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SHORT COMMUNICATION

# How do differences in the nutritional and hydrological background influence phytoplankton in the Vistula Lagoon during a hot summer day?

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## KEYWORDS

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Phytoplankton;  
Biomass

**Summary** The aim of this work was to find out whether the difference between the central Vistula Lagoon (the southern Baltic Sea) and the western lagoon was reflected in the relationships between nutrients and phytoplankton during one-day hot summer conditions when the water temperature exceeded 20°C. Significant differences in Soluble Reactive Phosphorus (SRP) and Dissolved Inorganic Nitrogen (DIN) concentrations, and also in the biomass of the dominant phytoplankton assemblage of Cyanoprokaryota, were noted in the studied parts of the lagoon. No such differences were found for the nitrogen to phosphorus ratio (N:P) or for the biomasses of Bacillariophyta and Chlorophyta. The very low values of N:P (on average 2.8 and 3.4) indicated strong nitrogen limitation. The Correspondence Canonical Analysis (CCA) showed that the central part of the lagoon could be defined as positively related to DIN and to N:P, and western part could be characterized by correlation with temperature, dissolved oxygen and SRP concentrations. Competition for the limited resources of Dissolved Inorganic Nitrogen in the western, shallower part of the lagoon was in favour of Cyanoprokaryota, to the detriment of other phytoplankton assemblages. In contrast, the Cyanoprokaryota biomass in the central part of the lagoon, where DIN concentrations were increased, was lower, and Bacillariophyta in particular prospered at their expense. Here, the competition for Soluble Reactive Phosphorus was not so clear-cut.

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## 1. Introduction

The eutrophication of shallow coastal lagoons and bays has recently become a leading topic in the ecology and biogeochemistry of temperate shelf seas (Lloret et al., 2008; Nixon, 1995; Su et al., 2015; Vidal et al., 1999). A number of research projects focus on the relations between nutrients like phosphorus (P) and nitrogen (N), and the consequent rapid increase in the primary production of phytoplankton, which manifests itself in blooms of Cyanoprokaryota, undesirable from the sanitary and economic state of seas worldwide (Nixon et al., 2001), including shallow coastal waters of the Baltic Sea (Pliński, 2005). The present work addresses this global phenomenon and attempts to demonstrate the spatial differentiation in the nutrient supply and its consequences for the relations between the main phytoplankton assemblages in the summer phase of their reproductive cycles in shallow coastal waters, which are characteristic for such shelf, semi-closed and catchment-dependent seas as the Baltic Sea. This study also refers to a number of publications on the effects of eutrophication in Baltic Sea coastal waters (Pilkaitytė and Razinkovas, 2006; Seppälä and Balode, 1999; Włodarska-Kowalczyk et al., 2014), and points out the spatial hydrological aspect of relationships between the distribution of nutrients and phytoplankton production and structure.

The horizontal distribution of algae in open oceanic waters is regulated by hydrodynamic processes like Kelvin waves and advection, chemical ones such as the differences in nutrient concentrations, and biological ones associated with the dynamics of grazing (Bidigare and Ondrusek, 1996; Lucas et al., 1999). The differences in the phytoplankton assemblage biomasses can also be found as an effect of competition among them for resources (Carey et al., 2014; Chakraborty and Feudel, 2014). The spatial distribution of phytoplankton structure and biomass in shallower coastal sea waters, like the Gulf of Riga (Baltic Sea), depends above all on the levels of nutrients supplied by river waters and subsequently disseminated by sea currents (Seppälä and Balode, 1999).

The general aim of the present work was to show the effect of the uneven distribution of assimilable P and N forms on the relations between the biomasses of the main phytoplankton taxonomic groups. It was achieved by comparing the various levels of N and P species in the two parts of the lagoon with the differences in the phytoplankton assemblage. The particular objectives of this work were to verify a hypothesis on whether the differentiation in water exchange between two parts of the shallow Baltic lagoon was reflected: (1) in the distribution patterns of biomass and dominant species, Cyanoprokaryota, Bacillariophyta and Chlorophyta correlated with N and P compounds and other basic environmental parameters, (2) in the relations between Dissolved Inorganic Nitrogen (DIN) and Soluble Reactive Phosphorus (SRP) and the biomass of the main phytoplankton assemblages during a hot summer day, when the water temperature in the lagoon exceeds 20°C.

The areas of the Vistula Lagoon to be compared in this respect were its shallower western part, influenced by inflows of inland waters but relatively isolated from the effects of the open sea, and its central part, which is deeper and whose waters are exchanged rather more quickly with the open Baltic. We expected to find different nutritional

factors responsible for phytoplankton structure, including Cyanoprokaryota domination, in relation to varied exchange of waters in shallow lagoons in the Baltic Sea. This can serve to expand our knowledge of the spatial hydrological causes of harmful algal blooms in shallow coastal water bodies and to find pointers for eliminating these undesirable phenomena.

