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Rheophilic fish in oxbow lakes of the Warta River – the effect of environmental conditions on habitat selection

by

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Abstract

Oxbow lakes are typical elements of meandering watercourses and are considered to be key components of floodplains of natural rivers. A permanent connection with the river promotes the use of these water bodies by ichthyofauna as spawning grounds, shelter for fry, feeding and wintering grounds. The aim of this study was to determine which rheophilic species inhabit oxbow lakes and how environmental conditions affect habitat selection and fish behavior. Analyses were conducted on six oxbow lakes of the Warta River in the Koło-Poznań section. Fish and water samples were collected for three years, in spring, summer and late autumn. Variation in environmental conditions in the analyzed water bodies results in a considerable diversity of the ichthyofauna, including rheophilic species, in individual seasons of the year. In the course of the study, nine rheophilic fish species were recorded, including four from the lithophilic reproductive guild having the highest environmental requirements. Relative abundance of rheophilic species in the dominance structure ranged from 0 to 100%, depending on the reservoir and seasons, with an average of 7% for all catches. For comparison, their relative abundance in the adjacent parts of the river was 12 and 23%.

Key words: lowland river, open oxbow lakes, backwaters, ichthyofauna, Poland

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Introduction

In order to preserve species diversity in a river ecosystem, particularly in the case of lowland rivers, areas with standing water are required as they increase the variability of environmental conditions. These areas called backwaters include flood polders and particularly oxbow lakes. Oxbow lakes are typical elements in meandering watercourses and are considered to be key components of floodplains in natural rivers (Hooke 1995; Van Geest et al. 2003). Many authors are of an opinion that oxbow lakes may have a considerable and varied effect on the diversity and viability of fish assemblages in rivers (Ward and Stanford 1995; Winemiller et al. 2000). Floodplains preserved in the natural conditions are of great importance to fish, since many species require different habitats in the course of their life cycle (Kurmayer et al. 1996; Buijse 2002; Starmach 2003). Open oxbow lakes are particularly important to ichthyofauna, i.e. those having a permanent connection with the main river channel. A permanent connection with the river has a positive effect on hydrological conditions of reservoirs and adjacent areas (e.g. water exchange), while it also promotes the use of these water bodies by ichthyofauna as spawning grounds, shelter for fry, as well as feeding and wintering grounds (Hohausowa 2000; Golski et al. 2005; Osorio et al. 2011). Both fish species characteristic of standing waters as well as rheophilic fish (preferring fast flowing waters), i.e. obligatory river species, occur in open oxbow lakes. This may indicate that in certain periods, these fish find better living conditions in lentic rather than lotic habitats. Among the large number of papers describing river ecosystems, there are only single publications or chapters related to backwaters (Penczak et al. 2000a; Winemiller et. al. 2000; Wiśniewolski et al. 2009). A few Polish scientists for years study oxbow lakes: Penczak (Penczak et al. 2000a,b; 2003a; 2005), Glińska-Lewczuk (Glińska-Lewczuk et al. 2005; 2015), Obolewski (Obolewski 2005; Obolewski et al. 2015).

In view of the fragmentary knowledge of the subject, the authors of this study decided to present the importance of these habitats of considerable conservation value for the entire river system, including rheophilic ichthyofauna, based on six oxbow lakes located in the middle course of the Warta River. The aim of this study was to determine which rheophilic species live in open oxbow lakes, whether their occurrence is permanent and whether environmental conditions connected with the type of water body and season of the year influence the habitat selection and fish behavior.

Materials and methods

Study area

The Warta is the largest right-bank tributary of the Oder and the most important watercourse in the Wielkopolska province. Analyses were conducted on six oxbow lakes of the Warta River along the Koło-Poznań section, between 409 and 277 km of the river (Fig. 1). The most important criterion for the selection of oxbow lakes was a permanent connection of the water body with the main river channel, maintained for min. 10 months a year. The oxbow lakes were described in terms of the degree of connection with the watercourse, the area of the oxbow lake, the depth, bottom substrate, their surroundings, aquatic vegetation and anthropopressure (Table 1). The Święte oxbow lake was the only analyzed water body with a permanent water flow. Despite the narrow embankments, the lake is not separated from the watercourse. On the contrary, it is connected with the river through two forks and it still serves the function of one of its channels. These two forks connect the water body with the river, even at low water stages. The continuous water flow prevents the development of plant communities, which are found here only in small coves. The smallest analyzed oxbow lakes were Tarnowa and Trzykolne Młyny, the area of which was max 1 ha at average water levels. The Tarnowa oxbow lake is surrounded by high shores, which considerably reduce the effect of wind, thus limiting the water mixing. In the period of low summer water levels, the narrow and shallow connection of

