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Original Research

Benthic Invertebrates in Floodplain Lakes of a Polish River: Structure and Biodiversity Analyses in Relation to Hydrological Conditions

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Abstract

Our study was carried out in the middle basin of the Biebrza River (NE Poland) in the periods of June and September in 2011 and 2012. From among numerous side-arms, four objects have been selected for analyses of macrozoobenthos structure and biomass. Two lakes exhibited a lentic character due to a long-lasting isolation from the river channel, one presented a lotic, and one was of a semi-lotic character. Differentiated hydrological conditions within the study period enabled comparative studies: in 2011 appeared low and high water levels, while in 2012 no low water appeared and high water levels prevailed, which influenced the wetland

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conditions and inhabiting aquatic zoocenoses. During the study 352 individuals of benthic invertebrates with a total biomass of 288 g of wet weight were collected. Among the studied lakes we found the highest values of biodiversity indices in a lotic reservoir, while the highest densities and biomasses were in a semi-lotic reservoir. Nevertheless, the composition and abundance of benthic invertebrates in the studied lakes differed significantly from type-specific communities found in the floodplain lakes in other regions. A substantially lower level of macrozoobenthos diversity in floodplain lakes of the Biebrza River is indicative of less favorable conditions for macrozoobenthos development due to frequent water level fluctuations.

Keywords: zoobenthos, oxbow lakes, water quality, hydrological connectivity, Biebrza River

Introduction

Floodplain lakes are an important and integral part of meandering river valleys. Their presence is very beneficial from an environmental point of view, as they increase the retention capacity of the floodplain. They are also recognized as valuable natural habitats for numerous hydrobionts, playing the role of "hot-spots" for biodiversity on a regional scale [1]. Much recent research has been focused on the restoration and use of lakes as buffer zones against river pollution from non-point sources. Due to the location between the catchment and the main river channel they regulate the migration of contaminants toward the river, functioning as biogeochemical filters [2].

The structure and functioning of riparian wetland ecosystems are directly or indirectly related to the distribution of water level fluctuations in the river channel [3, 4]. The amplitude of the water level fluctuations in the riverbed affects the hydrological connectivity of aquatic ecosystems within the floodplain. The level of their hydrological connectivity comes from several factors, which include:

(1) The distance from the lake to the river
(2) The existence of permanent versus temporary connections to the river
(3) The size and shape of a water body, which can be described by its length, width, depth, and sinuosity [5].

The combination of these features leads to the emergence of large mosaics of ecosystems, water, and land with a strong gradient of the indicators of biodiversity in the river – wetland system [6]. On the basis of biological diversity in aquatic ecosystems and habitat characteristics, the increased interest in standardized ecological models to support conservation and management of valuable natural areas has been noted [e.g. 4, 6-8]. Among freshwater organisms, benthic invertebrates are particularly excellent research facilities because they have short life cycles and high adaptive flexibility (e.g. body shape, cycles per year, resistance, and dispersion) to environmental factors [9]. A large number of benthic invertebrates is sensitive enough to any environmental alterations, so they can be useful in the monitoring of aquatic ecosystem quality, including floodplain lakes [e.g. 4, 6, 10, 11, 12].

This paper attempts to determine the relationship between the hydrological conditions, physical, chemical and biological properties wetlands of varying by lateral connectivity with the unregulated Biebrza River (NE Poland). Based on the hypothesis that the intensity of the contact of flowing river water with floodplain lakes affects the quantitative and qualitive structure of macroinvertebrate assemblages, four objects have been selected for the present study. At the same time, the identification and classification of water quality parameters was done, which affects the size of the invertebrate assemblages. Using multivariate ordination methods, it was possible to determine their role in the development of macrozoobenthos structure.

Material and Methods

Study Area and Sites Description

The Biebrza River is a medium-sized lowland river in NE Poland. Its catchment covers approximately 7,057.4 km^2, and the valley has an area of approximately 1,950 km^2. This is a typical lowland river with low slopes of riverbed (0.06-3.33‰). The river channel crosses boggy meadows and marshes, meandering considerably and forming a large number of old riverbeds and waterbodies in different stages of succession [13]. Almost the entire basin of the river is not altered by human activity and its natural character and hydrological patterns are almost wholly preserved, never having being dammed, diverted, regulated, or embanked. During the spring, the narrow river swells to form a vast shallow impoundment, in places a kilometer wide and lasting for several months. 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 [13]. The vast wetland area created by the numerous water bodies and regular flooding has abundant diversity. The whole river except 10 km is within a National Park and protected under the Ramsar Convention [14].

The Biebrza River valley consists of three basins – the Upper, Middle and Lower, which were separated on the basis of geomorphologic structure. The Middle Basin is separated from the Lower Basin by a thin constriction near the village of Osowiec, while the boundary of the Upper Basin runs in the vicinity of Sztabin [15]. The Middle Basin is covered with a peatland complex that covers an area of approximately 450 km^2 and the thickness of peat reaches 3 m.