## 2. Material and methods

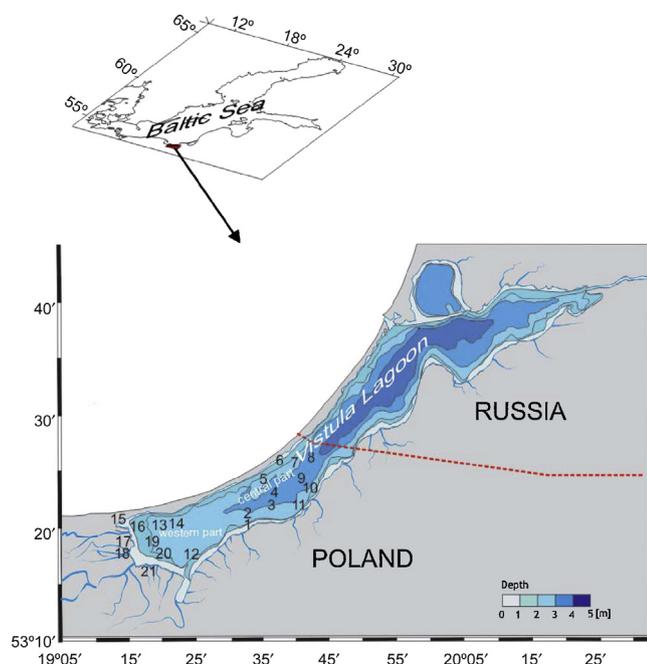
### 2.1. Study area

The Vistula Lagoon is a shallow coastal water body with specific hydrodynamic and trophic properties. A characteristic feature of the water exchange between the lagoon and the Baltic Sea is the presence of the only connection, the Baltiysk Strait, which cuts through the northern end of the Vistula Spit. The velocity of water movement in and out of the lagoon differs strongly: it is relatively fast mainly in the Russian part of the lagoon, but slow in the more enclosed Polish part. According to Bielecka and Kaźmierski (2003), the speed of inflowing or outflowing lagoon waters off Mamonovo (Kaliningrad Oblast) is 0.04–0.05 m s<sup>-1</sup>, off Frombork ca. 0.02 m s<sup>-1</sup> and near the Żuławy Wiślane (Vistula Delta lowlands) less than 0.01 m s<sup>-1</sup>. One consequence of this slowing down of current flows coming in from the sea and the flows of freshwater from the land is the salinity gradient in the Polish part of the lagoon (Bielecka and Kaźmierski, 2003). The depth of the lagoon and the nature of the bottom sediments are different too: in the deeper (3–4 m) eastern and central parts the sediments consist mainly of mineral matter such as sands and clays, whereas in the shallower (ca. 2 m) western part the emphasis shifts to organic alluvial deposits (Uścino-wicz and Zachowicz, 1996).

### 2.2. Field and laboratory methods

The fieldwork in the Vistula Lagoon was carried out in August 2011, a year with a typical hot summer when water temperature exceeded 20°C from July to the beginning of September: mean water temperature in August amounted 21.5°C near Nowa Pasłęka according to an ecohydrodynamical model simulation (Institute of Oceanography, University of Gdańsk) and phytoplankton growth was intensive. Samples were taken on one day (15 August) in the same meteorological condition and hydrodynamic relations, which guaranteed the high comparability of samples. Twenty-one sampling stations were designated in the two areas of the Polish part of the lagoon. Eleven sampling stations were located in the eastern area, between Frombork and Tolkmicko on the southern shore and Piaski and Krynica Morska on the northern one, and ten such stations were situated in the shallower western area bordering on the Vistula Delta lowlands (Fig. 1). Depth, Secchi Disc visibility, water temperature and dissolved oxygen content (by Hach LDO oxygen probe) were measured at each sampling station in situ.

The volume of 1 dm<sup>3</sup> of surface water (0–0.5 m depth) was taken using a vertical point water sampler at each point for chemical analysis in the laboratory. Samples were collected into dark bottles and cooled. Then, no more than a dozen or so hours later, the water samples were passed through a GF/C (1.2 µm) Whatman glass fibre filter. The



**Figure 1** Vistula Lagoon bathymetry and location of sampling sites in the Vistula Lagoon in August 2011 with delimitation of western and central parts; points with numbers indicate sampling sites.

sediment deposited on the filter was analyzed for its content, and the chlorophyll *a* level was estimated spectrophotometrically using the acetone method (Lorenzen, 1967). Soluble Reactive Phosphorus (SRP) was determined with the molybdate blue method, and total phosphorus (TP) by combustion in perchloric acid. Dissolved Inorganic Nitrogen (DIN) was defined as the sum of nitrate and ammonium nitrogen. Nitrate nitrogen ( $\text{NO}_3\text{-N}$ ) was determined by reduction to nitrite and ammonium nitrogen ( $\text{NH}_4\text{-N}$ ) using Kuderyarov's modification of Solerzano's method. Total nitrogen (TN) was obtained as the sum of Kjeldhal nitrogen as determined by combustion in sulphuric acid and of the nitrate content (APHA, 1996; Golterman et al., 1969).

For the phytoplankton analysis another  $1 \text{ dm}^3$  of water was taken from the same depth as that for chemical analysis; in addition, the phytoplankton were sampled for qualitative analysis by hauling a  $30 \text{ }\mu\text{m}$  plankton net through the water. Lugol's solution was used for sample preservation (Wetzel and Likens, 2000). The quantitative analysis was done on research material which was obtained from the  $1 \text{ dm}^3$  samples of water and densified by the sedimentation method (Hötzel and Croome, 1999). The counting units were cells, cenobia or trichomes  $100 \text{ }\mu\text{m}$  in length. The quantitative analysis was done in accordance to APHA (1996) methodology using  $1 \text{ cm}^3$  Sedgwick-Rafter cells. Magnifications of  $1 \times 10 \times 40$  and  $1 \times 10 \times 63$  (Carl Zeiss Axio Imager A1) were used for the microscopic analysis. The phytoplankton biomass was estimated by measuring cell volumes according to the recommendations of the Baltic Monitoring Programme (HELCOM). Dominant taxa in biomass on a specific site were those with shares in the total biomass of phytoplankton greater than 5%.

## 2.3. Statistical methods

Canonical Correspondence Analysis (CCA) was used to show the distribution pattern of the phytoplankton groups (Cyanoprokaryota, Bacillariophyta and Chlorophyta) biomass, dominant species of these assemblages in relation to basic physical (temperature, Secchi Disc visibility, dissolved oxygen concentration) and nutrient (SRP, DIN, N:P) parameters, as well as in relation to sampling stations and two parts of the Vistula Lagoon. Prior to CCA, Detrended Correspondence Analysis (DCA) was performed to determine the gradient length of phytoplankton composition. Results of DCA allow subsequent CCA performance due to the results of gradient length for the axes: 3.875 standard deviation. It is recommended to use unimodal methods as CCA when the gradient length is  $>3$  standard deviation (ter Braak and Šmilauer, 2002). Environmental variables were transformed logarithmically (ter Braak and Šmilauer, 2002) and analyzed with forward selection of the Monte Carlo permutation test (499 unrestricted permutations). CANOCO 4.5 software was used for the above ordination analyses. Two-factor correlation and regression analysis was used to demonstrate relationships among nutrients (SRP and DIN) and biomass of three dominant groups of phytoplankton in the western and central parts of the Vistula Lagoon. Test *t* for equality of means was used to compare environmental parameters of two parts of the Vistula Lagoon.

