Original Research

Effects of Hydrological and Physicochemical Factors on Phytoplankton Communities in Floodplain Lakes

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Abstract

The fate of phytoplankton communities in different hydrological and hydrochemical conditions was studied in the middle basin of the Biebrza River (NE Poland). Our results showed that hydrological connectivity significantly influenced phytoplankton abundance in floodplain lakes: minimal abundance was stated in lotic and maximal in lentic waterbodies. Phytoplankton diversity and species richness were related to changes in water levels. During the low-water phase, phytoplankton biodiversity was the lowest in lentic and the highest in lotic lakes. High water levels promoted exchanges in species among waterbodies and the river, which increased biodiversity indices. We concluded that the isolation of any floodplain lake from the river channel deteriorates its trophic conditions. Thus, the decrease in phytoplankton biodiversity in floodplain lakes should be regarded as an indirect feedback of the hydrobionts on the hydrological factors.

Keywords: phytoplankton, floodplain lakes, lowland river, water quality, hydrological connectivity

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Introduction

Cut-off channels, spreading along both sides of river beds, enrich the hydrographic and biocenotic structure of floodplains [1, 2]. Their value results from a wide spectrum of ecological benefits, including water purification processes, flood control, habitat features for freshwater biocenoses, and landscape virtues [2, 3]. Contrary to common opinion on boring semi-circle shapes and the similarity of morphometric and biocenotic features, the floodplain lakes located in lowland peat-formed floodplains are characterized by extremely abundant diversity of shapes, dimensions, and hence reactions toward hydrobiological processes [4, 5]. This diversity determines the changes of chemical components and the method of their internal circulation mainly due to the exchange at the boundary of aquatic environments and bottom sediments and bio-sorption, as well as the supply of components from a catchment, suitable for phytoplankton growth.

Resulting from applying new theories, e.g. flood pulse concept [6], flow pulse concept [7], and river continuum concept [8], recent years brought a considerable change in perception of a relationship between rivers and river-dependent aqueous ecosystems. Thus, the classification of aquatic ecosystems within floodplains proposed by Amoros and Roux [9] has been adopted worldwide, as it is based on the hydrological connectivity between present and former river channel sections, which is indicative of water exchange conditions and water retention time. The authors distinguished the following functional units: eupotamic (main channel and active side-channels), parapotamic (abandoned river meanders or channels with a downstream-arm connection, or backwaters), plesiopotamic (side channels and depressions with water table at high water levels), and paleopotamic (old river beds totally isolated from the river during low water stages). Hydrological typology of floodplain lakes, based on differences in the water movement, distinguishing lentic, semi-lotic and lotic habitats, is also used in the literature [10]. Regardless of the distinguished hydrological types, floodplain lakes provide valuable habitats for numerous representatives of fauna and flora [11-14]. The significant role of floodplain lakes in promoting phytoplankton biodiversity as well as their ecological values provide numerous studies carried out for the Vistula River [13, 15, 16], Bug River [17-19], and 52 oxbow lakes of 10 hydrobiologically diversified rivers [20]. An interesting analyses of qualitative and quantitative composition of phytoseston have also been preformed for a river-lake system for the Płociczna River in Drawieński National Park [21]. Taxonomical composition of phytoplankton in the floodplain lakes along the Biebrza River floodplain have already been recognized by Frąk et al. [22] and Hutorowicz et al. [23, 24]; however, their research did not contain a factorial approach.

Phytoplankton in floodplain lakes is determined by changes in many abiotic and biotic parameters in time and space [13, 25]. Among abiotic parameters the most important are nutrient availability and hydrological conditions. Phytoplankton abundance and biomass is related to the trophic status of each waterbody [26, 27]. In the case of lower trophy the diatom dominance was recorded by Frąk et al. [22] and Hutorowicz et al. [24]. Fertile water is usually distinguished by a higher share of cyanophytes and/or dinoflagellates, which was reported by Dembowska et al. [16], Owsianny et al. [20], or Padisák et al. [26], as well as euglenoids, which was stated both by Ligęza and Wilk-Woźniak [15] as well as Padisák et al. [26].

Hydrological processes are key factors in controlling the productivity and development of floodplain lakes. Overbank floodings change biotic and physico-chemical properties of aquatic habitats and allow for the exchange of matter and organisms among the ecosystems. During floods, a floodplain retains particular organic matter (POM) and can be an important source of organic compounds [28, 29] and plankton development [25]. After a flood event more homogenous distribution of the phytoplankton and decrease in its abundance and biomass was reported by Kasten [11]. In the phase of low water, when periodic isolation of lentic floodplain lakes occurs, higher phytoplankton abundance and biomass was recorded [17, 18]. During low water periods the most significant differences between riverine and floodplain lake phytoplankton communities, in terms of the phytoplankton structure, have been stated as well.

Genuine riverine phytoplankton (potamophytoplankton) is dominated mainly by diatoms and/or chlorophytes due to water velocity and turbulence [24, 30]. Lentic habitats are characterized by a greater stagnation of water (water retention time) and a higher share of flagellates algae [15, 18, 26]. In eutrophic floodplain lakes, similar to dammed eutrophic rivers [31], mass development of cyanophytes also has been recorded [16]. Pasztaleniec et al. [18, 19] also pointed out that the differences in phytoplankton parameters among biotic parameters are related to the presence/absence of macrophytes and their composition.

The knowledge of biogeochemical processes taking place in floodplains under certain climatic and hydrologic conditions is the basis of any activity toward conservation of natural values of its aquatic ecosystems. It concerns the Biebrza River, one of the few mean-sized rivers in Europe, which remained unaltered. The river and most of its tributaries have not been modified or polluted. Similarly, its catchment area, in spite of wetland drainage, has kept its natural character.

In our study we are presenting the diversity of plankton communities on the background of hydrological and hydrochemical properties of waterbodies located in a peat-formed floodplain of the Biebrza River. We have anticipated that the attribute of natural character of the floodplain lakes promotes high phytoplankton species diversity as well as densities. Thus, the aim of the present paper is to test a hypothesis that hydrological connectivity and hydrological conditions influence phytoplankton biodiversity in floodplain lakes. We assumed also that more fertile lentic water bodies create better conditions to phytoplankton growth then the lotic ones.

Material and Methods

Study Area and Site Description

Biebrza is a medium-sized low-gradient river in NE Poland. Its total catchment area amounts to 7,057.4 km^2, while the floodplain covers 1,950 km^2. The river slope is typical of lowland rivers and varies from 0.06 to 3.33‰. The river crosses fen meadows and marshes. It meanders considerably throughout its course and forms a large number of old riverbeds and floodplain waterbodies in different stages of succession. Despite intensive dewatering of the catchment area in mid-1970s, almost the whole floodplain of the river has not been altered by human activity and natural character of river flow and hydrological pattern are almost wholly preserved, never having being dammed, diverted, regulated, or embanked [32]. In the Biebrza River Valley three basins have been distinguished: the upper, middle, and lower, based on the differences in geomorphological structure. The middle basin of the Biebrza River is approximately 33 km long and spreads along its floodplain between villages of Osowiec and Sztabin [33]. The floodplain is peat-covered on the area of 450 km^2. The peat is 1-3 m thick and underlain by sands, with silts and clay within the area of interest.