Hydrological regime of the Biebrza River in its middle course shows a distinct natural flood-pulse, but with significant irregularity of flows [16]. The average flow rate in the years of 1984-2012 at a gauge in Osowiec was 22.78 $m^3 \cdot s^{-1}$, within the range of 3.08 to 360.00 $m^3 \cdot s^{-1}$. In Osowiec, the

ratio of the average maximum and minimum flows (MQ_{max}/MQ_{min}) for the multiannual period was 6.2, while the ratio of extremely high and low flows (HQ/LQ) was 117. Fluctuations of the water level are relatively high (265 cm).

In the period in which the study was conducted (2011-12), analysis of the water level data logger installed in the vicinity of Bednarka oxbow near the town of Goniądz, showed the significant hydrological activity of the Biebrza River (Fig. 2A) 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 (Fig 2B). The periods of overbank flooding (evaluated with the discharge rating curve method), calculated as the share of days exceeding bankfull level (BFL= 107.80 m a.s.l), amounted in 2011 and 2012 to 29% and 23%, respectively. The longest flood period in 2011 took place between January and April, and in 2012 between March and May (Fig. 2B). The differences in the pattern of water level fluctuations were advantageous for our hydrobiological studies.

Study sites [13] were located in four floodplain lakes with local names: Stara Rzeka, Bocianie Gniazdo, Budne and Bednarka, as well as in the main channel of the Biebrza River in the city of Goniądz (Fig. 1). The side-arms under the present study are remnants of the former river channel, representing a wide range of hydrological connectivity to the river: from the habitats preserving permanent connection to the main riverbed (Stara Rzeka and Bocianie Gniazdo), through the places of a temporary connectivity, depending on hydrological conditions (Bednarka) to the habitat of limited hydrological connectivity due to channel overgrowth and a significant distance (ca. 680 m) from the main riverbed (Budne). It should be noted that due to high hydrological activity of the Biebrza River, no object completely isolated from the influence of the river has been detected. Bednarka and Budne reservoirs do not have a constant hydrological connectivity with the river and show the lentic features, while Bocianie Gniazdo functions as a semi – lotic habitat connected with the lower arm to the Biebrza River. It shows a typical hydrological gradient: from lotic habitat in the downstream end to the lentic habitat at the upstream end. Stara Rzeka is a free-flowing side-channel of the Biebrza River with features typical of the lotic habitats [1]. Detailed morphometric data of individual reservoirs are given in Table 1.

Longer water age favors the intensity of biogeochemical processes, accumulation of autogenous matter accelerating succession of these reservoirs, and the silting and overgrowing by helo- and macrophytes with the domination of common reed (*Phragmites australis* (Cav.) Trin ex Steud.), yellow water lily (*Nuphar luteum* L.). The impact of agricultural land use in the vicinity of Budne as well as a large distance between the reservoir and the riverbed (over 680 m), and thus a limited exchange of water, caused severe hypertrophy of the reservoir. This feature made the floodplain lake different from other reservoirs under this study.

In the studied waterbodies, fishfauna is represented mainly by roach, (*Rutilus rutilus* L.), rudd (*Scardinius erythrophthalmus* L.), and pike (*Esox lucius* L.), the share of which in total ichthyofauna composition constitutes 41%, 15%, and 15%, respectively [17].

Sampling Procedures

In each floodplain lake three sampling sites have been selected to both physico-chemical and biological analyses: in the upstream, downstream, and middle parts of a given waterbody (N=12). Additionally, water and macrozoobenthos material from the Biebrza river have been taken (N=4). The sampling of water and macrozoobenthos took place simultaneously. *In situ* measurements of dissolved oxygen (DO), pH, electrolytical conductivity (EC), total dissolved