Figure 1
Location of six oxbow lakes of the Warta River

Table 1

Characteristics of oxbow lakes

Oxbow lake	Km	Area (ha)	Maximum length/width (m)	Max depth (m)	Bottom substrate (%)	Submerged vegetation	Surroundings (%)
Święte (SW)	409	1.5	570/40	2.5	90S; 10M	+	60M; 40SH
Madałowe (M)	359	2.6	620/50	3.5	70M; 20S; 10G	++	90M; 10F
Tarnowa (TR)	348	1.0	320/60	2.5	60S; 40M	+++	60M; 40SH
Trzykolne Młyny (TM)	278	0.9	280/35	2.0	80M; 20S	+++	70M; 30SH
Tuchoń (T)	278	4.7	1170/90	5.0	50S; 50M	++	70F; 30M
Święconka (SC)	277	6.0	970/130	4.5	80S; 10G; 10M	+++	40B; 60M

Bottom substrate: G – gravel, S – sand, M – mud; Submerged vegetation abundance: +small, ++ – medium, +++ – high; Surroundings: F – forest, M – meadow, SH – shrubs, B – buildings

Tarnowa with the river prevents fish migration. On the other hand, Tuchoń and Święconka are the largest oxbow lakes analyzed in this study. Tuchoń extends as a narrow channel among tall pine-oak forests, while the connection with the Warta is through a narrow and shallow isthmus, which does not provide sufficient connectivity during low water levels. In contrast, Święconka has a wide and deep connection with the main channel throughout the year, while during spring high-water stages, the lake is intensively washed by the flood wave. Tarnowa, Trzykolne Młyny and Święte are the shallowest oxbow lakes, whereas Tuchoń and Święconka are deep lakes. Bottoms of the analyzed water bodies are mainly covered by sand or organic sediments of varying thickness, while small sections of the bottoms in Madałowe and Święconka oxbow lakes are covered by pebbles and gravel. In Madałowe and Trzykolne Młyny, the contribution of organic matter in the bottom area may reach 80%, while sand definitely predominates in Święte, Tarnowa and Święconka. Abundant submerged vegetation overgrows the bottoms of Tarnowa, Trzykolne Młyny and Święconka oxbow lakes. The dominant plant species include rigid hornwort *Ceratophyllum demersum* (L.), Eurasian watermilfoil *Myriophylum spicatum* (L.) and curled pondweed *Potamogeton crispus* (L.). The water bodies are surrounded mainly by meadows, with buildings located only at the shore of Święconka.

Sampling methods

Analyses of the oxbow lakes of the Warta River within the Koło-Poznań section consisted of two stages: fish captures and collection of water samples for physicochemical analyses. Both stages were performed simultaneously during the same field trip. Each of the oxbow lakes was investigated for three years (2008, 2009 and 2010), three times a year: in mid-May, at the end of August or the beginning of September and in early December. The following parameters were determined in situ: temperature, dissolved oxygen content, oxygen saturation, reaction in the surface and bottom layers using a WTW MultiLine P3 ph/Oxi set, specific electrolytic conductivity was measured with a WTW LS 318/Set conductometer, while water transparency was determined using the Secchi disk. Biological material was collected using: [1] gillnets with specific mesh sizes ranging from 10 mm to 100 mm, [2] an IUP 12 Impulse Fishing Device (Radet Co.), [3] a combustion engine power generator equipped with a rectifier (Hans Grassl Co.). The number of nets used was constant and depended on the size of a given oxbow lake; nets differed in terms of mesh size. The net was set in the mornings between 6 and 7 a.m., depending on the season of the year. Electrofishing was performed in the littoral zone of the water bodies at a depth of max 1.5 m. The fish were collected into water-filled containers during a single boat tour around a given oxbow lake. After disembarking, they were identified to the species level, measured, weighed and released into the lake in locations selected so as to minimize the risk of their repeated capture in the net. Mesh size of the net dipper was 0.5 cm. Moreover, electrofishing in selected river sections in the area of the oxbow lakes was conducted three times during the study period using a combustion power generator equipped with a rectifier. The objective of all these methods applied was to obtain a representative sample, comprising all fish generations except for 0^+. At the same time, efforts were made to ensure the greatest possible repeatability of the methods. Juvenile forms were not included in the analyses, because they require different capture methods.

