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RESEARCH ARTICLE

Zooplankton and fish community structures in interconnected lakes

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Abstract. The aim of this study was to assess the species composition and structure of zooplankton and fish communities in lakes with similar ecological conditions that are connected by periodic streams. This was done by assessing the relative importance of local biotic and abiotic interactions associated with the species composition and structure of the zooplankton and fish communities. The study was conducted in three small, soft water lobelia lakes located in the source area of the Brda River, which were characterized by low trophic statuses and similar depths. A total of 15 Rotifera taxa, 18 Cladocera taxa, and nine Copepoda taxa were identified in the lakes analyzed. The lake zooplankton communities differed in species richness, total density, and biomass, while the Shannon–Wiener diversity indexes of the zooplankton communities were similar. Of the three lakes analyzed, the faunal similarity index was the highest in Lake Smołowe. Comparisons of the three lakes indicated there was greater similarity in the pelagic (42.7–50.0%) than in the littoral (20.1–26.8%) zones. The fish community of the three lakes consisted of eight species, and species richness ranged from two to eight fish species. Only perch (*Perca fluviatilis* L.) and pike (*Esox lucius* L.) were present in all three lakes. The fish groups also differed in terms of density and biodiversity indicators. Faunal similarity indicators showed significant similarity in the dominance structure of the fish communities.

Keywords: connectivity, isolation, lobelia, soft water lake, fish predation

Introduction

One of the central issues in ecology is understanding and predicting patterns in community species structure and spatial and temporal variability. Numerous studies report on links among multiple environmental gradients and the occurrence of different species along them. Fish distribution in water bodies is controlled by the availability of surface waters, while connections among water bodies facilitate fish movement and the colonization of uninhabited areas (Jackson et al. 2001, Olden et al. 2001, Laske et al. 2016, Kristensen et al. 2020). Climate and geological and hydrological factors influence the richness patterns of fish and their community structures along environmental gradients on regional scales (Brucet et al. 2013). However, in addition to water quality (Feiner et al. 2016), physical isolation also influences fish species richness and the structure of fish

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communities on local scales (Tonn and Magnuson 1982, MacDougall et al. 2018).

Zooplankton is a key intermediary in aquatic food webs that transfers energy from primary producers to consumers. Zooplankton species richness in lakes depends primarily on factors related to lake size (Dodson 1992), productivity (Sługocki and Czerniawski 2018), temperature (Hessen et al. 2007), water quality (Jeppesen et al. 2000), and fish predation pressure (Hessen et al. 2006). The location of lakes and their surface area in surrounding landscapes significantly influence zooplankton species richness, which suggests that the phenomena of dispersion might increase zooplankton species richness (Hobæk et al. 2002, Dodson et al. 2005).

Nutrient-poor, soft water lakes found in the temperate and boreal zones of the northern hemisphere are highly valuable ecosystem elements (Murphy 2002). The low nutrient content supports the occurrence of isoetids, which are becoming increasingly rare because of nutrient enrichment associated with changes in land use and urbanization (Weckström et al. 2010). These lakes usually have no inlets or outlets or are fed by periodic streams. The specific physicochemical conditions in soft water lakes include low mineralization (conductivity < 100 μS cm^{-1}), low calcium content, high water transparency, a pH range of 5.5–7.5, and low concentrations of nitrogen and phosphorous (Borowiak et al. 2020). Aquatic invertebrate diversity is also generally low in soft water lakes (Kuczyńska-Kippen et al. 2017), and they often have small numbers of fishes (Heese 2000, Kapusta and Czarkowski 2016).

Lakes located in areas of river sources can be isolated in the sense that they can be linked with other water bodies by periodic streams, and fish can even use such streams as colonization routes (Öhman et al. 2006, Heim et al. 2019). If environmental conditions in isolated lakes become inhospitable for fish breeding or survival, species can disappear for long periods of time, while lakes that are linked can be recolonized quickly. Therefore, environmental conditions have a greater influence on faunal community structure in isolated lakes than in those that are linked. The aim of this study was to assess the species compositions and structures of the zooplankton and fish communities in lakes with similar environmental conditions that are linked by periodic streams. The study was performed by assessing the relative importance of local biotic and abiotic interactions associated with the species composition and structure of the zooplankton and fish communities in three lakes.

