

Article



The Planktonic Rotifer Community in a Lake Restored with Selective Hypolimnetic Withdrawal

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Abstract: The objective of this study was to analyze variations in the planktonic rotifer community in a lake subjected to hypolimnetic withdrawal. The present study is also the first attempt to estimate the effects of changes in hypolimnion water withdrawal rates on the zooplankton community. The lake is located in northeastern Poland. Zooplankton were sampled in 1986, 2004 and 2013. Standard protocols of zooplankton sampling and elaboration were applied. Rotifer abundance, wet biomass, community structure, and species diversity were studied at different intensities of hypolimnetic water withdrawal. Trophic state indices based on rotifer abundance and species structure were used to evaluate changes in the trophic state of the lake. Our results showed increased planktonic rotifer species diversity over a period of years, which was a positive outcome of the restoration measures. Lower hypolimnetic withdrawal rates seemed to favor the development of a diverse rotifer community. Conversely, qualitative changes in zooplankton structure and a zooplankton-based assessment of the lake trophic state indicated that water eutrophication was progressing. Despite modifications to the operation of the pipeline, no significant differences in rotifer abundance or biomass were detected between the sites in each year or among years at each site.

Keywords: lake restoration; rotifers; Lake Kortowskie

1. Introduction

Lake restoration aims to recreate, initiate, or accelerate the recovery of ecosystems that have been disturbed. Various physico-chemical and biological methods for lake restoration have been developed around the world [1-3]. One such treatment involves the withdrawal of hypolimnetic water enriched with nutrients and reduced substances [4]. This method was first applied more than 60 years ago, and it has been used since then at many sites globally [5,6]. Considerable research has been done into lake restoration. Numerous studies have focused on the influence of restoration measures on the physico-chemical parameters of water, water quality, macrophytes, and phytoplankton [7–10]. Changes in zooplankton communities were also investigated [11–13]. This group of organisms was examined in particular in biomanipulated lakes [14,15]. However, little attention has been focused on zooplankton communities in lakes restored with hypolimnetic withdrawal, and there is scant information on the long-term effects of hypolimnetic withdrawal on zooplankton communities [5]. The only data available are from Lake Kortowskie, which was the first water body in the world to have been restored with selective hypolimnetic withdrawal [4]. The lake has been studied for several decades, and this research has generated valuable data on the impact of restoration on the physico-chemical parameters of the lake water, the phytoplankton, the benthic fauna, and water quality [16–21] and also on the biocenosis and water quality of the recipient river into which the hypolimnetic water is discharged [22,23]. Although lake restoration has been conducted for more than 60 years, the zooplankton of Lake Kortowskie has been studied only sporadically. Zooplankton data were published



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Copyright: © 2021 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). more than 30 years ago, are difficult to access and do not account for current changes in the hydrological regime of Lake Kortowskie or for changes in hypolimnetic withdrawal rates through the pipeline. Zooplankton studies focused primarily on crustacean plankton and did not consider planktonic rotifers [24–26].

Zooplankton is a key component of aquatic ecosystems. Its abundance and functioning are linked with numerous environmental factors, including hydrological and hydrochemical conditions, food resources, predation, and macrophyte cover [27–31]. Zooplankton responses to changes in environmental conditions can identify both functional disruptions and the regeneration of aquatic ecosystems. Among the components of zooplankton communities, planktonic rotifers deserve special attention. Because of the wide range of rotifer species in freshwaters and their ability to adapt to changing environmental conditions, planktonic rotifers are highly useful indicators for evaluating changes in aquatic ecosystems. Analyses of the species composition and abundance of rotifer communities support assessments of the trophic state of lakes [32–34]. The advantage of rotifers over planktonic crustaceans in water quality assessments stems from the fact that there is little direct trophic pressure on them from ichthyofauna, which can modify the composition and abundance of zooplankton. Therefore, planktonic rotifers are reliable indicators for assessing ecosystem recovery.

The aim of this study was to analyze variations in the planktonic rotifer community in a lake subjected to selective hypolimnetic withdrawal. Specifically, the goals of this research included: (1) quantitatively and qualitatively analyzing the rotifer community; (2) determining whether rotifer abundance, biomass, taxonomic structure, and species diversity changed significantly in years when the intensity of hypolimnetic water withdrawal differed; (3) evaluating the trophic state of the lake based on rotifer indices and identifying changes among years. Analyses of variations in rotifer communities could be helpful in assessing the influence of long-term restoration on lake ecosystems. The results could be useful for managing water bodies that are restored with hypolimnetic withdrawal in other parts of the world.

