The impact of an extreme flood in spring/summer 2010 on phytoplankton communities in oxbow lakes of the lower Vistula River, central Poland

Ewa A. Dembowska*

Department of Hydrobiology, Faculty of Biology and Environment Protection, Nicolaus Copernicus University, Lwowska 1, 87-100 Toruń, Poland

Abstract – In 2010, central Europe was hit by a massive flood. The main objective of this study was to assess the impact of this natural disaster on phytoplankton communities in four oxbow lakes of the lower Vistula River. In order to explain changes caused by the flood, the data from the year 2010 were compared with the data from the previous year. In summer 2009, the abundance and biomass of phytoplankton as well as chlorophyll *a* content in small isolated oxbow lakes were relatively low. Small nanoplankton flagellates prevailed. Much higher abundance and biomass of phytoplankton and chlorophyll *a* content were recorded in a large oxbow lake, characterized by the predominance of filamentous cyanobacteria. After the flood wave, the abundance and biomass of phytoplankton in the small oxbow lakes increased dramatically (18 and 7 times, respectively), but the number of species decreased. Filamentous cyanobacteria (*Dolichospermum*), euglenophyta and dinoflagellates were identified. In the large oxbow lake, the number of species increased but the abundance and biomass of phytoplankton decreased (by approximately 60 and 75%). There was a shift in dominant algal species. Cyanobacteria were replaced mainly by cryptophyta, small chlorophyta (*Chlamydomonas*) and xanthophyta (*Heterothrix*). The least significant changes were recorded in the Vistula River. Here, before and after the flood, the abundance and biomass of phytoplankton as well as chlorophyll *a* content and the dominant algal species remained unchanged. The massive flood caused severe environmental stress, which disturbed phytoplankton development and led to shifts between clear water and turbid states in the lakes.

Key words: Floodplain lake / phytoplankton / species diversity / functional groups / flood wave

Introduction

River Flood Pulse theory (Junk *et al.*, 1989) states that pulsing of river discharge is the most important environmental factor in floodplain ecosystems. According to this concept, river basins constitute an integral part of dynamic river systems, interconnected through hydrological and ecological processes. Systems of this kind are characterized by great diversity resulting from interactions between a flowing river, stagnant lakes and periodically flooded wetlands in the river valley. There is a constant exchange of energy and matter between land and water systems (Junk *et al.*, 1989; Tockner *et al.*, 2000).

Periods of flooding are followed by periods of hydrological drought. In the valleys of unregulated rivers, these phases occur in regular succession. Oxbow lakes are considered regular features of the valleys of large lowland rivers. Typically, they are shallow and elongated, though sometimes have a horseshoe shape. They can be partly connected with the river or completely isolated. The width of connection between these water bodies depends both on the water level in the river and the morphology of the oxbow (Tockner *et al.*, 1999; Ward *et al.*, 2002). The immense morphological, hydrological and biocenotic diversity of these lakes ensures their great ecological potential.

Valleys of many large European rivers have been heavily transformed as a result of river regulation and construction of flood defenses (Dynesius and Nilsson, 1994; Makowski, 1998). In the last century, more than 80% of large European rivers were regulated. As a consequence, the isolation of oxbow lakes (limnophase) may last as long as several years, and sometimes longer. Owing to anti-flood systems, water remains in the river channel even when its level is high. However, very high water inflow makes the river overflow and flood the valley causing major damage.

*Corresponding author: dembow@umk.pl

Table 1. Morphometric data for the studied lakes.

	W1	W1a	Ma	PD
Geographical location	N 53°01'E 18°39'	N 53°01'E 18°39'	N 53°00'E 18°34'	N 53°01'E 18°30'
Surface [ha]	1.5	2.5	2.8	71
Maximum depth [m]	1.8	2.5	2.5	11
Maximum length [m]	140	220	640	1800
Maximum width [m]	67	40	61	390

Phytoplankton communities in oxbow lakes follow a cyclical pattern of changes resulting from changing hydrological conditions. Hydrological changes affect the structure and productivity of these communities (Wojciechowska *et al.*, 2005; Stević *et al.*, 2013; Grabowska *et al.*, 2014; Dembowska and Napiórkowski, 2015). During the potamophase, oxbow biocenosis is removed and partly replaced by river biocenosis. Phytoplankton biomass is low due to physical disturbances and a large share of abioseston, which impedes photosynthesis. During the limnophase, light conditions are improved due to slower water flow and the sedimentation of suspension. This promotes the development of indigenous phytoplankton and blooms of cyanobacteria (Bovo-Scomparin and Train, 2008; Mihaljević and Stević, 2011; O'Farell *et al.*, 2014).