Materials and methods

Study area

The study was conducted on three, small oligotrophic lakes located in the source area of the Brda River (Table 1). The Brda flows out of Lake Smołowe (54°01’57,6”N; 17°04’38,6”E) as a periodic stream and into Lake Kamień (54°01’35,7”N; 17°03’47,6”E) and then into Lake Orle (54°01’05,5”N; 17°03’59,6”E). The stream flowing out of Lake Smołowe is 950 m long and reaches a flow rate of 0.1 L s^{-1}. The stream connecting lakes Kamień and Orle is 180 m long and has a flow rate of 0.5 L s^{-1}. The flow rate of the river at the Lake Orle outflow is up to 10 L s^{-1}. All of the lakes are post-glacial and are located in a forested watershed. Common features of these lakes include low conductivity, a similar pH range close to neutral, and low trophic status (Table 1). All three lakes are classified as nature reserves and fishing and recreational activities are prohibited in them. *Lobelia dortmanna*, *Isoëtes lacustris*, and *Littorella uniflora*, species that are typical of lobelia lakes, occur here.

Zooplankton sampling

Zooplankton samples were collected in March, June, and August 2013 in the pelagic and littoral zones of each lake. Samples for chemical and zooplankton analyses were collected with a TOŃ sampler with a capacity of 5 L (entire sample 25 L). The sampling stations in pelagic zone were located close to the deepest parts of the lakes. Samples were taken at 2 m

Table 1
Environmental parameters of the three studded lakes

Variable	Smołowe	Kamień	Orle
Altitude	180.8	172.0	170.3
Watershed area (km^2)	1.66	3.88	0.51
Lake area (ha)	35.5	49.4	11.2
Maximum depth (m)	12.2	15.2	10.8
Mean depth (m)	4.6	6.6	6.2
Conductivity (µS cm^{-1})	27	54	55
TDS (mg L^{-1})	17.5	34.5	35.5
pH	6.8	7.1	7.2
Oxygen in the epilimnion (mg O_2 L^{-1})	9.3	9.4	9.3
Secchi disc visibility (m)	3.5	3.6	3.3
Chl a (mg L^{-1})	5.3	4.6	2.1
TP (mg P L^{-1})	0.02	0.02	0.04
TN (mg N L^{-1})	0.99	0.73	0.83
TSI	39	38	39

intervals from the surface to the bottom. The water was filtered through plankton nets with a mesh size of 30 µm and fixed with Lugol's solution and ethyl alcohol. At the sampling site, Secchi depth (SD) was determined and water temperature, oxygen content, pH, and conductivity were measured with a YSI Professional Plus instrument (YSI Inc., Ohio, USA). Chemical analyses of the concentrations of total phosphorous (TP) and total nitrogen (TN) were performed in the laboratory with standard methods (APHA 1992). Chlorophyll a concentrations were determined with spectrophotometry. Zooplankton density was quantified with a Sedgwick-Rafter chamber under an optical microscope (Nikon Eclipse 80i). Zooplankton species were identified based on standard keys (Flössner 1972, Kiefer and Fryer 1978, Koste 1978, Radwan et al. 2004, Rybak and Błędzki 2005). Rotifer biomass was determined with formulas by Ejsmont-Karabin (1998), and Crustacea biomass was determined with formulas by Rybak and Błędzki (2005).

