ORIGINAL RESEARCH ARTICLE

A turning point in the development of phytoplankton in the Vistula Lagoon (southern Baltic Sea) at the beginning of the 21st century

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Summary Phytoplankton community structure was studied from 2002 to 2016 in the Vistula Lagoon (southern Baltic Sea) in the context of the 2010 shift in its population, as well as the reason for this shift and its environmental impact. This evident shift was indicated by Multidimensional Scaling at the Bray Curtis similarity level of 31%. Before 2010, the primary components of phytoplankton were Cyanobacteria (up to 98% of the biomass, October 2007) and Chlorophyta (40%, July 2002). After 2010, the contribution of Cyanobacteria considerably decreased, and the proportions of other phyla increased. The total phytoplankton biomass positively correlated with phosphorus, and Cyanobacteria biomass with silica. Evident changes were also observed in the seasonal dynamics of phytoplankton. Before 2010, the highest values of biomass occurred in autumn, and were related to high biomass of Cyanobacteria. Higher biomass has been recently reached in spring, during the dominance of Ochrophyta associated with Chlorophyta, Charophyta, and Cryptophyta. Generalised additive models showed a significant decreasing trend of the total phytoplankton biomass, Cyanobacteria, Chlorophyta, and flagellates, suggesting a decrease in eutrophication. This trend is concurrent with a considerable increase in the ratio of zooplankton to phytoplankton biomass since 2010. The increased ratio, however, did not result from elevated zooplankton biomass, but from the drop in phytoplankton biomass. Therefore,

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the most probable reason for the decrease in phytoplankton biomass was the simultaneous decrease in the concentration of all nutrients. The potential additional impact of filtration by a new alien bivalve *Rangia cuneata* G. B. Sowerby I, 1832 is also discussed.

1. Introduction

Lagoons are coastal marine ecosystems under a strong direct influence of land and rivers. Consequently, they are characterised by high productivity (Newton et al., 2014; Viaroli et al., 2008). The trophic status of lagoons shows considerable temporal inertia due to nutrient loads originating from both auto- and allochthonous matter accumulated over several years in sediments (Schernewski et al., 2011; Verdonschot et al., 2013). The gradual release of nutrients from sediments to the water column occurs under worsening oxygen conditions (Zilius et al., 2015), as well as through resuspension (Sondergaard et al., 1992). The latter phenomenon is common in lagoons due to the shallow depth of the water bodies and their high exposure to wind action. Phytoplankton is the primary beneficiary of a higher than the average level of nutrients (Eyto et al., 2018). The role of phytoplankton as a primary producer in lagoons is usually considerably greater than that of macrophytes, which predestines the systems to remain in a phytoplankton-dominated regime (Kornijów, 2018). This process bears consequences for the habitat conditions (worse light conditions, strong supply of organic matter to sediments, and periodical oxygen deficits), as well as for ecosystem services benefitting the human economy (Newton et al., 2014). The 2000s seem to have had the particular anthropogenic impact on the Vistula Lagoon (VL). Firstly, the economic transformation that commenced in the early 1990s (Eriksson et al., 2007) resulted in a considerable decrease in the nutrient load in the lagoon during the 2000s. It can be assumed to have caused a gradual decrease in the phytoplankton biomass and a transformation of its taxonomic composition as the bottom-up effect. At the same time, the food-web structure changed in the lagoon. In addition to the numerous alien species of invertebrates and fish already present in the lagoon (Grabowski et al., 2006; Jablonska-Barna et al., 2013), a new efficient bivalve filter-feeder appeared (Rudinskaya and Gusev, 2012; Warzocha et al., 2016).

Research on the phytoplankton of the Polish section of the lagoon has been occasionally conducted since the early 1950s (Kruk et al., 2016; Margoński and Horbowa, 2003; Margoński et al., 2003; Nawrocka and Kobos, 2011; Piwosz et al., 2016; Pliński, 1972; Pliński and Simm, 1978; Szarejko-Łukaszewicz, 1957). Previous research had been usually based on relatively short and non-continuous data series. The research shows that for more than half a century, the phytoplankton of the lagoon has been characterised by the dominance of blue-green algae (Cyanobacteria). Cyanobacterial blooms involved the appearance of species constituting potential producers of cyanobacterial toxins (Mazur-Marzec et al., 2010; Rybicka, 2005). These blooms occurring from May to Oc-

tober formed one vast peak lasting almost throughout the vegetation season, suggesting a disturbance of the typical order of seasonal phytoplankton succession in the waters of the temperate zone, usually consisting of spring, late spring, summer, and autumn peaks (Gasiūnaitè et al., 2005; Pliński and Simm, 1978; Wasmund et al., 1998; Witek et al.,1993). Whereas seasonal changes in the phytoplankton of the lagoon have been quite thoroughly investigated, publications concerning the long-term transformations occurring in the community are scarce. This publication shows changes in the phytoplankton structure in the Vistula Lagoon in the period 2002—2016, both in the seasonal and long-term aspect, as well as the verification of the hypotheses regarding causes of such changes and their effect for the environment. First, we hypothesised that the observed decrease in the concentration of nutrients in the lagoon should lead to changes in the seasonal development of phytoplankton, limiting the development of Cyanobacteria in the summer period and to a progressing decrease in its biomass in a long-term cycle (bottom-up effect).

Moreover, we verified whether the underlying causes were related to the pressure of filter-feeding zooplankton on the phytoplankton community as a top-down effect.

Finally, we assumed that water quality would considerably improve in terms of the concentrations of chlorophyll *a* and Cyanobacteria biomass.

2. Material and Methods

2.1. Study area

The Vistula Lagoon (VL), second largest coastal lagoon in the southern Baltic Sea (Witek et al., 2010), extends over approximately 90 km along the Polish and Russian coast of the Gulf of Gdańsk (Figure 1). Its width ranges from 8 to 19 km, and its depth reaches up to 5.1 m, averaging 2.4 m. To the north, the lagoon is separated from the open sea by the Vistula Spit, a shallow belt of sandy land with a width of 1—2 km and length of approximately 50 km. This estuarine system is exposed to strong land (inflow of fresh waters via rivers) and marine (intrusion of salt waters from the Baltic Sea via the Strait of Baltiysk) impacts. The annual freshwater influx is approximately 4 km^3, and the water retention time is approximately 4 months (Witek et al., 2010). Salinity decreases from 6.5 psu at the Baltiysk Strait to <1 psu at the mouths of the larger rivers.

In comparison to the water surface area (838 km^2) of the lagoon, its drainage area (23,871 km^2) is exceptionally large (Łomniewski, 1958). More than half of the area is under agricultural use, and approximately 25% is covered by forests. The total number of residents in the lagoon's catchment slightly exceeds one million. The industry is not extensive.
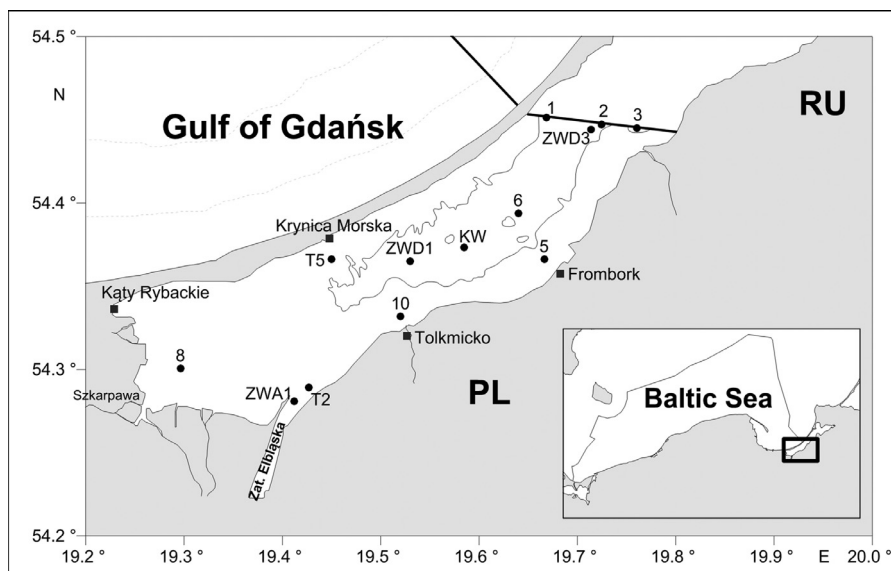
Figure 1   Location of sampling stations in the Polish part of the Vistula Lagoon.

The water level in the lagoon is subject to considerable fluctuations with an amplitude of up to 1.2 m, particularly in the period of autumn-winter storms (Chubarenko et al., 2012). Wave-induced mixing results in a continuous resuspension and homogeneous temperature distribution in the lagoon during the ice-free period (Chubarenko et al., 2017). The lagoon is under the influence of both maritime and continental climates, with air temperature reaching high annual amplitudes from −31°C to 36°C. During winter, VL may become covered by ice. Depending on the year, the ice may remain from several days to several months.

2.2. Physico-chemical parameters

Water temperature and salinity were measured *in situ* by means of a CTD probe. Transparency was measured with a Secchi disc as the Secchi disc depth (SDD). Physical parameters were measured simultaneously with phytoplankton sampling. Concentrations of nutrients (N-NO$_3$, N-NO$_2$, N-NH$_4$, total nitrogen (N$_{tot}$), P-PO$_4$, total phosphorus (P$_{tot}$), and dissolved silicate DSi) were determined using methods applied for the Baltic Sea to meet the objectives of the HELCOM monitoring programme (HELCOM, 2013). According to the HELCOM guidelines, the determination of nutrients is based on colorimetric methods (c.f. Grasshoff et al., 1983; Kirkwood, 1996). N/P ratio was calculated as N$_{tot}$ to P$_{tot}$ ratio.