Phytoplankton studies should focus not only on the species composition but also on the community structure. Assessing the role of functional groups of phytoplankton seems particularly useful (Reynolds *et al.*, 2002; Padisák *et al.*, 2009). The evaluation of the dynamics of changes within the groups shows the rate of environmental change.

The main aim of this study was to investigate the influence of an extreme flood from the river Vistula in May 2010 on phytoplankton communities in shallow oxbow lakes located in Toruń, lower Vistula valley. In order to evaluate the importance of the extreme conditions on the phytoplankton communities in 2010, the results were compared with those from 2009, obtained during the investigation carried under regular hydrological conditions.

The following hypotheses were analyzed:

(1) Changes in hydrological conditions in the oxbow lake cause changes in the phytoplankton biomass, species composition and functional groups. Functional groups of phytoplankton can be used to assess whether flood pulsing is a factor that stimulates or disturbs phytoplankton development.
(2) Within 1 to 2 months after the flood, algae carried by the river are deposited as sediment. Algal communities typical of oxbow lakes (found there before the limnophase) gradually recover.

Materials and methods

Study area

The study was conducted in four oxbow lakes of the lower Vistula River located in Toruń, between 730 and 742 km of the river course. Winnica 1 (W1), Winnica 1a (W1a) and Martówka (Ma) are shallow (1.8–2.5 m) and have a small surface area (1.5–2.8 ha). Lake Port Drzewny (PD) is shallow, but its surface area at the medium water level is 70.8 ha. All investigated lakes are located within a distance of 250–500 m from the river.

The studied lakes had different communities of vascular plants. The cover on lake W1, which appeared at the beginning of June, eventually covered its entire surface. Free floating plants included the following species: *Spirodela polyrhiza* (L.) Schleid., *Salvinia natans* (L.) All., and *Lemna minor* (L.). In lake W1a, submerged macrophytes included *Ceratophyllum demersum* L., *Myriophyllum spicatum* L., *M. verticillatum* L. and *Potamogeton* spp. Plants with floating leaves such as *Nuphar lutea* (L.) Sibth. & Sm. and *Hydrocharis morsus-ranae* L. were found near the banks. In lake Ma, the bottom was thickly covered with *Ceratophyllum demersum* L. The flora in lake Port Drzewny was poorly developed and consisted mainly of *Elodea canadensis* Michaux and *Potamogeton* spp. found near the banks. Morphometric data for all lakes are presented in Table 1.