## 3. Results

### 3.1. Differences in physicochemical characteristics

The two areas of the Vistula Lagoon selected for this study (Fig. 1) differed above all in their bathymetry. They shared some physicochemical characteristics but differed in others. Table 1 shows that the differences in location, depth and hydrodynamics between the two areas were the most likely reason for the statistically significant ( $p < 0.05$ ) differences in salinity and dissolved oxygen (DO) concentration. The  $\text{O}_2$  concentration in the central area of the lagoon ( $7.35 \text{ mg dm}^{-3}$ ) was significantly lower than in the western area ( $9.12 \text{ mg dm}^{-3}$ ) (Table 1).

Despite a number of significant differences in several physicochemical parameters, the two parts of the lagoon did not differ significantly with respect to levels of chlorophyll *a* ( $40\text{--}42 \text{ }\mu\text{g dm}^{-3}$ ); moreover, the Secchi Disc visibility was no greater than 50 cm in both parts.

The concentrations of N and P forms in the lagoon waters in summer 2011 differed widely. Mean TP and SRP levels in the shallower, western part of the lagoon were very high at  $233$  and  $34 \text{ }\mu\text{g dm}^{-3}$  respectively. These values were significantly higher than the equally fairly high mean levels noted in the central area of the lagoon:  $179 \text{ }\mu\text{g dm}^{-3}$  TP and  $23 \text{ }\mu\text{g dm}^{-3}$  SRP (Table 2). Total nitrogen (TN) levels were the same at ca.  $0.6 \text{ mg dm}^{-3}$  in both areas of the lagoon. But the mean level of Dissolved Inorganic Nitrogen (DIN) was significantly higher in the centre of the lagoon ( $44 \text{ }\mu\text{g dm}^{-3}$  DIN) than in its western part ( $29 \text{ }\mu\text{g dm}^{-3}$  DIN) (Table 2). The stoichiometric relationships between N and P did not differ significantly in the two parts of the lagoon and were very low

**Table 1** General characteristics of the two studied parts of the Vistula Lagoon in August 2011: *m* – mean, SD – standard deviation, *p* – significance level of test *t* for equality of means. Significance level *p* < 0.05 in bold font.

Parameter Unit	Depth [m]	Salinity <sup>a</sup> [PSU]	Temperature [°C]	Visibility of Secchi Disc [m]	O <sub>2</sub> dissolved [mg dm <sup>-3</sup> ]	Chlorophyll <i>a</i> [µg dm <sup>-3</sup> ]	
Central part ( <i>n</i> = 11)	<i>m</i>	3.3	2.5–4.0	20.2	0.44	7.35	42.0
	SD	0.8		0.4	0.08	0.48	24.4
Western part ( <i>n</i> = 10)	<i>m</i>	2.2	1.5–2.5	21.0	0.47	9.12	40.1
	SD	0.4		0.5	0.03	0.95	24.8
<i>p</i>		<b>0.0024</b>		<b>0.0004</b>	0.1999	<b>0.0001</b>	0.8587

<sup>a</sup> Multiyear ranges of mean salinity (Institute of Meteorology and Water Management data, 2011).

**Table 2** Nutrient concentrations in the two studied parts of the Vistula Lagoon in August 2011: *m* – mean, SD – standard deviation, *p* – significance level of test *t* of equality of means. Significance level *p* < 0.05 in bold font.

Parameter Unit	SRP [µg dm <sup>-3</sup> ]	TP [µg dm <sup>-3</sup> ]	DIN [µg dm <sup>-3</sup> ]	TN [mg dm <sup>-3</sup> ]	TN:TP	
Central part ( <i>n</i> = 11)	<i>m</i>	23	179	44	0.60	3.4
	SD	9	15	14	0.12	0.6
Western part ( <i>n</i> = 10)	<i>m</i>	34	233	29	0.64	2.8
	SD	13	31	9	0.20	0.9
<i>p</i>	<b>0.03711</b>	<b>0.00024</b>	<b>0.01115</b>	0.59622	0.11558	

in both. The N:P ratio in the water column was ca. 3 in both areas (Table 2).

### 3.2. Differences in phytoplankton

The dominant taxa in biomass were Cyanoprokaryota, Bacillariophyta and Chlorophyta. Among Cyanoprokaryota, the dominant genera were Aphanocapsa, Aphanothece, Chroococcus, Gloeocapsa, Gomphosphaeria, Microcystis, Dolichospermum, Woronichinia, Snowella and Merismopedia. Identified species were dominant on individual sites of each part of the lagoon. *Microcystis viridis* was the dominant species on sites 1–11 in the central part, but in the western part it dominated on sites 12–16 and 21. Other dominant species on different sites were *Microcystis flos-aquae*, *Microcystis botrys*, and *Microcystis aeruginosa*. The most significant differences in dominant *Microcystis* spp. were found on site 3. *Aphanocapsa holastica* dominated on sites 6–7 and 10–11 of the central lagoon, and on sites 13–21 in the western lagoon. The greatest taxonomic diversity of dominant Aphanocapsa species was found on site 6 in the central part of the lagoon and on sites 17 and 19 in the western part. These were the only sites where biomass was formed by dominant Aphanocapsa species such as *A. holastica*, *A. delicatissima* and *A. incerta*. *Dolichospermum spiroides* and *Dolichospermum flos-aquae* were dominant in biomass only on sites 8, 9 and 10, in the central lagoon. *Woronichinia compacta*, *Woronichinia elorante* and *Snowella lacustris* dominated in biomass only on sites 2, 5 and 7 in the central lagoon. *Gomphosphaeria salina* was also dominant on sites 4 and 9 of this part of the lagoon. Merismopedia species were

dominant on sites 12–18 and 19–21 in the western lagoon. The greatest diversity of dominant Merismopedia species (*M. glauca*, *M. punctata*, *M. tenuissima*) was found on site 14. Bacillariophyta dominant in biomass were represented by *Actinocyclus* spp. and *Camphylodiscus* spp. They were dominant on sites 1 and 2. *Camphylodiscus* spp. was also dominant in biomass on sites 3 and 4, and *Actinocyclus* spp. on sites 8–10 in the central lagoon. In the western part the only dominant was *Camphylodiscus* spp. on sites 17–21. Dominant Chlorophyta were represented by *Pediastrum* and *Scenedesmus* species. *Pediastrum boryanum* was dominant on sites 1, 2 and 6. In the central part *Scenedesmus* spp. was dominant in biomass on site 20 in the western part (Table 3).