2. Materials and Methods

The subject of this research was Lake Kortowskie, which is located in the city of Olsztyn in northeastern Poland (latitude—53°45′43″; longitude—20°26′42″). The lake has an elongated shape and an area of 89.7 ha. It has two basins: the northern basin with a maximum depth of 15.7 m, and the southern basin with a maximum depth of 17.2 m. The depth of the sill separating the two basins is 6.0 m [35]. Based on comprehensive studies conducted in 1952–1957, Lake Kortowskie was classified as a hypertrophic water body. Lake restoration began in 1956 by removing anoxic, nutrient-rich water from the hypolimnion and discharging it into a natural watercourse flowing out of the lake [4]. Hypolimnetic water is removed through a pipeline, the inlet of which is positioned in the deepest part of the southern basin (Figure 1).

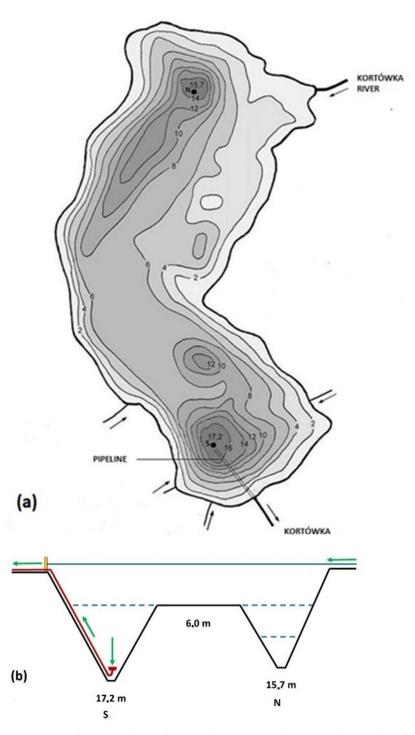


Figure 1. Study area and sampling site locations (S—the site in the southern basin of the lake, where the pipeline is located; N—the site in the northern basin of the lake) (**a**) and the cross section of Lake Kortowskie (**b**).

The amount of water flowing out of the lake is regulated by a weir located at the Kortówka River mouth, which is also where the pipeline outlet is located. The difference in the lake water surface level and the lower edge of the pipeline facilitated the process of syphoning and hypolimnetic water withdrawal. Initially, the pipeline was made of wood, and hypolimnetic water was discharged during the summer stagnation period at a rate of $180 \text{ L} \text{ s}^{-1}$. A fiberglass and polyester resin pipe was installed in 1976, and the hypolimnetic water withdrawal rate during the summer and winter stagnation periods was $250 \text{ L} \text{ s}^{-1}$. Between 1990 and 1994, the water withdrawal rate was limited to $50 \text{ L} \text{ s}^{-1}$. In the 1995–1998

period, the withdrawal rate was again at the maximum of 250 L s^{-1} , but it was decreased to 100 L s^{-1} between 1999 and 2001. Changes in the intensity of the water withdrawal rate beginning in 1990 stemmed from difficulties in maintaining the pipeline water flow at 250 L s^{-1} during the summer stagnation period because of the unfavorable hydrological balance in Lake Kortowskie. These changes were introduced to optimize the effects of restoration. Pipeline operation was halted in 2002 and 2003. In 2004, pipeline operation resumed at the beginning of summer stagnation at a flow rate of up to of 80 L s⁻¹, and, to date, hypolimnetic waters continue to be discharged into the Kortówka River at a similar rate during the summer stagnation period.

