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The impact of free-floating plant cover on phytoplankton assemblages of oxbow lakes (The Bug River Valley, Poland)

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Abstract: In the present study we focused on the impact of macrophyte cover (composed mainly of the *Lemna* genus) on phytoplankton taxonomic and functional diversity. Some important environmental parameters, mainly light (Kd_{PAR}), and the chemical conditions (pH, dissolved oxygen, ammonium, soluble and total forms of phosphorus) were closely related to the pleustophyte cover. Among them, the key factor in the phytoplankton ecology of the studied oxbow lakes was the dense macrophyte cover which strongly reduced the illumination of water. Neither differences in the mean nutrient concentrations between the lakes with FFP (Free Floating Plants) absence and those with FFP dominance nor significant relationships between nutrients and the phytoplankton structure were observed. The species composition of phytoplankton and the functional (FG) and morpho-functional (MFG) groups reflected the differences between the habitats connected with hydromacrophytes. The free-floating macrophyte cover favours mixotrophic and heterotrophic species, mainly Euglenophyta (coda **W1** and **W2**) and chrysophytes (codon **Ws**) as well as shade-adapted cyanobacteria with the high tolerance of the low oxygen content (codon **K**). In lakes with FFP absence – taxa from Chlorophyta and Bacillariophyceae (associations **X1**, **J**, and **D**), or filamentous cyanobacteria (codon **S1**) dominated the phytoplankton. MFG were less related to the oxbow type and exhibited greater similarity between lakes independently of the presence or absence of FFP. Only unicellular Cyanoprokaryota which created **MFG 4** and colonial chroococcales (**MFG 5b** and **5c**) reached a greater percentage share, especially in oxbow lakes with FFP dominance.

Key words: anoxic waters; functional groups, diversity; light limitation; oxbow lakes; phytoplankton

Introduction

The Bug River extends from the upland area of Ukraine (northeast of Lviv) to the Narew River, and for most of its course it is a border river. It has changed its course many times and the palaeographic changes in it have been well documented (Szwajgier 2002). Especially, the middle part of the Bug River meanders strongly and this has created a lowering of the old river bed which is now occupied by river lakes, also known as oxbow lakes (Dawidek & Turczyński 2006). Because of the location of border, a great part of them are mostly affected by natural factors and they have not undergone any significant anthropogenic changes. The Bug River‘s oxbow lakes are usually small, shallow, eutrophic and gradually overgrown by plants. In many lakes of the Bug Valley floor, the associations of pleustophytes – mainly *Lemnetea minoris* – dominate (Urban & Wójciak 2006). It was observed that a dense layer of free-floating plants, covering almost all the water surface of the oxbow lakes, could persist from year to year. In contrast, in the same lakes, pleustophytes are absent or their stands are rare and never cover a greater part of the lake. Aquatic plants play an important role in the structuring of the ecosystems of freshwater shallow lakes. The connection between submerged macrophytes and a clear water state was described (Scheffer 2001). As was described in the literature, in oxbow lakes, especially subtropical and tropical ones, the environmental biological parameter which can interact with the phytoplankton community is mainly free-floating aquatic vegetation; plants which create a dense cover on the lake surface cause a limitation of light and anoxic conditions (Izaguirre et al. 2001, 2004; O’Farrell et al. 2003). In temperate regions duckweeds (Lemnaceae), in conditions of high nutrient availability, are commonly found in small, shallow water bodies and ditches (Scheffer et al. 2003; Krasznai et al. 2010). These plants have the best position for competition for light, rapidly take nutrients from water and form dense beds over the water surface, that seems to be the key factor for phytoplankton growing. Investigations of Scheffer et al. (2003) suggest that the dominance of FFP can promote a self-stabilizing state. Thus, the result of higher nutrients level is phytoplankton-domination state or in case of smaller lakes – predominance of free floating plants.

The aim of the present study was to compare the phytoplankton biomass amount, the phytoplankton taxonomic structure and its diversity in oxbow lakes with a contrasting (present or absent) cover of pleustophytes.

Particularly, we focused on the following hypothesis:

(i) Abiotic parameters of water in FFP – dominated lakes are significantly different from those free from pleustophytes.

(ii) A dense cover of floating macrophytes strongly influences the lake phytoplankton structure in terms of its biomass and taxonomy.

(iii) Macrophyte-dependent differences of the phytoplankton quality structure can be expressed by the functional approach (functional groups – FG; according to Reynolds' theory; Reynolds et al. 2002) and/or morpho-functional groups – MFG (according to the pattern described by Salmaso & Padisak 2007).

Material and methods

In the present work eleven oxbow lakes situated within the left zone of the Bug River valley were studied. From the south they were – Uchańka, Hniszów, Bawole Rogi, Jama Roma, Wołczyny, Sobibór, Orchówek, Białe, Przewóz Nurski, Bużysko and Szumin. The lakes chosen for the study are small (with a surface area from 0.3 to 28.1 ha) and shallow (max. depth between 1.5 and 5.7 m); except one (Lake Szumin), they have no permanent connection to the river channel. In order to enable their location on the map Table 1 shows the geographic coordinates of the studied lakes.

Considering the aquatic vegetation, two groups of the lakes sampled can be differentiated. The first group includes seven lakes: Hniszów, Bawole Rogi, Jama Roma, Wołczyny, Sobibór, Białe and Bużysko; during the study period, all of them were covered by pleuston macrophytes. This macrophyte community was quite constant in terms of species composition, dominated by *Spirodela polyrhiza* (L.) Schleiden, *Lemna trisulca* L., *Lemna minor* L., *Hydrocharis morsus-ranae* L. and *Utricularia vulgaris* L. The plant cover created by these species was present, to a lesser or greater extent, on the surface of these lakes during all the seasons of vegetation growth. The percentage of the macrophyte cover was estimated during sampling, along the transect perpendicular to the shoreline. The level of overgrowth ranged from about 30 to 100% of the lake surface. The second group, Lake Orchówek, Lake Uchańka, Lake Przewóz Nurski and Lake Szumin, were water bodies always free from of floating vegetation cover and even if it appeared it was located in very sparse stands near the banks. This provided an opportunity to compare the effects of macrophytes (FFP) on phytoplankton development in oxbow lakes.

For phytoplankton and chemical analyses, samples were collected monthly between April and October in 2006 (Uchańka, Hniszów, Bawole Rogi, Jama Roma, Orchówek, Wołczyny, Sobibór) and 2007 (Uchańka) and three times a year (May/June, August, October) in 2009–2010 (Białe, Bużysko, Przewóz Nurski, Szumin).

Temperature, conductivity, pH and dissolved oxygen concentration were measured *in situ* (WTW OX196 oxymeter, YSI 650 MDS multiparametric probe). In all of the lakes, water was taken with a Ruttner type sampler ($2\ L^{-1}$ capacity), at 1 to 4 stations within a lake. The water column was sampled at one metre intervals and poured into one collective sample, or, in lake stations characterized by depth <2 m, from the depth 0.5 m.

Light was measured with a light meter (Underwater Quantum Sensor Li192 SA and Quantum Sensor Li 190SA, LI-COR Biosciences, Lincoln, IL, USA). Photosynthetically active radiation was recorded every 25 cm in the water column to calculate the vertical attenuation coefficient (Kd_{PAR}), Kd_{PAR} was calculated by log-transformed irradiance measurements against depth.