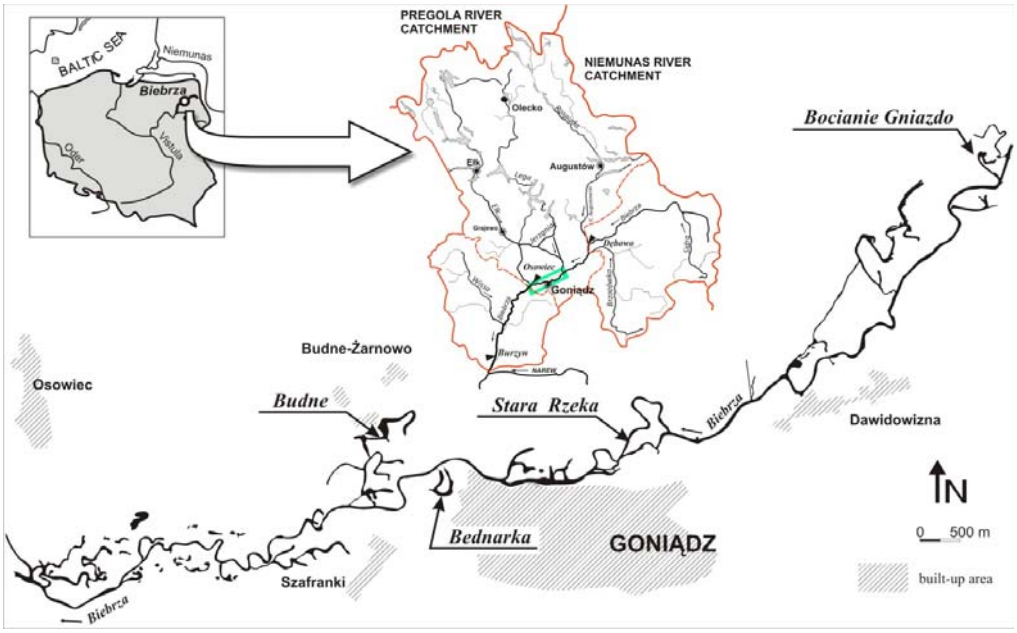

Fig. 1. Study site locations (four oxbow lakes and the river channel) in the Biebrza River floodplain, Poland.

Table 1. Select morphological parameters of the studied oxbow lakes in the Middle Basin of the Biebrza River.

Floodplain lake	Geographical coordinates	Type of connection with river	Length [m]	Width [m]	Area [ha]	Distance from river channel			Depth	
						Upper arm [m]	Lower arm [m]	Max. [m]	h_{avr} [m]	h_{max} [m]
Stara Rzeka	N:53º30'0.26" E:22º44'37.2"	Lotic (LO)	1380	24.00	3.31	0.0	0.0	523	2.2	3.4
Bocianie Gniazdo	N:53º31'15.47" E:22º47'55.62"	Semi-lotic (S-LO)	569	25.30	1.4	104.0	0.0	304	2.8	5.3
Budne	N:53º29'56.68" E:22º42"14.06"	Lentic (LE)	1652	26.80	4.41	407	380	680	1.2	1.8
Bednarka	N:53o29'31.51" E:22o42'43.46"	Lentic (LE)	740	29.20	2.16	50	42	313	1.6	2.6

solids (TDS), and salinity were performed using calibrated multiparameter probes YSI 6600R2 and YSI Professional Plus (USA). At the same time, water samples with a volume of 2.5L from a depth of about 20 cm were taken to acid-washed polycarbonate containers. Under laboratory conditions, within 24 h the samples were filtered on glass fiber filters Whatman® GF/F (incubation at 450ºC for 4h) to determine the amount of mineral matter (MM) [18]. The concentrations of orthophosphates, nitrates, nitrites, and ammonium ions as well as macroelements: main cations and ions were determined in the water samples, as well. Standard methods of analyses were applied [18]. A continuous flow analyzer (FLOWSYS-SYSTEA®) was used to determine total nitrogen (TN) and total phosphorus (TP) [18]. Chemical oxygen demand (COD) and the concentration of HCO_3^- were measured with the help of a DR-2800 spectrophotometer (Hach-Lange, USA) and the cuvette method.

Invertebrates were sampled with the Ekman's grab sampler (225 cm^2 surface) three times at each zone of the lakes. Those sites differed by the thickness of bottom sediments and their composition (e.g. the presence of leaves, branches, and submerged plants). The sediments were sieved through a 300 µm mesh size sieve, placed in containers, and fixed in 5% formalin. In the laboratory benthic invertebrates were identified to the lowest possible systematic level, except for Oligochaeta (class). To identify the invertebrates, commonly available keys have been used [10]. Results of that identification were considered in two ways: separately and altogether. Additionally, the following zoocenotic indices were used: Shannon diversity (H'), Pielou's evenness (J'), share in a single macrozoobenthos sample (%), share in the biomass (%), number of taxa, and total abundance. The diversity indices (H' and J') were calculated with the help of Past v.2.17c software [19].

Statistics

To assess the statistical differences among years for macro invertebrate data (grouped into classes/orders) and hydro-chemical data, the non-parametric analysis of variance (Kruskal-Wallis and Dunn's tests, $P \leq 0.05$) were performed. Canonical Correspondence Analysis (CCA) was applied to obtain a synthesized profile of macrozoobenthos taxa on the background of environmental conditions in the studied oxbow lakes and to evaluate similarities between