The distribution of dominant species varied in different parts of the lagoon. Species from genera Dolichospermum, Woronichinia, Snowella, Pediastrum and Actinocyclus were dominant in phytoplankton biomass only in the central area. Species representing Merismopedia and Scenedesmus were dominant only in the western area. Species representing Aphanocapsa, Aphanothece, Chroococcus, Gloeocapsa, Gomphosphaeria, Microcystis and Campylodiscus were dominant in both lagoon areas, but their distribution on individual sites varied in different parts of the lagoon (Table 3).

The dominant group of algae in the Vistula Lagoon in August 2011 was Cyanoprokaryota, with a mean biomass of 12.9 mg dm<sup>-3</sup> in the central area and 15.1 mg dm<sup>-3</sup> in the west. The respective mean biomasses of Bacillariophyta were distinctly lower at 2.4 and 2.9 mg dm<sup>-3</sup>, but more than those of Chlorophyta (1.3 and 1.6 mg dm<sup>-3</sup>). Only very low biomasses of species from the other groups were present (Table 4). The differences in the biomasses of the identified



**Table 4** Biomass [ $\text{mg dm}^{-3}$ ] of main phytoplankton taxonomic groups in the two parts of the Vistula Lagoon in August 2011.  $m$  – mean, SD – standard deviation,  $p$  – significance level of test  $t$  of equality of means. Significance level  $p < 0.05$  in bold font.

Parameter		Share of phytoplankton taxonomic groups				
Phytoplankton Group		Cyanoprokaryota	Euglenophyta	Pyrrophyta	Bacillariophyta	Chlorophyta
Central part	$m$	12.9	0.03	0.17	2.4	1.3
( $n = 11$ )	SD	2.0	0.05	0.07	0.9	0.4
Western part	$m$	15.1	0.03	0.16	2.9	1.6
( $n = 10$ )	SD	0.9	0.05	0.07	1.0	0.4
$p$		<b>0.0132</b>	1.00000	1.00000	0.17199	0.11690

groups of algae in the two areas of the lagoon were statistically significant only in the case of Cyanoprokaryota at the  $p < 0.05$  level (Table 4).

### 3.3. Relationships between phytoplankton and environmental parameters

The CCA ordination method was used to analyze distribution features of the phytoplankton groups' (Cyanoprokaryota, Bacillariophyta and Chlorophyta) biomass, their taxonomic composition and set of environmental parameters, including

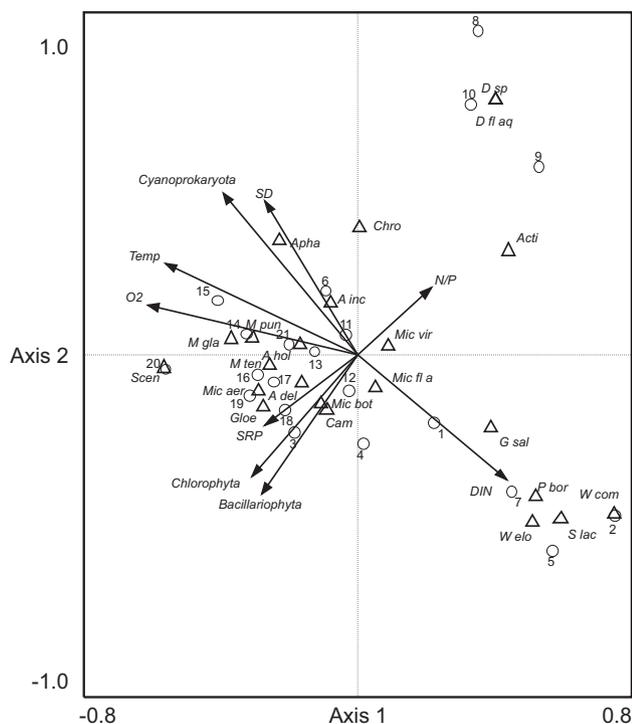
N and P compounds. The eigenvalues of first two axes were 0.120 and 0.104, and these axes explained 19.5 and 16.8% of the variation, respectively. The Monte Carlo test confirmed that the CCA model was significant with  $F$  ratio = 4.35 ( $p = 0.002$ ).

The CCA 1 axis was interpreted as a gradient of temperature (Temp), Dissolved Oxygen concentration (DO) and Dissolved Inorganic Nitrogen concentration (DIN) (Fig. 2, Table 5). The second axis was much more weakly defined by correlation with environmental variables. Only Secchi Disc visibility (SD) and biological variable Cyanoprokaryota biomass (Cyano) showed significant relations with this axis (Table 5).

The ordination analysis clearly showed an environmental separation between the main phytoplankton groups occurring in the Vistula Lagoon. Bacillariophyta and Chlorophyta biomass had significant positive relationships with SRP concentration and significant negative relationships with the nitrogen to phosphorus ratio (N:P). By contrast, Cyanoprokaryota biomass correlated significantly with the majority of physical-chemical parameters: Secchi Disc visibility (SD), water temperature (Temp), Dissolved Oxygen concentration (DO) (positively) and DIN (negatively), but did not correlate significantly with SRP and N:P (Fig. 2, Table 5).

The present CCA ordination analysis also allowed the identification and delimiting of a cluster of sampling stations belonging to the shallower western part of the Vistula Lagoon (Fig. 2). Assemblages in a limited and coherent area of cluster sampling stations from this part of the lagoon showed that the environmental, taxonomic and biomass relationships of phytoplankton were similar in this region. This contrasted, however, with a wider dispersion on the scatterplot distribution of sampling stations belonging to the deeper central part of the Vistula Lagoon (Fig. 2). Generally, the central part of the lagoon could be defined as positively related to DIN and N:P, and the western part could be characterized by a SRP, as well as by DO and Temp (Fig. 2).