The chemical analyses of soluble nutrients ($N\text{-}NH_4$, $N\text{-}NO_3$, $P\text{-}PO_4$), total values (TN and TP) and chloride ion concentrations were estimated in the laboratory according to standard methods (Hermanowicz et al. 1999). Samples for quantitative phytoplankton analysis were first fixed in Lugol's solution and then preserved in formaldehyde. Algal counts (cells, colonies and filaments) were evaluated with an inverted microscope, according to the Utermöhl method (Vollenweider 1969). For counting, samples were transferred to a settling chamber (5, 50, 100 ml capacities were used, depending on algal density) and at least 100 specimens of the most numerous algae were counted per sample. The biomass was estimated based on the phytoplankton number by making measurements of the species size. The biovolume was determined according to Hillebrand et al. (1999). Additional samples for taxonomic analysis were obtained with a 25 µm plankton net and the phytoplankton species composition was determined under a light microscope at magnification 400× to 1500× from living samples and those fixed with Lugol‘s solution. Due to the shallowness of the water bodies studied, the material could sporadically include species belonging to other ecological formations (periphyton or phytobenthos), mainly diatoms, and these were also counted. Measurements of chlorophyll *a* concentration involved filtering water through Whatman GF/C filters on the day of sampling, followed by extraction with ethanol and determination by the spectrophotometric method (Nusch 1980). The absorption of the extract was determined with a Beckman DU640B spectrophotometer, at wavelengths of 665 and 750 nm.

Statistical analyses were performed with the StatSoft Statistica 8 for Windows. The Kruskal-Wallis one-way analysis of variance by ranks and Wilcoxon rank-sum tests were used to reveal which means of abiotic and biotic parameters are significantly different between two types of lakes. The Spearman rank coefficient was used to determine the relationship between the abiotic and biotic parameters of water. The diversity, PCA and CCA analyses were carried with MVSP, Kov. Comp. Serv. 1985–2009. The principal component analysis (PCA) using environmental variables allowed to evaluate similarities between types of lakes. All the variables were centred and standardized prior to ordination. The functional groups (FG) were determined according to Reynolds et al. (2002) and Padisák et al. (2009) and so were the morpho-functional groups (MFG) according to Salmaso & Padisák (2007).

Results

Physical and chemical characteristics

Table 1 summarizes the physical and chemical variables of all the lakes sampled. Water temperature varied from 5.3 to 24.2 ℃. The lowest mean temperature (14 ℃) was measured in Lake Sobibór, which was covered by floating plants and shaded by near trees. The highest temperature was in Lakes Uchańka and Przewóz Nurski

Table 1. Morphometric and limnological parameters (mean, minimum and maximum values) of studied oxbow lakes.

	Hniszów	Bawole Rogi	Jama Roma	Wołczyny	Sobibór	Białe	Bużysko
Geographic coordinates	51°15′50″ N 23°43′01″ E	51°24′37″ N 23°41′42″ E	51°25′28″ N 23°40′49″ E	51°26′22″ N 23°40′20″ E	51°28′13″ N 23°39′36″ E	52°39′36″ N 22°19′11″ E	52°40′40″ N 21°54′40″ E
Max. depth (m)	1.5	3.1	3.7	4.1	3.3	3.9	2.7
Lake surface (ha)	0.3	2.4	2.7	2.3	1.7	1.1	15.8
Temperature (℃)	14.8 (7.8–20.0)	14.5 (7.8–18.3)	15.2 (7.7–18.4)	15.7 (12.4–17.6)	14.0 (12.3–15.3)	15.6 (5.6–17.6)	16.2 (5.3–21.9)
Kd (m^{-1})	6.7 (0.6–11.6)	6.0 (2.8–11.7)	4.6 (0.4–11.6)	9.7 (2.7–12.7)	13.4 (11.6–15.8)	8.3 (3.3–15.6)	3.6 (2.1–4.6)
pH	7.76 (6.98–8.19)	7.48 (6.99–8.29)	7.59 (7.04–8.26)	7.44 (7.28–7.53)	7.20 (6.85–7.48)	7.61 (7.23–7.53)	7.71 (7.47–7.53)
Conductivity (μS cm^{-1})	980 (785–1294)	731 (588–920)	616 (416–864)	658 (524–876)	737 (620–837)	410 (370–433)	396 (357–423)
Alkalinity (mval L^{-1})	5.8 (3.9–8.3)	4.7 (3.0–5.9)	3.4 (2.2–4.7)	4.5 (4.0–4.9)	5.9 (5.0–6.9)	5.2 (5.1–5.2)	4.9 (4.5–5.2)
Dissolved oxygen (mg L^{-1})	2.0 (0.1–8.4)	2.7 (nd-9.6)	1.9 (nd-6.5)	0.2 (nd-0.7)	0.3 (nd-0.8)	7.7 (1.2–12.3)	9.0 (6.3–10.1)
TP (mg L^{-1})	0.82 (0.33–1.56)	0.56 (0.13–1.62)	0.29 (0.14–0.74)	0.68 (0.2–1.24)	0.49 (0.3–0.67)	0.27 (0.15–0.53)	0.24 (0.09–0.46)
TN (mg L^{-1})	3.10 (2.04–4.78)	3.05 (1.93–3.92)	2.52 (1.68–3.89)	2.93 (1.83–3.98)	4.00 (2.75–5.13)	2.04 (1.73–3.00)	2.00 (1.35–2.68)
Orthophosphate (mg L^{1})	0.40 (0.03–0.95)	0.18 (0.02–0.39)	0.10 (0.02–0.17)	0.22 (0.08–0.32)	0.27 (0.15–0.5)	0.09 (0.01–0.20)	0.02 (0.01–0.40)
Nitrate (mg L^{-1})	1.13 (0.41–1.93)	0.95 (0.19–2.48)	0.65 (0.19–1.00)	0.74 (0.54–1.06)	0.94 (0.90–1.01)	0.17 (0.04–0.28)	0.12 (0.13–0.14)
Ammonium (mg L^{-1})	1.07 (0.37–2.68)	1.14 (0.39–2.96)	0.81 (0.36–1.85)	1.29 (1.09–1.67)	2.13 (1.78–2.96)	0.11 (0.01–0.52)	0.01 (0.01–0.01)
Chloride (mg L^{-1})	28.2 (17.8–36.2)	15.3 (12.0–18.1)	11.6 (9.8–14.2)	12.6 (8.2–17.7)	19.7 (10.3–26.9)	ND	ND
Chl-*a* (μg L^{-1})	98.2 (1.0–503.7)	59.9 (17.1–100.2)	67.9 (15.3–173.9)	40.7 (10.9–99.8)	190.4 (72.6–351.2)	19.26 (10.4–32.2)	14.90 (4.4–27.2)
Biomass (mg L^{-1})	3.3 (0.1–14.2)	3.1 (0.1–9.0)	4.7 (0.3–16.0)	0.8 (0.6–1.2)	4.6 (1.7–8.3)	6.8 (0.2–26.7)	7.4 (1.3–15.4)
Species number/sample number	17 (5–33)/7	15 (7–28)/7	20 (17–27)/7	10 (5–14)/4	11 (9–16)/4	14 (8–23)/8	23 (14–30)/7
Shannon-Weaver index	1.52 (0.95–2.46)	1.97 (1.15–2.80)	2.52 (1.51–3.21)	1.44 (1.02–1.72)	1.16 (0.38–0.80)	2.14 (1.31–3.04)	2.42 (0.72–3.69)
Evenness index	0.41 (0.20–0.51)	0.54 (0.40–0.80)	0.59 (0.39–0.68)	0.44 (0.32–0.52)	0.32 (0.12–0.53)	0.56 (0.41–0.67)	0.53 (0.36–0.78)
Character of floating vegetation	*Spirodela polyrhiza* *Lemna minor* *Lemna trisulca* *Wolffia arrhiza*	*Spirodela polyrhiza* *Lemna minor* *Lemna trisulca*	*Spirodela polyrhiza* *Lemna minor* *Lemna trisulca* *Hydrocharis morsus-ranae*	*Spirodela polyrhiza* *Lemna trisulca* *Lemna minor*	*Lemna minor* *Lemna trisulca* *Spirodela polyrhiza*	*Spirodela polyrhiza* *Lemna trisulca* *Lemna minor*	*Spirodela polyrhiza* *Lemna trisulca* *Lemna minor* *Hydrocharis morsus-ranae* *Utricularia vulgaris*
Macrophytes cover (%) (min–max)	30–100	30–100	30–100	30–100	70–100	30–100	30–70