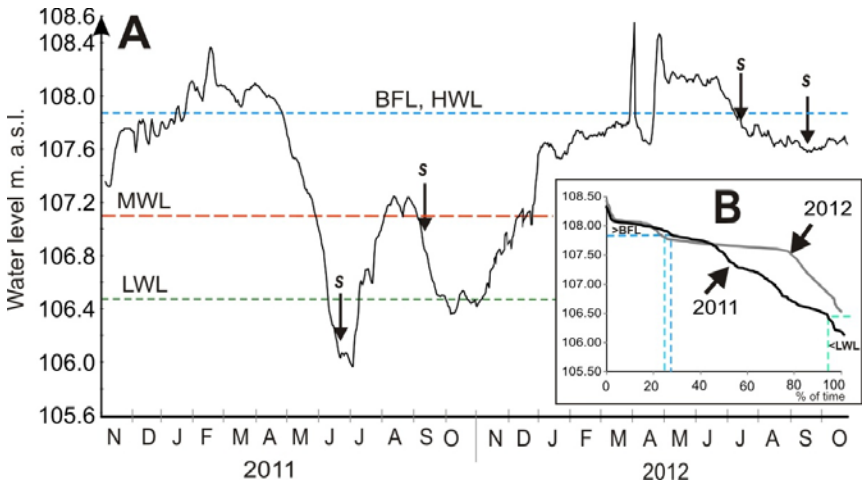

Fig. 2. Water level characteristics of the Biebrza River at Goniądz cross-section in 2011-12. In the hydrograph arrows indicate macrozoobenthos samplings (s), BFL – bankfull level, HWL – high water level, MWL – mean water level, LWL – low water level. (B) Water level duration curves.

Table 2. Physico-chemical parameters of oxbow lake water (mean and ±standard devations (±SD)) and the Biebrza River.

Parameter	Unit	N	Floodplain lakes								Biebrza River	
			Stara Rzeka		Bocianie Gniazdo		Budne		Bednarka			
			Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD
pH, -		12	7.88	0.28	7.73	0.23	7.78	0.31	7.98	0.15	7.96	0.21
DO	$mg \cdot dm^{-3}$	12	8.01	1.61	5.36*	1.74	6.32	2.70	7.56	1.32	7.48	0.87
COD_{-Cr}	$mg \cdot dm^{-3}$	12	36.68	10.15	45.11	8.14	74.88*	23.81	41.68*	12.30	33.25	7.52
EC	$uS \cdot cm^{-1}$	12	512	77	513	87	649*	110	533	71	516	76
NO_2^--N	$mg \cdot dm^{-3}$	12	0.013	0.011	0.004	0.001	0.006	0.006	0.007	0.003	0.013	0.012
NO_3^--N	$mg \cdot dm^{-3}$	12	0.17*	0.09	0.10	0.03	0.10	0.03	0.12	0.02	0.19*	0.11
NH_4^+-N	$mg \cdot dm^{-3}$	12	0.16*	0.09	0.20	0.05	0.34*	0.11	0.33*	0.42	0.17	0.13
TN	$mg \cdot dm^{-3}$	12	0.96	0.22	1.58*	0.44	1.89*	0.49	1.58*	0.63	1.02	0.22
PO_4^{3-}-P	$mg \cdot dm^{-3}$	12	0.11*	0.04	0.06	0.02	0.11*	0.04	0.07	0.03	0.09	0.04
TP	$mg \cdot dm^{-3}$	12	0.26	0.11	0.25	0.10	0.38	0.14	0.40	0.24	0.20	0.12
Salinity	$g \cdot dm^{-3}$	12	0.24	0.04	0.25	0.05	0.30	0.07	0.25	0.04	0.22	0.08
TDS	$mg \cdot dm^{-3}$	12	336	49	338	56	436*	69.55	341	50	347	48
MM	$mg \cdot dm^{-3}$	12	249	38	247	44	331*	57.79	256	38	245	44
HCO_3^-	$mg \cdot dm^{-3}$	12	209	7	209	6	249*	16.80	211	8	207	7.67
Ca^{2+}	$mg \cdot dm^{-3}$	12	70.97	3.49	71.42	4.79	78.97*	4.90	73.62	2.77	69.90	4.34
Na^+	$mg \cdot dm^{-3}$	12	8.83	0.88	9.61	1.05	22.73*	8.36	8.33	0.64	8.85	0.88
K^+	$mg \cdot dm^{-3}$	12	3.18	0.70	3.25	0.47	2.63	1.30	2.83	0.52	3.23	0.73
Cl^-	$mg \cdot dm^{-3}$	12	9.50	0.90	10.25	0.86	23.29*	9.27	10.25*	1.71	9.75	2.06
Mg^{2+}	$mg \cdot dm^{-3}$	12	13.90	1.79	12.53	1.47	13.28	2.15	14.05	1.25	12.90	1.69

Units are in $mg \cdot dm^{-3}$ unless otherwise indicated.
*denotes significant differences among water quality parameters in the floodplain lakes and the Biebrza River in a non-parametric Kruskal-Wallis test and Dunn's test followed by Shapiro-Wilk test for normality, $P \leq 0.05$.

taxa. It is a highly useful ordination method that supports the multivariate analysis of variance (MANOVA) among selected environmental factors and water quality data and macroinvertebrate assemblages. The method also facilitates the interpretation of complex correlations and a synthetic presentation of the obtained results.

CCA was used between 23 environmental variables (hydrological and water quality parameters) and 9 groups of macroinvertebrates with the use of the CANOCO 4.5 software package [20]. The data have been transformed to logarithms log $\sqrt{n+1}$ and centered by species. Because environmental gradients had not previously been evaluated in the study area, we ran a manual, forward-selection procedure using the Monte Carlo Permutation Test, which included variables that had a conditional effect significant at the 5% level ($P \leq 0.05$) [21].

