 km^3 [23], containing 111.5×10^3 and 6.6×10^3 t of bulk nitrogen and phosphorus, respectively. A significant part of the easily degradable organic matter (OM) is mineralized in the Gdansk Bay. Dilution of the river water with seawater results in the allochthonous OM becoming less available to bacteria. In the water area studied, the autochthonous source is therefore more convenient for utilization by bacterioplankton during the second half of the vegetation period.

Relatively high abundance of bacteria was observed in winter, although the processes of production and destruction were slow at low water temperatures. This was probably associated with the stable OM accumulated during summer due to excessive primary production or brought with currents from other regions and by the coastal flow. High coefficients of determination for bacterial numbers and organic species of nitrogen and phosphorus resulted mostly from the analysis of the late winter and autumn data. This suggestion is supported by the more pronounced dependence of bacterial numbers from organic phosphorus, since "old" OM is known to be phosphorus-poor [12].

Allochthonous OM probably arrives into the investigated part of the Gdansk Basin by alongshore transfer of desalinated water from the Vistula estuary in its southern part. This agrees with the general scheme of the circulation of the Baltic Sea upper layer determined by the prevalence of western winds in moderate latitudes. The hypereutrophic Curonian Lagoon may act as a source of OM under continuous northern wind. Terrigenous inflow is the third possible source of OM. The elevated bacterial numbers at the northern shore of the Sambia peninsula in March 2008 most probably resulted from arrival of additional dissolved and suspended organic matter from the land. The least saline waters were found close to the shore at the sites of inflow of the numerous small rivers. A general decrease in bacterioplankton numbers with increasing salinity is evident from Fig. 6.

The favorable effect of stirring-up of the bottom sediments by storm winds on bacterial cell number was described, for example, for the near-bottom water layer (3 m above the bottom) in the Kiel Bay [9]. Our findings, however, indicate an opposite dependence for the Russian sector of the Gdansk Basin (Fig. 7). Under strong wind, bacterial numbers decreased more significantly in the open sea than in the coastal areas. Bacterioplankton number was higher at the western wind. When the wind was northern or eastern, cell numbers decreased, probably as a result of uplifting of deep water less rich with microbial cells due to the upwelling along the Curonian Spit [29]. Comprehensive investigation in the Vigo Bay (Spain) revealed that "moderate" upwelling provided for an increase in bacterial abundance, while the "strong" one resulted in its decrease [30].

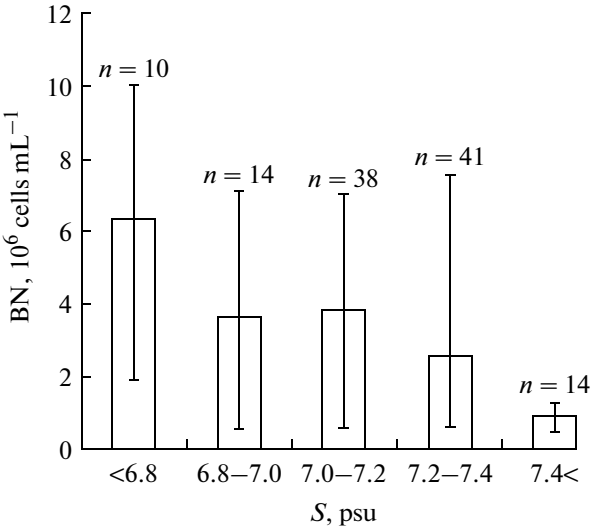

Fig. 6. Bacterial number (BN) depending on salinity (*S*) within the 0–20 m layer.