2.3. Phytoplankton

2.3.1. Chlorophyll *a*
Chlorophyll *a* (Chl *a*) concentrations were analysed in accordance with the HELCOM recommendations for the fluorometric method (Edler, 1979; Evans et al., 1987; HELCOM 1988, 2015; Strickland and Parsons, 1968). Although all measurements were performed using the same method as that applied in the monitoring programme, the data for the period 2007—2017 were a raw database, and

those for the period 2002—2006 were obtained from the study by Kobos and Nawrocka (2018).

2.3.2. Species composition, abundance, and biomass
The data shown in this study come from the analysis of 443 samples collected monthly from April to November during the period 2002—2016 with one gap in 2004, when phytoplankton monitoring was not conducted. In some years (2011, 2014—2015), samples were also collected in winter (Supplement Table 1).

The research was conducted at 13 stations relatively evenly distributed in the Polish part of the lagoon (Figure 1).

Surface water was collected by means of a 5—10 litre bathometer or another plastic container, and 250 ml samples were immediately fixed with acidic Lugol's solution to a final concentration of 0.5%. Subsamples of 2, 10, or 20 ml were analysed using an inverted microscope following the method of Utermöhl (Edler and Elbrächter, 2010; Utermöhl, 1958). Individual phytoplankton cells were counted in accordance with the HELCOM recommendations (HELCOM, 1988, 2006). The wet weight biomass and carbon content in the phytoplankton cells were calculated in accordance with Olenina et al. (2006). Phytoplankton organisms were identified to the lowest possible taxonomic rank. Their names and classification complied with the accepted binomial nomenclature of the World Register of Marine Species (version 2016).

Flagellates and *Others* were differentiated as artificial groups aggregating cells impossible to identify, divided into size classes.

As the samples were collected over a period of almost 20 years (a period of numerous changes in the phytoplankton taxonomy due to the development of molecular biology techniques), and analysed in various research centres, harmonisation of the data was necessary at the initial stage (Derolez et al., 2020; Munitz et al., 2020). This process resulted in a unified database for further analysis. The harmonisation of the database involved the unification of the

names of taxa often occurring as synonyms of the same species. Then the organisms were aggregated to higher taxonomic units, phyla, classes, orders, and genera. The calculation of annual average values was always preceded by the calculation of the monthly average.

2.4. Zooplankton

Zooplankton data were needed for the determination of the potential impact of zooplankton on phytoplankton. Water sampling and quantitative and qualitative laboratory analysis of the samples were conducted in accordance with the HELCOM COMBINE methodology applied in the monitoring of the Baltic Sea (HELCOM, 2017; Hernroth, 1985).

Zooplankton in the mezo-size fraction, i.e. 0.2—20 mm, was sampled at the same time and place as phytoplankton, by means of single vertical tows performed with the Hydro-Bios (Germany) limnological standard plankton net (25 cm in diameter and a mesh size of 100 μm). The samples were preserved in ~4% formaldehyde solution buffered to pH 8—8.2 with disodium tetraborate (borax).

To highlight certain mechanisms of food-web interactions, the ratio between zooplankton and phytoplankton biomass (Bzoo/Bphyto) was calculated. This ratio is considered sensitive to changes in the top-down control through cascading trophic interactions (Carpenter et al., 1985) from fish to zooplankton and from zooplankton to phytoplankton (Gyllstrom et al., 2005; Hessen et al., 2003; Jeppesen et al., 2000). The ratio was calculated based on the analysis of samples collected at station KW during the period 2003—2016. Average annual biomasses of phytoplankton and zooplankton were used. The total zooplankton biomass covered *Copepoda, Cladocera, Rotifera*, and others that comprised meroplankton organisms.

2.5. Statistical analysis

The statistical significance of the differences in the taxonomic structure of phytoplankton was determined with the application of a one-way ANOSIM test. Multidimensional scaling (MDS) and cluster analyses were performed for the visualisation of the similarity of the structure of phytoplankton communities in years and seasons (months). Both the ANOSIM test and the MDS procedure were based on the Bray-Curtis distance matrix calculated based on the biomass of individual phylum ($\log(x+1)$ transformed data). The analysis was performed in the PRIMER 6 Version 6.1.15 package.

At least 10-year time series for the biomass of phytoplankton phyla were analysed for six selected months by means of generalised additive models (GAMs) (*gam* function, R package "mgcv", Wood, 2014). GAMs were run separately for each response variable vs. year. The possible autocorrelation between years was modelled with AR1 (autocorrelation structure with lag 1). Curves estimated with GAMs and 95% confidence limits were plotted on the data to visualise the direction of statistically significant long-term changes (i.e. decreasing, increasing, or non-linear trends). The total phytoplankton biomass and biomass of each phylum served as variables in the first stage of GAMs analysis. At the second stage, the biomass of each genus (or aggregation at class or order level) within the phylum was analysed.

The Pearson rank correlation (r) was used to evaluate the relations between environmental variables and phytoplankton biomass (at the level of total biomass, phylum, and genus) as well as between phytoplankton and zooplankton biomass. The Pearson correlation and statistical significance of correlations were determined (*cor* and *cor.test*, functions, R package "stats").

The statistical significance of temporal changes in the physico-chemical parameters was confirmed or rejected after the verification of whether the coefficient of the slope of the regression line was significantly different from 0. Such analysis permits trend detection. A test probability value of $p < 0.05$ was considered for rejecting the hypothesis of the lack of a trend (*lm* function, R package "stats").

3. Results

3.1. Physical and chemical water properties

3.1.1. Temperature
The mean water temperature recorded during the growing season (March—November) of the period 2002—2016 was 15.6°C (Figure 2). Statistically, no evident trends occurred over the analysed years. There were, however, slight differences in the two periods. Before 2010, the mean temperature was 16.3°C, with the highest values in July and June. After 2010, the warmest months were August and July, and the mean temperature dropped to 14.7°C (Figure 2).

3.1.2. Salinity
The mean water salinity measured at station KW, located in the centre of the Polish part of VL and providing the longest time series of data, was 3.6 psu throughout the study period, and showed minor fluctuations (Figure 2). Linear regression showed a slight although not statistically significant increasing trend ($p > 0.05$) in time. Moreover, the comparison of the years before and after 2010 showed the same mean values for both differentiated periods and multiannual means. In November, the salinity was the highest (5.5 psu), and slightly higher during the second period.

3.1.3. Transparency
The mean water transparency (SDD) recorded during the period 2002—2016 was 0.57 m. During the first period, 2002—2009, values of SDD readings were relatively uniform and always lower than the multiannual value. Later, considerable fluctuations occurred with a strongly increasing tendency in the years 2013—2016 (Figure 3, top panel). The increasing trend of water transparency in time, in terms of maximum, average, as well as the minimum values, was statistically significant ($p < 0.05$).

During the first period, the lowest average values occurred in early spring and in autumn (Figure 3, middle panel), while during the second period (Figure 3, bottom panel), they occurred in summer from May to July as well as in late autumn (November). Then, very high maximum values of up to 2 m were recorded. These values were at least twice as high as the maximum values during the first period.
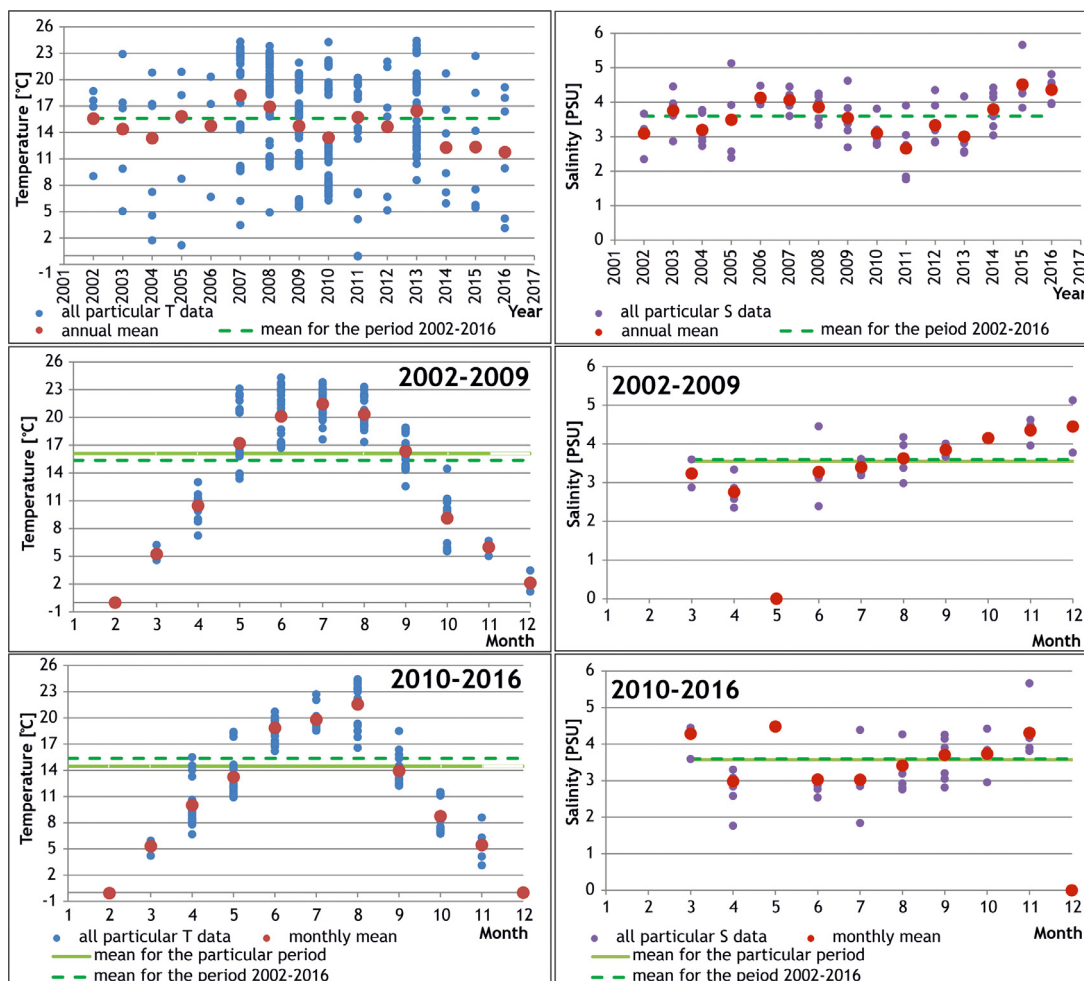
Figure 2 Temperature and salinity in VL. Multiannual changes during the study period (top panel) and seasonal changes during the two differentiated periods (middle and bottom panels).