Data analysis

The following parameters characterizing the ichthyofauna of the investigated oxbow lakes were determined: the number of species, relative abundance (specimens ha^{-1}), biomass (g ha^{-1}), the mean individual mass (g), the percentage of individual species in the population (D%) and constancy of occurrence (C%). Apart from the percentage of species,

also the percentage of ecological reproductive guilds in assemblages was calculated. Names of reproductive gilds regarding the spawning substrate were used after Balon (1990). The basic statistics were determined for the above-mentioned indices and parameters: the arithmetic mean, extreme values, and standard deviations. Significance of the effect of experimental factors (site of capture, time of capture) was analyzed using the two-way analysis of variance with interaction according to the linear model given below:

$$y_{ijk} = \mu + m_i + s_j + ms_{ijk} + e_{ijk}$$

where:

- y_{ijk} – value of the analyzed trait;
- μ – mean of the analyzed population;
- m_i – fixed effect of the ith capture site (oxbow lake) (i=1,2,…,6);
- s_j – fixed effect of the jth season of capture (j=1,2,3);
- ms_{ijk} – interaction of capture site × season;
- e_{ijk} – random error.

Calculations were performed using Microsoft Excel, STATISTICA v. 10 Statsoft Polska and SAS v. 9.4 (2014) package by SAS Institute Inc., Cary, NC, USA.

Results

Environmental conditions

The investigated oxbow lakes differ in terms of the area, shape, depth, surroundings, the exposure index and bottom substrate (Table 1). The variation in morphometric parameters of the investigated water bodies is reflected in the statistically significant differences in the physicochemical indices, primarily oxygen content and temperature at the bottom. Despite the shallow depth of the Tarnowa oxbow lake, the oxygen content at its bottom decreases already in early summer (Fig. 2). In the deep Tuchoń oxbow lake, sheltered from the wind, thermal and oxygen stratification may be observed in summer. Starting from mid-May, the most severe oxygen deficits in this water body were also recorded in the bottom zone. Despite the considerable depth of the Święconka oxbow lake, thermal stratification is small, while oxygen saturation of the water near the bottom may be considered satisfactory. A considerable reversed thermal stratification was observed in all the studied water bodies in the autumn-winter season, except for the flow-through lakes Święte and Tarnowa.

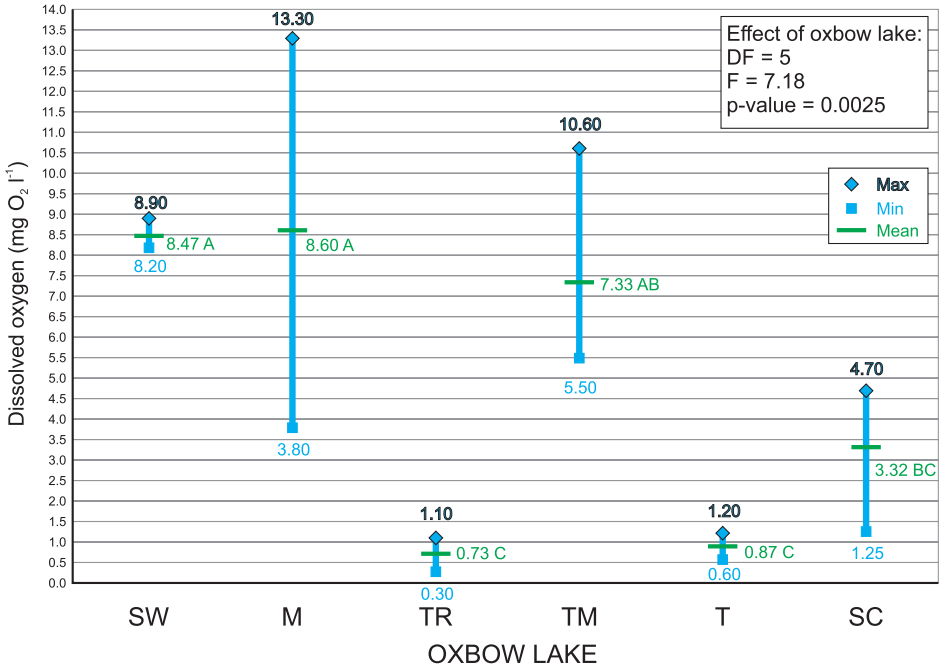

Figure 2

Dissolved oxygen concentration in the benthic zone in the summer (minimum,maximum, mean); means with the same letter don`t differ statistically

Rheophilic ichthyofauna in oxbow lakes

A total of 26 fish species were recorded during the 3-year study in the six oxbow lakes, including 9 rheophilic species, i.e. chub (*Leuciscus cephalus*), asp (*Aspius aspius*), vimba (*Vimba vimba*), nase (*Chrondostoma nasus*), dace (*Leuciscus leuciscus*), ide (*Leuciscus idus*), blue bream (*Abramis ballerus*), gudgeon (*Gobio gobio*) and burbot (*Lota lota*) (Table 2). In terms of relative abundance, the phyto-lithophilic reproductive guild significantly dominates, including three rheophilic species as well as eurytopic taxa, such as the white bream, perch and roach, which together account for as much as 70% of all fish. The constancy of occurrence of rheophilic fish in the oxbow lakes varied greatly, ranging from 2% for the burbot to 67% for the ide. The percentage of rheophilic species in the fish assemblage was only 7% throughout the study period (Fig. 3). However, analysis of individual catches and investigated periods reveals considerable fluctuations in the population density, and thus the dominance