Table 1. (continued)

	Uchańka	Orchówek	Przewóz Nurski	Szumin
Geographic coordinates	51°05′10″ N 23°52′08″ E	51°31′36″ N 23°34′18″ E	52°39′59″ N 22°15′54″ E	51°26′22″ N 23°40′20″ E
Max. depth (m)	5.2	2.9	5.7	3.6
Lake surface (ha)	3.5	8.2	21.8	5.4
Temperature (℃)	17.4 (8.8–23.6)	16.1 (12.5–21.0)	17.2 (6.4–24.2)	16.8 (5.7–22.6)
Kd (m^{-1})	4.7 (0.2–7.9)	3.4 (2.0–6.4)	3.4 (0.4–7.6)	4.6 (3.3–7.6)
pH	8.38 (7.66–8.78)	7.84 (7.55–8.30)	8.43 (7.73–8.30)	8.44 (8.15–8.30)
Conductivity (µS cm^{-1})	805 (702–949)	627 (529–700)	327 (269–380)	452 (415–489)
Alkalinity (mval L^{-1})	4.7 (3.4–6.9)	4.0 (2.9–4.6)	4.1 (3.9–4.3)	5.1 (4.3–5.5)
Dissolved oxygen (mg L^{-1})	5.8 (0.5–11.8)	2.9 (1.2–7.8)	13.42 (3.9–18.9)	12.83 (3.9–22.2)
TP (mg L^{-1})	0.62 (0.28–1.56)	0.41 (0.12–0.99)	0.37 (0.25–0.47)	0.36 (0.13–0.59)
TN (mg L^{-1})	2.69 (0.51–4.10)	3.03 (2.09–4.43)	2.06 (1.30–3.27)	1.09 (1.54–2.45)
Orthophosphate (mg L^{-1})	0.12 (0.02–0.24)	0.19 (0.03–0.5)	0.16 (0.10–0.29)	0.16 (0.05–0.24)
Nitrate (mg L^{-1})	0.88 (0.24–1.96)	0.65 (0.14–0.97)	0.15 (0.06–0.30)	0.22 (0.09–0.63)
Ammonium (mg L^{-1})	0.79 (0.33–1.37)	1.27 (0.39–3.72)	0.46 (0.01–1.31)	0.07 (0.01–0.14)
Chloride (mg L^{-1})	25.6 (16.9–30.1)	22.2 (15.1–26.9)	ND	ND
Chl-*a* (µg L^{-1})	34.2 (7.5–66.3)	63.5 (22.9–105.8)	15.45 (6.9–53.2)	54.26 (12.4–133.0)
Biomass (mg L^{-1})	6.5 (0.2–17.5)	5.5 (0.5–13.9)	17.7 (2.47–41.9)	27.5 (2.58–80.9)
Species number/sample number	32 (13–58)/13	33 (18–56)/6	22 (15–26)/11	41 (29–51)/12
Shannon-Weaver index	2.63 (1.56–3.54)	2.80 (1.88–3.47)	2.06 (0.63–2.93)	3.24 (1.6–4.63)
Evenness index	0.49 (0.16–0.82)	0.57 (0.42–0.77)	0.46 (0.15–0.62)	0.61 (0.30–0.79)

ND – Not Determined, nd – not detectable.

– shallow lakes, with a wide surface area and free from floating vegetation (Table 1). In most lakes, the light attenuation coefficient (Kd$_{\mathrm{PAR}}$) reached high values and was the highest (Kd$_{\mathrm{PAR}}$ > 4 m^{-1}) during the summer season. The mean values of Kd$_{\mathrm{PAR}}$ were significantly lower in lakes free from pleustophytes than in the overgrown ones (4.3 m^{-1}and 7.3 m^{-1}, respectively; $n = 74$, $H = 5.22$, $p = 0.022$). Kd$_{\mathrm{PAR}}$ was at the maximum (Kd$_{\mathrm{PAR}}$ > 8 m^{-1}) when FFP created dense mats covering 70%–100% of the water surface, whereas in the lakes free from FFP it never exceeded the value of 8 m^{-1}. The mean pH, usually neutral or alkaline (varied between 6.98–8.78), also exhibited statistically significant differences between abovementioned types of lakes (with mean values of 8.26 and 7.55, respectively; $n = 74$; $H = 36.04$, $p = 0.000$). The oxygen conditions were usually significantly worse (with anoxia in the summertime) in the lakes dominated by FFP than those free from FFP (with mean values of 7.3 and 3.3, respectively; $n = 74$; $H = 14.08$, $p = 0.000$). The values of conductivity were always rather high and usually exceeded 400 µS cm^{-1}, except for Lake Przewóz Nurski (Table 1). The highest conductivity value (1294 µS cm^{-1}) in the Lake Hniszów waterbody coincided with the highest concentrations of chlorides (36.2 mg dm^{-3}) and nitrates (1.93 mg dm^{-3}). For all of the lakes, there was a correlation between conductivity and chloride ions ($r = 0.76$, $n = 38$, $p < 0.05$). All the studied lakes revealed an eutrophic character with relatively high values of nutrient concentrations. The mean values of phosphorus and nitrogen compounds were similar in lakes with FFP absence and those with FFP dominance (Table 1).

The PCA of abiotic variables in lakes free from FFP suggests that the considerable variability (50.5%) can be explained by nutrients, light availability and dissolved oxygen concentration connected with these parameters (Fig. 1). There was an inverse relationship of dissolved oxygen and pH, with nitrogen compounds and conductivity. There was also a negative relationship with TN and TP, suggesting that the ammonium and other nitrogen compounds could be related to a greater extent to decomposition processes. In the PCA for FFP-dominated lakes the greatest interlake variation resulted from differences in light penetration (macrophyte cover and Kd$_{\mathrm{PAR}}$) (Fig. 1). Contrary to the previously described type of lakes, the concentrations of some nutrients were strongly correlated with each other. Moreover, light deficiencies were positively related to conductivity, ammonium and orthophosphates and negatively correlated with oxygen and pH. Across all the lakes, the total biomass of phytoplankton strongly covaried with the main principal components. In oxbow lakes free from FFP there was a positive but not statistically important relationship between biomass and Kd$_{\mathrm{PAR}}$, while in water bodies dominated by FFP the biomass was significantly negatively correlated with Kd$_{\mathrm{PAR}}$.