Methods

Phytoplankton was collected in July and August 2009 (before the flood) and in July and August 2010 (after the flood). Sample collection sites were located in the central part of each lake. Plankton in the Vistula River (at 732 km of its course) was also analyzed. A total of 20 phytoplankton samples were collected from the lakes and the river during the research. For qualitative studies, the material was collected with a plankton net with a mesh diameter of 10 μm from the water column, and preserved with formaldehyde. For quantitative analyses, non-concentrated samples were collected from beneath the surface, *i.e.* at a depth of about 0.5 m. Material for quantitative analyses was immediately preserved with Lugol's solution (J in KJ). The following physicochemical parameters of water were also determined: temperature (WT, °C), pH, electrolytic conductivity (EC, μS.cm^{-1}) and the oxygen content (DO, mg.L^{-1}; DO, %), using a WTW MultiLine P4 multi-parameter probe. Water transparency (SD, m) was measured by Secchi disc. For chlorophyll *a* (Chl *a*, μg.L^{-1}) content, water was filtered through a Whatman GF/C glass fiber filter and extracted with ethanol. Chl *a* contents were measured and calculated according to the Nusch (1980) method. Absorbance was measured with a Jasco UV/VIS V-530 spectrophotometer.
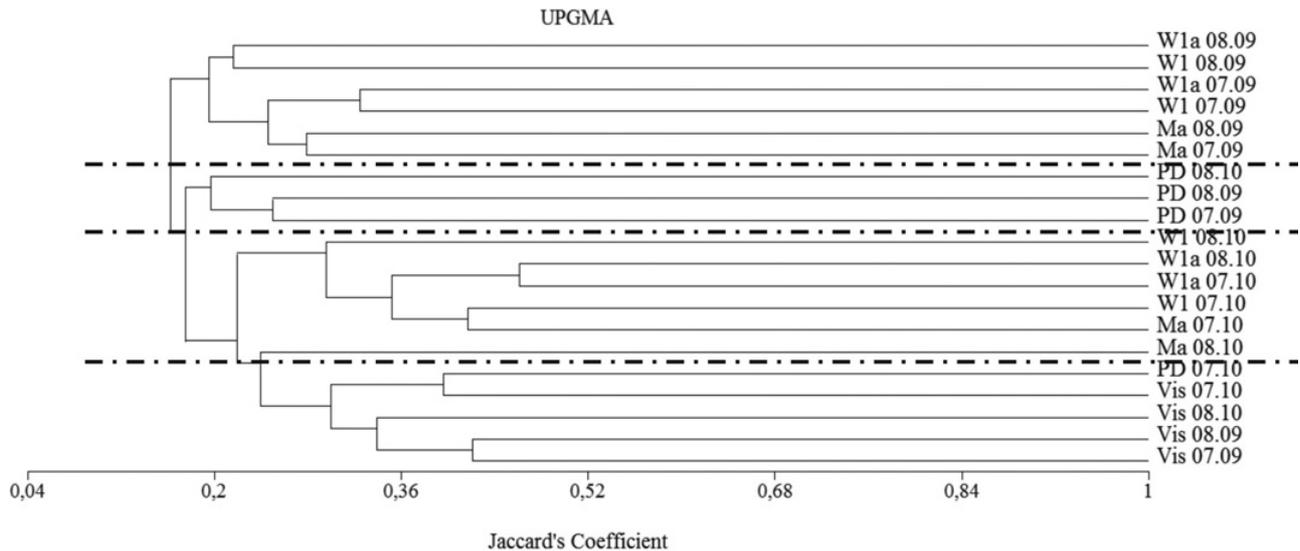
Fig. 1. Dendrogram of phytoplankton similarity in oxbow lakes and the Vistula River in the year preceding the flood (2009) and in the year of the flood (2010).

Phytoplankton species were identified using a light microscope (Nikon Alphaphot-2). To identify diatom species, samples were treated with HCl and about 30% H_2O_2. The abundance of algae was determined with the Utermöhl (1958) method, and the biomass with the volumetric method (Hillebrand et al., 1999; Sun and Liu, 2003), assuming that 1 mm^3 of algae is equal to 1 mg. The abundance of each species is presented as the number of individual cells per liter (N, ind..L^{-1}). Biovolume (B) was expressed as $mg.L^{-1}$ fresh mass. Dominant phytoplankton species were estimated from the percentage contribution of individual species to the total biomass. Only the species with a minimum of 5% contribution to the total biomass were considered dominant. Dominant species described in this paper were classified into functional groups, based on the studies by Reynolds et al. (2002); Reynolds (2006) and Padisák et al. (2009).

In order to assess similarity between phytoplankton communities (Jaccard's coefficient), species diversity (Shannon-Weaver, evenness) and the relationship between dominant species and environmental variables (CCA), MVSP 3.2 (multivariate statistical package, www.kovcomp.com/mvsp) was applied.

Results

Water levels in the years 2001–2009 were moderate. The average annual water level of the Vistula River in Toruń within this period was 280 cm (low medium level). In May 2010, an extreme flood occurred. The maximum water level was recorded on May 24 (856 cm, flow 5800 $m^3.s^{-1}$). The massive inflow of river water affected the quality of water in the analyzed oxbows, with water transparency and electrolytic conductivity changing the most significantly. In lakes Ma, W1 and W1a, water transparency decreased dramatically in 2010, while in lake PD, it increased by 1.5 times. In 2010,

electrolytic conductivity in the Vistula and all oxbows was lower than in 2009. The largest decrease was observed in lake Ma: 970 $\mu S.cm^{-1}$ in July 2009 and 923 $\mu S.cm^{-1}$ in August 2009. In the following year, the values decreased further to 503 $\mu S.cm^{-1}$ and 482 $\mu S.cm^{-1}$. All physical and chemical parameters are presented in Table 2.