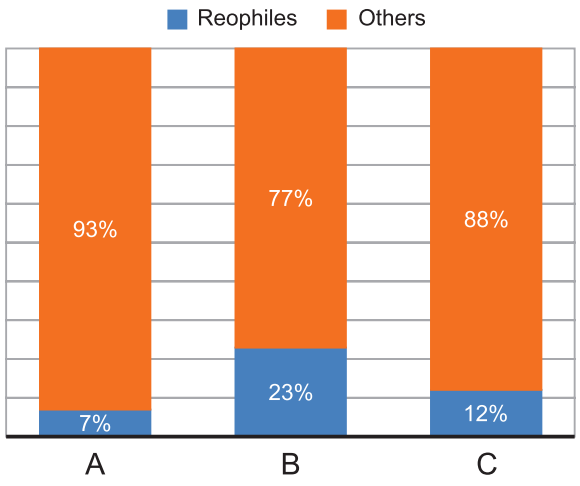

Figure 3

Average contribution of rheophilic species to the dominance structure of ichthyofauna in oxbow lakes (A), in the Warta near Pyzdry (B), and in the Warta near Rogalin (C)

Table 2

Fish species recorded in six oxbow lakes (C – constancy of occurrence in all catches; D – percentage in dominance structure; rheophilic species are given in bold)

No.	Species	SW	M	TR	TM	T	SC	C [%]	Reproductive guilds, contribution (D%)
1	***Leuciscus cephalus***	0	+	+	+	0	+	17	Lithophils, 2.1
2	***Aspius aspius***	+	+	0	+	+	+	44	
3	***Vimba vimba***	0	0	0	+	0	0	4	
4	***Chondrostoma nasus***	0	+	0	0	0	0	2	
5	***Leuciscus leuciscus***	0	0	+	0	+	0	7	Phyto-lithophils, 85.2
6	***Leuciscus idus***	+	+	+	+	+	+	67	
7	*Blicca bjoerkna*	+	+	+	+	+	+	89	
8	*Perca fluviatilis*	+	+	+	+	+	+	96	
9	*Gymnocephalus cernuus*	0	+	+	0	0	+	20	
10	*Rutilus rutilus*	+	+	+	+	+	+	96	
11	*Alburnus alburnus*	0	+	+	+	+	+	46	
12	*Abramis brama*	+	+	+	+	+	+	85	
13	***Abramis ballerus***	0	0	0	+	0	+	17	
14	*Esox lucius*	+	+	+	+	+	+	96	Phytophils, 12.1
15	*Scardinius erythrophthalmus*	0	+	+	+	+	+	65	
16	*Tinca tinca*	+	+	+	+	+	+	80	
17	*Carassius carassius*	0	+	+	0	+	+	30	
18	*Carassius gibelio*	0	+	+	0	+	+	43	
19	*Cyprinus carpio*	0	0	+	0	0	0	2	
20	*Misgurnus fossilis*	0	+	+	0	0	+	6	
21	*Cobitis taenia*	+	+	+	+	+	+	41	
22	*Silurus glanis*	+	+	0	+	0	0	6	
23	*Stizostedion lucioperca*	+	+	0	+	+	+	19	
24	***Gobio gobio***	+	0	0	0	0	0	2	Psammophils, 0.1
25	***Lota lota***	+	+	0	0	0	0	9	Litho-pelagophils, 0.3
26	*Rhodeus sericeus*	0	0	+	0	0	0	9	Ostracophils, 0.2
	Number of species	13	20	18	16	15	18		

structure, as well as certain regularities (Fig. 4, 5). Moreover, catches in the two sections of the Warta River indicate a clear dominance of indifferent species, also in the main river channel (Fig. 3). The highest percentage of chub is observed in autumn, when small specimens of this species flow into the standing waters to spend winter there (Fig. 5). The highest density of asps was recorded in the Madałowe oxbow lake in summer. Large specimens of over 1 kg migrated to that oxbow lake to feed there intensively. In the autumn season, overwintering juvenile specimens of asps were found in Trzykolne Młyny (similarly as chubs). Among rheophilic species, the ide is the most common species reported from the oxbow lakes. The highest percentage in the assemblage was recorded in the autumn in the Święte flow-through oxbow lake, as well as in Trzykolne Młyny and Święconka. The blue bream, a species characteristic of confluence sections of large