Changes in the relevant physical and chemical variables were investigated along the increasing attenuation coefficient (Fig. 2). In the case of oxbow lakes free from floating vegetation, none of the parameters showed a close relationship with the light conditions. But in lakes with a macrophyte cover, pH and some others chemical parameters (ammonium, dissolved oxygen, soluble and total phosphorus), were associated with Kd$_{\mathrm{PAR}}$ (Fig. 2). The alkaline water reaction (with a mean of about 8) occurred for the best light conditions and it decreased as the plant cover gathered. pH was lowest under a total vegetation layer when Kd$_{\mathrm{PAR}}$ > 8 m^{-1}. Such a negative relationship was even more evident in the case of oxygen saturation, where the concentration decreased dramatically as the Kd$_{\mathrm{PAR}}$ increased (Fig. 2). The oxygen content was high in spring, while in the following months it decreased to an undetectable level. The variability in

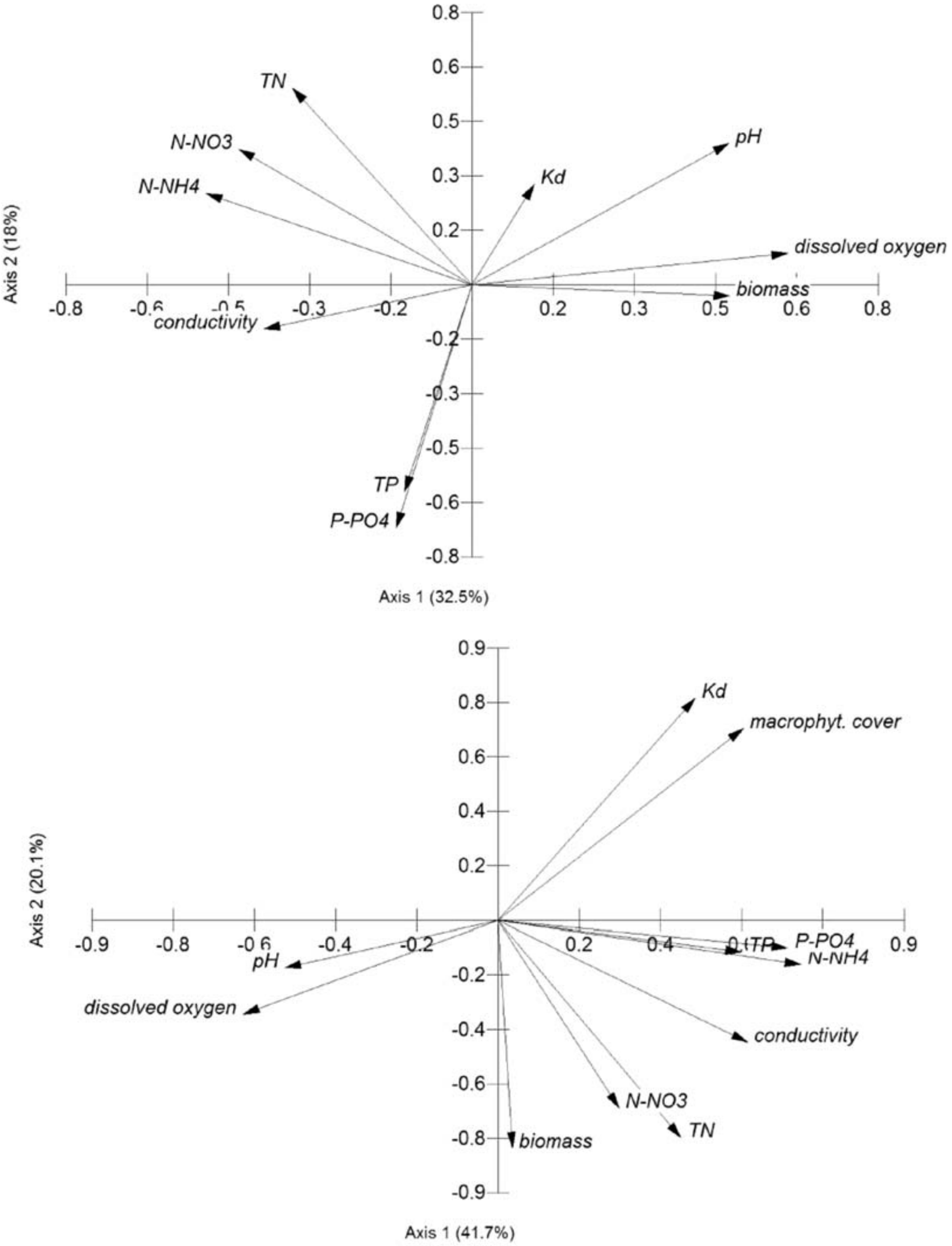

Fig. 1. Covariance of water quality with the first and second principal components in a PCA of all variables and samples (top – FFP absence, below – FFP dominance)

oxygen concentration corresponded to changes in water transparency. When Kd_{PAR} exceeded 6 m^{-1}, oxygen depletion was noted, and as a result five of the lakes, i.e. Hniszów, Bawole Rogi, Jama Roma, Wołczyny, Sobibór and Białe, remained anoxic for almost the entire study period, whereas in lakes free from FFP waters were usually oxygen saturated (Table 1, Fig. 2). The opposite pattern was found for ammonium ions, where their concentration increased in anoxic waters and was about 60% higher in lakes entirely shaded by macrophytes (Kd_{PAR} above 8 m^{-1}) than in waters with better possibilities of irradiation. The Spearman rank coefficients between $N\text{-}NH_4$ and dissolved oxygen and between $N\text{-}NH_4$ and Kd_{PAR} were respectively: $r = -0.47$ and -0.71 ($n = 41$, $p < 0.05$). There was also a correlation between orthophosphate concentrations and the light conditions ($r = 0.44$, $n = 41$, $p < 0.05$).

Taxonomic composition

Phytoplankton was represented by a total of 322 taxa distributed into eight algal groups: Cyanoprokaryota, Euglenophyta, Dinophyceae, Cryptophyceae, Chrysophyceae, Xanthophyceae, Bacillariophyceae and Chlorophyta. The occurrence of the Xanthophyceae was ob-