A total of 125 taxa of algae were identified. With 66 species, lakes Ma and PD were the richest in species. The species composition changed distinctly after the flood (Table 2). Thirty-eight algal taxa were identified in the Vistula in the year preceding the flood, and 47 in the following year. The lowest number of taxa was recorded in W1a: 31 before the flood and only 26 after the flood. In lakes W1 and Ma, the number of taxa also decreased after the flood. An increased number of species in 2010 was recorded only in lake PD (40 in 2009 and 48 in 2010).

Before the flood, the phytoplankton abundance in the small isolated oxbow lakes was low and ranged from 0.719 10^6 ind..L^{-1} (August 2009) in lake Ma to 1.570 10^6 ind..L^{-1} (also August 2009) in lake W1a. The most abundant were nanoplankton flagellates (FGs W2, X2, X1, Y), cryptophyta (Cryptomonas spp., Plagioselmis nannoplanctica (H. Skuja) G. Novarino, I. A. N. Lucas & S. Morrall), euglenophyta (Trachelomonas spp. of the Volvocinae group) and small chlorophyta (Chlamydomonas spp., Monoraphidium minutum (Nägeli) Komárková-Legnerová). Much higher phytoplankton abundance in August 2009 was noted in the large lake PD, where it reached 17.888 10^6 ind..L^{-1}. The predominance of filamentous cyanobacteria (Aphanizomenon flos-aquae Ralfs ex Bornet et Flahault, Planktothrix agardhii (Gomont) Anagnostidis et Komárek), centric diatoms (Actinocyclus normanii (W. Gregory ex Greville) Hustedt, Aulacoseira granulata (Ehrenberg) Simonsen), cryptophyta, euglenophyta, small chlorophyta and xantophyta Heterothrix stichococcoides (Pascher) P.C.Silva (FGs D, H1, J, P, S1, W2, Y) was observed.

Table 2. Average physico-chemical and biological parameters of oxbow lakes before 2009 and after the 2010, flood.

	Vistula		W1		W1a		Ma		PD	
	2009	2010	2009	2010	2009	2010	2009	2010	2009	2010
SD [m]	–	–	1.55	0.6	1.3	0.65	1.95	0.4	0.9	1.4
DO [mg.L^{-1}]	5.38	7.03	1.51	4.57	2.48	4.63	7.12	5.09	6.06	7.75
DO [%]	61.3	82.4	16.7	52.9	28.0	52.0	82.8	59.0	65.9	90.0
WT [$^{\circ}$C]	21.8	22.3	18.6	20.4	19.6	20.9	23.4	21.5	22.4	21.2
pH	8.16	8.32	7.75	7.89	7.74	7.97	8.08	8.17	8.34	8.18
EC [μS.cm^{-1}]	572	483	780	703	789	651	947	493	683	620
Chl a [μg.L^{-1}]	17.15	31.79	13.80	98.78	11.92	93.56	6.68	71.26	33.77	26.69
N	38	47	47	38	31	26	43	39	40	48
N [10^6 ind..L^{-1}]	1.177	1.591	0.893	6.861	1.300	23.296	0.435	5.466	10.780	4.623
B [mg.L^{-1}]	1.440	1.700	4.405	8.653	1.963	13.015	1.434	9.542	12.558	3.272
H'	2.598	2.414	2.536	2.367	2.092	1.370	2.125	2.695	2.168	2.433
e	0.714	0.627	0.659	0.651	0.609	0.420	0.565	0.735	0.588	0.629

SD, Secchi disc visibility; DO, dissolved oxygen content; WT, water temperature; pH, reaction; EC, electrolytic conductivity; Chl a, chlorophyll a content; n, number of phytoplankton taxa; N, phytoplankton abundance; B, phytoplankton biomass; H', Shannon-Weaver index; e, evenness.

Phytoplankton abundance in the Vistula was similar to that of the small oxbows: 0.552 10^6 ind..L^{-1} in July 2009 and 1.802 10^6 ind..L^{-1} in August 2009. However, dominant algae were different: centric diatoms, *Cryptomonas erosa* Ehrenberg and coccal chlorophyta (FGs *C*, *D*, *J*, *X1*) were the most abundant.