Inside the delimited cluster area on the scatter plot of CCA analysis, referred to as the western part of the Vistula Lagoon, we can find a number of phytoplankton species occurring only in this region (Table 3) as belonging to Cyanoprokaryota *M. punctata* (*M pun*), *M. glauca* (*M gla*), *M. tenuissima* (*M ten*) or Chlorophyta genus *Scenedesmus* spp. (*Scen*) (Fig. 2).



**Figure 2** Ordination diagram of Canonical Correspondence Analysis (CCA) including phytoplankton groups Cyanoprokaryota, Bacillariophyta and Chlorophyta biomass (arrows), dominant taxa (triangles – codes are given in Table 3), environmental variables (arrows, bold font – codes are given in Table 5) and sampling sites (circles). The position of sampling sites is divided into the western part (limited by a cluster) and the central part of the Vistula Lagoon.

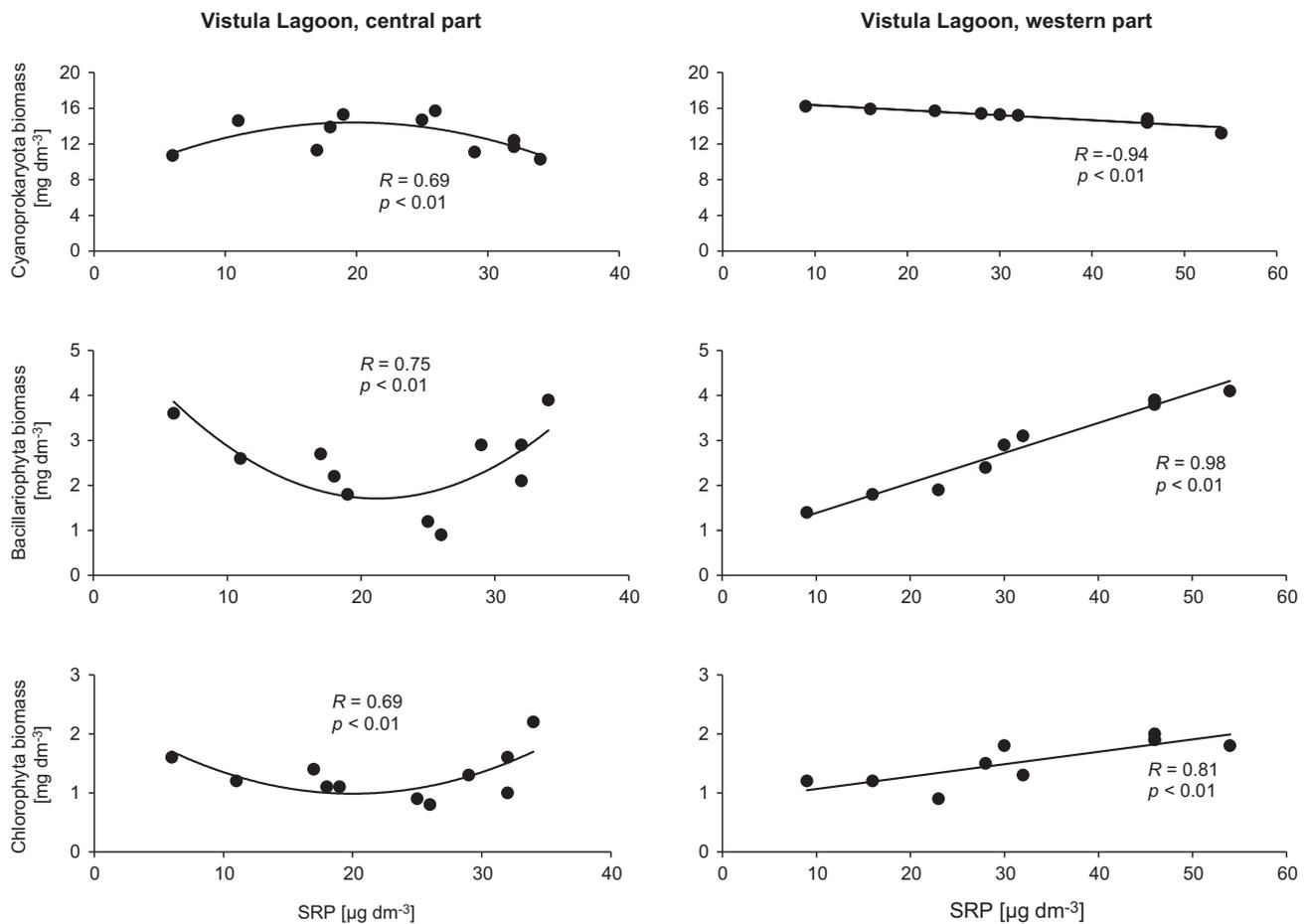
**Table 5** Correlations between environmental and biological (phytoplankton groups biomass) variables and CCA axes (Fig. 2) in the Vistula Lagoon:  $p < 0.5$ ,  $p < 0.01$  (with asterisk),  $n = 21$ .

Variables	Axis 1	Axis 2	SD	Temp	DO	SRP	DIN	N/P	Cyano	Bac	Chlo
Secchi Disc visibility (SD)		0.45					-0.57*		0.62*		
Temperature (Temp)	-0.56*		0.54*		0.93*		-0.66*		0.77*		
Dissolved Oxygen (DO)	-0.61*						-0.58*		0.69*		
Soluble Reactive Phosphorus (SRP)							-0.41	-0.60*		0.61*	0.59*
Dissolved Inorganic Nitrogen (DIN)	0.44								-0.74*		
Nitrogen to phosphorus ratio (N/P)										-0.43	-0.42
Cyanopokaryota (Cyano)		0.47								-0.46	
Bacillariophyta (Bac)											0.90*
Chlorophyta (Chlo)											

### 3.4. The influence of nutrient spatial differentiations on phytoplankton biomass

It is evident from Table 2 that the statistically significant differences in nutrient levels in the two parts of the lagoon with respect to algal biomass were accompanied by a similar

difference only in the case of Cyanopokaryota (Table 4). The CCA results also confirmed differences in SRP and DIN directly assimilated by phytoplankton, with biological parameters between the central and western parts of the lagoon. Given the dominance in the biomass of Cyanopokaryota and also of Bacillariophyta and Chlorophyta, the two groups with the