Results

Physical and chemical properties of water and the significant differences between the investigated objects are shown in Table 2. Water quality in the Biebrza River is high due to the neutralizing and protective action of a broad area of flooded meadows, peatlands, and marshes which means that settlements and fertilized arable land are on the valley margins. The pH of the river water amounted to 7.15-8.34 as acidity is buffered by higher calcium concentrations. Oxygen saturation was relatively high and ranged from 80 to 93% at the water surface. Electrolytical conductivity (EC) was found to be stabile along the whole study period at the level of 514±86 $\mu S \cdot cm^{-1}$.

Physico-chemical parameters of water varied among floodplain lakes in terms of the nutrient concentrations (NH_4^+-N, NO_3^--N, PO_4^{3-}-P, Cl^-). Lotic objects (the Biebrza River and Stara Rzeka) were characterized by higher concentrations of mineral forms of nitrogen, especially NO_2^--N and NO_3^--N, and lower concentrations of TP and PO_4^{3-}-P compared to habitats with a less intensive water exchange. Lentic and semi-lotic habitats (Budne and Bednarka) had significantly higher concentrations of NH_4^+-N and TP when compared to lotic habitats.

The qualitative structure of benthic macroinvertebrates in the distinguished hydrological types of floodplain lakes

Table 3. The presences of benthic invertebrates in the studied floodplain lakes and the Biebrza River in the studied years.

Taxa	Floodplain lake								Biebrza River	
	Stara Rzeka		Bocianie Gniazdo		Budne		Bednarka			
	2011	2012	2011	2012	2011	2012	2011	2012	2011	2012
OLIGOCHAETA	+	+	+				+	+		
HIRUDINEA										
Erpobdella octoculata L.	+	+						+	+	+
Glossiphonia complanata L.		+		+						
Helobdella stagnalis L.		+								
ODONATA										
Gomphus vulgatissimus L.							+			
Cordulegaster annulatus Latreille		+								
Lestes viridis Vander Linden							+			
MEGALOPTERA										
Sialis fuliginosa L.	+									
TRICHOPTERA										
Cyrnus sp.					+	+				
HETEROPTERA										
Sigara sp.						+				
DIPTERA										
Sylvicola fenestralis Scopoli								+		
Chaoborus sp.			+	+			+			
Bezzia sp.								+		
Procladius sp. Skuse							+	+		
Chironomus plumosus L.	+	+	+	+	+	+	+	+		
GASTROPODA										
Viviparus viviparus L.									+	
Radix auricularia L.	+	+			+					
Lymnaea stagnalis L.			+	+						
Theodoxus fluviatilis L.										+
BIVALVIA										
Anodonta anatina L.		+								
Anodonta cygnea L.		+								
Unio pictorum L.				+					+	
Unio tumidus Philipsson	+			+						
Pisidium sp.	+	+	+	+					+	
No. of taxa	7	10	5	7	3	3	6	6	4	2

in 2011 and 2012 are shown in Table 3. A total of 352 individuals of benthic fauna collected belonged to worms, insects, and molluscs. The benthos abundances between the lakes differed significantly (Kruskal-Wallis test, P = 0.023). Gastropoda and Diptera were the most common invertebrate classes (each with 5 taxa). In the Biebrza River the most numerous were gastropods (mainly *T. fluviatilis*, 56% – percent in the collection), although bivalves (Table 4)

Table 4. Invertebrate composition and metrics in the floodplain lakes and the Biebrza River.

	Floodplain lake								Biebrza River N=4	
	Stara Rzeka N=12		Bocianie Gniazdo N=12		Budne N=12		Bednarka N=12			
No. of taxa	12		8		4		9		5	
Shannon index (H')	2.211±0.640		1.088±0.376		1.332±0.345		1.898±0.379		1.303±0.417	
Pielou index (J')	0.890±0.462		0.523±0.290		0.961±0.379		0.864±0.441		0.809±0.423	
	A	B	A	B	A	B	A	B	A	B
Total	680.9±62.1	995.32±164.59*	3718.2±446.1*	3232.12±677.36	88.8±18.4*	4.18±0.81*	725.7±72.9	31.06±5.30	1435.2±202.7	167.41±30.28
Oligochaeta	118.4 (17.4)	1.00 (1.0)	1896.2 (51.0)	3.4 (0.1)	0	0	88.8 (12.2)	1.20 (3.9)	0	0
Hirudinea	44.4 (6.5)	2.12 (0.2)	14.8 (0.4)	1.42 (0.0)	0	0	14.8 (2.0)	1.54 (5.0)	14.8 (11.1)	0.24 (0.2)
Odonata	29.6 (4.4)	11.45 (1.2)	0	0	0	0	104 (14.3)	18.94 (61.0)	0	0
Trichoptera	0	0.00	0	0	14.8 (16.7)	0.29 (6.9)	0	0.00	0	0
Heteroptera	0	0.00	0	0	14.8 (16.7)	0.38 (9.1)	0	0.00	0	0
Megaloptera	14.8 (2.2)	0.59 (0.1)	0	0	0	0	0	0.00	0	0
Diptera	207.3 (30.4)	7.45 (0.7)	1614.7 (43.4)	4.26 (0.1)	29.6 (33.3)	0.29 (6.9)	518.1 (71.4)	9.38 (30.2)	0	0
Gastropoda	29.6 (4.3)	55.20 (5.5)	103.7 (2.8)	12.29 (0.4)	29.6 (33.3)	3.22 (77.0)	0	0.00	88.9 (66.7)	42.16 (34.7)
Bivalvia*	236.8 (34.8)	917.51* (92.2)	88.8 (2.4)	3210.75* (99.3)	0	0	0	0.00	29.6 (22.2)	79.11 (65.1)