In 2010, after the flood, phytoplankton abundance in small isolated oxbow lakes increased dramatically. In lake Ma, the highest abundance was recorded in August (7.800 10^6 ind..L^{-1}), in lakes W1 and W1a, in July (12.724 10^6 ind..L^{-1} and 30.814 10^6 ind..L^{-1}, respectively). Dominant algal species were different. In lake Ma, the proportion of small nanoplankton flagellates (*Y*, *W2*) was still high, but cyanobacteria *Dolichospermum flos-aquae* (Brébisson ex Bornet & Flahault) P.Wacklin, L.Hoffmann et J.Komárek (FG *H1*) were also abundant.

In W1 and W1a, previously dominant cryptophyta and *Chlamydomonas* spp. (FGs *Y*, *X2*) were accompanied by abundant euglenophyta (*W2*), centric diatoms (**C**) and chrysophyta *Synura uvella* Ehrenberg (*Ws*). In PD, phytoplankton abundance dropped to 5.465 10^6 ind..L^{-1} in July 2010 and 3.780 10^6 ind..L^{-1} in August 2010 (similar to the value recorded in July 2009). The dominant algal species included cryptophyta, *Chlamydomonas* spp., *Heterothrix stichococcoides,* and nanoplankton cyanobacteria *Synechocystis aquatilis* Sauvageau (FGs *Y*, *X2*, *X1*).

In the Vistula, phytoplankton abundance remained unchanged (2.491 10^6 ind..L^{-1} in July 2010 and 0.690 10^6 ind..L^{-1} in August 2010). Moreover, centric diatoms and coccal chlorophyta were still predominant (FGs *C*, *D*, *J*, *X1*). All dominant FGs are presented in Table 3.

Before the flood, the average phytoplankton biomass in the small oxbow lakes was low and ranged from 1.434 mg.L^{-1} in lake Ma to 4.405 mg.L^{-1} in W1. In lake Ma, predominant species included cryptophyta (*Cryptomonas* spp., *Plagioselmis nannoplanctica*), chlorophyta (*Chlamydomonas* spp.) and chrysophyta *Uroglena* sp., in lake W1, chrysophyta *Uroglena* sp, and in lake W1a,

Aphanizomenon flos-aquae, *Planktothrix agardhii* and cryptophyta. At the same time, water bloom was observed in lake PD and phytoplankton biomass ranged from 6.255 to 18.860 mg.L^{-1}. Cyanobacteria (*Aphanizomenon flos-aquae*, *Microcystis wesenbergii* (Komárek) Komárek ex Komárek, *Planktothrix agardhii),* centric diatoms (mainly *Actinocyclus normanii)* and cryptophyta had the greatest contribution to the biomass.

Phytoplankton biomass in the Vistula was low and ranged from 0.639 mg.L^{-1} to 2.241 mg.L^{-1}. Predominant algae belonged to centric diatoms (*Cyclotella meneghiniana* Kützing and *Actinocyclus normanii*) and coccal chlorophyta (*Pediastrum boryanum* (Turpin) Meneghin, *P. duplex* Meyen, *P. simplex* Meyen and *Desmodesmus communis* (E. Hegewald) E. Hegewald).

In 2010, phytoplankton biomass in the small oxbow lakes increased significantly. In all lakes, its maximum value was recorded a month after the flood wave, *i.e.* in July: 11.100 mg.L^{-1} in Ma, 15.683 mg.L^{-1} in W1 and 17.119 mg.L^{-1} in W1a. During the next month, the biomass dropped by almost 30% in Ma, by 90% in W1 and by about 50% in W1a. After the flood, *Dolichospermum flos-aquae*, *Cyclotella meneghiniana*, *Peridinium cinctum* (O.F.Müller) Ehrenberg, *Euglena* spp. and *Trachelomonas hispida* (Perty) F.Stein dominated in the biomass of lake Ma. In W1 and W1a, *Chlamydomonas* spp., *Peridinium cinctum*, *Euglena* spp. and *Cyclotella meneghiniana* prevailed.