Fish sampling

Fish samples were collected according to the Norden standard for gillnet survey during the period between July and August of 2013. Each lake was divided into depth strata, and each stratum was randomly sampled by a defined number of benthic and pelagic gillnets (Appelberg 2000). Pelagic nets were located close to the deepest places in the lakes. Benthic gillnets, 1.5 m in height, 30 m in length, composed of 12 panels with mesh sizes from 5 to 55 mm. Pelagic gillnets, 6 m in height, 27.5 m in length, composed of 11 panels with mesh sizes from 6.25 to 55 mm. Gillnets exposition time was approximately 12 h, and fishing began at approximately 18:00. The specimens caught were identified to the species, counted, and measured. The next stage of analysis was to determine the numerical share of each species. The dominance index was calculated for each species:

$$(D_i): D_i = 100 \times n_i \times (\Sigma\, n_i)^{-1},$$

where: n_i – number of specimens of species *i*.

Further data analysis focused on determining abundance per unit of fishing effort. The catch per unit effort (CPUE) was the total number of fish caught during one night in one net. Fish density, expressed based on the CPUE, was calculated per 100 m^2 of net surface area.

Data analysis

The similarities among the structures of the zooplankton communities in the lakes analyzed and among the fish communities in the lakes analyzed were determined with the Renkonen percentage similarity index (Kwak and Peterson 2007). This index compared the relative proportions of the species in each lake, where relative proportions were normalized as the percentage of all species observed. The percentage of similarity fluctuated from 0% for completely different communities to 100% for very similar communities. This simple percentage of similarity was robust to sample size and species diversity and served as a quantitative measure of community structure (Krebs 1989). Species richness, Shannon–Wiener diversity, and Shannon–Wiener evenness were calculated to compare the overall patterns in the zooplankton and fish communities among the lakes. Diversity indicators were calculated individually for each dataset representing the results of the fish catch in individual nets and zooplankton samples. The Shannon–Wiener diversity (H') index was calculated with the following formula (Krebs 1989):

$$H' = -\Sigma p_i \times ln(p_i)$$

where p_i is the share of specimens of species i in the whole sample. Shannon–Wiener evenness (J) was calculated for each set as:

$$J = H' \times ln(S)^{-1}$$

where S is the total number of species in the sample.

Species richness, the Shannon–Wiener diversity index, and the Shannon–Wiener evenness index were compared among the lakes analyzed with non-parametric ANOVA (Kruskal-Wallis test) and the Mann–Whitney U test in *post hoc* analyses. The Bonferroni method for correction of significance level was used to decrease the probability of committing a type I error. All statistical analyses were performed with Statistica 12 (StatSoft, Inc.).

Results

Zooplankton composition

A total of 15 Rotifera taxa, 18 Cladocera taxa, and nine Copepoda taxa were identified in the three lakes analyzed (Table 2). The total zooplankton abundance and biomass differed significantly in the lakes (Fig. 1a). Higher abundance was primarily associated with rotifer abundance. Rotifers dominated in lakes Smołowe and Orle at a mean share of 62%, while in Lake Kamień Copepoda (36.2%) and Cladocera (35.5%) were the dominants. The most isolated of the lakes, Smołowe, had the lowest zooplankton biomass (Fig. 1b). Cladocera was the main component of zooplankton biomass in all the lakes.

Zooplankton species richness differed significantly among the lakes (H = 7.17, P = 0.028, Fig. 2). Much higher species richness was recorded in Lake Orle than in Lake Kamień (P < 0.01). The values of the Shannon–Wiener diversity index for zooplankton in the lakes analyzed were similar (H = 0.81, P = 0.669, Fig. 2). However, the values of the Shannon–Wiener evenness index for zooplankton were varied in the compared lakes (H = 7.88, P = 0.02, Fig. 2), and zooplankton evenness was much higher in Lake Kamień than in Lake Orle (P < 0.01).