Data are total density (A– indiv·m^{-2} ± SD) and biomass (B– g_{ww}·m^{-2} ± SD) from samples collected in 2011 and 2012. A share of each taxon in total metrics was given in parentheses. Significant differences are marked with * (non-parametric Kruskal-Wallis test and Dunn's test, $P \leq 0.05$).

were also abundant and significantly affected the densities. In the floodplain lakes with reduced hydrological connectivity to the river (Bednarka and Budne) the most numerous were Insecta, including larvae of the Diptera family (mainly *Chaoborus* sp., 30%) and Odonata larvae (*L. viridis*, 10%). Bocianie Gniazdo, having a limited contact with the river via a single arm, showed the lowest biodiversity dominated by oligochaetes and flies (*Ch. plumosus*, 40%). In the lake with double-sided connections with the riverbed (Stara Rzeka) the highest biological diversity (H'= 2.202) was recorded. The most numerous were bivalves represented mainly the Unionidae family (28%) and accompanied by a large number of Chironomidae larvae (28%).

The total biomass of macrozoobenthos in the studied lakes amounted to 288g of wet weight, and its values in each floodplain lake differed significantly (Kruskal-Wallis test, P = 0.023). The most significant differences were noted between the lotic reservoir Stara Rzeka, and lentic reservoir Budne (Table 4). In the river channel benthos biomass was affected by the presence of bivalves (*U. pictorum*), with a significant share of Gastropoda (*V. viviparus*). Bivalvia were the most abundant in the floodplain lakes with low residence time. The share of the Unionidae family in biomass in the lotic lake constituted 91%, whereas in the semi-lotic lake *U. tumidus* prevailed (69%). Opposite two other types of lakes, standing water of lentic lake promoted the