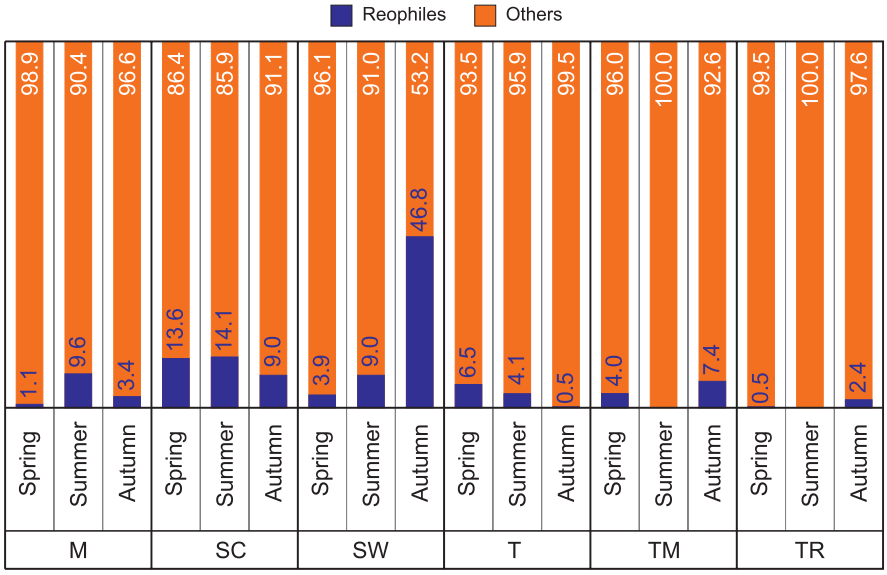

Figure 4

Fluctuations in the contribution of rheophilic species in the dominance structure in catches from six oxbow lakes in three periods.

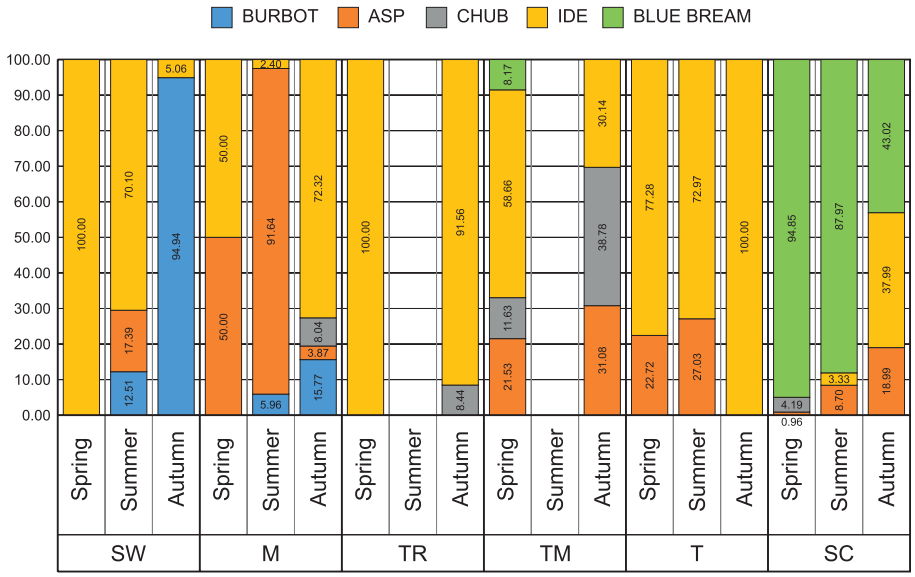

Figure 5

Fluctuations in the contribution of selected species in the dominance structure of rheophiles from six oxbow lakes in three periods.

Table 3

Statistical influence of experimental factors on the analyzed traits

Experimental factor	DF	Analyzed traits							
		Number of species		Number of specimens		Mass		Mean individual mass	
		F	p	F	p	F	p	F	p
Oxbow lake	5	3.80	0.0075	3.68	0.0088	4.98	0.0015	9.04	0.0001
Season	2	6.02	0.0057	0.65	0.5297	1.65	0.2075	2.79	0.0754
Oxbow lake × Season interaction	10	5.49	0.0001	1.61	0.1454	1.53	0.1712	7.92	0.0001

Effects of factors: – highly significant (P≤0.05); – significant (P≤0.1); – non-significant (P>0.1)