The species structure of planktonic crustaceans and rotifers differed in the lakes analyzed. Only four Rotifera species were noted in all the lakes: *Conochilus unicornis*; *Kellicotia longispina*; *Keratella cochlearis*; *Polyarthra major*. Only three Cladocera species were noted in all three lakes: *Bosmina coregoni*; *Ceriodaphnia quadrangula*; *Holopedium gibberum*. The Copepoda species noted in all the lakes were *Eudiaptomus gracilis*, *Heterocope appendiculata*, *Macrocyclops albidus*, and *Thermocyclops crassus*. The highest value of the similarity index within the lakes for the habitats (littoral vs. pelagic zones) analyzed was recorded in Lake Smołowe (57.3%; Fig. 3). However, comparison among the lakes indicated more similarity in the pelagic (42.7–50.0%) than in the littoral (20.1–26.8%) zones.

Table 2

Species composition and mean zooplankton abundance in littoral and pelagic zones of the three connected lakes in March, June, and August

	Smołowe		Kamień		Orle	
	littoral	pelagic	littoral	pelagic	littoral	pelagic
Rotifera						
Ascomorpha ovalis	4.5					
Asplanchna herrickii	1.0	1.0			1.0	3.0
Asplanchna priodonta				3.0		2.0
Conochilus unicornis	30.0	45.0		10.5	2.0	26.8
Filinia longiseta						1.0
Gastropus stylifer		17.5				
Kellicotia longispina		1.5	13.0	3.8	19.0	79.6
Keratella cochlearis	3.0	10.5		1.3	22.0	66.8
Keratella cochlearis f. hiemalis				1.5	1.0	1.7
Keratella cochlearis f. tecta						1.0
Keratella quadrata		4.0			2.0	2.7
Lecane curvicornis	4.0					
Lecane lunaris			1.0			
Polyarthra major	60.0	50.5	3.0	3.0	3.0	49.4
Testudinella mucronata	32.0					1.0
Total Rotifera	134.5	130.0	17.0	23.2	50.0	234.9
Cladocera						
Acroperus harpae	1.0	2.0				
Alona guttata	1.0					
Alonella nana	3.5	1.0	1.0			
Bosmina coregoni		5.0		3.0		2.0
Bosmina longirostris			2.0	3.4	2	1.0
Bosmina longispina		9.5				3.0
Ceriodaphnia quadrangula	2.0	29.5	5.0	1.0	13.1	11.0
Chydorus sphaericus	1.0		1.0			
Daphnia cucullata						13.3
Daphnia cristata				20.5		36.0
Daphnia longiremis						1.0
Diaphanosoma brachyurum				1.5		
Dunhevedia crassa	1.0					
Eurycercus lamellatus	2.0					
Holopedium gibberum		1.0		3.7		4.0
Pleuroxus uncinatus	2.0					
Polyphemus pediculus			3.0			
Sida cristalina				1.0		1.0
Total Cladocera	13.5	48.0	12.0	34.1	15.1	72.3
Copepoda						
Cyclopoida naupli	34.0	21.3	3.0	8.1	86.0	55.4
Cyclops bohater	1.0				3.0	0.0
Eudiaptomus gracilis	2.0	3.7	17.0	4.8		2.7
Heterocope appendiculata		7.0		4.0		5.0
Harpacticoida			3.0			1.0
Macrocyclops albidus	11.5	8.5	15.5	3.2		7.5
Macrocyclops distinctus						2.0
Paracyclops affinis			1.0	1.0		
Thermocyclops crassus	4.0	8.0	3.0	8.8		36.7
Total Copepoda	52.5	48.4	42.5	29.8	89.0	110.2