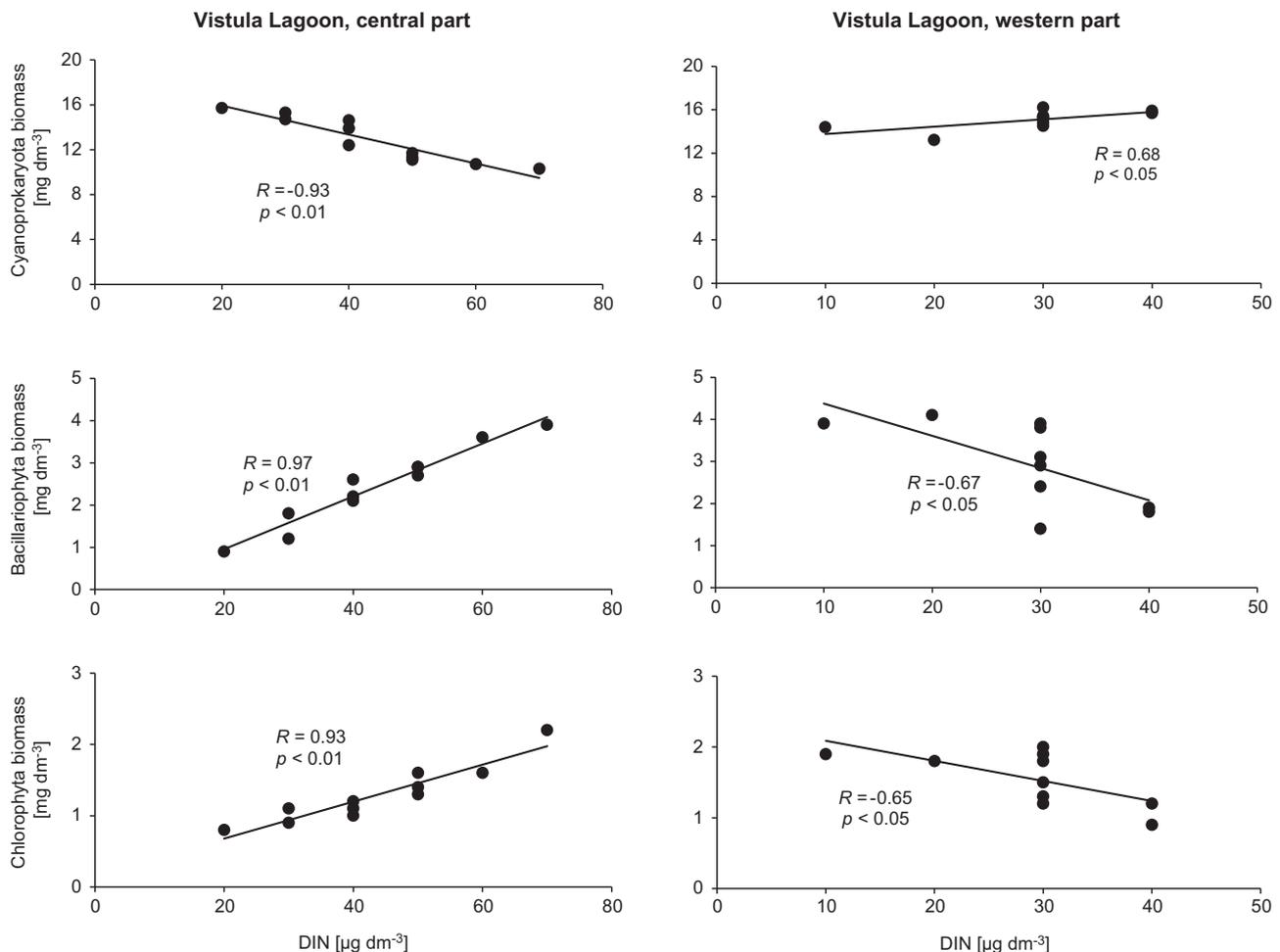
**Figure 3** The relationship between concentrations of Soluble Reactive Phosphorus (SRP) [ $\mu\text{g dm}^{-3}$ ] and Cyanopokaryota, Bacillariophyta and Chlorophyta biomass [ $\text{mg dm}^{-3}$ ] in the central and western parts of the Vistula Lagoon in August 2011.

next-highest biomasses, we analyzed how the variability in the different SRP and DIN contents in the two lagoon areas affected the biomass of these groups of algae. It turned out that there were distinct differences in the reactions of Cyanoprokaryota on the one hand, and those of Bacillariophyta and Chlorophyta on the other, to changing nutrient levels in the two areas of the Vistula Lagoon.

SRP levels in the western lagoon were relatively high (mean =  $34 \mu\text{g dm}^{-3}$ , Table 2). The relationships between the biomass of Cyanoprokaryota and this nutrient were such that for lower SRP levels the biomass of Cyanoprokaryota was at its highest, whereas that of Bacillariophyta and Chlorophyta was low. Conversely, when SRP levels were higher, the biomass of Cyanoprokaryota was lower, and that of Bacillariophyta and Chlorophyta higher. The relationships between these taxa and SRP levels are described by high correlation coefficients:  $R = -0.94$  for Cyanoprokaryota,  $R = 0.98$  for Bacillariophyta and  $R = 0.81$  for Chlorophyta at a significance level of  $p < 0.01$  (Fig. 3). In contrast, in the central part of the lagoon, where SRP levels were lower (mean =  $23 \mu\text{g dm}^{-3}$ , Table 2), the relationships between the variability in SRP concentrations and the biomass of these three groups of algae were not linear; they can be described by a polynomial function. As in the western part of the lagoon, a higher biomass of Cyanoprokaryota coincided with a minimal

biomass of Bacillariophyta and Chlorophyta, whereby the most Cyanoprokaryota were present at SRP levels between 20 and  $30 \mu\text{g dm}^{-3}$  and relatively fewer at higher and lower concentrations. These non-linear relationships between the biomass of phytoplankton groups and SRP levels are described by correlation coefficients of  $R = 0.69$  for Cyanoprokaryota,  $R = 0.79$  for Bacillariophyta and  $R = 0.69$  for Chlorophyta at a significance level of  $p < 0.01$  (Fig. 3).