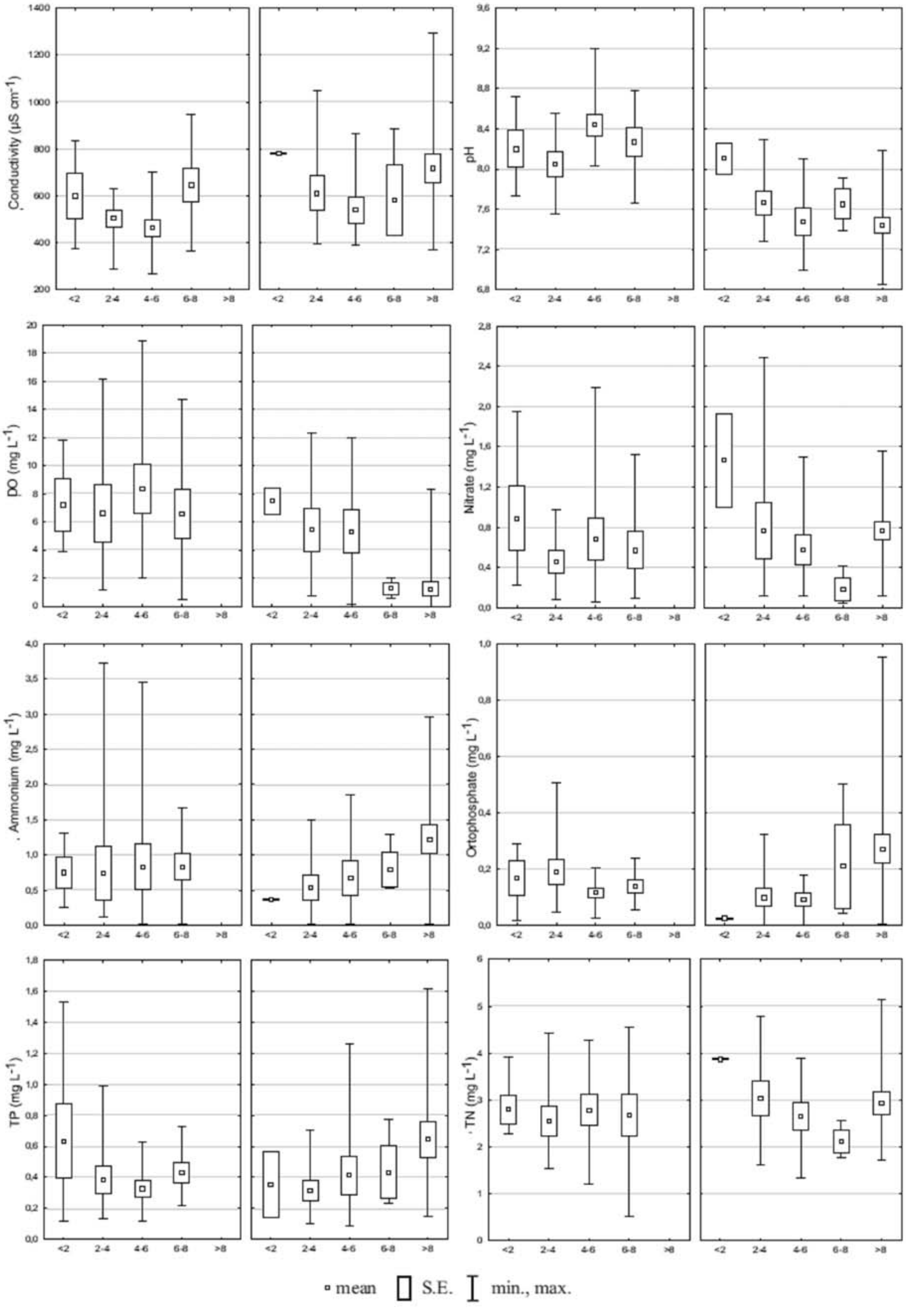

Fig. 2. Characteristic physical-chemical parameters (mean, S.D., min., max.) along different light conditions expressed as attenuation coefficient (Kd_{PAR}). The left column – FFP-absence, right – FFP dominance.

served, but its percentage share in the total number of species was small and did not exceed 10% of total density. The Bacillariophyceae, Chrysophyceae, Cryptophyceae, Chlorophyta and Cyanoprokaryota gener-

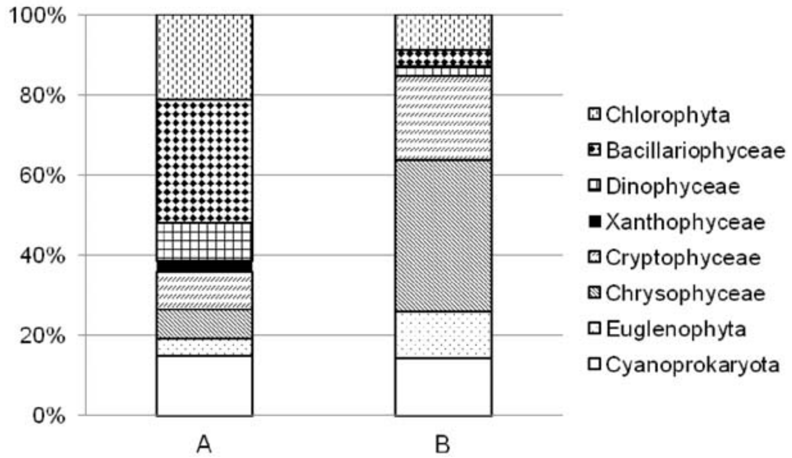

Fig. 3. Relative average biomass of phytoplankton taxonomic groups in different types of lakes (A – FFP – absence, B – with FFP domination).

ally reached the greatest percentage share in the total biomass. The composition of phytoplankton species differed between lakes without FFP and those with FFP (Fig. 3). Diatoms were especially numerous in lakes without FFP, centrales from genera *Stephanodiscus* (*S. hantzschii* Grunow) and *Cyclotella* (*C. meneghiniana* Kütz., *C. comta* (Ehrenb.) Kütz.), also *Aulacoseira granulata* var. *granulata* (Ehrenb.) Simonsen or *Chaetoceros muelleri* Lemmerm. Pennated forms, such as *Ulnaria ulna* (Nitzsch) P.Compère, *U. acus* (Kütz.) M.Aboal and *Meridion circulare* (Grev.) C.Agardh, were less abundant. In some lakes dominated by FFP, under a dense macrophyte cover, typical peryphytic algae (*Epithemia* spp., *Gomphonema* spp.) reached a great percentage share.

The taxonomic groups which achieved predominance in pleustophyte-dominated lakes, especially in the spring and the autumn, were chrysophytes and/or cryptophytes (Fig. 3). The biomass of Chrysophyceae increased in lakes when the surface of water was covered by macrophytes to a lesser extent, but their abundance was considerable (more than 20% of the total biomass) only when the oxygen conditions were sufficient (at least 2 mg L^{-1}). The most numerous species in this class were: *Synura uvella* Ehrenb., *Dinobryon sociale* (Ehrenb.) Ehrenb., *D. divergens.* O.E.Imhof and *D. bavaricum* Imhof.

Green algae dominated the phytoplankton structure, especially in lakes free from FFP, and this class was especially rich in taxa. Their most abundant species belonged to the order Volvocales: *Pandorina morum* (O.F.Müller) Bory de Saint-Vincent, *Eudorina elegans* Ehrenb., *Gonium pectorale* O.F.Müller, *Pyrobotrys incurve* Arnoldi*, Phacotus lenticularis* (Ehrenb.) Stein*, Carteria* spp. and Chlorococcales: *Coelastrum sphaericum* Nägeli, *Monoraphidium contortum* (Thuret) Komárková-Legnerová, *M. minutum* (Nägeli) Komárková-Legnerová, *Crucigeniella rectangularis* (Nägeli) Gay, *Micractinium pusillum* Fresenius. The same species occurred in lakes covered by FFP and reached a considerable percentage share in some samples.

Under duckweed mats, Cyanoprokaryota comprised from 20 to almost 100% of the biomass of planktonic algae in particular lakes and was usually composed of a few species – almost exclusively: *Synechococcus mundulus* Skuja, *Merismopedia insignis* Skorbatov, *M. tenuissima* Lemmerm., *Woronichinia elorantae* J.Komárek & J.Komárková-Legnerová, *Coelosphaerium aerugineum* Lemmerm., *Oscillatoria limosa* C.Agardh and an unidentified *Arthrospira* species. In lakes free from FFP, Cyanoprokaryota occurred in low numbers and the abovementioned species were very rare or absent. Instead of them, among Cyanoprokaryota, filamentous as well as colonial forms were most numerous (*Planktothrix agardhii* (Gomont) Anagnostidis & Komárek and *Microcystis* spp.).

Other groups with relatively high biomass were: Dinophyceae (with dominants: *Gymnodinium uberrimum* (G.J.Allman) Kofoid & Swezy, *Peridinium inconspicuum* Lemmerm., *Woloszynskia leopoliensis* (Woloszynska) R.H.Thompson – in lakes with FFP absence, and euglenoids (a group relatively rich in species), frequent in FFP-covered lakes (Fig. 3). The dominants among euglenophytes were: *Lepocinclis acus* (O.F.Müller) Marin & Melkonian, *L. ovum* (Ehrenb.) Lemmerm., *Euglena hemichromata* Skuja*, Monomorphina strongyla* (Playfair) Marin & Melkonian*, Trachelomonas volvocinopsis* Svirenko*, T. hispida* (Perty) F.Stein, *T. armata* (Ehrenb.) F.Stein, *Phacus helicoides* Pochmann.