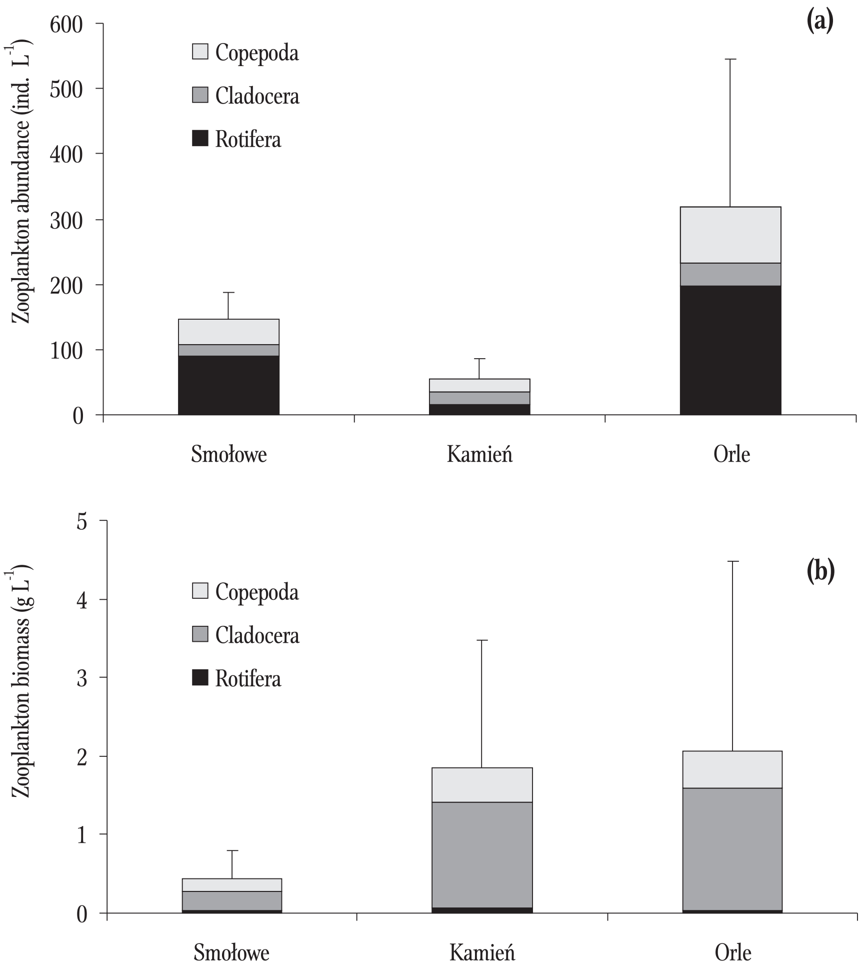

Figure 1. Mean abundance (a) and biomass (b) of Rotifera, Cladocera, and Copepoda in the lakes analyzed.

Fish composition

A total of 944 fishes belonging to eight species were caught. Percids and cyprinids dominated the overall catches. Perch (*P. fluviatilis*) dominated in lakes Smołowe and Kamień, while roach (*Rutilus rutilus* (L.)) did so in Lake Orle. Perch (58.1% total catch) and roach (34.6% total catch) were caught most frequently, and combined, these two species were 92.7% of the specimens examined. Perch and pike (*E. lucius*) were the only species that occurred in all of the lakes. Vendace (*Coregonus albula* (L.)) only occurred in Lake Kamień. No alien fish species were caught in the lakes. The highest value of the domination structure similarity index was noted between lakes Kamień and Orle (Table 3). The mean CPUE values for lakes Smołowe (90.2 ± 25.3) and Kamień (91.3 ± 56.2) were significantly statistically lower than that for Lake Orle (135.7 ± 116.7; $H = 6.20$, $P = 0.045$). Species richness per unit of fishing effort differed significantly among the lakes analyzed ($H = 6.38$, $P = 0.041$, Fig. 2). Species richness was much higher in Lake Kamień than in Lake Smołowe ($P < 0.01$). The Shannon–Wiener diversity index values per unit of fishing effort differed significantly in the lakes analyzed ($H = 6.20$, $P = 0.045$, Fig. 4). Fish diversity was much higher in Lake Kamień than that in Lake Smołowe ($P < 0.01$). The Shannon–Wiener evenness value per unit of fishing effort also differed in the lakes analyzed ($H = 6.20$, $P = 0.045$, Fig. 2), and fish evenness in Lake Kamień was much higher than that in Lake Smołowe ($P < 0.01$).