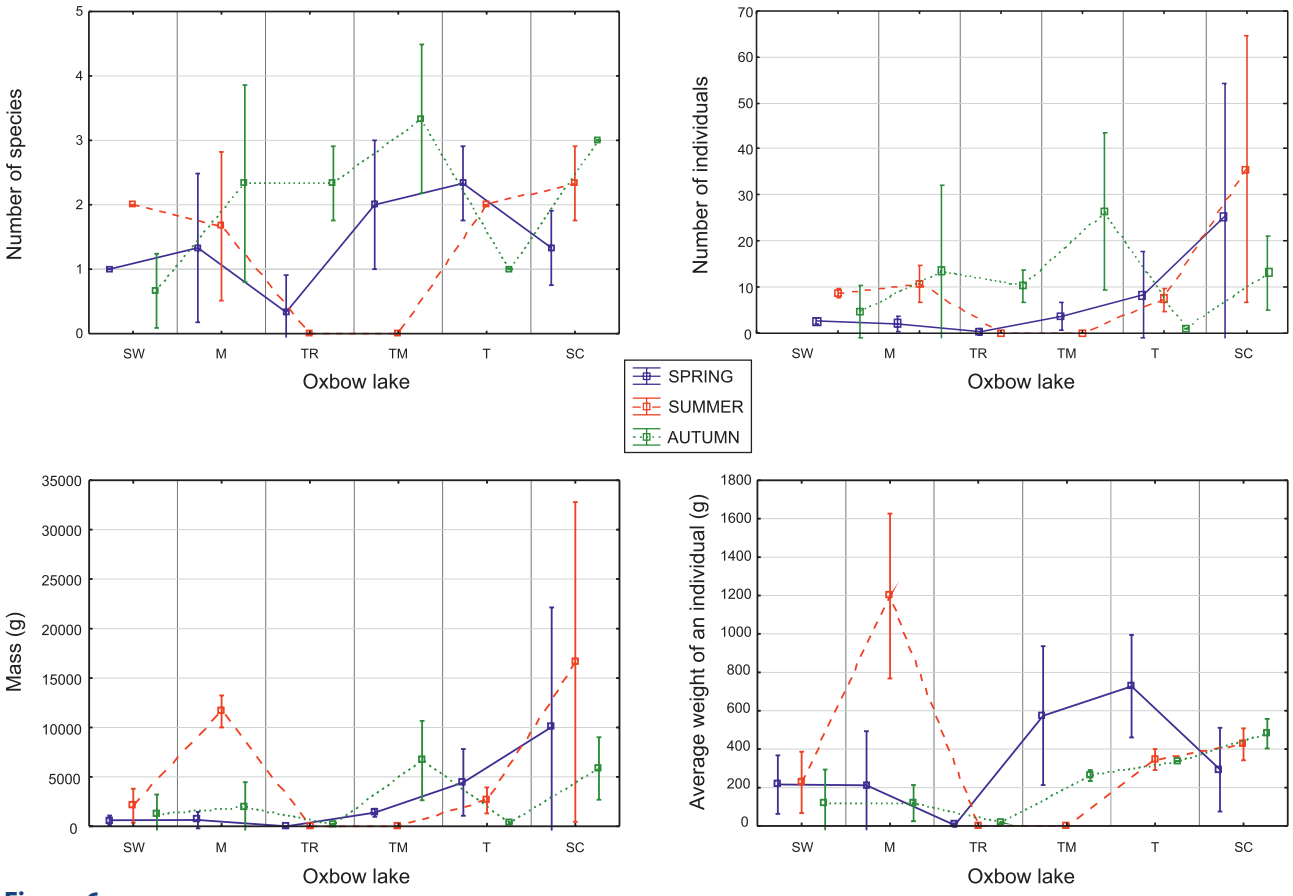

Figure 6

Fluctuations in four traits of all rheophilic species (chub, asp, vimba, nase, dace, ide, blue bream, gudgeon, burbot) in six oxbow lakes throughout the year (Mean, SE, SD)

rivers, was caught almost exclusively in the Święconka oxbow lake, where it probably forms a stationary population. Higher population density of the burbot was recorded only in the Święte flow-through oxbow lake, where it accounted for up to 100% of all fish in autumn. The vimba and the burbot are found in the oxbow lakes in very small numbers. However, results of unpublished studies by the authors of this study as well as literature data indicate that these species are also rarely found in the river channel. Taking into consideration all the water bodies together and the entire study period, the one-way analysis of variance showed a statistically highly significant effect of the capture site (oxbow lake) on the number of species, population density, biomass and the mean individual mass of rheophilic fish species (Table 3). Differences between the investigated water bodies in terms of their size, depth, wind shielding and connection

with the river result in fluctuations of all analyzed parameters. The largest number and the highest density of rheophilic species were found in Święconka (SC), while the lowest values of these parameters were determined in Tarnowa (TR) and Święte (SW) (Fig. 6). The Madałowe oxbow lake is distinguished from the other reservoirs by the mean individual mass. The analysis showed that the seasons of the year primarily affect the number of species and, to a lesser extent, the size of specimens and the population density (Table 3). In terms of the number of rheophilic species found in the oxbow lakes, the autumn season was statistically significantly different from the two other seasons (Fig. 6). In the autumn, all species living in the river system (including vimba and burbot) can be found in the investigated water bodies. In the summer, obligatory river fish species were not observed in the small and shallow oxbow lakes Tarnowa and Trzykolne Młyny. The total effect of location and season is highly significant for the number of species and the specimen size.