The hydrological regime of the Biebrza in its middle course has a natural pattern of high and low water levels fluctuating within the range of 264 cm. According to the classification of the regimes of Polish rivers by Dynowska [34], the Biebrza is characterized by a snowy, distinctly formed regime, with a domination of intensive spring floodings. The average multiannual flow (1984-2012) at the gauge in Osowiec amounts to 22.78 $m^3 \cdot s^{-1}$ within the range from 3.08 to 360.00 $m^3 \cdot s^{-1}$. The ratio of annual mean maximal and minimal flows (MQmax/MQmin) was 6.2, while the ratio of extreme flows (HQ/LQ) reached 117. Irregularity of flows was confirmed by a relatively high variability coefficient *cv* = 17%.

The most important factor of ecological functioning of floodplain lakes along the Biebrza is the reach, depth, and length of the periods of inundations (> bankfull level (BFL). During the spring, the narrow river swells to form a vast shallow impoundment, in places a kilometer wide and lasting for several months. The long periods of saturation create ideal conditions for mosses. In this stable undisturbed environment, the deposits accumulate to form peat, in places up to 10 m deep, and estimated to be more than 10,000 years old [33]. The vast wetland area created by the abundance of floodplain water bodies and regular flooding has abundant diversity. River floodwater aids the maintenance of species rich, moderately nutrient-rich fen, and meadow vegetation. The whole river except for 10 km is within Biebrzański National Park and protected under the Ramsar Convention.

Study sites have been located on three floodplain lakes with local names: Bednarka (BED), Mostek (MOS), and Glinki (GLI), as well as in the main river channel of the Biebrza River at Goniądz (Fig. 1). The floodplain lakes under this study show a wide spectrum of hydrological connectivity: from lotic (*eupotamal*) habitats (Mostek), through semi-lotic (*parapotamal*) (Glinki) until lentic (*plesiopotamal*) habitats of distinct periodical river-depended supply (Bednarka). Bednarka, although connected by narrow (ca. 1.0 m wide) canals with the Biebrza River channel, is a lentic habitat due to periodic isolation from the main river channel during low and mean water stages. Glinki is connected with the river channel via the downstream arm and represents a typical zonation for semi-lotic habitats: from lotic (downstream arm) till stagnant waters (upstream arm). Mostek is a fully passable side-arm with properties typical of lotic habitats. Morphometric details of the studied floodplain lakes are given in Table 1.

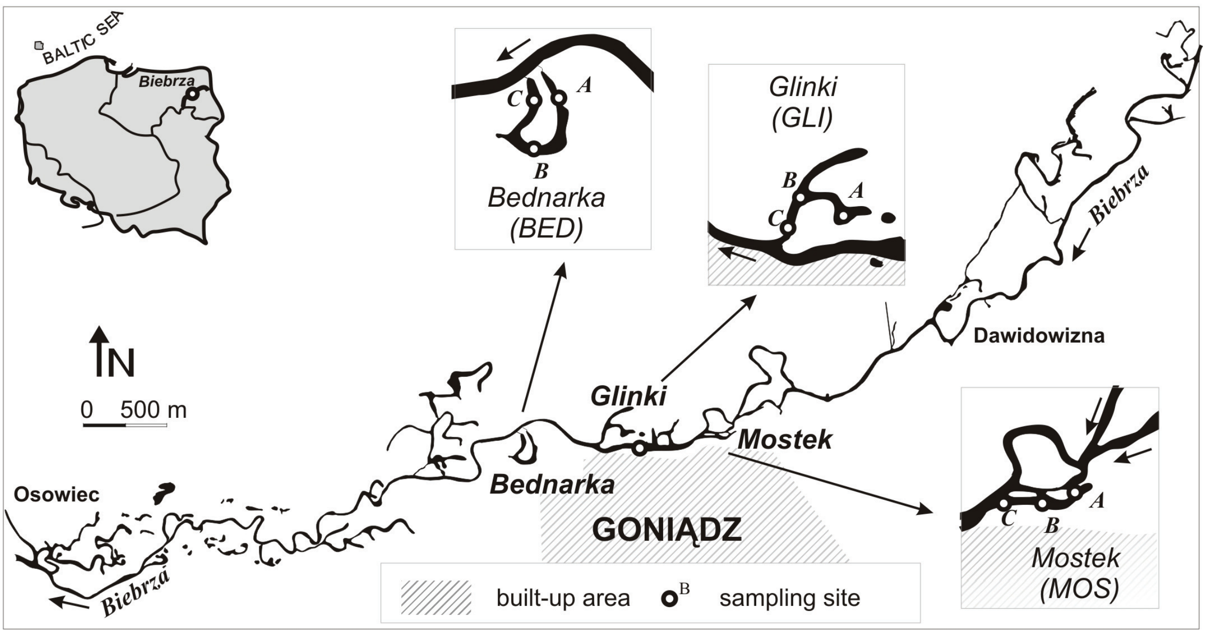


Fig. 1. Location of study sites in the middle basin of the Biebrza River.

Table 1. Morphometric characteristics of the studied floodplain lakes in the middle basin of the Biebrza River.

Floodplain lake (local name)	Hydrological type of floodplain lake	Geographical coordinates	Area (ha)	Length (m)	Avr. width (m)	Max. depth (m)	Max. distance from the river channel (m)
Mostek (MOS)	Lotic (eupotamon)	N:53º29'35.9" E:22º44'15.95"	0.62	306	20	1.4	50
Glinki (GLI)	Semi-lotic (para-potamon)	N:53º29'40.29" E:22º43'28.94"	1.48	459	32	5.5	226
Bednarka (BED)	Lentic (plesio-potamon)	N:53º29'31.51" E:22º42'43.46"	2.16	740	29	2.6	313

Sampling and Analytical Procedure

Phytoplankton was collected twice a year in June and September, 2011-12, from three floodplain lakes and the river. The sample collection site took place from a boat from three sites in each reservoir and one sample was taken from the river (Fig. 1). For quantitative analyses, unthickened samples were collected from beneath the surface directly into bottles (20 ml), i.e., at a depth of approximately 0.10 m. Sampled material was preserved with Lugol's solution. The counting units were cells, colony, and trichomes with length of 100 µm. Phytoplankton abundance was determined according to the Utermöhl method [36] using an inverted microscope (Olympus CX 41). Additionally, phytoplankton was collected from the surface water column with a plankton net (10 µm). The Shannon-Weaver diversity index (H') was calculated with the help of Past v.2.17c software.