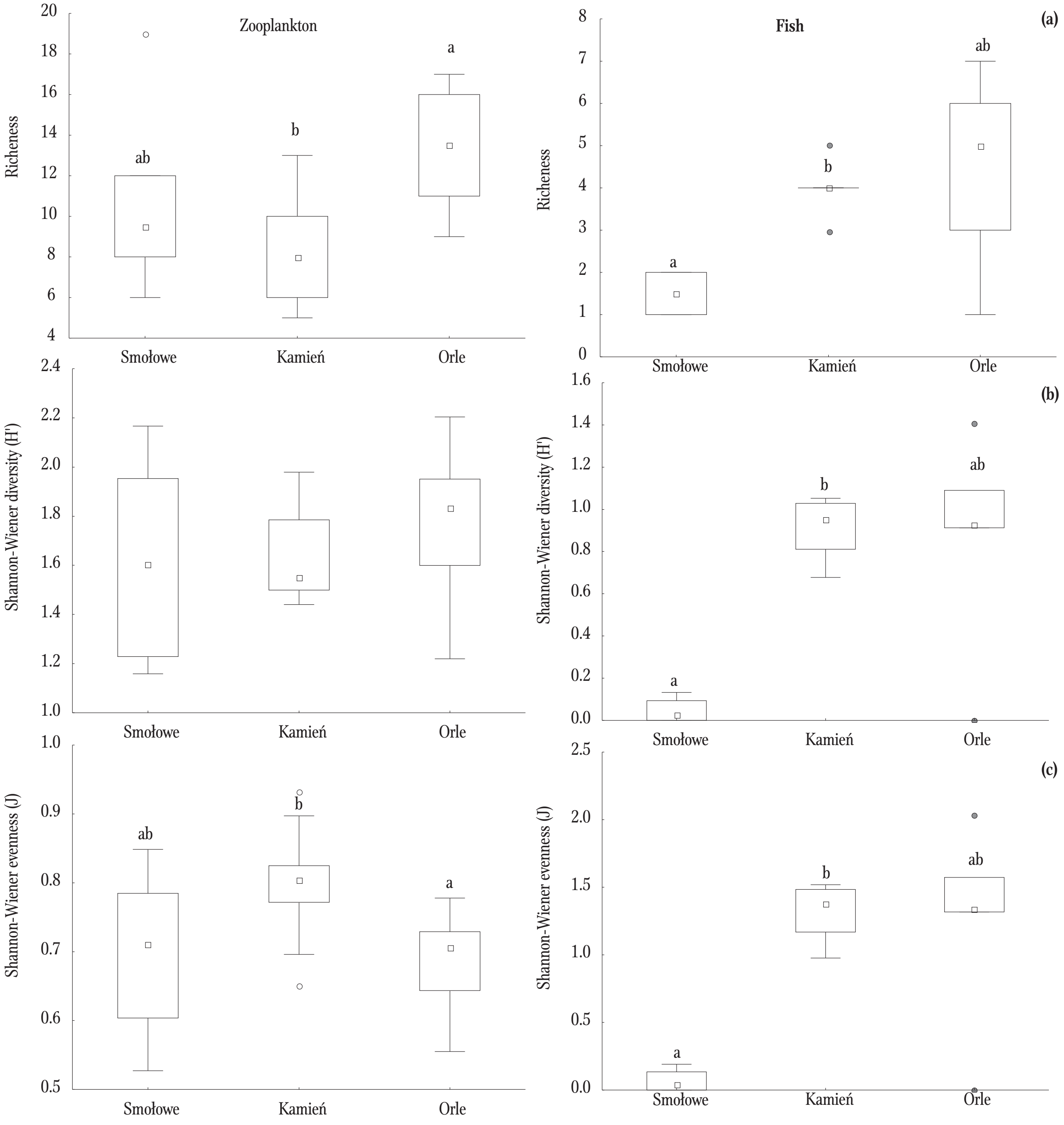

Figure 2. Species richness (a), Shannon–Wiener diversity index (b), and Shannon–Wiener evenness index (c) of the zooplankton and fish communities in the lakes analyzed. Values are median (small square), 25%, and 75% percentiles, whiskers are non-outliers, and points are outliers. Different letters above the boxes indicate significant differences among lakes as indicated by the post hoc analysis of non-parametric ANOVA.