Discussion

Clear variation in environmental conditions in open oxbow lakes in the middle Warta River is confirmed by the results of research on oxbow lakes of this river in the area of the Jeziorsko dam reservoir (Penczak et al. 2000a; 2003a), the Pilica River (Penczak et al. 2000b, 2005), the Łyna River (Glińska-Lewczuk 2005) and the Słupia River (Obolewski 2005). Differences concern oxbow lakes as well as individual seasons of the year. The major differentiating factors, directly affecting the behavior of fish, are water temperature and dissolved oxygen content. Temperature has a very strong effect on the behavior of river ichthyofauna (Opuszyński 1983; Pliszka 1964; Nunn 2003). In late autumn and winter, due to the lack of flow and thermal stratification, water at the bottom of oxbow lakes may be warmer than in the river, even by several degrees. This lead to the development of favorable overwintering conditions for fish, including rheophilic species. Typical wintering grounds for river species are primarily Madałowe and Trzykolne Młyny oxbow lakes, in contrast to the flow-through Święte oxbow lake where limited numbers of ide and burbot were reported in autumn. In the summer, water temperature in oxbow lakes on the one hand reduces the dissolved oxygen content, while on the other hand, it creates optimal conditions for eurytopic species, e.g. the bleak (*Alburnus alburnus*). The bleak is followed into the oxbow lake by asp. This is confirmed by the example of Madałowe where asp spectacularly hunted for bleak in the summer and reached the maximum biomass in the catches. These predators used oxbow lakes only as feeding grounds and returned to the river immediately after feeding. Large asps, i.e. above 0.5 kg, were fished almost exclusively during their spectacular hunt for bleak. Apart from Święte, periodical deficits of dissolved oxygen were observed in each of the analyzed water bodies, with the most adverse oxygen conditions being recorded at the bottom of Tarnowa and Tuchoń oxbow lakes. Based on the considerable decrease in the dissolved oxygen content with increasing depth, it may be concluded that large areas of the bottom in those water bodies were deoxygenated in critical periods and thus unavailable to the fish. If there is no permanent connection with the main river channel, oxbow lakes may act a deadly trap for rheophilic fish (having higher environmental requirements) in the summer. The research conducted on oxbow lakes of the Morava River confirm that oxygen is an important parameter differentiating both habitats (lentic vs. lotic), thus affecting their species structure and the fish population size. Migrations of fish from oxbow lakes to the river are accelerated in the summer due to the reduction in the dissolved oxygen content or high temperature (Hohausowa 2000, Hohausowa et al. 2003). When considering all the oxbow lakes together over the entire study period, the percentage of rheophilic species in the total population appears to be low. However, a comprehensive picture was provided based only on the fluctuations in the dominance index for individual species in three seasons of the year in each oxbow lake separately and the comparison of the fish species structure in the river and in a given oxbow lake. It appears that the ichthyofauna is strongly dominated by indifferent species also in the main channel, while the contribution of individual rheophilic species in the water bodies ranges from 0 to 100%, depending on the conditions. The problem of a decline in rheophilic species and the increasing dominance of species with reduced environmental requirements is observed not only in the Warta River, but also in other rivers throughout Europe and for this reason, intensive measures need to be implemented to support the declining species (Grows et al. 1998; Kruk 2004). In their research on the ichthyofauna of the Warta River upstream of Jeziorsko and of the Pilica River, Penczak et al. (2000b; 2005) reported that oxbow lakes of both catchments are visited by obligatory river species, yet rheophilic species become less common and some of them are no longer found in the main channel and therefore, they are very rarely observed in oxbow lakes. Quantitative indices for these oxbow lakes greatly fluctuated, which was confirmed by the high values of the coefficients of

variation, exceeding 100%. The high variability of natural lotic assemblages was also presented by Grossman et al. (1990), Grows et al. (1998) and Golski et al. (2010). Fluctuations in open oxbow lakes are directly related to the behavior of fish. Based on the observations of changes in the population size over a period of several years, as well as those of the fish biomass and the dominance structure of rheophilic species in the investigated oxbow lakes, it may be concluded that these fish use both habitats with varied intensity throughout the season. This conclusion is consistent with the results of other studies (Hohausowa 2000; Wolter, Bischoff 2001; Hohausowa et al. 2003; Fladung et al. 2003). With regard to the middle Vistula River, Wiśniewolski et al. (2009) reported that a permanent connection of lotic and lentic elements in the river system supports an increase in their overall diversity and the number of species sensitive to habitat transformation.