Water for chemical analyses was sampled simultaneously with phytoplankton sampling. *In situ* measurements of dissolved oxygen (DO), pH, electrolytical conductivity (EC), and total dissolved solids (TDS) were done using calibrated multiparameter probes YSI 6600R2 and YSI Professional Plus. Water transparency was measured with a Secchi disk. The content of orthophosphates, nitrates, nitrites, and ammonium ions as well as macroelements: main cations, and anions were determined in the water samples as well. Standard methods of analyses were applied for the determinations [36]. Colorimetric measurements were done using a Shimadzu UV 1601 spectrophotometer. Total organic carbon (TOC) concentration was determined in unfiltered samples; dissolved organic carbon (DOC) was quantified following filtration through 0.45 µm pore size nitrocellulose membrane filters (Millipore). TOC and DOC were analyzed via high-temperature combustion (HTC) (Shimadzu TOC 5000 analyzer, Japan). Standards were prepared from reagent grade potassium hydrogen phthalate in Milli-Q Plus Ultra Pure Water. Samples and standards were acidified to pH 2 with 2M HCl and purged with carbon dioxide-free carrier gas for 5 min at a flow rate of 125 $ml \cdot min^{-1}$ to remove inorganic carbon prior to injection onto a heated catalyst bed (0.5% Pt on alumina support, 680ºC, regular sensitivity). A non-dispersive infrared detector measured carbon dioxide gas from the combusted carbon. Each sample was injected 3 times. The coefficient of variation (*cv*) for the repeated analysis was 2% [37].

Statistical Procedures

To assess the general differences among floodplain lakes, physico-chemical parameters of water and the phytoplankton abundance, non-parametric analysis of variance was applied. The statistical analysis consisted of the Shapiro-Wilk's test ($P<0.05$), to test the assumption of normality, followed by non-parametric Kruskal-Wallis and Dunn's tests ($P \leq 0.05$). Correlation coefficients were calculated with the use Spearmann ranks ($P \leq 0.05$). The response of the phytoplankton communities to the environmental conditions was analyzed using multivariate statistical analyses. Detrended correspondence analysis (DCA) and redundancy analysis (RDA) (CANOCO 4.5 for Windows [38]) were used to analyze data of phytoplankton abundance. DCA was used first to determine the character of variability in the studied assemblages: if the length of the first gradient is greater than 2 standard deviations, we can assume a unimodal variation; a length smaller than 2 SD indicates a linear variation [39].

The length of the first gradient for the phytoplankton communities amounted to 1.64 SD, which indicated a linear variation, providing justification for the further use of redundancy analysis. RDA is a direct gradient analysis that summarizes relations between phytoplankton species and environmental parameters [39]. RDA was used to obtain an overview of the combined effects of water quality parameters and retention time, distance from the river channel, and water level at the community level. Statistical significance of the canonical axes was determined using Monte Carlo permutation tests [39]. The forward selection was to find a sufficient subset of the explanatory variables that represents the relationship between the species and environmental data (Table 3). The dataset was centered by species, as it is obligatory for the constrained linear method (RDA). RDA detects a gradient along which all species are correlated. The variance explained by the first (canonical) axis is represented by its eigenvalue ($\lambda 1$). Statistical significance of variable correlations λ was:

$$((Axis\ 1 + Axis\ 2)/Sum\ of\ canonical\ eigenvalues)\times 100$$

Thus, $\lambda > 0.3$ was considered a strong gradient, while $\lambda > 0.4$ a very good separation of species.

Generalized additive model (GAM, $P \leq 0.05$) has been provided towards correct interpretation of ordination dia-

Table 2. Select physico-chemical parameters of floodplain lakes water (mean and ±standard devations (±SD)) and the Biebrza River.

Ecosystem	Mostek lotic habitat		Glinki semi-lotic habitat		Bednarka lentic habitat		Biebrza River	
Parameter	Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD
pH, –	7.77	0.25	7.79	0.30	7.98	0.16	7.94	0.31
EC, $\mu S \cdot cm^{-1}$	550.7[a]	97.5	698.1[b]	148.9	533.1[a]	71.9	513.8[a]	85.9
TDS	360.4[a]	63.4	453.6[b]	96.8	341.7[a]	50.6	333.5[a]	56.5
DO	7.70[a]	1.43	8.07[a]	1.41	7.56[a]	1.33	8.52[b]	1.90
DO, %	78.98	11.39	80.78	11.71	79.55	13.23	87.83	12.77
COD-Cr	37.59	9.87	42.98	9.95	41.68	12.31	35.65	9.11
NO_2^--N	0.019	0.015	0.005	0.003	0.007	0.003	0.012	0.009
NO_3^--N	0.23[b]	0.08	0.12[a]	0.03	0.12[a]	0.02	0.18[a]	0.12
NH_4^+-N	0.12	0.03	0.24	0.10	0.33	0.43	0.17	0.12
TN	1.16	0.33	1.61	0.45	1.58	0.63	1.12	0.25
PO_4^{3-}-P	0.13	0.08	0.05	0.02	0.07	0.03	0.10	0.03
TP	0.27	0.16	0.34	0.15	0.40	0.25	0.23	0.15
TOC	11.79	4.37	18.77	4.61	15.04	6.04	12.89	1.51
DOC	9.77	3.68	15.56	3.04	11.22	2.68	10.47	1.16
HCO_3^-	203.4[a]	16.6	260.8[b]	24.5	211.1[a]	8.3	226.5[a]	40.1
Cl^-	10.96[a]	2.38	24.22[b]	8.71	10.25[a]	1.71	9.75[a]	2.06
Ca^{2+}	71.18	5.65	78.58	9.01	73.62	2.77	69.90	4.35
Na^+	9.89[a]	1.89	26.03[b]	10.10	8.33[a]	0.64	8.95[a]	1.01
K^+	3.75	1.20	3.09	0.98	2.83	0.53	3.20	0.74
Mg^{2+}	13.62[ab]	2.60	15.34[b]	1.55	14.05[ab]	1.26	12.58[a]	2.20

Units except those indicated in the table are $mg \cdot L^{-1}$. Different letters denote groups of significantly different means among water quality parameters in the oxbow lakes and the Biebrza River in a nonparametric Kruskal-Wallis test, followed by the Shapiro-Wilk test for normality, $P \leq 0.05$, N=40.

grams computed for the Shannon-Weaver biodiversity index of phytoplankton in relation to water levels using CANOCO for Windows 4.5 software. Terms that were not significant ($P \geq 0.05$) were dropped from the model. The Akaike information criterion (AIC) is given in the model. The GAM built here was useful to model biodiversity index/habitat relationships, and to predict its spatial variations.