In lake PD, the biomass decreased to 4.656 mg.L^{-1} in July 2010, and to 1.888 mg.L^{-1} in August 2010. Predominant species belonged to cryptophyta and chlorophytes of the genus *Chlamydomonas*. In the Vistula, the phytoplankton biomass was similar to that recorded the previous year (2.685 mg.L^{-1} in July 2010 and 0.715 mg.L^{-1} in August 2010). Centric diatoms (*Melosira varians* C.Agardh) and coccal chlorophyta (*Coelastrum microporum* Nägeli in A.Braun*, Pediastrum duplex, Desmodesmus communis*) were predominant.

Jaccard similarity analysis (Fig. 1) indicates a close similarity of the three small isolated lakes before flooding

Table 3. Functional groups of phytoplankton, representative species and their dominance based on abundance $> 5\%$ in at least single samples in total abundance before 2009 and after the 2010, flood.

FG	Main representatives	Dominance before flood	Dominance after flood
C	*Cyclotella meneghiniana* Kützing	Vistula	Ma; W1
D	*Actinocyclus normanii*	W1; PD	
E	*Dinobryon divergens* Imhoff		
F	*Oocystis lacustris* Chodat	PD	
H1	*Aphanizomenon flos-aquae*, *Dolichospermum flos-aquae*, *Dolichospermum heterosporum* (Nygaard) P. Wacklin, L. Hoffmann & J. Komárek, *Dolichospermum* sp. div.	W1; PD	Ma
J	*Coelastrum astroideum* De Notaris, *C. microporum* Nägeli, *Crucigenia/Crucigeniella* sp. div., *Desmodesmus communis* (E. Hegewald) E. Hegewald, *D. denticulatus* (Lagerheim) S. S. An, T. Friedl & E. Hegewald, *D. intermedius* (Chodat) E. Hegewald, *Pediastrum boryanum* (Turpin) Meneghini, *P. duplex* Meyen, *Tetrastrum glabrum* (Y. V. Roll) Ahlstrom & Tiffany	Vistula; Ma; W1; PD	Vistula; Ma; PD
Lo	*Peridinium cinctum* (O. F. Müller) Ehrenberg, *Peridiniopsis cunningtonii* Lemmermann		
MP	*Cymbella* sp., *Navicula tripunctata* (O. F. Müller) Bory, *Navicula* sp. div.	W1a	
P	*Aulacoseira granulata* (Ehrenberg) Simonsen, *Fragilaria crotonensis* Kitton, *F. capucina* Desmazières	PD	Vistula
S1	*Planktothrix agardhii* (Gomont) Anagnostidis & Komárek, *Pseudanabena limnetica* (Lemmermann) Komárek	W1a; PD	
W1	*Euglena* spp., *Lepocinclis acus* (O. F. Müller) B. Marin & Melko		Ma
W2	*Trachelomonas volvocina* (Ehrenberg) Ehrenberg, *T. volvocinopsis* Svirenko, *Trachelomonas* sp. div.		Ma; PD
Ws	*Synura uvella*		W1; W1a
X1	*Monoraphidium contortum* (Thuret) Komárková-Legnerová, *Monoraphidium grifithii* (Berk.) Komárková-Legnerová, *M. minutum, Synechocystis aquatilis*	W1	Vistula; W1; Ma; PD;
X2	*Plagioselmis nannoplanctica, Chlamydomonas* spp.	All stations	All stations
Y	*Cryptomonas erosa, C. marssonii* Skuja, *C. obovata* Skuja, *C. ovata* Ehrenberg, *C. rostratiformis* Skuja	All stations	All stations
?	*Heterothrix stichococcoides*	Vistula; PD	Vistula; PD

(2009). The same lakes after flooding also constitute a group with a high similarity coefficient. Samples collected from the Vistula (regardless of hydrological conditions) are yet another group with the highest similarity coefficient.