3.1.4. Nutrients

The course of the mean annual concentrations of total nitrogen showed considerable fluctuations (Figure 4a), with the highest values (up to 328 μmol L^{-1}) between 2007 and 2009 and in 2013. The comparison of both periods revealed a decrease in the monthly mean N_{tot} concentrations below the multiannual average (127 μmol L^{-1}) during the period 2010—2016, and in the mean value for that period (112 μmol L^{-1}) compared to the multiannual average. Moreover, in the case of P_{tot} (Figure 4b) and Si (Figure 4c) concentrations, the comparison of data from before 2010 with data after 2010 showed a decrease in nutrient concentrations in recent years. It is worth emphasising that over the multiannual course of changes, a statistically significant downward trend occurred in P_{tot} concentration (p <0.05), whereas for N_{tot}, Si, and N_{tot}/P_{tot}, the value of p>0.05 for linear regression indicated no trends.

Until 2006, the ratio between total nitrogen and phosphorus remained at an even level close to or slightly above the Redfield ratio. Between 2007 and 2016, the N/P ratio showed fluctuations analogous to those of the total nitrogen concentrations, with maximum values in 2009 and 2013, and values approximately equal to the initial values in 2012 and 2015 (Figure 4d).

The mean annual silicon concentrations were maintained at a level approximately equal to the multiannual mean value for the entire study period (96 μmol L^{-1}). Silicon concentrations only decreased in recent years (2014—2016), in 2015 by almost 50% in comparison to the multiannual average (Figure 4c).

3.1.5. Abiotic variables as drivers of phytoplankton biomass

The Pearson rank correlation (r) demonstrated positive correlations between the total phytoplankton biomass and (i) phosphorus (P-PO4 and P_{tot}) concentration, (ii) suspension, and (iii) Chl *a* concentration. In contrast, the total biomass was negatively correlated with transparency. A considerably higher correlation of transparency with suspension than with the total phytoplankton biomass or Chl *a* concentration deserves particular attention. A positive correlation occurred between transparency and *Mesodinium rubrum* Lohmann, 1908 (Ciliophora), and a negative correlation was determined between transparency and Cyanobacteria and Chlorophyta.

No significant correlations were determined between the phytoplankton biomass and water temperature, the concentration of total nitrogen and its different forms, or
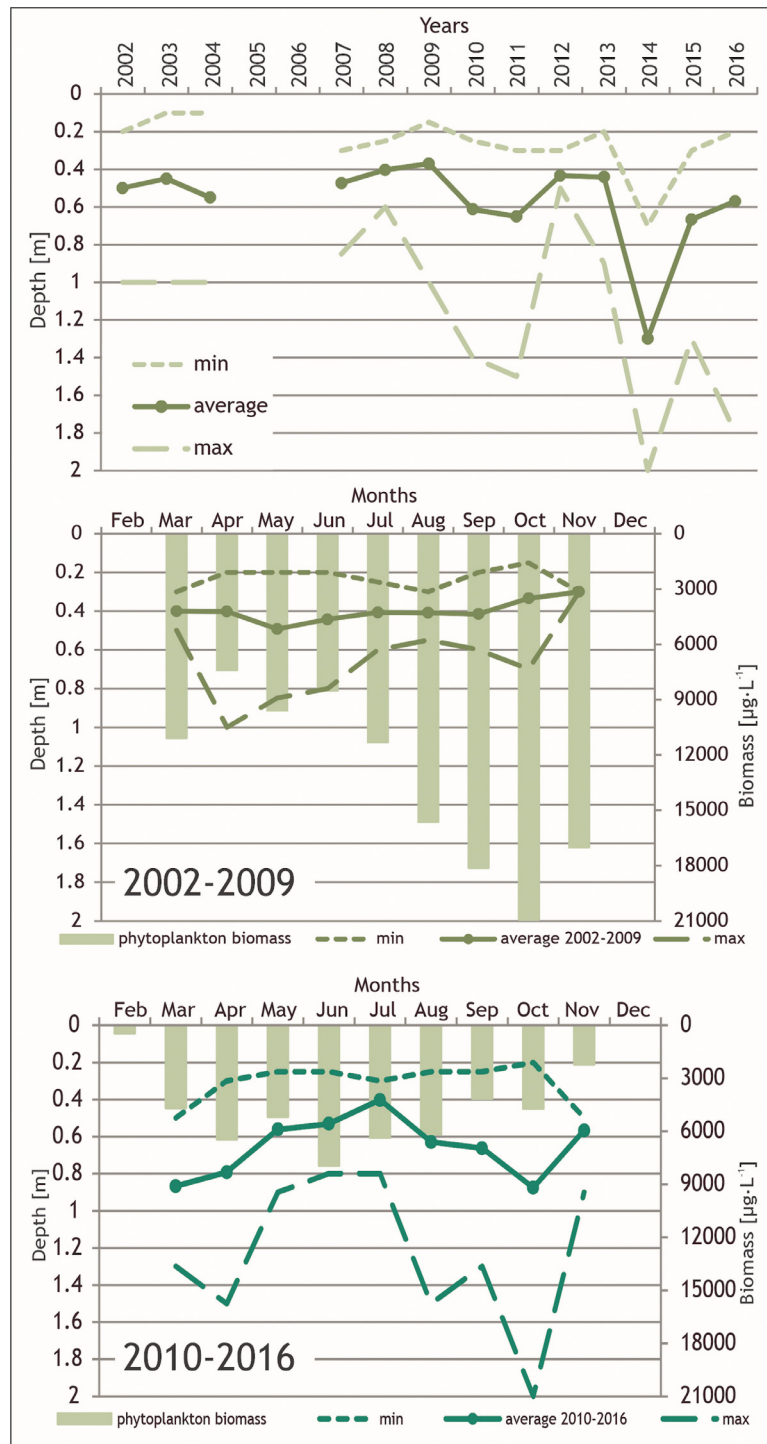
Figure 3 Transparency (SDD) versus phytoplankton biomass in VL. Multiannual changes during the study period (top panel) and seasonal changes during the two differentiated periods (middle and bottom panels).

the N/P ratio (with the exception of Chlorophyta which was positively correlated with N_{tot}). Silica was positively correlated with Cyanobacteria biomass, including genera such as *Snowella* Elenkin, 1938 and *Woronichinia* Elenkin, 1933, as well as genera belonging to Chlorophyta, namely, *Planctonema* Schmidle, 1903 and *Ankistrodesmus* Corda, 1838. The highest number of genera was correlated with total phosphorus and phosphate phosphorus (*Ankistrodesmus*,

Aphanotheceae/Anatheceae, Gleocapsopsis Geitler ex Komárek, 1993, *Lemmermanniella* Geitler, 1942, *Monoraphidium,* Komárková-Legnerová, 1969, *Planctonema, Snowella,* and *Woronichinia* and biomass of Cyanobacteria, *Chlorophyceae* and *Oscillatoriales*). Cyanobacteria showed a positive correlation with salinity, including those from genera *Snowella* and *Woronichinia*, and a negative correlation was found for Ochrophyta (*Nitzschia* A.H. Hassall,
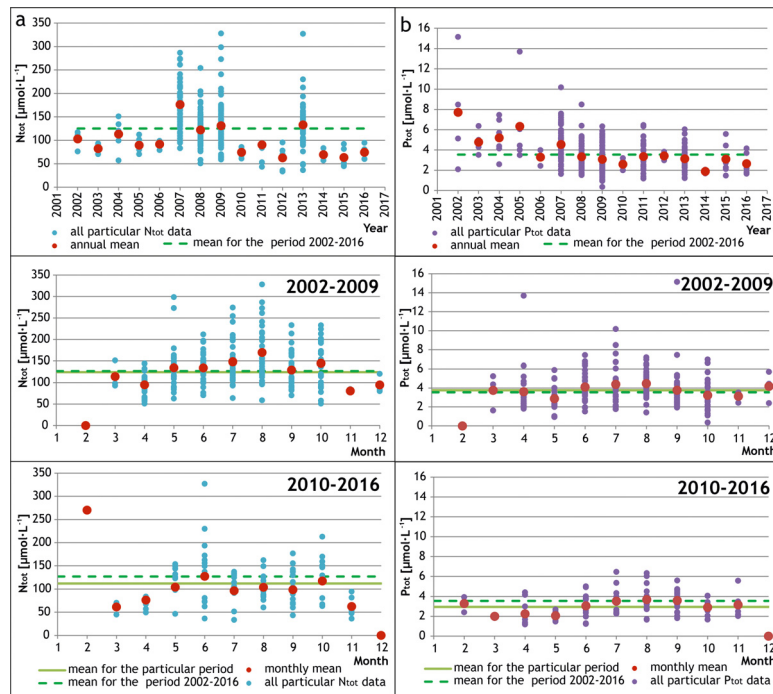
Figure 4   Total nitrogen (a), phosphorus (b), and silicon (c) concentrations and N/P ratio (d) in VL. Multiannual changes throughout the study period (top panel) and seasonal changes during the two differentiated periods (middle and bottom panels).