The ide showed different habitat preferences, depending on the season of the year (Rakowitz, Zweimuller 2000). In the Danube backwaters, fish were found during the period of intensive feeding as well as overwintering, both in the river and oxbow lakes, mainly in the periods of higher water levels. During the spawning season, ides from the Elbe (Germany) and the Vecht (the Netherlands) were found only in the river (Winter, Fredrich 2003; Fredrich 2003). These data are confirmed by the catches made within the framework of the authors' studies. Other available literature data also indicate that ides may spawn in oxbow lakes (Witkowski et al. 1997). Based on the studies conducted in the 1950s, Jaskowski (1962) reported that ides are found in greater numbers in sections with numerous sandbars and oxbow lakes. Penczak reported that asps in the 1960s were frequently caught in oxbow lakes of the Warta River, yet the species was found in very small numbers during the studies conducted 30 years later (Penczak 1969b; Penczak et al. 2000a). In the Elbe River, asps rarely visited natural oxbow lakes to overwinter or to feed. In washlands, the species was found rarely and only very close to the main channel, as most fish overwintered in the river. The water level had no effect on the habitat use. Based on the habitat use, the asp may be classified as a definitely rheophilic species (Fredrich 2003). The results of the presented study indicate a different behavior of this species, as asps from the middle Warta River system – in contrast to the population from the Elbe – regularly use oxbow lakes as wintering grounds and feeding grounds. According to the abiotic typology, the Elbe is a large lowland river, one of the longest in Europe and therefore different from the Warta River in many ways, including depth, flow velocity, microhabitat heterogeneity. Perhaps in the case of the Elbe River, fish may find more convenient places for feeding and overwintering. In water bodies permanently connected with a river, Penczak (1986) observed greater species richness and the presence of asps in the summer season, which largely confirms the results of the studies conducted by the authors of this study. The blue bream (not reported in the Warta by Ciepłucha et al. 2014) is found in considerable numbers in the Święconka oxbow lake. Typical habitats of the rheophilic blue bream include lower river sections and estuaries, where its population may achieve considerable density (Brylińska et al. 2000; Kompowski 1991). The first report on the occurrence of blue breams in the Warta near Poznań was published by Kaj (1956). Findings of the report were confirmed by Jaskowski (1962) who caught two specimens at Wronki and Poznań. Previously, Puszczykowo near Poznań was the farthest documented location of this species (Kaj 1956). There are no data in the Polish or foreign literature on the occurrence of blue breams in oxbow lakes. Święconka is the only oxbow lake described to date with such a large population of blue bream. Furthermore, so far this location represents the southern limit of this species' range in the Warta. The other rheophilic species were found only in the autumn. The chub was recorded in larger numbers in Madałowe and Trzykolne Młyny oxbow lakes, two nase specimens were caught in the Madałowe oxbow lake, while one specimen of gudgeon and one specimen of vimba were caught in Święte and Trzykolne Młyny oxbow lakes. The dace was recorded only in the Tarnowa oxbow lake, located opposite to the confluence of the Prosna and the Warta River. In the Spree, chubs were found only in the main river channel where flow velocity ranged from 0.15 to 0.6 ms^{-1} (Fredrich 2003). Large numbers of daces in the confluence section of the Prosna were reported by Penczak et al. (2003b). Data collected in the 1960s by Penczak (1969a; 1969b) showed that daces and gudgeons were not found in the oxbow lakes of the Warta River upstream of Sieradz, while single specimens of chub and burbot were caught only in the winter during the ice phenomena. Promising findings are related to the burbot and vimba caught in the last year of the study, as they were previously found in large numbers in the Warta, which was documented by Rychlicki (1933), Dziekońska (1948), Iwaszkiewicz (1969), Jaskowski (1962), Mastyński (1992), Andrzejewski and Mastyński (2005). According to Penczak et al. (2005), the chub, asp and burbot are rarely found in oxbow lakes of the upper and middle course of the Warta River.

Conclusions

The results of this study clearly show that open oxbow lakes may play an important role in the functioning of ichthyofauna through their permanent connection with the main riverbed. This is consistent with most available literature data on the subject.

Of the nine rheophilic species, five are found in greater density, depending on the season and the nature of the water body. Significant fluctuations in the number of species and their relative densities were observed in individual oxbow lakes.

Open oxbow lakes are used primarily as wintering and feeding grounds.

Larger oxbow lakes, connected with the main channel through a large confluence at one end only, are characterized by greater diversity and density of the rheophilic ichthyofauna. In smaller water bodies with a limited connection with the river, particularly in summer, the river species are basically not found and these oxbow lakes may act as traps for fish.

Implementation of conservation measures is required in order to maintain the ecological functions of these valuable habitats. Regulation of river banks prevents large rivers from meandering and thus new oxbow lakes are not formed. Moreover, fish poaching was observed mainly in backwaters and not in the river channel. For this reason, it is important to maintain a permanent connection with the river and to fight poaching.

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