Table 3

Species composition, relative abundance, and similarity index percentages of fish communities caught in the lakes analyzed. Lines indicate the lakes used to calculate similarity index percentages

Species	Smołowe	Kamień	Orle
Perch *Perca fluviatilis*	99.4	46.3	42.0
Pike *Esox lucius*	0.6	0.3	0.7
Roach *Rutilus rutilus*		44.0	49.5
Rudd *Scardinius erythrophthalmus*		0.3	5.2
Tench *Tinca tinca*		0.8	1.6
Bleak *Alburnus alburnus*		3.3	1.0
Vendace *Coregonus albula*		1.8	
Ruffe *Gymnocephalus cernua*		3.5	
	46.5		
	42.6		
		88.4	

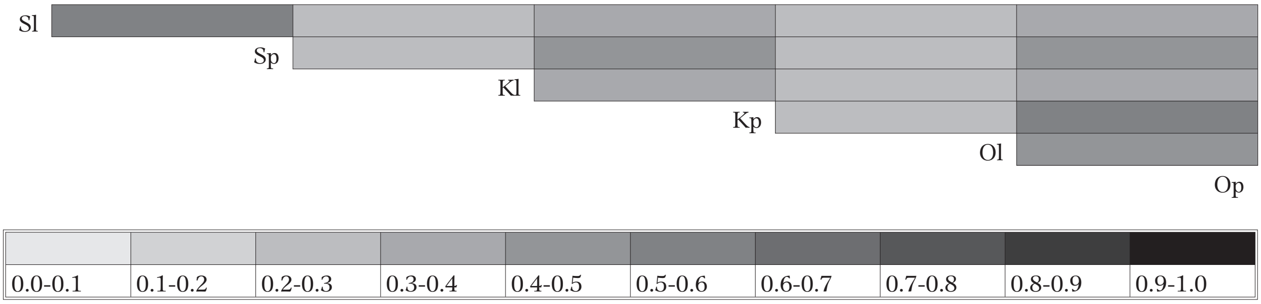

Figure 3. Renkonen's percentage of similarity, between the littoral and pelagic zones for zooplankton communities in the three connected lakes. Sl – Smołowe in littoral, Sp – Smołowe in pelagic, Kl – Kamień in littoral, Kp – Kamień in pelagic, Ol – Orle in littoral, Op – Orle in pelagic.

Discussion

Soft water lobelia lakes are considered to be poor in terms of species richness and are characterized by low zooplankton abundance and biomass (Romanowicz et al. 1994, Kraska et al. 2006, Bogacka-Kapusta 2016). Previous studies on these types of lakes indicated that zooplankton density and biomass increased with increasing water trophic status (Romanowicz et al. 1994, Bogacka-Kapusta 2016). Zooplankton species richness was similar in the three lobelia lakes without inlets or outlets located in the vicinity of Bytowa (Kuczyńska-Kippen et al. 2017). In total, we confirmed 21 Rotifera, 13 Cladocera, and two Copepoda species. The results of the present study indicated that even lakes of very similar ecological conditions that are in close physical proximity differ significantly in terms of species richness. Comparisons of this parameter with the results of earlier studies of the zooplankton of lobelia lakes highlighted that analyzing zooplankton in two habitats, i.e., the pelagic and littoral zones, significantly influenced the values of species richness. The littoral zone in relatively small, shallow lakes has a significant influence on zooplankton species composition, quantitative structure, and size. For example, large cladocerans can survive in lakes with plentiful macrophyte cover that provides sufficient shelter from planktivorous fishes (Jeppesen et al. 1998). Macrophytes occurring in lake littoral zones play important roles in increasing habitat heterogeneity, and in the lakes analyzed they could have been a key factor in determining the species richness patterns and ecologically unique zooplankton communities observed.