1845), and a representative of Chlorophyta genus *Desmodesmus* (R. Chodat) S.S. An, T. Friedl & E. Hegewald, 1999 (Supplement Table 2).

3.2. Phytoplankton

3.2.1. Chlorophyll *a* (Chl *a*)
Although mean Chl *a* concentrations (range: 21—70 mg m^{-3}) showed no significant differences (p>0.05) throughout the period (2002—2017), considerable differences were observed in the maximum concentrations between the years (Figure 5). Maximum Chl *a* concentrations reached values of more than 100 mg m^{-3}, particularly during the period 2002—2008 (up to 520 mg m^{-3} in 2002). The amplitude of the fluctuations considerably decreased after 2009, not exceeding 100 mg m^{-3} (except for 2013). The described changes, however, were of periodical character, with no statistically significant trend (p>0.05).

3.2.2. Species composition and dominance structure
A total of 170 taxa were identified before 2010, and approximately twice more (323) during the period 2010—2016. During the period 2002—2009, no Myzozoa such as *Prorocentrum cordatum* (Ostenfeld) J.D. Dodge, 1975, *Heterocapsa triquetra* (Ehrenberg) F. Stein, 1883, or *Oblea rotunda* (Lebour) Balech ex Sournia, 1973 were observed in VL. Among Ochrophyta, no genera such as *Chaetoceros* C.G. Ehrenberg, 1844, *Diploneis* (C.G. Ehrenberg) P.T. Cleve, 1894, *Achnanthes* Bory, 1822, or *Dinobryon* Ehrenberg, 1834 were documented, either.

Phytoplankton in VL was dominated by picoplanktonic (diameter <2 μm) Cyanobacteria-forming colonies belonging to genera *Anatheceae (Aphanotheceae* C. Nägeli, 1849*), Cyanodictyon* (Komárek & Anagnostidis) Komárek,

Kastovsky & Jezberová, 2011, *Lemmermanniella, Woronichinia, Aphanocapsa* C. Nägeli, 1849, and *Merismopedia* Meyen, 1839, particularly during summer and autumn. During the period 2002—2009, the abundance of coccal Cyanobacteria reached 1.7 ·10^{10} cells L^{-1}. At the same time, the mean abundance of nano- and microplanktonic Cyanobacteria was 6 ·10^8 cells L^{-1}, and the abundance of other components of phytoplankton ranged between 6 ·10^5 and 7 ·10^8 cells L^{-1}. During the period 2010—2016, the abundance of picoplanktonic Cyanobacteria decreased by an order of magnitude (10^9 cells L^{-1}), but still exceeded the abundance of the remaining phytoplankton components (nano- and microplanktonic Cyanobacteria abundance was 1.7 ·10^6 cells L^{-1}, and the abundances of the remaining components were between 5 ·10^5 and 7 ·10^8 cells L^{-1}).

The dominant taxa were recognised as those with biomass exceeding 30% of the total phytoplankton biomass in a sample (Supplement Table 3). Among such established dominants, only six dominated throughout the study period (2002—2016), namely: *Dolichospermum* (Ralfs ex Bornet & Flahault) P. Wacklin, L. Hoffmann & J. Komárek, 2009 with coiled trichomes, *Microcystis aeruginosa* (Kützing) Kützing, 1846, *Microcystis* Lemmermann, 1907, *Snowella* spp., *Aphanizomenon* spp., and *Cyclotella* (F.T. Kützing) A. de Brébisson, 1838. During the initial period of the study (2002—2009), along with these taxa, dominants included 9 others, whereas after 2010, the presence of 29 other periodically dominant taxa was recorded (Supplement Table 3).

3.2.3. Long-term changes in the taxonomic composition and phytoplankton biomass
Statistical analyses aimed at the assessment of the effect of station location on the distribution of phytoplankton in the Polish part of VL showed no significant differences. There-
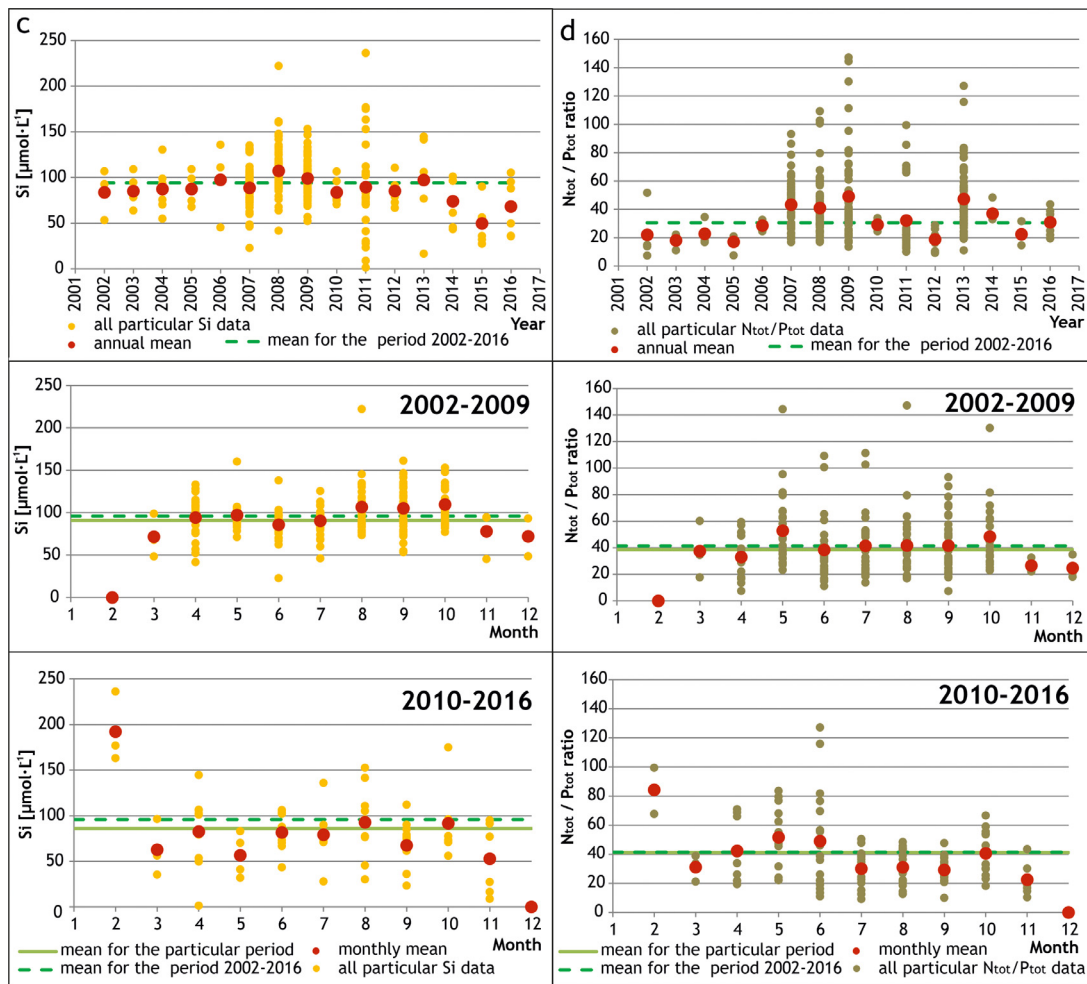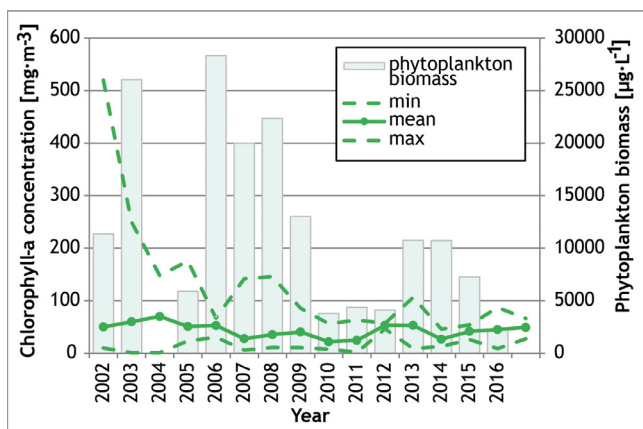
Figure 4   *Continued.*

Figure 5   Multiannual changes in Chl *a* concentrations.

fore, the spatial distribution of phytoplankton will not be subject to further analysis. In contrast, a significant effect of time (year) on phytoplankton biomass was determined (one-way ANOSIM, p=0.001). It was revealed in a significant decrease in the total biomass and evident reorganisation of the taxonomic structure of the phytoplankton community (Figure 6).

For better visualisation of the observed changes in phytoplankton biomass during the period 2002—2016, the MDS analysis with phytoplankton biomass at the level of genus was applied. The analysis revealed two groups of data (Bray Curtis similarity at 31%), marked in Figure 7. One of the groups covers data from years 2002—2009, and the other from the period 2010—2016. Therefore, all further analyses were conducted with consideration of the division into these two time periods.