Results

Hydrological Conditions

Hydrological conditions of the Biebrza River in the period of study (2011-12) characterized by higher water stages in comparison to multiannual period of 1984-2010. The periods of inundation in 2011 and 2012, calculated as a share of days exceeding bankfull level (BFL= 107.70 m a.s.l) amounted to 29 and 23, respectively (Fig. 2A). Prolonged spring flooding creates a system of hydraulic and ecological connectivity among all water ecosystems in the floodplain (Fig. 2B). The years 2011 and 2012 were hydrologically different. Fluctuations of water table in 2011 amounted to 200 cm, while in 2012 to 80 cm. Stages below low water level (LWL) occurred only in 2011 and lasted 8% of the year. The differences in a pattern of water level fluctuations were advantageous for our hydrobiological studies.

Hydrochemical Properties of Water

The hydrological conditions in the Biebrza River-floodplain system influenced the hydrochemistry to a varying degree. The physical parameters as well as nutrient dynamics during the investigation period showed considerable differences between the studied objects presented in Table 2. Water in the floodplain lakes was characterized by medium mineralization (334-454 $mg \cdot L^{-1}$) and electrolytic conductivity (514-698 $\mu S \cdot cm^{-1}$). Lower values in the brackets represented lotic habitats while higher values were associated with lentic habitats. Water had a slightly basic pH (7.77-8.03). The dominant hydrogeochemical process found in the Biebrza peatlands is dissolution of calcium carbonate-containing minerals. Thus the contents of HCO_3^- and Ca^{2+} was high and ranged from 203 to 261 mg·L^{-1} and from 69.9 to 78.6 mg·L^{-1}, respectively. Organic matter from allochtonic sources as leaching of peatlands is in the form of humic compounds and decay of organic litter. Increase in COD was observed at higher water levels (in 2012) when humic compounds supplied the lakes.

The content of total sum of mineral forms of nitrogen (TIN) was similar in studied floodplain lakes (0.35-0.45 mg·L^{-1}), but the contribution of each N-form differed in relation to retention time: in lentic habitats ammonium nitrogen dominated (69%), whereas in lotic nitrate nitrogen dominated (62%). In the river water, the share of both N forms was equal and amounted to 48%. Also, the differences between the NO_3^--N and PO_4^{3-}-P concentrations in the river water and floodplain lakes decreased with increasing lentic character of ecosystems. Among water quality parameters only dissolved oxygen concentrations differentiated the Biebrza River from the studied floodplain lakes (Table 2). River water oxygenation was statistically higher (8.52 mg DO·L^{-1}; Dunn's test, $P \leq 0.05$) and more stabile when compared to other habitats.

Analysis of RDA (Fig. 3A) showed that water retention time, TN, NH_4^+-N, COD, Ca^{2+}, and transparency were highly correlated with the first component Axis 1 (41.7 % of variance). These variables can be directly related with the gradient of enrichment with nutrient turnover. On the other hand, other mineral forms of nitrogen (NO_3^--N, NO_2^--N), orthophosphates (PO_4^{3-}-P) as well as TOC and DOC, Na^+, Cl^-, HCO_3^- and water retention time were significantly correlated with the second component (23.1% of variance), (Table 3).

Water sampled at three sites within each lake showed a significant heterogeneity of its physico-chemical parameters, particularly in the case of semi-lotic habitats (Bednarka and Glinki). A distinct gradient along the backwater (Glinki) was detected for dissolved oxygen concentration, which decreased from site C near the connection to the river channel (8.90 mg DO·L^{-1}), through middle part B (7.98 mg DO·L^{-1}) until site A in the upstream part (7.34 mg DO·L^{-1}). A clear but increasing tendency was observed for COD between the same sites C-A (40-45 mg·L^{-1}), NH_4^+-N (0.17-0.34 mg·L^{-1}), TN (1.39-1.84 mg·L^{-1}) and Ca^{2+} (70.60-84.27 mg·L^{-1}). Among the studied floodplain lakes, Glinki was significantly different from the other two ecosystems in terms of the highest values of NH_4^+-N, HCO_3^-, Cl^-, and Mg^{2+}, which created the groups of homogenous means in Dunn's test (P<0.05). Significantly lower water quality parameters showed the river water and Mostek as for NO_3^--N (0.18 mg·L^{-1}), but higher as for PO_4^{3-}-P (0.12 mg·L^{-1}).

Based on the cluster analysis of physico-chemical variables of water quality (Ward's method, Fig. 4) there is a clear gradient of dissimilarity between river water and the increase in water retention time in the studied floodplain lakes. Thus, more lentic habitat (Glinki), particularly at sites located a distance from the main river channel (A: see

Table 3. The explanatory variables selected that represent a significant relationship between the species (marginal and conditional effects).

Variables	Marginal Effects	Conditional Effects		
	λ 1	λ A	*P*	F-value
Water retention time	0.16	0.16	0.004	6.65
TN	0.10	0.04	0.054	2.32
HCO_3	0.09	0.08	0.008	3.74
NO_2-N	0.07	0.07	0.018	3.16
NH_4-N	0.07	0.03	0.046	2.29
Water level	0.05	0.06	0.016	3.41
TDS	0.04	0.10	0.004	6.91
DOC	0.03	0.03	0.040	2.69
TOC	0.03	0.05	0.044	2.31

Lambda denotes the amount of variability in the species data that would be explained by a constrained ordination model using that variable as the only explanatory variable.
Variables not used in the table were statistically insignificant.