The relationships between DIN and the biomass of the dominant groups of algae in the Vistula Lagoon were different. In the western part the DIN content was distinctly lower than in the central part (mean =  $29 \mu\text{g dm}^{-3}$ ) (Table 2). Under such conditions the algal assemblages occurred mainly (in 8 cases out of 10) where DIN levels were higher ( $30\text{--}40 \mu\text{g dm}^{-3}$ ). Here, at higher DIN levels the biomass of Cyanoprokaryota rose but that of Bacillariophyta and Chlorophyta fell. These relationships are described by correlation coefficients of  $R = 0.68$  for Cyanoprokaryota,  $R = -0.67$  for Bacillariophyta and  $R = -0.65$  for Chlorophyta at a significance level of  $p < 0.05$  (Fig. 4). However, if DIN levels were higher (mean =  $44 \mu\text{g dm}^{-3}$ ) (Table 2), as it was in the central part of the lagoon, lower DIN levels (up to ca.  $20 \mu\text{g dm}^{-3}$ ) correspond to maximum biomass of Cyanoprokaryota (ca.  $16 \text{ mg dm}^{-3}$ ) and to minimum that of Bacillariophyta and Chlorophyta. And vice versa: when DIN concentrations were



**Figure 4** The relationship between concentrations of Dissolved Inorganic Nitrogen (DIN) [ $\text{mg dm}^{-3}$ ] and Cyanoprokaryota, Bacillariophyta and Chlorophyta biomass [ $\text{mg dm}^{-3}$ ] in the central and western parts of the Vistula Lagoon in August 2011.

higher (over  $50 \mu\text{g dm}^{-3}$ ), the biomass of Cyanoprokaryota fell to ca.  $10 \text{ mg dm}^{-3}$  but that of Bacillariophyta rose to ca.  $4 \text{ mg dm}^{-3}$  and that of Chlorophyta to ca.  $2 \text{ mg dm}^{-3}$ . These relationships are strongly correlated with one another:  $R = 0.93$  for Cyanoprokaryota,  $R = 0.97$  for Bacillariophyta and  $R = -0.93$  for Chlorophyta at a significance level of  $p < 0.01$ ) (Fig. 4).

#### 4. Discussion and conclusions

The waters of the Vistula Lagoon are enriched principally by N and P compounds entering from point sources (sewage outfalls) and rivers, and released from bottom sediments that have been accumulating pollutants for many decades at least (Kruk, 2012; Pliński, 2005). One result of the presence of N and P loads in the Lagoon's waters is the regular occurrence of Cyanoprokaryota blooms, especially on summer days (Rybicka, 2005). The Lagoon has long been classified as a hypertrophic water body (Nawrocka and Kobos, 2011; Pliński, 2005). However, hydrodynamic differences between the more shallow western part and the deeper part, with faster water exchange, cause various nutrient distributions and may imply differences in eutrophication effects.

In what way do the differences in the spatial distribution of nutrient concentrations affect the biomass of the phytoplankton assemblage under the special conditions of a hot summer day in the shallow Vistula Lagoon? To answer this question, it is important first of all to note that in the areas of the Lagoon we studied, there were significant differences both in SRP and DIN levels, and in the biomass of the dominant phytoplankton assemblage of Cyanoprokaryota. In contrast, no such differences were recorded for the N:P ratio or the biomasses of Bacillariophyta and Chlorophyta. The very low N:P ratios, ranging from barely 2.8 to 3.4, indicated unequivocally that nitrogen was very strongly limited in both areas of the lagoon. At the same time, the western area of the lagoon exhibited distinctly higher SRP and lower DIN levels in relation to the central area. The question therefore arises as to why, despite the similar stoichiometric relations, the spatial distribution of nutrients gave rise to a significantly higher biomass of Cyanoprokaryota in the shallower, less saline and more stagnant waters of the western Vistula Lagoon (Bielecka and Kaźmierski, 2003) than in the central area, which receives more inflows of water from the open Baltic Sea. As shown in the Canonical Correspondence Analysis (CCA), environmental differences between both parts of the Vistula Lagoon, described above, influenced the biomass of dominant phytoplankton assemblages and the taxonomic composition of these groups.

The phytoplankton community acquires nutrients from the water in accordance with Monod's (1942) model, and their assimilation into algal cells under good thermal and light conditions – and such were the conditions prevailing during our study – can take from a matter of minutes to one day (Olsen et al., 2013). The stimulator of algal cell growth, inter alia of ribosomal RNA, is above all assimilable phosphorus (Arrigo, 2005), which is not limited in the Vistula Lagoon. Under such benign conditions, the only possible limitation to the growth of the assemblage of algae living in the lagoon's waters appears to be competition between the various taxonomic groups of algae (and also bacteria) for the available nitrogen.

For simplification, the present study took no account of the range of nutrient assimilability, different in various taxa (Tilman, 1982), the possibility that phytoplankton can assimilate tiny fractions of organic nutrient elements (Davidson et al., 2012; Glibert et al., 1991), or the additional effects of competitive displacement by Cyanoprokaryota such as allelopathy (Suikkanen et al., 2005) or shading (Zevenboom et al., 1982). It was not ruled out, however, that the conspicuously different levels of salinity in the two areas of the lagoon could affect the biomass of algae, including that of Cyanoprokaryota (Rakko and Seppälä, 2014). Moreover, the consumption of phytoplankton by zooplankton seems to be an insignificant factor in the Vistula Lagoon, which is indicated by the lack of proportional relation between the phytoplankton biomass recorded in our study and zooplankton biomass (Cladocera species feeding on algae) in the central and western parts of the Vistula Lagoon (Paturej and Kruk, 2011).

Some species of Cyanoprokaryota are said to be capable of enzymatically fixing atmospheric nitrogen, which in this way makes up for the deficit of nitrogen in algal cells due to the lower N:P ratio (Knuuttila et al., 1994; Smith, 1982). Even though exceptionally low N:P ratios were recorded in our study, the participation of Cyanoprokaryota species potentially capable of binding atmospheric nitrogen appears to be marginal. Here, we have only *D. flos-aquae*, *D. spiroides* (at 3 sampling stations in the central basin). Even under conditions of nitrogen limitation in eutrophic water bodies, the share of Cyanoprokaryota assimilating atmospheric N is no more than a few per cent: this was estimated on the basis of incubational and isotopic studies by Ferber et al. (2004). Therefore, the binding of atmospheric nitrogen by Cyanoprokaryota in the waters we studied was probably of marginal significance in the assimilation of this element and did not affect the relations between these algae and the forms of Dissolved Inorganic Nitrogen in the water.