The differences in environmental conditions between lake types (with the pleustophyte mats and without it) were related with reduce the amount of phytoplankton biomass, richness and diversity (Table 2). These parameters were lower in lakes covered by macrophytes and within this group of oxbow lakes there was a negative, but not statistically significant, relationship between diversity and increasing $\mathrm{Kd}_{\mathrm{PAR}}$ coefficient ($r = -0.29$, $n = 44$, $p < 0.05$). This result was connected with the development of *Synechococcus mundulus*, *Coelosphaerium aerugineum,* which species were the only dominants (above 60% of total biomass) under a dense plant cover and anoxic conditions. In contrast, in lakes without pleustophytes, the phytoplankton bio-

Table 2. Mean values of the amount of phytoplankton and its diversity in both types of studied oxbow lakes. Also the standard deviations (S.D.), statistical significance (p, Wilcoxon signed rank test) for the differences between the mean values in FFP absence and FFP dominance.

	FFP absence ($n = 42$)		FFP dominance ($n = 44$)		p
	Mean	S.D.	Mean	S.D.	
Chl-a (μg L^{-1})	40.5	32.8	59.6	93.0	0.930
Biomass (mg L^{-1})	15.0	17.5	7.4	15.2	0.000
Shannon-Weaver index	2.68	0.90	1.96	0.81	0.000
Evenness index	0.54	0.15	0.50	0.15	0.140
Species number	33	13	16	7	0.000

diversity (the Shannon-Weaver coefficient) was slight, but positively related to an increase in the light attenuation coefficient ($r = 0.26$, $n = 42$, $p < 0.05$). Surprisingly, the chlorophyll a concentration was very high in most of FFP dominated lakes and reached an extremely elevated level (above 200 μg L^{-1}) even when the illumination of water was very poor (Kd_{PAR} above 11 m^{-1}). There was no significant difference in the mean value of chlorophyll a concentration between the two types of the studied lakes (Tables 1 and 2).

Characteristic assemblages

Using the trait-based approaches developed by Reynolds (Reynolds et al 2002) and Salmaso and Padisák (2007), phytoplankton species were classified into functional (FG) and morpho-functional groups (MFG). According to the FG scheme, species were assigned to 23 coda. Among them, the most abundant (min. 30% of total biomass at least in one sample) were: **D**, **G**, **J**, **K**, $\mathbf{L_M}$, $\mathbf{L_O}$, **M**, **MP**, **S1**, **W1**, **W2**, **Ws**, **Y**, **X1**, **X2**. Some of them occurred in both lake oxbow types and were characterised by similar taxonomic composition; i.e., codon **G** with *Pandorina morum* and *Eudorina elegans* as dominants; **Ws** – *Synura uvella*, **W1** – *Trachelomonas* spp., *Strombomonas* spp. or **Y** – composed of different species of the *Cryptomonas* genus. Coda which were frequent in the absence of FFP as well as with FFP dominance were also noted; however, their dominants were different, e.g. for codon $\mathbf{L_O}$ the highest biomass was reached by: *Ceratium hirundinella* (O.F.Müller) Dujardin, *Woloszynskia leopoliensis*, *Peridinium* spp., or *Coelosphaerium aerugineum*, *Merismopedia insignis*, *M. tenuissima* with FFP absence and FFP dominance, respectively. Moreover, in lakes with a clear surface, the following associations were abundant: **S1** (*Planktothrix aghardii* (Gomont) Anagnostidis & Komárek, *Limnothrix redekei* (Van Goor), *Planktolyngbya limnetica* (Lemmerm.) Komárková-Legnerová et G.Cronberg, *Pseudanabaena limnetica* (Lemmerm.) Komárek, **X1** (*Monoraphidium komarkovae* Nygaard, *M. contortum*, *Didymocystis* sp.), **X2** (*Carteria compressa* Pascher, *C. excentrica* Printz, *Phacotus lenticularis* Ehrenb. Stain, *Pteromonas* sp.) and **J** (*Pediastrum boryanum* (Turpin) Meneghini, *P. duplex* Meyen, *Scenedesmus quadricauda* (Turpin) Brébisson). In contrast, under a partial or total pleustophyte cover, the species of codon **J** were almost absent or rare. There were coda which were specifically connected with oxbow lakes with FFP dominance: **K** (*Synechococcus mundulus*, *Arthrospira* sp.), $\mathbf{L_M}$ (*Microcystis aeruginosa*, *Ceratium hirundinella*), **MP** (*Epithemia* spp., *Gomphonema* spp., *Oscillatoria* spp.), **W1** (*Lepocinclis ovum* (Ehrenb.) Lemmerm., *Euglena* spp., *Gonium pectorale*) and **M** (*Microcystis aeruginosa, M. wesenbergii* (Komárek) Komárek).

According to the MFG classification, phytoplankton species were assigned to 27 groups. All of them occurred in all the studied lakes, except for group **9d** (*Trachychloron* sp., *Goniochloris laevis* Fott, *G. contorta* (Bourrelly) Ettl), whose representatives were noted almost exclusively in lakes without FFP, and group **4** (unicellular cyanobacteria – i.e. *S. mundulus*), typical of FFP – dominated lakes. Generally, in the latter type of lakes, a greater percentage share in the total biomass was reached, by large, vacuolated and non-vacuolated chroococcales such as *M. aeruginosa* or *C. aerugineum* (MFG – **5b** and **5c**) as well as by large and small euglenophytes i.e. *L. acus*, *L. ovum* or *T. volvovinopsis* (**1c** and **2c**) (Fig. 4).

The canonical correspondence analysis revealed that PAR irradiation, conductivity, dissolved oxygen and pH were the main determinants in the separation of samples. These variables differentiated the FG and MFG with distinct requirements for light and oxygenation conditions (Fig. 5). Coda **K**, $\mathbf{L_M}$, $\mathbf{L_O}$, **M**, **W1** and groups **4**, **5c** and **5b** exhibited a correlation with samples from lakes with worse light conditions, while associations **S1**, **J**, **D**, **Y** and **X1** and groups **8a** (large unicellular chlorophytes) and **1b** had better light penetration in water and a higher level of oxygen saturation. Coda **W1, M,** $\mathbf{L_O}$ were positively correlated to an increase in nutrient concentrations. The only associations which correlated in a significantly positive manner with TP were $\mathbf{L_O}$, $\mathbf{L_M}$ and **W1** and so did **Ws** with TN. There was no more significant relationship between FG and nutrients. A more statistically significant relationship with nitrogen and phosphorus compounds was noted in the case of MFG (Fig. 5). The positive relation to TP and TN was exhibited by groups **1b** (large Dinophytes) and **1c** (large euglenophytes), while a negative one was demonstrated by **2d** (Cryptophytes). An inverse relation was observed between groups **2d**, **5a** (filamentous Cyanoprokaryota) and **9b** (small chlorococcales) in relation to ammonium and nitrate concentrations.