Before 2010, the primary components of the phytoplankton community were Cyanobacteria, accounting for 53—98% of the total phytoplankton biomass, and Chlorophyta, with a contribution of 14—40%. Other phytoplankton groups only occasionally reached a higher share of the total biomass, e.g., diatoms in 2002 and cryptophytes in 2007 (15% and 20% of the total biomass, respectively). The highest total phytoplankton biomass of $6 \cdot 10^4$ µg L^{-1} was observed in 2006 and 2008. Ten times lower total biomass was observed in 2010. In 2011 and 2012, the maximum values of phytoplankton biomass did not exceed $2 \cdot 10^4$ µg L^{-1}. Subsequently, until the end of 2015, they did not exceed $4 \cdot 10^4$ µg L^{-1}. The lowest biomass was recorded in 2016, not exceeding $3 \cdot 10^3$ µg L^{-1}.

The taxonomic reorganisation of the phytoplankton community resulted in an equalisation of the contribution of
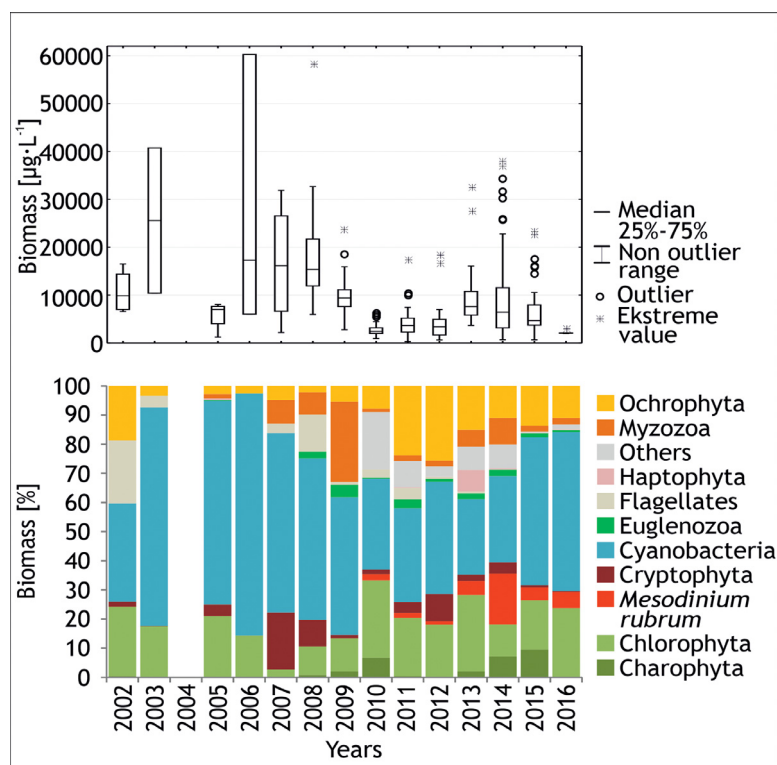
Figure 6   Multiannual changes in phytoplankton biomass (top panel) and its structure shown as percentages of the main groups (bottom panel) during the period 2002—2016.
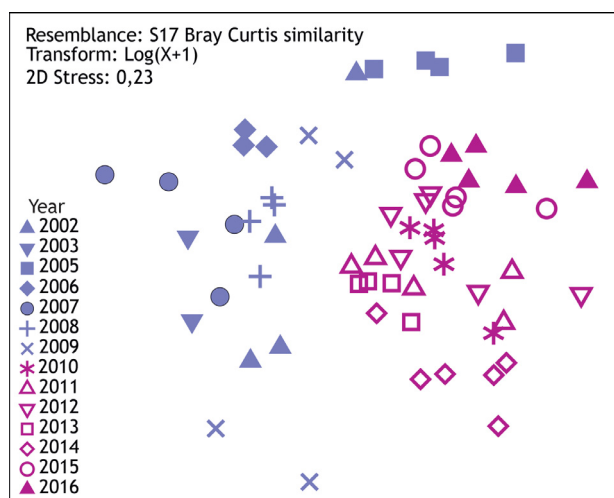

Figure 7   Multidimensional scaling (MDS) for phytoplankton biomass (at genus level) at station KW during the period 2002—2016.

particular phyla to the total phytoplankton biomass after 2010 (Figure 6, bottom panel). The most important changes included (i) the reduction of the proportion of Cyanobacteria biomass almost by half; (ii) an increase in the proportion of Ochrophyta, Charophyta, and Chlorophyta; (iii) the appearance of the mixotrophic ciliate *Mesodinium rubrum* with a proportion in certain events in autumn 2014 reaching 98% in the eastern part of VL, but with an average share of 21%.

3.2.4. Seasonal changes in phytoplankton biomass

Phytoplankton biomass underwent statistically significant monthly changes (one way ANOSIM, p=0.001). MDS analysis covered phytoplankton biomass at the genus level. It showed that all monthly data from the period 2002—2009 were mixed without grouping into seasons (Figure 8). In contrast, during the period 2010—2016, data from summer months formed one group, while those from spring months formed a second group. The results from autumn months were less pronounced. September data were combined with summer data, October data with spring data, and November data remained separate. The division of data was not as strong as that in the case of years (Bray Curtis similarity >50%), but it pointed to at least three seasons in the annual vegetation cycle in comparison with the period 2002—2009, when the data were mixed with no pattern. The analysis of phytoplankton biomass at the phylum level during the period 2002—2009, however, showed seasonal succession consisting of two stages (Figure 9). The stage lasting from March to April was followed by the stage from May to November. In early spring, there was a small peak of biomass of the complex primarily consisting of cryptomonads and Chlorophyta, diatoms, euglenids, and flagellates, with a small share of cyanobacteria. At the second stage of succession, phytoplankton biomass dominated by Cyanobacteria gradually increased, culminating in October.

During the period 2010—2016, phytoplankton succession showed three stages of development (Figure 9). The first spring stage lasted from March to May with a maximum in April. At that time, the community was primarily composed of diatoms and representatives of Charophyta, Chlorophyta, Cryptophyta, Myzozoa, and inconsiderable quantities of
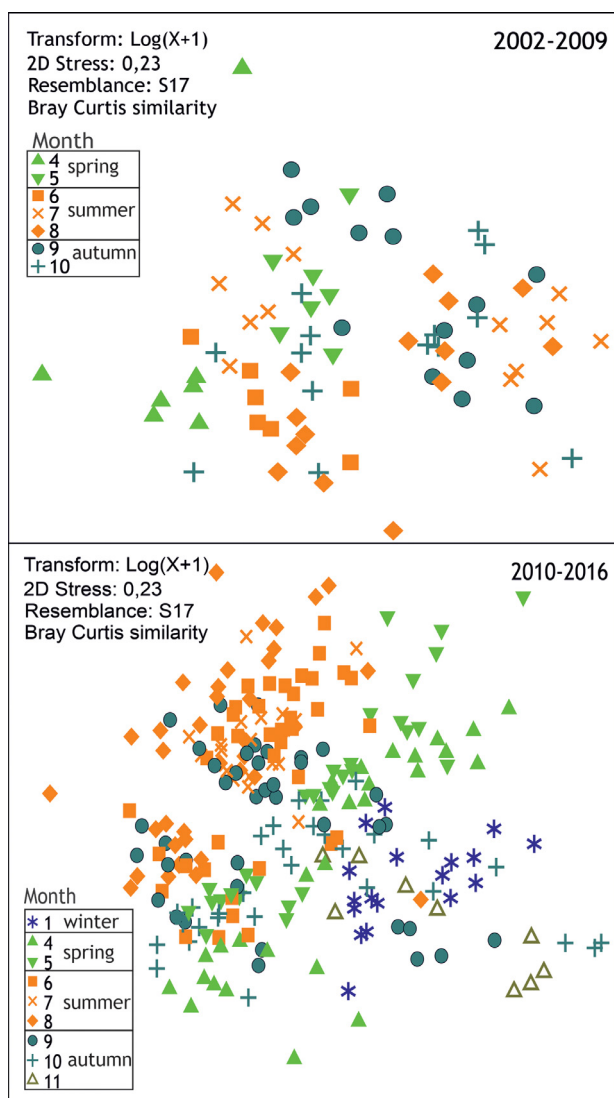
Figure 8 Multidimensional scaling (MDS) for phytoplankton biomass (at genus level) in two periods: 2002—2009 (top panel) and 2010—2016 (bottom panel).

Figure 9 Seasonal changes in monthly biomass of the main taxonomic groups in VL during the periods 2002—2009 and 2010—2016. The values are means for all the analysed stations.

Cyanobacteria. The summer stage of the succession lasted from June to August, with a maximum in June, and was dominated by Cyanobacteria, primarily accompanied by Chlorophyta and Ochrophyta. During the autumn stage, lasting from September to November, the taxonomic composition was similar to that in summer, with an additional considerable share of *Mesodinium rubrum* (Ciliophora). The biomass peaked in October, although its mean value was 5 times lower than during the period 2002—2009.