In the light of our results and the above considerations regarding the part played by different environmental factors capable of modifying the relations between nutrient supply and phytoplankton biomass in a shallow, oligohaline lagoon (Paturej, 2005), we can now put forward the following scheme for the different reactions of the phytoplankton assemblage to the varying supply of assimilable N and P in the central and western areas of the Vistula Lagoon. In the western part, where SRP levels are quite considerable, there is competition for P between Cyanoprokaryota and Bacillariophyta and Chlorophyta, especially when those levels are low. The biomass of Cyanoprokaryota peaks at SRP levels from 15 to  $30 \mu\text{g dm}^{-3}$ ; when SRP is higher. However, competition on the part of Cyanoprokaryota weakens, and the biomasses of Bacillariophyta and Chlorophyta then increase.

Bacillariophyta and Chlorophyta require higher SRP concentrations for growth than Cyanoprokaryota (Watson et al., 1997; Zhu et al., 2010). The latter begin to age and die off only when the P supply is completely exhausted (Lafforgue et al., 1995). Moreover, the P resources in the water can maintain Cyanoprokaryota at a relatively constant level, enabling them to grow even when SRP is low. This is because they can accumulate P in larger amounts than other algae (Jensen and Andersen, 1992). As their phosphatase activity is greater, they can assimilate organic P more efficiently (Giraudet et al., 1997; Hadas et al., 1999; Shapiro, 1990), this being a product of their own metabolism, as well as of

competing algae and the excreta of zooplankton (Elser et al., 1987; Keating, 1977).

In the western lagoon there was also a relatively lower supply of DIN; this probably elicits stiff competition for this nutrient. An increase in its concentration led to an almost equivalent increase in the biomass of Cyanoprokaryota at the expense of the biomass of the subdominant algae.

In the conditions of shallow, stagnant waters of the western lagoon, favouring the growth of Cyanoprokaryota, these algae could win the competition for N resources against other phytoplankton groups by bringing into play their specific physiological adaptation mechanisms. In consequence, by producing gas vacuoles and controlling their turgor Cyanoprokaryota are capable of vertical migrations in the water; this enables them to choose habitats that are optimal not only with regard to temperature and illumination, but also to food resources (Dokulil and Teubner, 2000; Humphries and Lyne, 1988). The ability of vertical migration in the stagnating waters of the western lagoon, where the penetration of light to the deeper layers of water was limited by the intense growth of phytoplankton, frequently dominated by the Cyanoprokaryota themselves, also gave them an advantage in their development over other algae (Dokulil and Teubner, 2000; Ganf et al., 1989). A strong correlation between the Cyanoprokaryota biomass and Secchi Disc visibility demonstrated in the study suggests a decisive effect of these algae on water transparency in the Vistula Lagoon.

The competition between the algal groups in the central area of the lagoon, where relatively less SRP and more DIN were recorded, takes on a different aspect. Here, the competition for phosphorus (SRP) was non-linear: in the SRP range from ca. 15 to 25  $\mu\text{g dm}^{-3}$ , Cyanoprokaryota appeared to be the winners, but above and below this range Bacillariophyta and Chlorophyta came into their own. In contrast, increasing levels of DIN in this part of the lagoon favoured the growth of Bacillariophyta in particular (a fourfold increase) but Chlorophyta to a lesser extent; the biomass of Cyanoprokaryota decreased in these conditions. This means that Bacillariophyta found better conditions for growth in the water flowing in from the open sea, probably because the silica content in this water was higher; in addition, its higher salinity might retard the growth of some species of Cyanoprokaryota.

The basic factor limiting the growth of Cyanoprokaryota is the movement of water masses: these algae grow best when the mixing of waters is weak (Berman and Shteinman, 1998; Lafforgue et al., 1995; Lindenschmidt and Chorus, 1998). A change in weather conditions, strong winds, intense rainfall, stronger wave action and other water movements often cause the growth of Cyanoprokaryota to break down. The aquatic environment of the central part of the Vistula Lagoon, periodically affected by the inflow of brackish waters through the Baltiysk Strait and more exposure to air movements, was far less static than the stagnant western part. Under such conditions, the chances of algae other than Cyanoprokaryota ones growing here were much greater. The pressure on the part of Cyanoprokaryota, thus attenuated, could benefit diatoms arriving with the inflows of water from the sea. The most common diatoms are typically brackish-water species, which do not occur in fresh waters. These propitious environmental conditions could have given Bacillariophyta a competitive advantage in the acquisition of food

resources and in utilizing the high DIN levels in this part of the lagoon for their growth.

The CCA ordination analysis showed differences between the two parts of the Vistula Lagoon by delimitation a cluster of sampling sites belonging to the shallower western part. Environmental, taxonomic and biomass relationships in sampling stations were similar in this region in comparison with the deeper central part. Generally, the central part of the lagoon could be defined as positively related to nitrogen compounds and to the N to P ratio, and the western part could be characterized by a correlation with a wider range of environmental variables, in which SRP play a significant role.

The differences in the levels of assimilable N and P available to algae between the more 'closed' western area of the Vistula Lagoon and the more 'open' central area, may be shaping the competition for resources between Cyanoprokaryota on the one hand and Bacillariophyta and Chlorophyta on the other; they may explain the differences between these two areas as regards the intensity of Cyanoprokaryota blooms during a hot summer. The biomass of Cyanoprokaryota was greater than that of the other groups of algae when they were competing for the meagre resources of Dissolved Inorganic Nitrogen in the western area of the Lagoon. By contrast, the biomass of Cyanoprokaryota was smaller in the more open central area of the Lagoon, with its higher DIN levels, where the growth of Bacillariophyta superseded that of Cyanoprokaryota. Competition for SRP was not so clear-cut; this was due to the very low N:P ratio characteristic of the trophic status of the entire Vistula Lagoon.

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