Discussion

In summer 2009, average water levels were recorded in the river based on the data from the last 10 years. Lakes Ma, W1 and W1a were isolated from the river. In lake W1, a thick layer of pleustophyta disturbed phytoplankton development (Dembowska, 2015). The bottoms of lakes Ma and W1a were covered with dense submerged vegetation, mainly *Ceratophyllum demersum*. Phytoplankton growth was limited, and both phytoplankton biomass and chlorophyll *a* content were low. Lakes Ma, W1 and W1a had characteristics of shallow macrophyte lakes (Scheffer and Jeppesen, 1998), in which competition and allelopathic interactions between macrophytes and phytoplankton result in high water transparency (Van Donk *et al.*, 1993). Lake PD was connected to the river. The submerged vegetation was found only near the shores. Phytoplankton grew abundantly, with annual summer blooms of *Aphanizomenon flos-aquae* (Dembowska *et al.*, 2012).

The hydrological state, which lasted for several years changed in 2010. Central Europe (Austria, Czech Republic, Germany, Poland, Serbia, Slovakia, Ukraine and Hungary) was hit by a massive flood. It is expected that climate change may increase the frequency and extent of these natural disasters (IPCC, 2012).

In the study area (the lower course of the Vistula River in Toruń), the highest water level was recorded in the evening of May 23, 2010 (859 cm). The alert level (650 cm) was exceeded by more than 2 m. On June 10, the flood returned, but this time the water level was lower (790 cm). The river valley was under water. The oxbow lakes Ma, W1 and W1a, which had been isolated from the river for many years (Dembowska, 2015) were also flooded.

The flood drastically changed environmental conditions in the studied lakes. Electrolytic conductivity decreased as a result of water dilution with floodwater. In three lakes, it decreased by only around 10–20%. However, in lake Ma, it dropped by 50%. The lake is actually a pond located in the center of the town and the impact of storm water is the strongest here. Its high EC is usually caused by the inflow of saline water rich in chlorides during spring thaw.
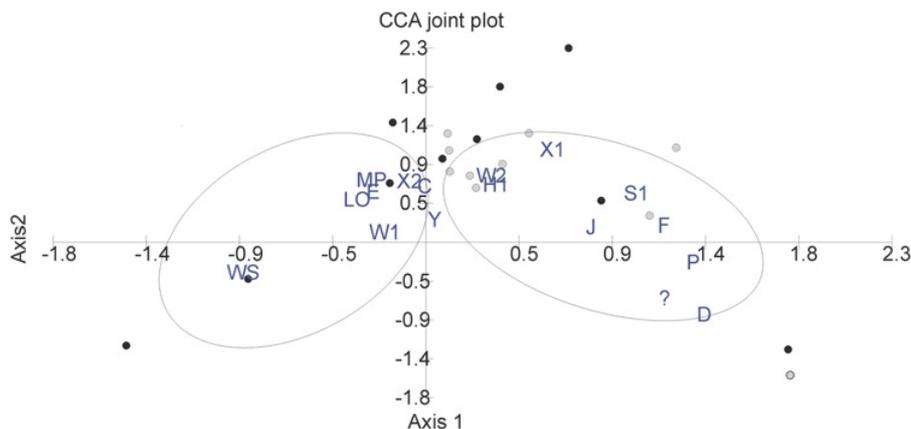
Fig. 2. Results of CCA analysis. Symbols (C, D, E, F, H1, J, LO, MP, P, S1, W1, W2, WS, X1, X2, Y, ?; see Table 3) indicate predominant FGs of phytoplankton. Gray circles represent dates before the flood, black circles, after the flood. The first axis explains 22.051% of the variation, the other axis explains 12.846% of variability.

In lakes Ma, W1 and W1a, isolated from the river before the flood, water transparency decreased significantly after flooding (approx. 0.4–0.65 m Secchi disc visibility). Flood water carries large amounts of inorganic suspended matter (Wetzel, 2001). This limits light penetration efficiency and impedes the development of primary producers (phytoplankton, submerged macrophytes and periphytic algae), especially in the initial phase of the flood. Previous studies (Huszar and Reynolds, 1997; Train and Rodrigues, 1998) indicate that during flooding, phytoplankton abundance and biomass in oxbows is low but species diversity is the highest (Huszar and Reynolds, 1997; Wojciechowska et al., 2005).

Better oxygen saturation was recorded in the lakes after the flood. This may have been caused by good oxygenation of flood water. Moreover, increased phytoplankton abundance and biomass may have also led to better oxygenation of the water in the studied lakes. Higher primary production is also connected with a larger amount of produced oxygen.