The above observations were also confirmed by the results of the GAMs analysis used for the detection of long-term trends in phytoplankton biomass and structure (Figure 10, Supplement Table 4). GAMs indicated a decreasing trend of the total phytoplankton biomass in August, September, and October (Figure 10a), and a similarly decreasing trend for Cyanobacteria (Figure 6b). This group was the most important component of phytoplankton biomass (20—63% depending on the season).
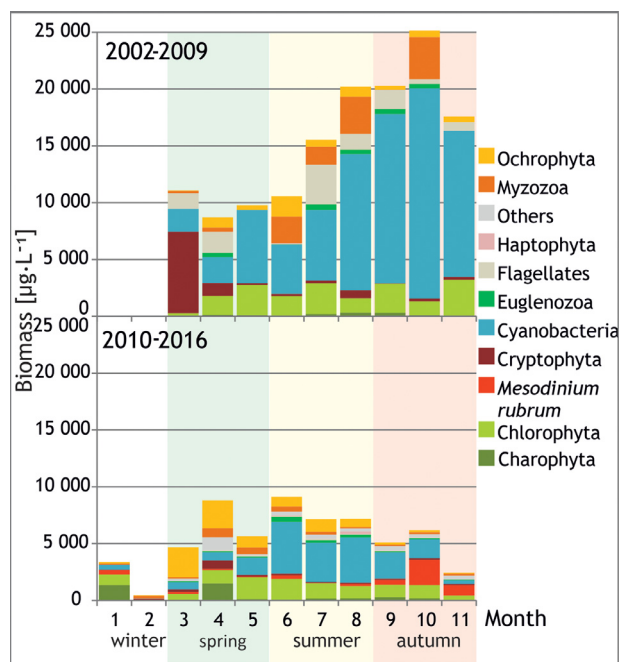
Chlorophyta (with a share of total phytoplankton biomass ranging from 14 to 23% depending on the season) and flagellates (1—8%) also showed a decreasing trend. In the case of Chlorophyta, it was recorded in July and October (Figure 10d, Supplement Table 4), and for flagellates (Figure 10c) also in April. In both cases, in autumn, the trend was non-linear, with a significant decrease during the period 2002—2008 followed by stabilisation until 2016.

At the same time, ciliate *Mesodinium rubrum* (0.1—8% of the total phytoplankton biomass in different seasons), Cryptophyta (1—14%), and Myzozoa (1—6%) showed an increasing tendency. Whereas in the case of *M. rubrum* this trend was evident in spring and autumn, in the case of Cryptophyta and Myzozoa a regular trend occurred in September and October (Figure 10e—f, Supplement Table 4). The GAMs analysis was also used to detect the long-term trends in Cyanobacteria and Chlorophyta biomass and taxonomic structure, i.e. the most important components of the phytoplankton community in VL (Supplement Table 5 and Table 6). Decreasing trends occurred in the months from August to October for the following genera dominant in the total biomass of Cyanobacteria: *Woronichinia, Snowella, Cyanodictyon,* and *Aphanotheceae (Anatheceae)*, as well as for the order of Oscillatoriales, primarily represented by *Planktolyngbya capillaris* (Hindák) Anagnostidis & Komárek, 1988 /*contorta* (Lemmermann) Anagnostidis & Komárek, 1988 (Supplement Table 3 and Table 5). No significant trends occurred in the biomass of potentially toxic diazotrophic Cyanobacteria causing blooms in June—July—August from genera *Aphanizomenon* and *Dolichospermum* (with the exception of *Aphanizomenon* in August, when an increasing trend occurred).

The decreasing trends occurred during months from July to October for the following genera: *Tetraëdron* Kützing,

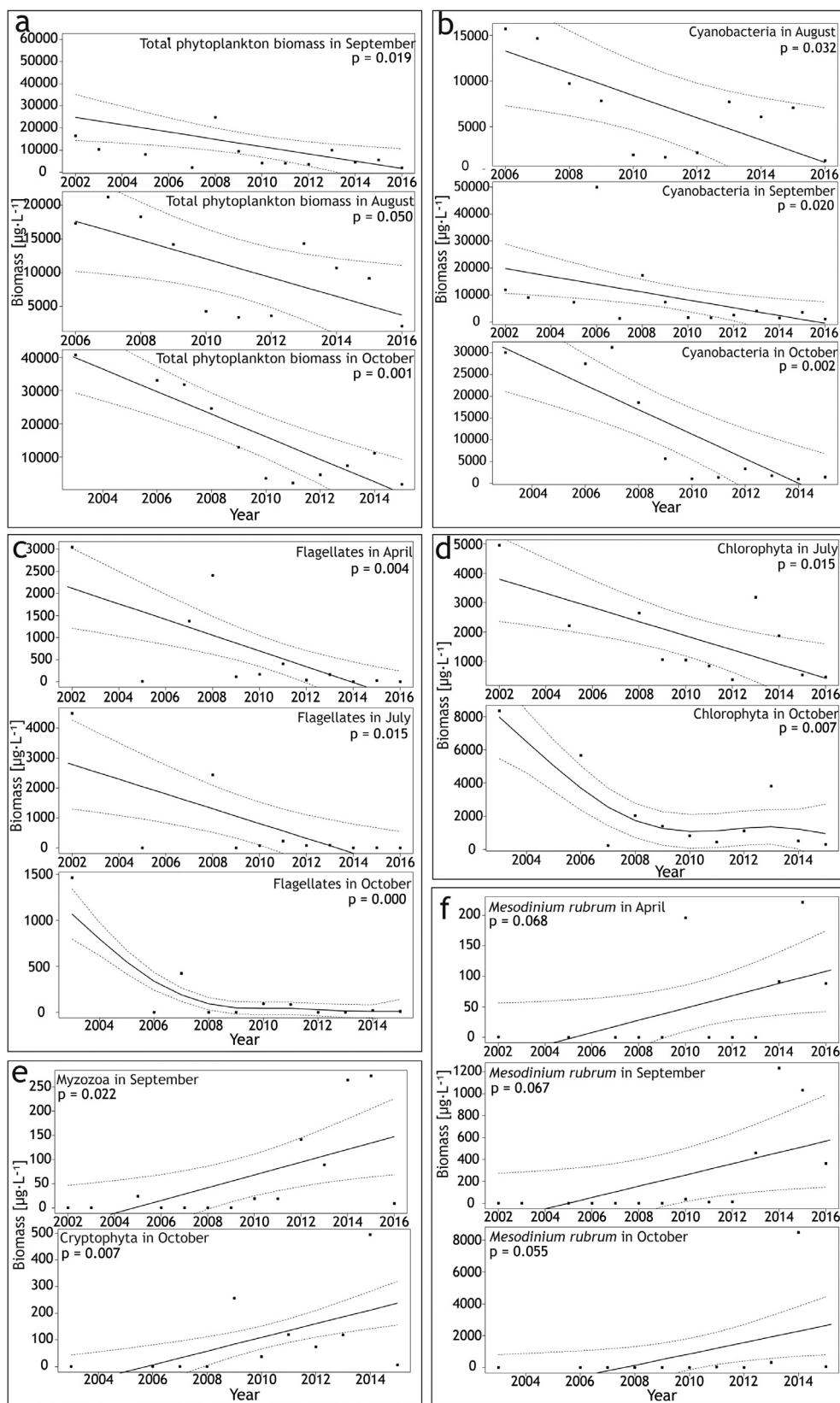**Figure 10** Significant long-term trends in total phytoplankton biomass (a) and biomass of Cyanobacteria (b), flagellates (c), Chlorophyta (d), Myzozoa and Cryptophyta (e), and *Mesodinium rubrum* (f) in VL. For variables with a statistically significant trend (p < 0.05), a GAM curve (solid line) is plotted with a 95% confidence interval (dashed line). Annual averages are plotted as filled squares.
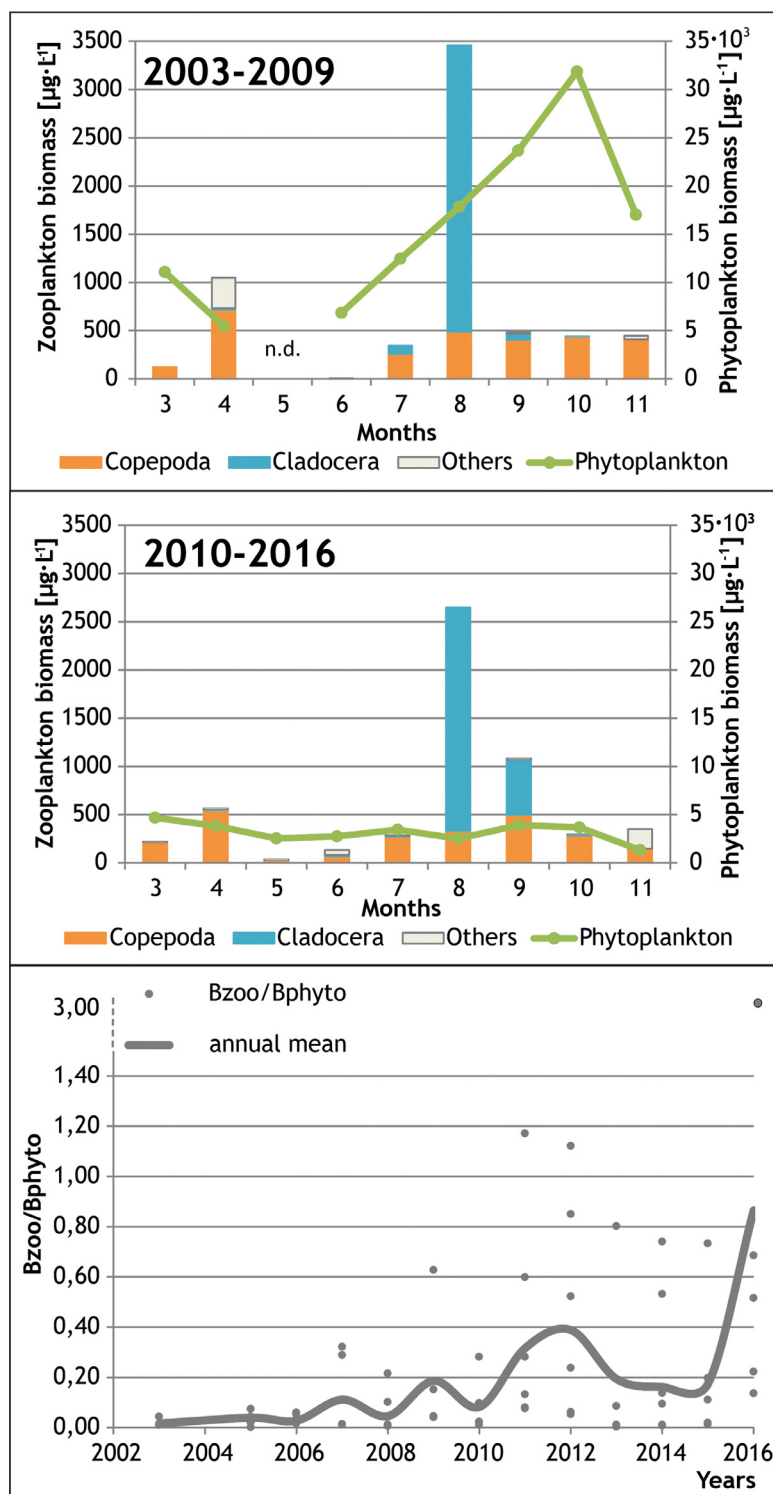
Figure 11 Comparison of monthly mean phyto- and zooplankton biomass at station KW in the differentiated periods (top and middle panels). Zooplankton to phytoplankton biomass ratio (B_{zoo}/B_{phyto}) in subsequent years (bottom panel). n.d. = no data.