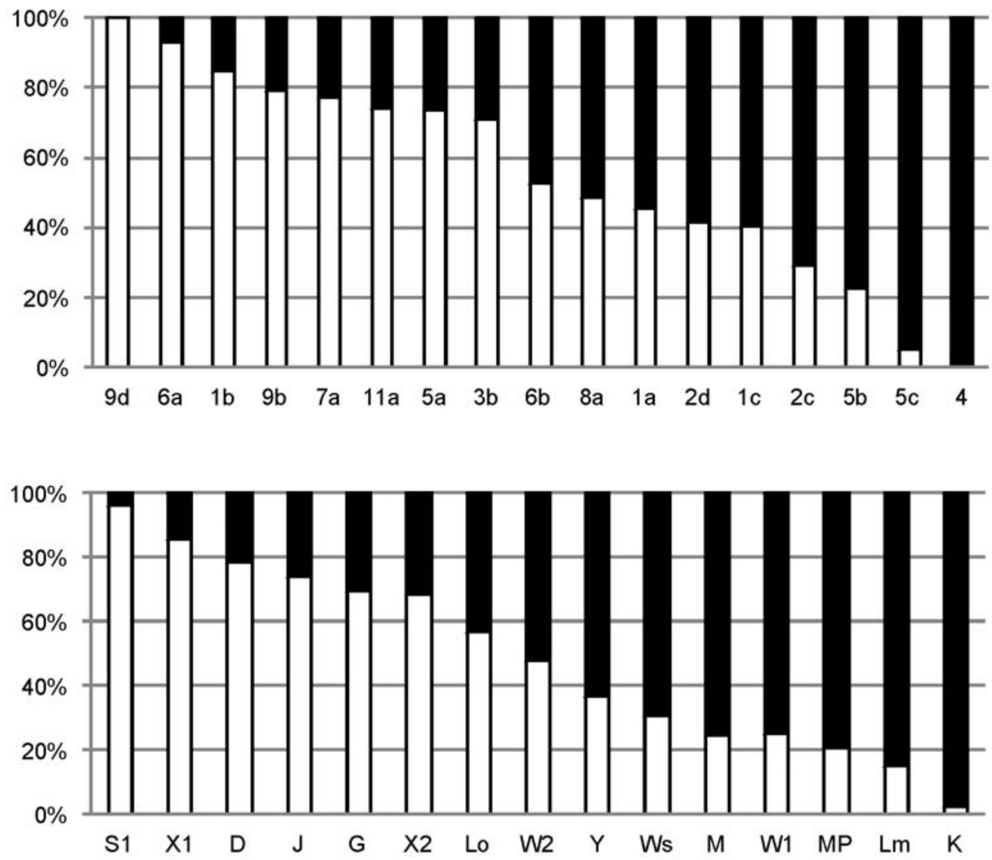

Fig. 4. Relative average share of the main MFG (diagram above) and FG (below) in total phytoplankton biomass of oxbow lakes with FFP absence (white columns) and FFP domination (black columns).

Discussion

In general terms, the structure and composition of the phytoplanktonic community in oxbow lakes were significant influenced by site environmental factors, mainly the free-floating plant cover. The pleustophyte cover displayed variations in its density and extent during the vegetation season, but it considerably influenced the phytoplankton structure in oxbow lakes from the spring to the early autumn.

On the basis of physicochemical results, as well as earlier investigations (Wojciechowska et al. 2005, 2007), just as many other such types of waterbodies, all the lakes can be classified as eutrophic ones. In the studied oxbow lakes, nutrients do not play a critical role in regulating the composition and biomass of phytoplankton. Similar results in these types of oxbow lakes were published by Krasznai et al. (2010) who emphasised that the role of nutrients is limited because in these ecosystems their concentrations highly exceed those that can be considered as limiting (Reynolds 2006). Thus, there was no clear relationship between TP and biomass as well as phytoplankton assemblages. The main differences in water parameters of the oxbows were caused by a dense FFP cover, which had overgrown most of them. Under such a FFP carpet, oxygen depletion appears, pH is circumneutral and the ammonia concentration is high. When the lake surface was 'clean', the oxygen concentration was high, pH – alkaline and ammonia low.

The high values of conductivity, chlorides and nitrates in Lake Hniszów in the summer indicate that this lake must have another source of water containing these ions, other than the Bug River. Lake Hniszów is a small oxbow (0.3 ha) and 30% of its catchment consists of arable fields (Dawidek & Turczyński 2006). The agricultural activities in the fields surrounding the lake could account for the increase of Cl^- and NO^{-3} ions in groundwater which supplies the lake during the isolation phase. Pithart (1999) observed a similar situation in another extremely small and shallow oxbow lake.

The species composition of phytoplankton and its life strategies expressed as functional and morphofunctional groups reflect the differences of habitats. Beside algal assemblages common in eutrophic, small water bodies of different types, in studied oxbow lakes the high biomass reached groups which usually are marginal in other lake type (**Ws**, **Y**, $\mathbf{L_O}$, **W1**, **K**, **MP**). The elements of codon **Ws** (*Synura* spp.) must use carbon dioxide as a source of inorganic carbon (Reynolds 2006) and, therefore, avoid eutrophic ecosystems with high pH (Krasznai et al. 2010). The members of this codon prevail in macrophyte-dominated lakes but only when oxygen conditions were sufficiently good (min. concentration 2 mg L^{-1}). The high biomass of chrysophytes (mainly *Synura uvella*, *Dinobryon sertularia* and *Uroglena* sp.) in oxbow lakes of the Bug river valley in