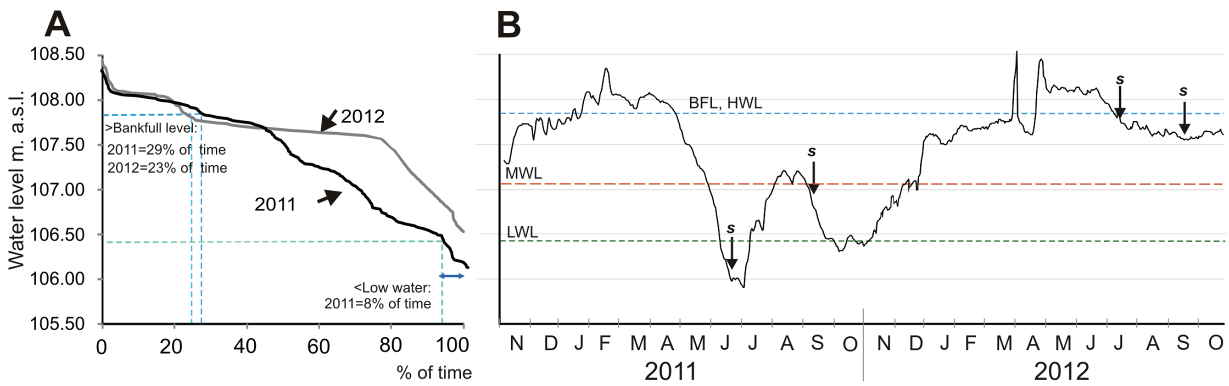
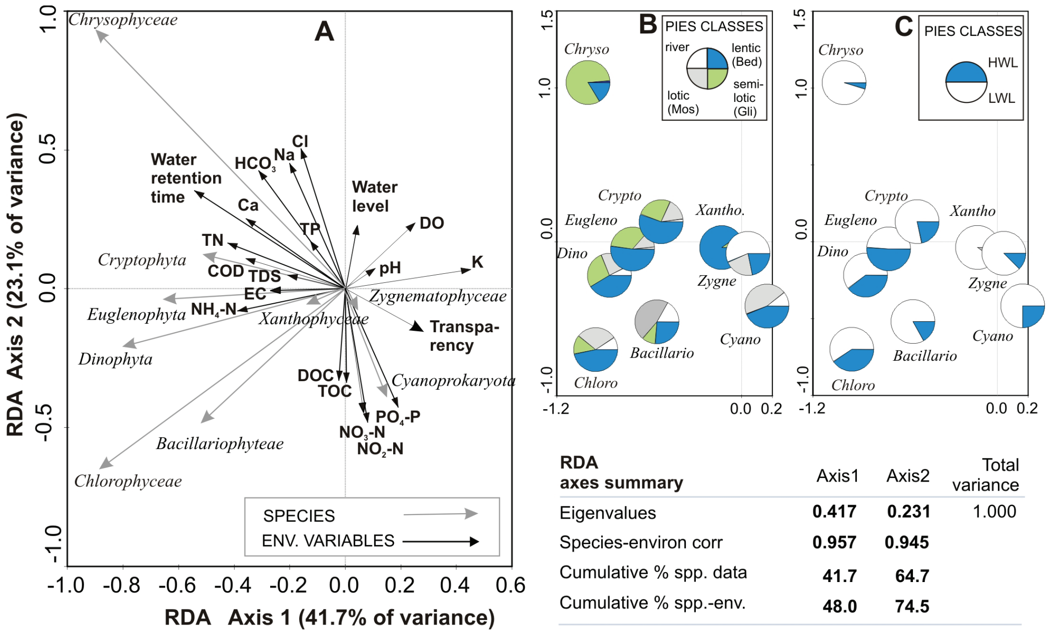


Fig. 2. Hydrograph of water levels in the Biebrza River extrapolated from Osowiec gauge station to the cross-section at Goniądz for two hydrological years (2011 and 2012). The levels of BFL (bankfull level), HWL (high water level), MWL (mean water level), and LWL (low water level) have been calculated for the period of 1984-2012. Arrows with "s" denote sampling events.



RDA axes summary	Axis1	Axis2	Total variance
Eigenvalues	0.417	0.231	1.000
Species-environ corr	0.957	0.945	
Cumulative % spp. data	41.7	64.7	
Cumulative % spp.-env.	48.0	74.5	

Fig. 3. (A) Ordination plot of Redundancy analysis (RDA) for phytoplankton communities (species) and hydrological and hydrochemical data (environmental variables) for floodplain lakes and the Biebrza River. (B) Relative values of phytoplankton communities in pie classes represented by hydrological types of floodplain lakes. (C) Relative values of phytoplankton communities in pie classes in relation to high (HWL) and low (LWL) water levels.

Fig. 1), showed remarkably higher values of EC, TDS, salinity, HCO_3^-, Cl^-, and Mg^{2+} (Dunn's test, P≤0.05). Concentrations of DOC, TOC, and COD were also higher in the floodplain lake than in the main channel, although this was not statistically justified.

Phytoplankton Communities

The total number of species found in the studied floodplain lakes and the Biebrza River was 245. The species belong to 9 taxonomic groups (Table 4). The greatest number of species was identified for Bacillariophyceae (99) and Chlorophyceae (74). Many species belonged to Cyanoprokaryota (18), Euglenophyta (17), and Chrysophyceae (12). Other algae phyla (Dinophyta, Cryptophyta) or classes (Xanthophyceae, Zygnemathophyceae) were represented by a few species.

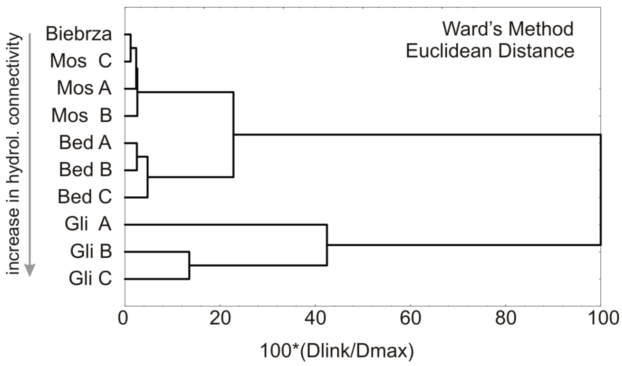


Fig. 4. Tree diagram of cluster analysis of study sites based on hydrochemical and phytoplankton data, obtained by using Ward's method as linkage rule and Euclidean distances as the metric for distance calculation.

The highest number of species was recorded in lotic Mostek (111) and the lowest in semi-lotic Glinki (74). In the latter, only 6 taxa per sample were identified in September 2011 during the chrysophytes bloom, while the highest number of taxa (43 taxa per sample) was found in the Biebrza River in June 2011.

In the period of study the total abundance of phytoplankton (TPA) ranged from 0.11 to 3.23×10^6 ind.·L^{-1} in the Biebrza River, from 0.12 to 7.78×10^6 ind.·L^{-1} in floodplain lakes (Table 4) but the changes depended on hydrological situation as well as water quality parameters. At all sampling sites the highest TPA were recorded in July 2011 during the lowest level of water. During this time the semi-lotic floodplain lake showed the highest increase in abundances, but a considerable drop in biodiversity (Figs. 3A and B).

With regards to hydrological connectivity of floodplain lakes with the parent river, the lowest TPA was noted in lotic environments (Biebrza and Mostek). Significantly higher (2-3 times, on average) values of TPA were stated in the lentic lake Bednarka, and semi-lotic lake Glinki (Dunn's test; P≤0.05). The contribution of Cyanoprokaryota, Euglenophyta, Dinophyta, Xanthophyceae, and Zygnematophyceae did not exceed 10% of the total phytoplankton abundance (Table 4). Generally, the highest contribution of chrysophytes to TPA was recorded in lentic and semi-lotic lakes while diatoms were in the river and lotic lake. The studied floodplain lakes differed statistically in terms of TPA and abundances of chrysophytes, euglenophytes, cryptophytes, and zygnematophytes (Table 4). The value of TPA positively correlated with COD (Spearman rank correlation coefficient, r_s= 0.573), NH_4^+-N (r_s= 0.605), TN (r_s= 0.407), while negatively correlating with dissolved oxygen (r_s= -0.345).