1845, *Scenedesmus* Meyen, 1829, *Acutodesmus* (Hegewald) Tsarenko, 2001, and *Monoraphidium* belonging to phylum Chlorophyta. Among them, only *Tetraëdron* was included in the dominant taxa (Supplement Table 3). In April, a decreasing trend was determined for the dominant genus *Desmodesmus*. In summer months, however, this genus showed an increasing trend similar to those of *Dictyosphaerium* Nägeli, 1849 and *Tetrastrum* Chodat, 1895. Among the genera dominant in phylum Chlorophyta, *Pediastrum* Meyen, 1829 and *Oocystis* Nägeli ex A. Braun, 1855 showed no trend, and *Crucigenia* Morren, 1830 exhibited an increasing or decreasing trend depending on the month.

3.2.5. Ratio between zoo- and phytoplankton biomass

Throughout the study period, zooplankton biomass ranged between 4 μg L^{-1} in June 2005 and 64 000 μg L^{-1} in August 2016. The highest biomass was always observed in August. In spite of the evident seasonal variability of zooplankton, no significant variability was determined between years. During the period 2003—2009 in March, June, and September, zooplankton biomass was usually lower than in the years 2010—2016. In April, August, October, and November, the opposite dependency was observed (Figure 11, top and middle panels). The mean values of zooplankton biomass in the first and second period were very approximate, and reached 874 and 882 μgL^{-1}, respectively. During both study periods, i.e. 2002—2009 and 2010—2016, considerable differences occurred in the structure of the phytoplankton community (Subchapters "*Long-term changes in the taxonomic composition and phytoplankton biomass*" and "*Seasonal changes in phytoplankton biomass*"), but no substantial changes were observed in the development of the zooplankton community. These observations suggest that changes in the B_{zoo}/B_{phyto} ratio were associated with changes in phytoplankton biomass rather than zooplankton (Figure 11, bottom panel).

During the period 2003—2009, the B_{zoo}/B_{phyto} ratio gradually increased from 0.02 to 0.19. In 2010, it decreased to a value of 0.08, and from 2011, its further increase was observed until it reached a maximum value of 0.86 in 2016.

The Pearson rank correlation (r), used to evaluate the relations between zooplankton and phytoplankton biomass, demonstrated that total phytoplankton biomass was not correlated with the total zooplankton biomass or with any of the identified groups of zooplankton (Supplement Table 7). A correlation was determined for the total zooplankton biomass, including superorder *Cladocera*, with colony-forming coccal cyanobacteria from genera *Aphanocapsa*, *Cyanodictyon,* and *Lemmermanniella,* and the Chlorophyta *Monoraphidium*. *Rotifera* was correlated with phytoplankton phylum Euglenozoa and genus *Coelastrum* Nägeli, 1849 (Chlorophyta), whereas *Copepoda* was correlated with a very rarely occurring genera *Anabaenopsis* V.V.Miller, 1923 and *Phacotus* Perty, 1852.

4. Discussion

4.1. Abiotic and biotic variables as the potential drivers of the long-term changes in the structure of the phytoplankton community

A rapid improvement in water quality in the Polish part of VL since 2010 is suggested by SDD measurements showing an outstanding increase in water transparency. SDD measurements reveal not only the effect of plankton on water transparency, but also the effect of suspension originating from periodical intensive resuspension. Therefore, these are not the mean annual SDD measurements as such, but rather the amplitude of their values that are useful for the assessment of the trophic status of a water body (Kornijów, 2018; Margoński and Horbowa, 2003; Margoński et al., 2003). This interpretation is confirmed by results of the present study indicating a higher negative correlation of SDD with the total suspension (coefficient -0.71) than with the total phyto-

plankton biomass (coefficient -0.25) or Chl *a* concentration (coefficient -0.34).

Margoński and Horbowa (2003) observed significant changes in SDD measurements in the Polish part of VL between the 1950s and 1990s. The range of the recorded SDD was much broader (0.2—1.7 m) and the mean values higher during the 1950s than 1990s (0.1—1.1 m). An analogous situation occurred in the compared periods 2002—2009 and 2010—2016. The former period shows a continuation of the situation from the 1990s, with a characteristic low amplitude of the measurement values and highest transparency in April (maximum up to 1 m). The latter period (2010—2016) reflects the situation from the 1950s, with two peaks of the maximum transparency: a smaller one (approximately 1.5 m) in spring, and a higher one (even up to 2 m) in autumn.

Considerable differences between the two analysed periods also occurred in the taxonomic composition and biomass of phytoplankton, as well as Chl *a* concentration. The question arises as to what the cause of the observed changes in phytoplankton after 2010 could have been. Potential causes include abiotic factors (temperature and nutrients) as well as trophic interactions occurring in food webs.

The mean water temperature in the study period 2002—2016 (15.6°C) was 2.1°C higher than the mean value in 1953 (Szarejko-Łukaszewicz, 1957). This finding corresponds with the observations of Dailidienė et al. (2011), who estimated the warming trend of the mean surface water temperature in the lagoons of the southern and eastern Baltic Sea at 0.03°C year^{-1} (during period 1961—2008). An increase in temperatures, however, proved not to be significantly correlated with the phytoplankton biomass. Moreover, an increase in temperature occurred gradually; hence, this factor cannot be attributed to the considerable changes in phytoplankton observed at the turn of 2009 and 2010.

Changes in nutrient concentrations involved a gradual decrease in phosphorus, whereas changes in nitrogen fluctuated with no evident trend. In 2010, very low concentrations of both elements overlapped, including the mean as well as maximum values. Moreover, according to Burska et al. (2018), a significant decrease in the concentrations of not only total N and P but also their inorganic undissolved forms occurred during this period. Furthermore, the maximum concentrations of Si in 2010 proved the lowest in comparison to previous years. Therefore, the changes can be presumed to have been at least one of the causes of a decrease in the phytoplankton biomass in the Polish part of VL. This conclusion is confirmed by a statistically significant correlation between the total phytoplankton biomass and its different components, primarily showing a decreasing trend (Cyanobacteria, *Chlorophyceae, Woronichinia, Snowella, Oscillatoriales, Aphanotheceae/Anatheceae*) and phosphorus concentrations (as P-PO$_4$ and P$_{tot}$), and to a lower degree also with Si and N$_{tot}$ concentrations. This confirms our first hypothesis that one of the causes of the changes observed in the phytoplankton community could have been a decrease in the concentration of nutrients.

Among biotic factors controlling the development of phytoplankton from the top of the trophic pyramid (top-down effect), the greatest role is traditionally ascribed to grazing by filter-feeders, including zooplankton (Jeppesen et al., 1994; Moss, 1994). The comparison of phyto- and zooplank-

ton biomass presented in this study, however, suggest no significant role of zooplankton as a factor controlling phytoplankton development. The determined positive correlation of Cladocera biomass with colony-forming coccal cyanobacteria points only to the promotion of the growth of colonial cyanobacteria through the selective eating of competitive phytoplankton by selective filter-feeder cladocerans (Haney, 1987). It is, however, necessary to find a factor that would limit rather than promote the development of cyanobacteria with the strongest decreasing trend.

The feeding pressure exerted by zooplankton on phytoplankton can be determined based on the B_{zoo}/B_{phyto} ratio. The values of the coefficient provided for the Baltic lagoons refer to relatively short periods (Dmitrieva and Semenova, 2011; Kornijów et al., 2020; Krylova, 1985). They still correspond with the values measured by us for the same years of research.

The study results indicate a considerable increase in the B_{zoo}/B_{phyto} ratio beginning in 2010. A more thorough analysis of both components of the indicator, however, shows that the increased B_{zoo}/B_{phyto} ratio observed in recent years did not result from the elevated biomass of zooplankton. The zooplankton biomass was very similar in subsequent years of both compared periods. In contrast, the phytoplankton biomass during the second period was considerably lower than during the preceding period. Therefore, our second hypothesis regarding the limiting effect of zooplankton on the development of phytoplankton in the second study period was not supported.