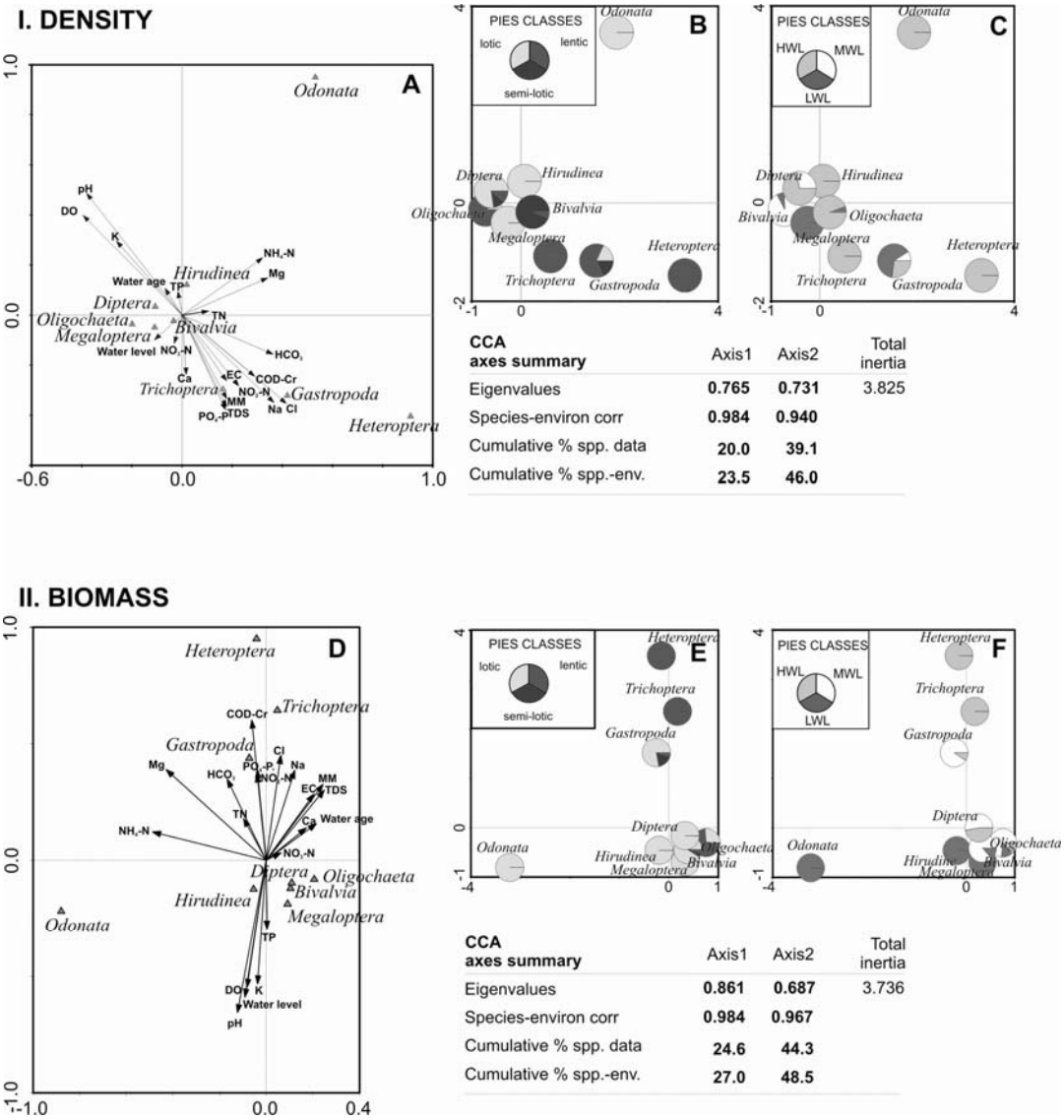

Fig. 3. Results of canonical correspondence analysis performed with invertebrate and environmental data from the Biebrza River floodplain lakes using a forward selection of variables (P≤0.05).
I. Density: (A) Biplot of significant environmental variables, invertebrate density, and sample scores of axis 1 and 2; (B) Biplot showing significant invertebrate density in relation to a hydrological type of floodplain lake; (C) Biplot showing invertebrate density during low and high water periods.
II. Biomass: (D) Biplot of significant environmental variables, invertebrate biomass, and sample scores of axis 1 and 2; (E) Biplot showing significant invertebrate biomass in relation to a hydrological type of oxbow lake; (C) Biplot showing significant invertebrate biomass during low and high water periods.

development of Insecta, the biomass of which was dominated (40%) mainly by the Odonata family (*G. vulgatissimus*). Among the identified groups of benthofauna, only biomass of Bivalvia differed significantly among the studied objects (Kruskal-Wallis test, P = 0.040).

From among 20 pre-analyzed environmental variables in the CCA model, finally 19 were selected as having a major impact on the quality of the model (Figs. 3A and D). CCA explained 46% of the total variation of density structure of invertebrates and all canonical axes were significant (Monte Carlo test, P = 0.002). Most of the analyzed environmental parameters affected the increase in density of Gastropoda and Trichoptera, whereas hydrological conditions (water level) determined the abundances of Megaloptera and Oligochaeta (Fig. 3A). Analysis of invertebrate preferences in relation to a relevant hydrological type of floodplain lake (Fig. 3B) showed that four taxa dominated in the lotic and lentic ecosystems, but only one (Bivalvia) preferred a semi-lotic habitat.

CCA for the relationship between environmental factors and biomass explained 48.5% of the variation (Fig. 3D). The biomass of Gastropoda representatives was related to the concentrations of two nutrients: nitrate nitrogen and phosphate phosphorus. By far the greatest weight was found in invertebrates in lotic habitats (Fig. 3E) during average water levels (Fig. 3F), which confirms our assumption on hydrological connectivity as a key determinant of habitat suitability for macrozoobenthos.