Table 4. Phytoplankton richness, diversity, and abundance (10^6 ind.·L^{-1}) in the studied floodplain lakes and the Biebrza River.

Parameter	Biebrza River N=4		Mostek N=11		Glinki N=9		Bednarka N=12	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Number of species	33-43	37	19-37	31	6-34	18	10-40	27
Shannon-Weaver index	2.40-2.88	2.64	2.20-3.12	2.51	0.23-2.70	1.39	0.94-3.16	2.24
Total abundance of phytoplankton (TPA)	0.11-3.23	0.98[a]	0.15-6.70	1.15[a]	0.12-7.78	3.58[b]	0.19-3.75	1.75[ab]
Percentage of phytoplankton groups in total abundance								
% Cyano.	0.00-8.80	3.70	0.00-8.20	3.10	0.00-1.10	0.10	0.00-5.00	1.50
% Eugleno.	0.20-1.20	0.70[a]	0.00-3.30	1.00[ab]	0.00-6.80	1.80[bc]	0.50-3.90	1.70[c]
% Crypto.	1.10-39.2	16.7[a]	1.20-49.4	19.7[a]	0.60-18.8	6.50[ab]	8.10-55.6	22.7[b]
% Dino.	0.00-1.60	0.50	0.00-5.80	1.20	0.00-2.80	0.70	0.00-4.90	1.40
% Chryso.	0.50-4.60	2.50[a]	0.50-17.9	5.90[a]	3.70-96.7	56.2[b]	1.40-83.9	27.6[a]
% Xantho.	0	0	0	0	0	0	0.00-0.60	0.10
% Bacilla.	29.4-65.4	46.3	17.0-77.0	37.0	0.70-67.0	16.1	2.00-44.6	14.8
%Chloro.	10.0-45.2	30.3	1.80-66.2	31.9	0.20-56.9	18.6	1.50-67.7	30.2
%Zygne.	0.00-0.80	0.40[b]	0.00-0.50	0.10[a]	0	0	0.00-0.60	0.10[a]

Groups of means statistically different in the non-parametric Dunn's test ($P<0.05$) were denoted with superscripts.

In 2011, during low water levels, the main dominants were cryptophytes together with centric diatoms and chlorophytes in the river, lotic lake Mostek and lentic Bednarka (Table 5). The highest abundance reached solitary diatoms such as *Cyclostephanos dubius* (Fricke) Round, *C. invisitatus* (M.H. Hohn et Hellerman) Theriot, Stoermer et Hakansson, *Stephanodiscus hantzschii* Grunow, *S. minutulus* (Kützing) Cleve et Möller and chain-forming diatom *Melosira varians* Agardh.). Chlorophytes were represented by *Monoraphidium contortum* (Thuret) Komárková-Legnerová, and *Dictyosphaerium* sp. Additionally, the chrysophytes *Dinobryon divergens* O.E. Imhof or *Synura uvella* Ehrenberg co-dominated with other groups in Bednarka. At the same time, the dominant species among phytoplankton in Glinki was *S. uvella* (> 55% TPA). In June-September 2012, during a period of high water levels, the new group of co-dominants was pennate diatoms (Asterionella formosa Hassall, *Cocconesis placentula* Ehrenberg, *Nitzschia acicularis* (Kützing) W.Smith, *Fragilaria* spp.), while in Mostek and Bednarka the highest abundance reached *Pandorina morum* (O.F. Müller) Bory (chlorophytes). In Glinki in September 2012, similar to September 2011, the predominance of chrysophytes (*S. uvella*) over other groups of phytoplankton was observed. The contribution of this species to TPA varied between 6% and 83.2%. Its lowest values were recorded at site C near the river channel.

In Mostek, water current was favourable for numerous centric diatoms and many pennate diatoms such as *Gomphonema gracile* Ehrenberg, *G. pseudoaugur* Lange-Bertalot, *Meridion circulare* var. constrictum (Ralfs) Van Heurck, *Karayevia laterostrata* (Hustedt) Bukhtiyarova, and *Placoneis gastrum* (Ehrenberg) Mereschkowsky. Dinophyta such as *Peridiniopsis kevei* Grigorszky et Vasas in Grigorszky and *P. elpatiewski* (Ostenfeld) Bourrelly preferred the stagnant water of Bednarka, where it reached the highest abundance.

A comprehensive tool in the description of relationships between the stated communities (species and environmental variables) is redundancy analysis (RDA) with a forward selection with the Monte Carlo permutation tests. Based on the analysis of gradients related to the first and second components, one may conclude that the variance explained between phytoplankton and environmental variables is high and amounts to 95.7 and 94.5%, respectively. The relationships are the strongest between COD, TDS, EC, and NH_4^+-N and Cryptophyceae, Euglenophyta and Dinophyta, and to a lesser extent Bacillariophyceae and Chlorophyceae. The presence of Cyanoprokaryota showed similar gradient to ortophosphates, and related to NO_2^--N and NO_3^--N (Fig. 3A).

A considerable role among the variables is played by hydrological conditions: water retention time and water level. The first variable explained 16% of variance and the second 5% ($P\leq0.05$). In the case of water retention time, both conditional and marginal effects are identical (0.16 of explained variance), which proves the linear independency of that variable (Table 3). The discrepancy in the importance of other explanatory variables, as judged by their marginal effects and their conditional effects, is caused by the correlations between those explanatory variables.

Table 5. Dominants of phytoplankton during low and high water levels.

Site	Low water level		High water level	
	June 2011	September 2011	June 2012	September 20112
Biebrza River	*Cyclostephanos dubius*, *C. invisitatus*, *Stephanodiscus hantzschii*, *S. minutulus*	*Cryptomonas* spp., *Rhodomonas* spp.	*Asterionella formosa*, *Cocconesis placentula*	*A. formosa*, *Cryptomonas* spp.
Mostek	*Cyclostephanos dubius*, *C. invisitatus*, *Stephanodiscus hantzschii*, *S. minutulus*	*Cryptomonas* spp., *Rhodomonas* spp., *Melosira varians*	*Pandorina morum*	*Melosira varians*, *Nitzschia acicularis*, *Fragilaria* spp., *Cryptomonas* spp.
Bednarka	*Cryptomonas* spp., *Monoraphidium contortum*, *Dictyosphaerium* sp., *Dinobryon divergens*	*Cryptomonas* spp., *Rhodomonas* spp., *Synura uvella*	*P. morum*, *Rhodomonas* spp., *M. contortum*, *S. uvella*, *D. divergens*	*S. uvella*, *D. divergens*, *C. dubius*
Glinki	n.d.	*S. uvella*	*D. divergens*, *M. contortum*, *A. formosa* *C. dubius*	*S. uvella*

Figs. 3B and 3C present a graphical interpretation of the share of the studied phytoplankton groups in relation to hydrological types of the floodplain lakes and water levels. Only Euglenophyta showed no differences between LWL and HWL (Fig. 3C). Cluster analysis (Fig. 4) comparing the phytoplankton abundance and water chemistry, showed a good division between the fertile backwater of Glinki and the river with the other lakes. The cluster was characterized by the highest phytoplankton abundance and the strongest predominance of Chrysophyceae over the other algal groups (Fig. 3B and Fig. 4).