The zooplankton communities of the lakes analyzed were formed by species that are common in temperate zone lakes, including *C. unicornis*, *K. longispina*, *K. cochlearis*, *P. major*, *B. coregoni*, *C. quadrangula*, *M. albidus*, and *T. crassus*. Similar results were confirmed by studies conducted in lakes in northeastern Poland (Ejsmont-Karabin et al. 2020, Karpowicz and Ejsmont-Karabin 2021) and in three soft water lobelia lakes (Kuczyńska-Kippen et al. 2017). Rare species also occurred, including *Daphnia longiremis*, *H. gibberum*, and *H. appendiculata*, which are considered glacial relics in Poland (Karpowicz and Ejsmont-Karabin 2021). *H. gibberum* is a species considered to have low Ca requirements (Jeziorski and Yan 2006), which could explain its frequent occurrence in dystrophic (Karpowicz and Ejsmont-Karabin 2021) and lobelia (Kuczyńska-Kippen et al. 2017) lakes.

The connectivity of the lakes could have had a significant influence on overall species richness of both zooplankton (Hobæk et al. 2002, Cottenie and De Meester 2003, Scheffer et al. 2006) and fishes (Magnuson et al. 1998, Öhman et al. 2006, Bellard et al. 2019). Fish are visual predators that target large prey, which leads to zooplankton communities that are characterized by species and specimens of small body sizes (Vanni 1987, Li et al. 2017). The lakes analyzed were characterized by significant shares of zooplankton of large body sizes (*H. gibberum*, *H. appendiculata*, *Daphnia cristata*), which indicated that the predation pressure of planktivorous fishes was not high. Additionally, fish density in the lakes analyzed was significantly lower than that in harmonic lakes in northeastern Poland (Kapusta et al. 2021).

The abundance and diversity of fish differed significantly in the lakes analyzed. The lowest fish species richness was confirmed in Lake Smołowe, which previously had much lower water pH (Banaś and Gos 1998). The physicochemical parameters of the lake most probably changed as the result of natural processes that occurred from the periodic mortality of submerged sphagnum populations (Bociąg et al. 2013). The release of organic matter from sediments led to dystrophication and increased pH. Previously, the water pH was 5–5.4, which is why it is not surprising that only perch and pike inhabited the lake since these species are resistant to water acidification (Holmgren and Appelberg 2000, Öhman et al. 2006). Changes in water pH, which are advantageous for fishes that are sensitive to low pH, did not alter fish species composition. Lake Smołowe remained inhabited only by those species that are resistant to low pH. It is plausible that the most important factor influencing the distribution of fishes in the lakes analyzed was colonization potential. The periodic stream connecting lakes Smołowe and Kamień did not provide a good dispersion route for fishes from the neighboring water body.

This study indicated that many uncertainties remain concerning the significance of hydrological connectivity in shaping zooplankton communities in soft water lobelia lakes. Significant differences in zooplankton communities in lakes with different connectivity conditions suggest that lake isolation could be a predictor of ecological processes that shape zooplankton communities. Hydrological connectivity in lakes influences the potential of fish colonization. This study indicated that fish were not evenly distributed in the three lakes; however, fish community similarity was not correlated with zooplankton community similarity. Perhaps this was because all the lakes differed significantly in terms of fish species richness. Furthermore, invertebrate predators could have exerted substantial predation pressure on the zooplankton in the lakes analyzed, particularly since fish abundance was low. These possibilities, which have yet to be studied, underscore the necessity of conducting further research on zooplankton communities of soft water lakes.

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Author contributions. E.B.K. designed the study, analyzed the zooplankton, and drafted the manuscript; M.B. analyzed the zooplankton data and revised a draft of the manuscript; A.K. analyzed the fish fauna data and drafted the manuscript.

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