Discussion

In floodplains of lowland rivers, side-arms are an important component of riparian wetlands as they play a significant role in the biodiversity enhancement. River flooding through surface connection with the main channel is an important determinant of benthic macrofauna composition. Aquatic ecosystems located in the Middle Basin of the Biebrza River create favorable conditions for certain groups of benthic macroinvertebrates as insects, worms and molluscs, which confirms the results obtained for other European floodplain lakes [e.g. 7, 8, 10]. In contrast to other river lakes studied by both the authors of this article and researchers in the world, the bottom of floodplain lakes along the middle course of the Biebrza River is devoid of crustaceans. This group has been reported as the main component of the benthic fauna, e.g. in the Słupia floodplain lakes [10, 22]. The cause comes from a strong pressure of predatory fish, for which the crustaceans are the basis of diet [11, 24], or adverse environmental conditions, especially long-term oxygen deficits in the near-bottom zone. This explains the higher abundance of bentofauna in Bocianie Gniazdo than in Budne and Bednarka, despite its penetration by the fish. At the same time, low abundance and biomass of bentofauna in lotic habitats of Stara Rzeka and the Biebrza River may be caused by predation of fish (perch, ruff) and juveniles, who first eat zooplankton and then feed on benthos. In some isolated oxbow lakes, relatively long periods of stability and rare periods of "refreshment" with well-oxygenated river water cause the accumulation of taxa that have longer life cycles and less effective strategies for colonization. Similarly, insects that have short life cycles (e.g. Chironomidae) reach peaks of their abundances and biomasses in semi-lotic floodplain lakes (Table 4). They are accompanied by Oligochaeta, for which the semi-lotic systems tend to be suitable. According to Kasprzak [25], the level of Oligochaeta density is influenced by the water level and age of the sediments. Based on the results of the presented CCA model, this group of benthic fauna preferred higher levels of water in the lakes (Fig. 3C), giving greater body weight at the average water level (Fig. 3F). Previous studies [e.g. 4, 12] showed that the optimal conditions for the benthos development represents the semi-lotic type of floodplain lakes. However, the present study only partially confirms these observations. In fact, in the studied three lakes within the floodplain of the naturally meandering the Biebrza River, values of density and biomass have been noted as the highest, whereas biological diversity (Shannon index) was the lowest. In this context, the optimal conditions for the biodiversity development seem to represent waterbodies with active exchange of water. On the basis of the conducted two-year studies, we can conclude that this may be the effect of high water in the Biebrza River in 2012 (Fig. 2). It is known that both environmental and hydrological factors influence either directly or indirectly the communities of hydrobionts [26, 27]. The concentrations of elements and trophic components of water as well as pH level, total hardness, and conductivity are hydrologically dependent and considered by some authors as key variables for the richness of species, diversity, density, and composition of macrozoobenthos [28, 29]. The mentioned environmental factors are shaped by the supply of nutrients from external (allochtonous) or internal sources (autochthonous). During isolation from the main riverbed, increased levels of conductivity and total dissolved solids are usually noted [4]. In the case of frequent mixing processes in the isolated lake basin, a lake is a subject for secondary pollution with P and enhanced processes of oxygen consumption [1]. This might have a limiting effect on the benthic invertebrates. On the contrary, in the passable lakes the water flow washes out the sediment from the bottom (particularly an organic fraction), which in turn reduces secondary contamination [2]. The storage capacity (retention) of nitrogen also depends on many factors such as intensity of flow, water depth, and water retention time [30]. During high flows the ability to neutralize N is limited. Denitrification processes occur most efficiently in the overgrown sites of oxbow lakes, e.g. mainly along bank zones. The open water is not a suitable habitat for the growth of bacteria, where there are fewer plant roots and less organic substance providing carbon for denitrifying bacteria [30, 31].

Water bodies located densely along the same river channel within the area of the same geomorphologic characteristics and origin can vary significantly from each other. Lateral connection and thus the exchange of water, as well as mineral and organic matter between the riverine water and water filling the floodplain lakes, is very important for the functioning and dynamics of the floodplain ecosystem

as a whole (river and flood system). That includes the structure of macroinvertebrates, too. It turns out that the distance between floodplain lakes and the parent river is also an important factor influencing the obtained results. The two tested lakes of limited water exchange (Bednarka and Budne) are inhabited by structurally different benthic fauna. Budne, situated at a distance from the riverbed (Table 1), is characterized by bottom fauna of low density and biomass, while the zoobenthos of Bednarka, situated near the riverbed, shows 8 times higher density and 7 times higher biomass (Table 4). This might be indicative of internal (autogenic) matter cycling prevailing in Budne lake, which was confirmed by the species adapted to anaerobic conditions prevailing at the bottom.

An important factor decreasing the aeration of water in lentic floodplain lakes is organic matter supplied from the area of extensive peatlands in the floodplain during the rising water level. Intensive utilization of oxygen takes place in the process of decomposition of organic matter. Only periodic overbank flooding linking all water bodies may "refresh" aquatic ecosystems by increasing oxygen resources and facilitate the migration of aquatic organisms between ecosystems [1, 20, 32]. It seems, however, that fluctuations in water levels and periodic inundation of river floodplains, according to Junk's *Flood Pulse Concept* [3], are necessary to preserve a high level of biodiversity of benthic invertebrates.

Conclusions

Our studies performed in the Middle Basin of the Biebrza River showed that the variation in the qualitative and quantitative structure of benthic invertebrates in floodplain lakes is largely determined by differences in water-level fluctuations and lateral connectivity. Higher biodiversity indices of benthofauna were recorded in lotic water bodies, constantly rinsed by river waters with an open pathway for the migration of benthic organisms. Both density and biomass were the highest in the semi-lotic ecosystem with a richer mosaic of microhabitats. The results showed that the quality, abundance, and biodiversity of benthic invertebrates in the studied floodplain lakes along the Biebrza, an unaltered lowland river, is quite different from those recorded in other, although regulated, floodplains in NE Poland.

Fluctuations in the water levels of the Biebrza River, beneath the bankfull level (BFL), may be destructive to a very vulnerable group of benthic invertebrates, due to the oxygen depletion. As the macrozoobenthos belongs to the groups of aquatic organisms with a relatively narrow tolerance to changes in abiotic parameters of the environment, it is important to take into account suitable management to enhance the ecological status of the Biebrza River floodplain lakes.

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