Among the physico-chemical variables of water quality, a significant relationship has been found between Shannon-Weaver H' index and water temperature (Spearman rank correlation r_s=0.519, P≤0.05) and HCO_3^- (r_s=-0.503). The composition of phytoplankton species and Shannon-Weaver indices changed significantly between low and high water levels (Figs. 5 and 6). The Shannon-Weaver biodiversity indices (H') were the highest at high water levels regardless of type of floodplain lake. The changes in the diversity of phytoplankton in the studied floodplain lakes in relation to low (A) and high (B) water levels are presented in the projection of the generalized additive model (Fig. 5). During periods of low water we simulated significant differences between habitats from the lowest H' in intermittent waterbodies (H'<0.7) to the highest H' in lotic ecosystems (0.6 > H' > 2.6). The model confirmed that during high water exchange, species make the H' biodiversity indices more homogeneous: from ca. 1.0 > H' > 2.8 in lentic and semi-lentic to 2.2 > H'> 2.8 in lotic ecosystems.

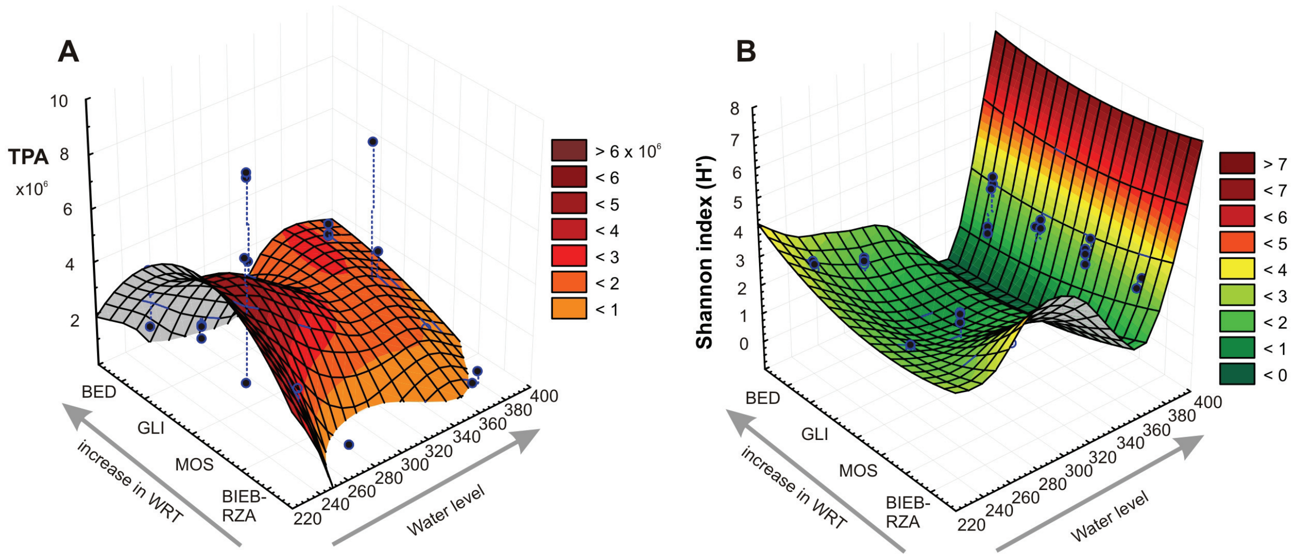


Fig. 5. A) Changes in total phytoplankton abundance (TPA) and B) Shannon-Weaver Index (H') in relation to hydrological connectivity and water levels. The data in Fig. A present abundances in × 10^6 ind.·L^{-1}.

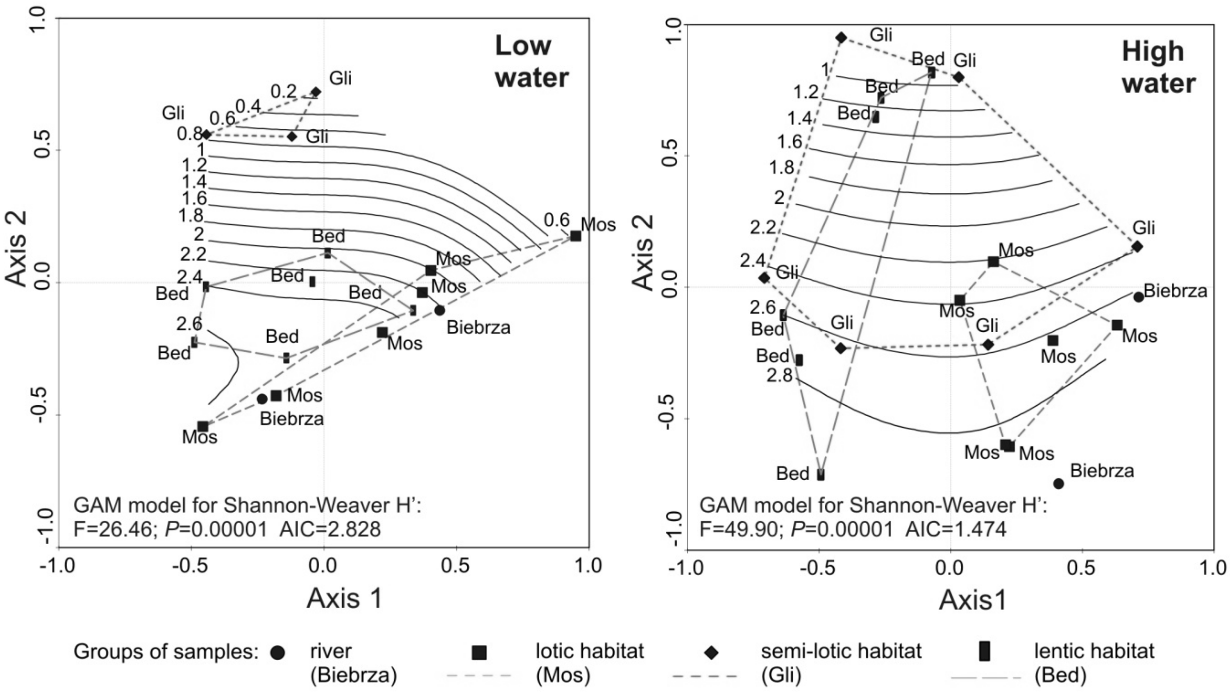


Fig. 6. Projection of GAM model (P≤0.05) performed for Shannon-Weaver diversity indices as a response to water level as an explanatory variable.