The rotifer community in Lake Kortowskie was studied in three periods of selective hypolimnetic withdrawal: in 1986 at the maximum withdrawal rate of 250 L s^{-1} ; in 2004 when pipeline operation was resumed at a maximum withdrawal rate of 80 L s⁻¹; and in 2013, when the maximum hypolimnetic water withdrawal rate was 80 L s⁻¹. The zooplankton study performed in 2004 aimed to illustrate the response of zooplankton to the resumption of the restoration process with reduced hypolimnion water withdrawal. The aim of the research conducted in 2013 was to identify temporal changes in zooplankton under conditions of long-term reduced hypolimnion water withdrawal. Unpublished rotifer data from 1986 were retrieved from the archives of the Department of Tourism, Recreation and Ecology, University of Warmia and Mazury in Olsztyn. In 2004 and 2013, zooplankton was sampled using the same methods as in 1986 to ensure reliable comparison of results. Zooplankton was collected from two sampling sites (Figure 1): the deepest point (17.2 m) in the southern basin of Lake Kortowskie from which hypolimnetic water is withdrawn (site S) and the deepest point (15.7 m) in the northern basin of the lake (site N). Samples were collected from both sites monthly from April to October from the water column from the lake surface to the bottom at 2 m intervals with a 5 L Patalas sampler. During sampling, water temperature was measured using a YSI 58 m. The total number of samples collected in each sampling period was 14. The samples collected were concentrated by sieving them through a 30 µm plankton net; then, they were preserved with Lugol's solution and fixed in a 4% formalin solution. Qualitative and quantitative analyses of rotifers were conducted using a Zeiss Axio Imager microscope (at a magnification of \times 400). Biomass was calculated based on standard wet weights [36]. The variability index (%) was calculated as the quotient of the standard deviation and the mean abundance or biomass. Five classes of variability were distinguished: low (0–20%), moderate (21–40%), high (41–100%), very high (101–150), and extremely high (>150%) [37]. The zooplankton dominance structure was determined according to Kasprzak and Niedbała [38]. The dominance index was based on zooplankton abundance and was divided into 5 classes: eudominants >10.0%; dominants 5.1-10.0%; subdominants 2.1–5.0%; recedents 1.1–2.0%; subrecedents \leq 1.0%. The Shannon-Wiener index (H) was calculated to evaluate zooplankton diversity [39]. Rotifer trophic state indices (TSI_{ROT}) were calculated to assess the trophic state of the lake [33] using additional zooplankton samples that were collected annually in August from the lake epilimnion, which was determined based on water column temperature. The following rotifer indices were analyzed: rotifer numbers (Nr); total rotifer community biomass (Br); the percentage of bacterivores in total rotifer numbers (Bac%); the ratio of biomass to numbers (B/N); the percentage of the *tecta* form in the population of *Keratella cochlearis* (Tecta%); and the contribution of species in the indicatory group numbers that indicate a high trophic state (Iht). TSI_{ROT} values below 45 indicate mesotrophic status; TSI_{ROT} values of 45–55 indicate meso-eutrophic status; TSI_{ROT} values of 55–65 indicate eutrophic status; and TSI_{ROT} values above 65 indicate hypertrophic status. The significance of differences in rotifer abundance, wet biomass, and diversity were tested with the Mann-Whitney U test (differences between sampling sites) and the Kruskal–Wallis test with post-hoc comparisons of ranks for all groups (differences among years). A proportion test was applied to determine the significance of differences among years in the proportions of individual species in the total rotifer community. All differences were significant at p < 0.05. Statistical analyses were performed with Statistica 13.0.

3. Results

At site S, the annual mean rotifer abundance increased from 418 indiv. L^{-1} (±687 SD) in 1986 to 499 indiv. L^{-1} (±312 SD) in 2013 (Figure 2). At site N, the highest abundance was noted in 1986 at 453 indiv. L^{-1} (±785 SD). In 2004, the mean rotifer abundance decreased to 264 indiv. L^{-1} (±314 SD), and then it increased to 390 indiv. L^{-1} (±250 SD) in 2013.

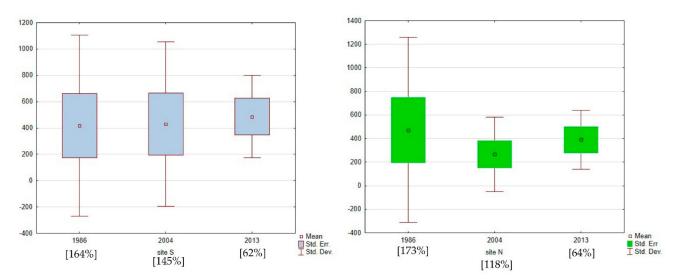


Figure 2. Temporal variability (mean values, standard error, standard deviation) of rotifer abundance [indiv. L^{-1}] at the sites in Lake Kortowskie; all differences were insignificant (p > 0.05). S–the site in the southern basin of the lake, where the pipeline is located; N–the site in the northern basin of the lake; [variability indices in parentheses].