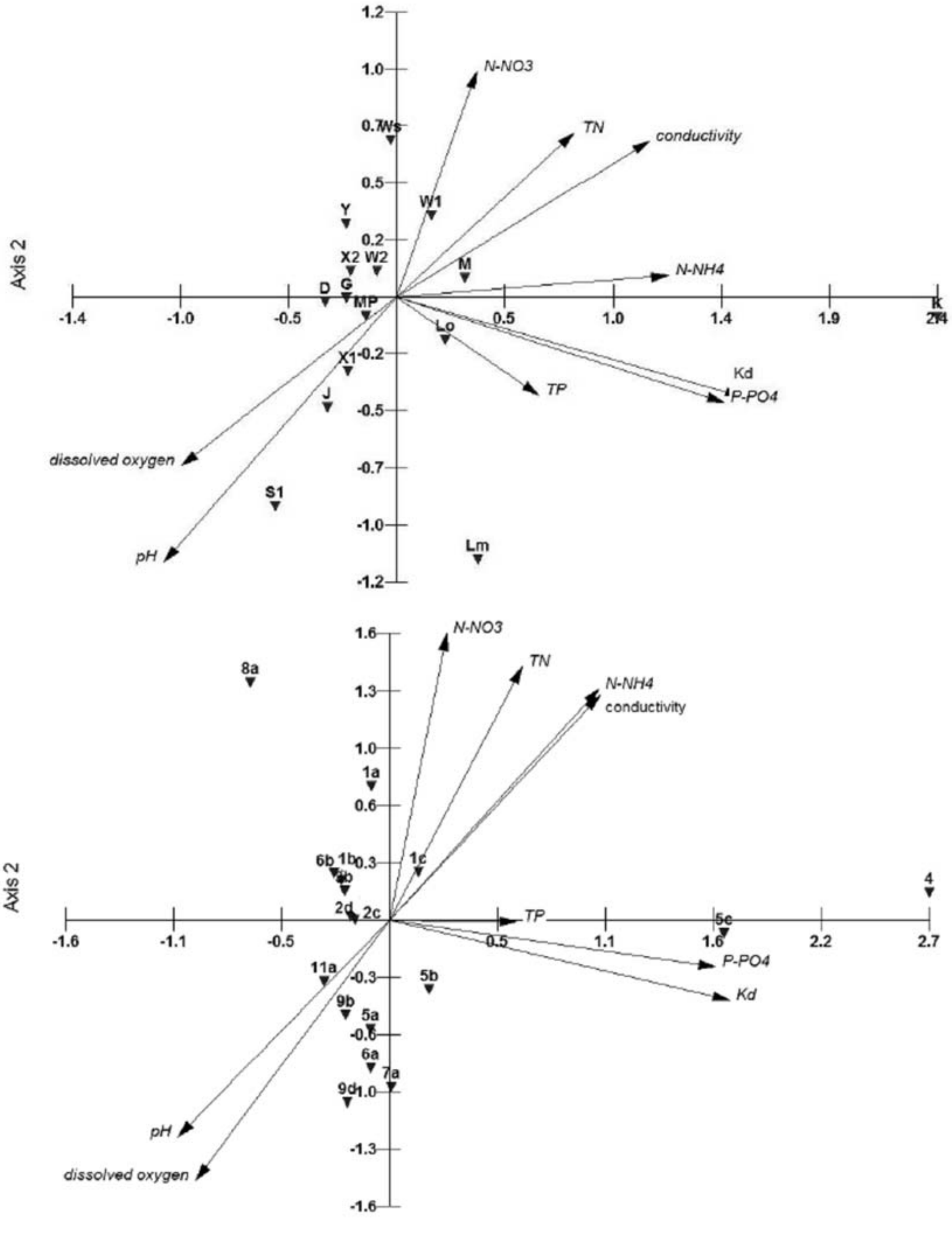

Fig. 5. CCA ordination among main FG (at the top)/ MFG (below) and significant abiotic variables in all studied oxbow lakes.

March and April, under good water oxygenation, was also observed in earlier investigations (Wojciechowska et al. 2007). In the present study, *Synura* genus was numerous as well in spring as in autumn, in differentiated light conditions (Kd_{PAR} varied between 0–8.4 m^{-1}). Its relatively great percentage share in total phytoplankton biomass, even under partial FFP cover, could be caused by the variant sensitivity of *Synura* species to ultraviolet radiation (UVR) which potentially inhibit photosynthesis. As described Scott et al. (2009) based on microcosm experiments, UVR had strong negative effect on the growth of *Synura* sp. in July and much weaker effect in April, with no differences in colony structure observed.

In oxbow lakes covered by FFP during vegetation season flagellates were dominants (mainly belonging to functional groups **Y, L_O** and **W1**). They are known as mixotrophic (using osmotrophy or phagotrophy strategy to survive in periods of low light) and they are enable to effective competition with other planktonic species to organizing the additional source of carbon – in form of DOC (dissolved organic carbon) or POC (particulate organic carbon) (Jones 2000). The bloom of euglenoids in a small oxbow lake of the Vistula River was observed by Ligęza & Wilk-Woźniak (2011). As mentioned authors described, rapid increases in the populations of *Euglena pascheri* and *Lepocinclis ovum* were accompanied with low pH values, oxygen deficits and high concentrations of nitrogen compound, chlorides, Fe, Mn, Zn and Cd, but with low concentrations of easily assimilated inorganic forms of phosphorus. In our studies, the increase of biomass of euglenophyta species (from *Euglena* and *Lepocinclis* genera) in oxbow lakes: Hniszów, Jama Roma, Bawole Rogi, also appeared in conditions of low oxygen concentrations and high concentrations of chlorides. Mean values of orthophosphates in these lakes were low and did not exceed 0.4 mg L^{-1}. Opposite to situations described by Ligęza & Wilk-Woźniak (2011), water pH values didn't decrease to acidic level. The possible factor promoting the growth of *Euglena* and *Lepocinclis* species in such habitat conditions could be their ability to combining phototrophy and consumption of organic carbon compounds.

The key factor in the phytoplankton ecology of studied oxbow lakes was a dense macrophyte cover. Interestingly, the increase in chlorophyll was especially high in FFP covered lakes, under a complete plant cover, when the environmental conditions, darkness and anoxia left scarce opportunities for the growth of planktonic algae. In these conditions, the mean value of chlorophyll *a* was about 200 µg L^{-1}, while in Lake Hniszów the maximum concentration reached as high as 503.7 µg L^{-1}. Simultaneously, the average biomass was low (approximately 4.5 mg L^{-1}). We can suppose that in poor light conditions the chlorophyll *a* content significantly increased per unit of biomass. As stated Felip & Catalan (2000), the maximum values of chlorophyll in the cells of algae were recorded in the deep hypolimnion of mountain lakes and under the ice layer, and were not correlated with the maximum values of biomass. According to these authors, the increase of algal biomass in water was associated with improvement of light conditions, while the increase in the concentration of chlorophyll *a* depended on its content in the cells as well as the taxonomic composition of phytoplankton. In the oxbow lakes of the Bug River the species responsible for such high concentrations of chlorophyll *a* belonged to shade-adapted blue-green algae with a high tolerance of a low oxygen level. The cyanoprokaryotic species identified for oxygen deficits, dominated by *Synechococcus mundulus*, resemble the assemblages described in the oxbow lakes of the Paraná River by Izaguirre et al. (2001, 2004) and by O'Farrell et al. (2003). These assemblages were mainly made up from small Chroococales (*Synechococcus* spp. and *Synechocystis* spp.) and *Arthrospira* sp. These small cells have a large surface to volume ratio, and so compete effectively for nutrients with any larger cells. They can occur in deeper water where they contribute to the "deep chlorophyll maximum" in spite of the very low light levels, because of their adaptive properties concerning photosynthetic active pigments in cells (Veldhuis et al. 2005). Picoplanktonic species have been also reported in the literature as probably being capable of mixotrophic anoxygenic photosynthesis (Izaguirre et al. 2001; O'Farrell et al. 2003). Moreover, the mass development of a Cyanoprokaryota species *S. mundulus*, shown in the present work, was accompanied by unidentified oscillatorian species, probably assigned to the genus *Arthrospira*. According to its morphological description and its environmental requirements, this species resembled *Arthrospira* sp. described by Izaguirre et al. (2001).

The species richness of oxbow lake ecosystems is generally high, as noted in the river lakes of European rivers (Van den Brink et al. 1993; Kylbergerova et al. 2002; Kasten 2003) and in other continents and climatic zones (García de Emiliani 1993; Zalocar de Domitrovic 2003). On the other hand, the mosaic of environmental conditions which exists even within the same lake also causes a high diversity of planktonic algae (Wilk-Woźniak & Ligęza 2005; Wojciechowska et al. 2005). In the oxbow lakes of the Bug River, during the study periods, 322 species were recorded, and because some of the lakes chosen for the study were covered by a dense pleustophyte layer, the conditions did not favour the development of numerous autotrophic species (the lack of light and oxygen); therefore, the lakes were characterised as poor in terms of species richness. The data published earlier demonstrated a high number of phytoplankton species in the oxbow lakes of the Bug River (Wojciechowska et al. 2005; 2007). There were identified 290 species and, in addition, many euryoecious taxa with several rare or little known algae were also found (e.g. *Coelosphaerium aerugineum*, *Synechocystis minuscula*, *Phacus elegans*, *Ph. horridus*, *Sporotetras pyriformis* or *Hemitoma meanderocystis*). Differences in the aquatic plant cover were the most important environmental factor, among other factors studied, determining phytoplankton biodiversity. The Shannon-Weaver Index and the number of species were strongly related to the FFP. Under a full cover of free-floating plants (70%–100%, $\mathrm{Kd_{PAR}} > 8\ \mathrm{m^{-1}}$), the successful species were those that needed specific types of habitat with low oxygen availability (e.g. *Synechococcus* spp. and *Arthrospira* spp.), and could tolerate low light conditions. The highest values of oxygen concentration and light intensity were noted for lakes which were free or almost free from vegetation. In conclusion, the environmental conditions created by the macrophytes cover influence on the phytoplankton assemblages resulting in the specific taxonomic and functional structure and diversity. The role of physical and morphological changes was more considerable for phytoplankton assemblages than availability of nutrients.

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