To conclude, significant year-to-year variability of the parameters of bacterioplankton should be noted. The summer samples collected in about the same time in July for three years are especially demonstrative, with each subsequent value of bacterial number, biomass, and production was higher than the previous ones. On the contrary, the efficiency of bacterial production decreased with increasing biomass. The anomalously low number and biomass of bacteria in 2007 resulted from a combination of factors, such as low water temperature, predominance of strong and fresh eastern winds, and the onset of the summer phytoplankton "bloom" probably postponed by cold weather. The high P/B coefficients (0.68–3.70) therefore resulted from the exponential growth of bacteria, simultaneously with the increase in primary production. Enormous efficiency of bacterial production along the shore of the Curonian Spit (3.44–5.00) may be associated with the inflow of the water enriched with labile OM. In July 2009, the highest observed values of bacterial numbers and biomass resulted from the favorable combination of high OM concentration, temperature, calm weather, and terrigenous flow caused by abundant rainfall prior to the expedition.

Our data agree with the major patterns of activity of the bacterioplankton community previously described for the Baltic Sea. The differences in the levels of bacterial production determined by the radiocarbon and thymidine methods result from the procedural errors, year-to-year variability, and/or irregular character of most investigations.

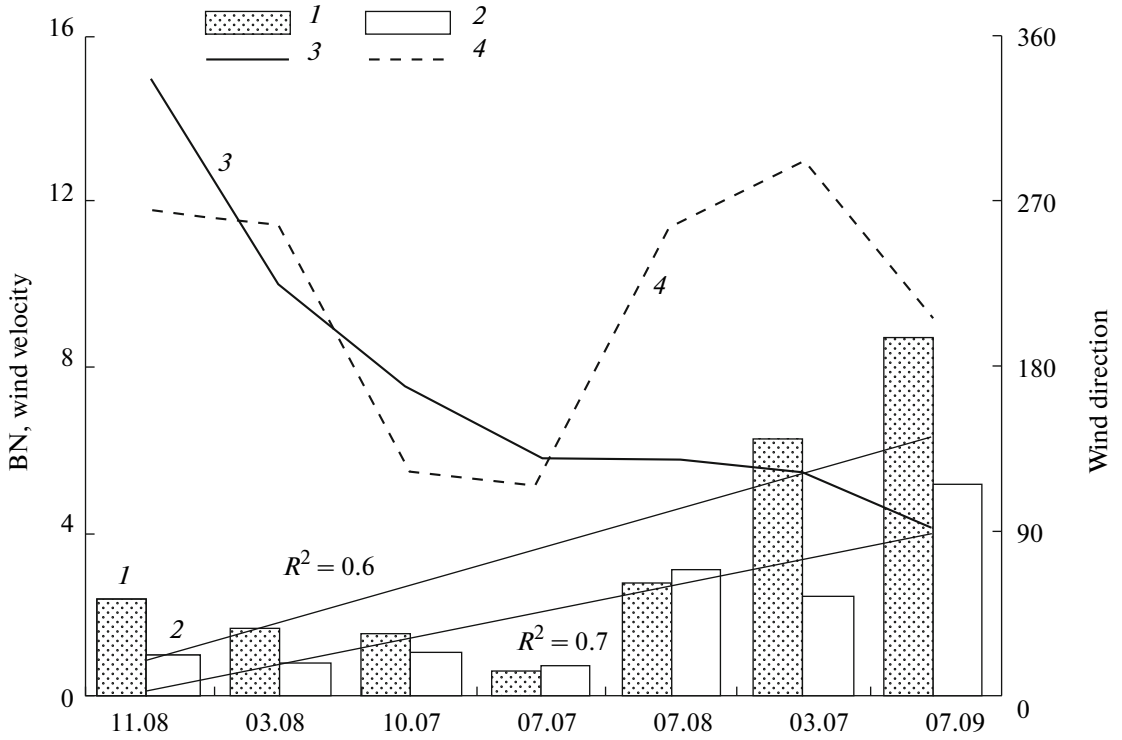

Fig. 7. Variations in average bacterial numbers (BN) in the 0–20 m layer depending on the average wind speed: coastal stations (*1*), open-sea stations (*2*), wind velocity (*3*), and wind direction (*4*).

According to the values of bacterial number, biomass, and production, the Russian sector of the Gdansk Basin (Baltic Sea) should be characterized as a mesotrophic–eutrophic one [12], with eutrophic water predominant along the coast and mesotrophic ones, in the open sea.

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