Other efficient filter-feeders consuming phytoplankton may include e.g. bivalves (Derolez et al., 2020, Strayer et al., 1999). Until 2010, these organisms were represented only by *Dreissena polymorpha* Pallas, 1771 in VL. Their abundance, however, shows strong decreasing tendencies, and their current occurrence is scarce, patchy and limited to near-shore hard substrates (Rychter and Jabłońska-Barna, 2018). Therefore, it is difficult to attribute the effect on phytoplankton and suspension at the scale of the entire ecosystem to the bivalve.

The opposite conclusions can be drawn for another bivalve clam *Rangia cuneata* G.B. Sowerby I. 1832, a non-intentionally introduced alien species originating from the Gulf of Mexico. *R. cuneata* probably arrived in VL in the years of 2007—2008, and was first observed in the Russian part of VL in 2010 (Rudinskaya and Gusev, 2012). The clams probably appeared in the Polish part of the lagoon in 2008 or 2009, because the first reports concerning their presence originate from 2012 when it was already 30—40 mm in length (Warzocha et al., 2016).

During the period 2012—2016, the clam spread over the Polish part of VL, where it became the dominant component of the benthos. Its biomass periodically reached up to 1750 g/m^2 (Kornijów et al., 2018; Warzocha et al., 2016). Such high biomass had not been previously reported for any benthic invertebrate in VL.

The literature provides examples of the strong controlling effect of *R. cuneata* on phytoplankton, resulting in an improvement of water transparency and recovery of submerged vegetation at the biomass several times lower than in VL (e.g., Cerco and Noel, 2010 in oligohaline and tidal fresh regions of the Chesapeake Bay; Wong et al., 2010 in the coastal lakes of south-eastern Louisiana).

The appearance of *R. cuneata* in VL coincided with a decrease in the phytoplankton biomass and considerable structural changes in the community, particularly in the case of Cyanobacteria. These changes could have been both directly caused by the clam through filtration, and indirectly through the utilisation of phosphorus compounds deposited in bottom sediments (Tenore et al., 1968). In addition to detritus, sand, organic matter, remnants of vascular plants, and bacteria derived directly from the sediments, several dozen species of phytoplankton (Hopkins et al., 1973; Olsen, 1976), including cyanobacteria as well as diatoms (Rudinskaya and Gusev, 2012) have been identified in the stomachs of *R. cuneata*.

It is worth mentioning, however, that after the appearance of the *R. cuneata* population, changes in the phytoplankton of the Russian part of the lagoon were different. They involved a considerable decrease in the contribution of Chlorophyta and diatoms in the total phytoplankton biomass (Semenova and Dmitrieva, 2013). At the same time the contribution of Cyanobacteria in the total phytoplankton biomass considerably increased, resulting in a competitive advantage when the biomass of Chlorophyta decreased.

Next to a drop in nutrient concentration, the sudden appearance and rapid development of the *R. cuneata* population at the end of the first decade of the 21st century could have likely been an additional cause of a decrease in the phytoplankton biomass at the turn of 2009 and 2010. After all, both factors (nutrients and *R. cuneata*) could have permitted a new balance between phytoplankton and filtering invertebrates, including zooplankton. As a result, the current values of the B_{zoo}/B_{phyto} ratio are a promising predictor for the efficient control of phytoplankton by zooplankton, especially that it is accompanied by a gradual decrease in nutrient load.

4.2. Impact on the environment quality

The phenomena described above, observed in the environment of VL (a decrease in nutrient concentration, and particularly P_{tot}; increase in water transparency; decrease in phytoplankton biomass, and increase in the B_{zoo}/B_{phyto} ratio), point to the improvement of its ecological state since 2010, i.e. from the moment of appearance of *Rangia cuneata*. Other consequences of the changes also deserve attention, such as a decrease in Cyanobacteria biomass and decrease in Chl *a* maximum concentration.

According to Wasmund et al. (1998), nitrogen-fixing Cyanobacteria can be considered as "blooms" at a biomass concentration of approximately 200 μg L^{-1}. Current calculations revealed that even after 2010, the average biomass of nitrogen-fixing Cyanobacteria is still much higher than 200 μg L^{-1} (1016 μg L^{-1}), although it decreased 3.6 times in comparison to those from the period 2002—2009. Statistical analyses showed no significant trends in the biomass of potentially toxic diazotrophic cyanobacteria causing blooms from genus *Dolichospermum,* but an increasing trend occurred in August for *Aphanizomenon*. The shift in the occurrence of blooms in months is very interesting. Before 2010, diazotrophic Cyanobacteria occurred from June to November with a maximum in September, but after 2010, they started blooming earlier, from May to September, with a

maximum in June and August. This phenomenon is proba-
bly related to the filtration activity of *R. cuneata* during
the summer season, or to the ongoing climate change in
the Northern Hemisphere. Both experimental results and
models have indicated that cyanobacteria respond more
strongly to the climate change than do diatoms or Chloro-
phyta (De Senerpont Domis et al., 2007; Moore et al.,
2008).

In addition to nitrogen-fixing Cyanobacteria, a signifi-
cant seven-fold decrease in biomass after 2010 occurred
in orders Chroococcales and Synechococcales. These orders
were abundant in VL year round, with particular intensity
between March and November. Within the aforementioned
orders, decreasing trends in months from August to October
were observed in the following genera dominant in the to-
tal cyanobacterial biomass: *Woronichinia, Snowella, Cyan-
odictyon*, and *Aphanotheceae (Anatheceae)*. Genus *Woroni-
chinia* and morphologically similar genus *Snowella* are char-
acteristic of standing-water ecosystems. The *Woronichinia
compacta* (Lemmermann) Komárek & Hindák, 1988 complex
was predominant in the Polish part of VL, and is known as
a dominant species in eutrophic ecosystems, including lakes
(Nowicka-Krawczyk and Żelazna-Wieczorek, 2017) and the
Curonian Lagoon connected to the Baltic Sea (Krevs et al.,
2007). According to Sagert et al. (2008), *W. compacta* oc-
curring along the German coast of the Baltic Sea can be
considered a species indicating an increase in eutrophica-
tion. Therefore, a considerable decrease in the biomass of
the species in the Polish part of VL confirms a decrease in
the level of eutrophication in the water body. A decrease in
the biomass of *Woronichinia* could have also had a positive
effect on zooplankton invertebrates. Representatives of the
genus often blooming in the plankton of meso-eutrophic to
eutrophic water bodies have been found to be able to pro-
duce toxins (microginin FR3) active towards invertebrate
zooplankton (Bober and Bialczyk, 2017).

Mean Chl *a* concentrations did not differ significantly
between the start and end of the study period, and were
maintained at the same level as concentrations recorded
by Margoński and Horbowa (2003), Renk et al. (2001) and
Witek et al. (2010) throughout the period 1970—2000. This
stability of the mean Chl *a* concentrations over more than
45 years is interesting in the context of evident changes
in phytoplankton biomass. Although the Pearson rank cor-
relation (r) demonstrated positive correlations between
total phytoplankton biomass and Chl *a* concentration, max-
imum Chl *a* concentrations were better harmonised with
phytoplankton biomass (Figure 5). This was not the exact
relationship, however, because the highest peak of Chl *a*
in 2002 did not correspond to the highest phytoplankton
biomass recorded in 2006. This is because the concentration
of Chl *a* depends on the phytoplankton species composi-
tion, development stage, and environmental conditions. A
particularly large discrepancy between the Chl *a* concen-
tration and phytoplankton biomass is observed at the high
abundance of picoplankton organisms in the environment
(Albertano et al., 1997; Hawley and Whitton, 1991), as is
the case for VL. The picoplankton fraction cannot be prop-
erly analysed by means of the Utermöhl method applied in
this study, because the colonies of very small cells, solitary
Cyanobacteria, and Chlorophyta in the picoplankton range
are often overlooked (Albrecht et al., 2017). Reliable

quantitative counting of the picoplankton fraction requires
fluorescence microscopy or flow cytometry (HELCOM, 2017).
The decreasing tendency of the maximum Chl *a* concen-
trations indicates a less intensive or shorter duration of
phytoplankton blooms. From this point of view, Chl *a* con-
centrations found in VL also suggest better environmental
quality of this estuary during the second study period. Based
on the above, our third hypothesis regarding the progressive
improvement of water quality in the Vistula Lagoon was
confirmed.

5. Conclusions

1. The turn of 2009 and 2010 marked a breakthrough in
   the recent history of the phytoplankton community (its
   biomass and taxonomic structure) in the Vistula Lagoon.
2. The range of variability of phytoplankton biomass was
   considerable in time, in both the multiannual and sea-
   sonal aspect, and inconsiderable in space.
3. Evident decreasing trends of changes occurred in sum-
   mer and autumn months from July to October, and were
   determined for Cyanobacteria and Chlorophyta, reaching
   the highest contribution in the total biomass.
4. The most probable factors that caused a decrease in the
   phytoplankton biomass included a simultaneous decrease
   in the concentrations of all nutrients (N, P, Si) in 2010,
   and the occurrence of a new filter-feeder *Rangia cuneata*
   at the same time. Due to the lack of availability of spe-
   cific data on the development dynamics of the clam in
   VL, however, its impact on phytoplankton remains largely
   undetermined. Final confirmation of this conclusion re-
   quires further research.
5. A decrease in phytoplankton biomass triggered a de-
   crease in the Chl *a* concentration, increase in the water
   transparency, and increase in the B_{zoo}/B_{phyto} ratio. The
   observed changes point to an improvement of the eco-
   logical state of the Polish part of VL.

Vistula Lagoon. Finally, we thank the Reviewer and the Editor for their valuable comments on the first version of this manuscript.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at https://doi.org/10.1016/j.oceano.2020.08.004.

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