Disscussion

Diversity of waterbodies in every floodplain represents a broad range of habitats and eco-hydrological parameters satisfying numerous assemblages of hydrobionts [1, 20, 40, 41]. Analyses of phytoplankton in the Middle Basin of the Biebrza River demonstrated that retention time, or water retention time, is a major factor controlling the diversity and abundance of phytoplankton. Hydrological conditions control the extent of the water exchange, which influences substantially the relative importance of autochthonous and allochthonous sources of mineral and organic matter to site channels and cut-offs in the floodplains [42, 43]. Retention of nutrients in a floodplain lake, processes of denitrification, uptake by submerged macrophytes and helophytes, periphyton and microorganisms, and deposition and binding in bottom sediments are important regulators of nutrient abundance in water. The intensity of nutrient cycling within any floodplain depends on nutrient availability (N and P, mainly), related to a significant extent to oxygen resources in the lake. However, storage, decomposition, and transformation of organic and mineral matter have temporal and spatial significance in the case of subsystems with elevated hydrological retention [5, 21, 28].

Water level fluctuations strongly influence physico-chemical parameters of water in a given water body [10, 32, 42]. Our results confirm that the alternating periods of high and low water increase nutrient cycling, which in turn stimulates biodiversity and productivity of shallow water bodies. As reported by Schiemer et al. [44], for the Danube, at high water levels, water from the river dominates the backwater hydrochemistry through accompanying connections of the various water bodies. Surface connection via the inflow causes an increase in inorganic nutrients in the side channels, which was also found e.g. by Hein et al. [5] for the Rhine River, Glińska-Lewczuk [10] for the Łyna River, and Knösche [28] for the Havel River. The increased retention time of water has a significant influence on phytoplankton abundance. Even a little slowdown of water velocity in comparison to the free-flowing river resulted in a small increase in the phytoplankton abundance and number of taxa. Natural water movement in eupotamic habitats (Biebrza River and Mostek) created favorable conditions for diatoms and chlorophytes, which are common constituents of lowland potamophytoplankton as it was previously reported by Grabowska [31]. These sites also had lower trophy than other floodplain lakes with longer water retention time. The most favourable conditions for phytoplankton growth were detected in lakes Glinki and Bednarka with stagnant water and high nutrient availability. That significant increase in phytoplankton abundance appeared at low water conditions. Thus, we could anticipate high phytoplankton abundances in semi-lotic backwaters at low water stages during hot summers. In contrast, high water levels were responsible to a great extent for the decrease in phytoplankton abundance, which is attributed to the diluting or wash-out effects [16].

Semi-lotic floodplain lakes, as other young ecosystems, connected with the river channel via downstream arm (herein Glinki site C), showed a lateral gradient of microhabitats resulting from the connectivity and rate of water exchange with the river channel. This connection between the river and a floodplain lake plays a significant role in phytoplankton growth and biodiversity enhancement. Phytoplankton communities near the river channel showed similarity to potamoplankton (e.g. centric diatoms). A more distal part of the floodplain lake with stagnant water favored flagellate algae (e.g. *S. uvella*).

The increase in the number of phytoplankton species and Shannon-Weaver biodiversity indices has been noted during the increased phase of water table and re-connecting of previously isolated ecosystems. Since that time the phytoplankton communities in floodplain lakes can be characterized as a mix of potamophytoplankton and species typical of more stagnant waters [11].

Our results confirmed that floodplain lakes, without or with limited human impact, are important hotspots for rare and/or endemic species. We identified rare species of pennate diatoms such as *Gomphonema gracile*, *G. pseudoaugur*, *Meridion circular*e var. *constrictum*, *Karayevia laterostrata,* and *Placoneis gastrum*, which are typical of waters characterized by lower trophy [12]. The presence of such dinoflagellates taxa as *Peridiniopsis kevei* in the stagnant zones in river channels was also reported by Owsianny [20].

In the Biebrza River floodplain we have noted the strongest growth of one species, *S. uvella*. The species was limited to the Glinki floodplain lake, representing a water body rich in nutrients. Similar growth was described by Padisák [26] for three Hungarian oxbow lakes. Lack of Cyanoprokaryota and Euglenophyta blooms in the Biebrza River floodplain lakes indicates a lower level of their trophy compared to the Vistula oxbow lakes [15, 16]. Except for Glinki, the Biebrza floodplain lakes also had higher values of diversity indices than the Vistula [16] and Bug oxbow lakes [17, 18].

Our research confirmed the research outcomes of Hutorowicz [24], that the lower abundance of phytoplankton is in the river (0.98×10^6 ind.$\cdot$L^{-1}) than in floodplain lakes (1.15-3.58×10^6 ind.$\cdot$L^{-1}). However, total phytoplankton abundance in the Biebrza River was much lower than that stated for some other lowland rivers, e.g. the Morava [30] and Narew [31] rivers. In comparison to the studies of Hutorowicz [24] conducted in 1999 on phytoplankton in the Biebrza River and its floodplain lakes, our results indicated the increase in TPA in the river by ca. 18% (0.1-0.8 ind.$\cdot$L^{-1}). The abundance of phytoplankton in the lakes in 1999 varied from 0.4 to 6.1×10^6 ind.$\cdot$L^{-1} and was lower when compared to our data. The number of identified species has not changed (37 species found in the Biebrza River). The most diversified group of phytoplankton remained Bacillariophyceae and Chlorophyceae. Although the increase in phytoplankton abundance in the studied ecosystems may be judged as relatively small and slow, it can be indicative of anthropogenic influences, resulting from agricultural disturbance throughout the nutrient over enrichment. Thus, further control of both abiotic and biotic parameters is recommended, otherwise subsequently, the floodplain lakes in the Biebrza River floodplain may lose their natural values due to deterioration of the trophic state of the water bodies.

Conclusions

Floodplain lakes located in the floodplains of lowland rivers are differed by numerous biotic and abiotic factors. Variability of physico-chemical conditions of water, being the result of differences in hydrological connectivity, influence the qualitative and quantitative structure of phytoplankton. We conclude that the highest abundance of phytoplankton (TPA) is likely to appear in semi-lotic floodplain lakes at low water stages during warm summers. Analyses of phytoplankton assemblages showed higher indices of biodiversity in lotic (eupotamic) habitats. Regardless of the hydrological type of floodplain lake, overbank flooding promotes the exchange of species with a simultaneous decrease in their abundance. This study brought an important conclusion: that hydrological parameters, and particularly hydrological connectivity and water level, are basic tools in proper lake management toward biodiversity improvement.

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