Extreme flooding of rivers significantly changes species communities (Follner et al. 2010). After the flood of the river Vistula in spring/summer 2010, the phytoplankton species composition also changed. Cluster analysis and CCA analysis indicated that phytoplankton communities changed in all the studied water bodies (Fig. 1, Fig. 2). In addition, the species diversity indices (Shannon-Weaver index and evenness) changed as well: in lake Ma, they increased (Table 2), in the Vistula and lakes W1 and PD, they remained almost the same and in W1a, they decreased. In W1a, they may stem from the fact that the population of macrophytes was damaged. Macrophytes constituted a suitable substrate for periphytic algae, common in the water column. Lack of substrate for periphyton reduced diversity (lower diversity indices).

For 1 or 2 months following the flood, phytoplankton can develop rapidly (Schemel et al., 2004; Wojciechowska et al., 2005). In this study, abundance and biomass of phytoplankton in the investigated lakes were more than ten times higher. The share of cyanobacteria in phytoplankton also increased. The success of phytoplankton is due to several factors.

Firstly, violent flooding destroys macrophytes, which are natural competition for phytoplankton (Bakker and Hilt, 2016). Later, suspended matter prevents the restoration of the vascular plant community. Secondly, phytoplankton spores and cysts, inactivated in bottom sediments, are revived. This applies particularly to Cyanobacteria akinetes, which retain the ability to germinate for many years. Cyanobacteria can grow faster under poorer lighting conditions than eukaryotic algae (Mur et al., 1999). Thirdly, a smaller share of Cladocerans in zooplankton may be another reason. According to Napiórkowski and Napiórkowska (2014), there was an 18-fold decrease in the abundance of crustacean zooplankton in the studied oxbow lakes. Although these authors noted a 15-fold increase in the abundance of rotifera, these small forms may only impair the development of the smallest pico- and nanoplankton. They do not affect the development of large forms of phytoplankton.

In lake PD, the reverse situation was observed: after the flood water transparency increased (up to 1.8 m in August 2010). Lake PD differs significantly from the other studied oxbows. It is large (surface area 71 ha), very shallow (average depth 1.5 m), and is connected to the Vistula. Before the flood, *Aphanizomenon flos-aquae* blooms were a regular occurrence. Every summer, water transparency was low, while phytoplankton biomass and chlorophyll *a* content were high (Dembowska et al., 2012). In this lake, spring and summer floods in 2010 impeded phytoplankton development. Similarly, a reduction of phytoplankton biomass during the potamophase was recorded in lake Sakadaš in the Danube valley by Mihaljević et al. (2009). Immediately after the flood, picoplankton cyanobacteria species *Synechocystis aquatilis* developed rapidly. However, due to the small cell size, their biomass was low. Originally, this species was included in the functional group *Z* (Reynolds et al., 2002), but because of its habitat it is now classified in group *X1* (de Melo and Huszar, 2000).

Flooding prevented another algal bloom by removing algae and introducing water without cyanobacteria. Cyanobacteria of the order Nostocales, sensitive to mixing water, are replaced by algae which can tolerate such conditions. A similar mechanism was confirmed by Mihaljević *et al.* (2010, 2013) in lake Sakadaš. A shift from a turbid state to clear water state was the result of extreme flooding. However, it is expected that the studied ecosystems will return to previous states in response to various hydrological impacts. A similar pattern was observed in the oxbow lake of the Danube River (Mihaljević and Stević, 2011). This research shows that after just 1 to 2 months, phytoplankton communities in the river returned to the state typical of moderate water levels. The phytoplankton number, biomass and biodiversity indices were similar in both years.

Summary and conclusions

Studies on the effects of extreme flooding of the Vistula in 2010 on phytoplankton in the oxbow lakes indicate changes in their ecological states. The low abundance and biomass of phytoplankton and low Chl *a* content were typical of a clear water state in lakes normally isolated from the river. Extreme flooding caused severe environmental stress, which affected phytoplankton growth. In three lakes, a clear water state with the dominance of submerged macrophytes changed into a turbid state with the dominance of planktonic algae. In one lake, a turbid water state shifted into a clear water state. The results indicate that extreme flooding can lead to changes in alternative states of oxbow lakes. Further research should analyze whether and when the studied oxbow lakes will return to the states from before the flood.

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