The differences observed in mean rotifer abundance were insignificant among years at each site (p > 0.05; Kruskal–Wallis test) and between the sites in given years (p > 0.05; Mann–Whitney U test). The variability indices of rotifer abundance at both sites were extremely high in 1986, very high in 2004 and high in 2013.

The maximum mean rotifer wet biomass at site S was 0.89 (\pm 1.31 SD) mg L⁻¹ in 2004 (Figure 3).

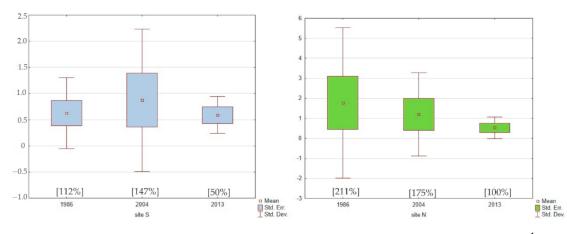


Figure 3. Temporal variability (mean values, standard error, standard deviation) of rotifer biomass $[mg L^{-1}]$ at the sites in Lake Kortowskie; all differences were insignificant (p > 0.05). S–the site in the southern basin of the lake, where the pipeline is located; N–the site in the northern basin of the lake; [variability indices in parentheses].

In the other two years, the mean biomass of the rotifer community was similar at approximately 0.6 mg L⁻¹ (±0.7 SD in 1986 and ± 0.3 SD in 2013). The mean biomass at site N decreased successively in subsequent years from 1.8 mg L⁻¹ (±3.8 SD) in 1986 to 0.5 (±0.5 SD) mg L⁻¹ in 2013. The differences in mean rotifer biomass were insignificant among

years at each site (p > 0.05; Kruskal–Wallis test). The differences in wet biomass between sites in given years were not significant (p > 0.05; Mann–Whitney U test). The variability indices of rotifer biomass were very high at site S and extremely high at site N in 1986, extremely high at both sites in 2004 and high at both sites in 2013.

Pooling zooplankton data from both sites, the mean rotifer abundance fluctuated from 347 (±482 SD) indiv. L⁻¹ in 2004 to 501 (±748 SD) indiv. L⁻¹ in 1986, while the mean rotifer biomass changed from 1.20 (±2.67 SD) mg L⁻¹ in 1986 to 0.61 (±0.43 SD) mg L⁻¹ in 2013 (Figure 4); however, the differences among the values calculated were statistically insignificant (p > 0.05; Kruskal–Wallis test).

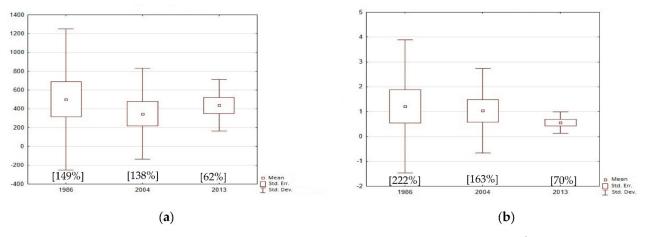


Figure 4. Variability (mean values, standard error, standard deviation) of the abundance [indiv. L^{-1}] (**a**) and biomass [mg l^{-1}] (**b**) of rotifers in Lake Kortowskie; all differences were insignificant (p > 0.05); [variability indices in parentheses].

Both for abundance and biomass, the variability index was the lowest in 2013. A total of 35 planktonic rotifer taxa were identified in Lake Kortowskie (Table 1). The overall, annual mean abundance (pooled zooplankton data from both sites were used) of the most important rotifer species in Lake Kortowskie (Figure 5) and their quantitative share in the community changed significantly in the different years of the study.

Table 1. Planktonic rotifer species (percentage of abundance) recorded at the sites in Lake Kortowskie (S-the site in the southern basin of the lake, where the pipeline is located, N-the site in the northern basin of the lake). The level of species dominance (D) is indicated as follows: *** eudominant; ** dominant; * subdominant.

Species	1986		2004		2013	
	S	Ν	S	Ν	S	Ν
Anuraeopsis fissa		9.2 **			1.7	0.1
Asplanchna priodonta	3.4 *	5.2 *	10.0 **	21.0 ***	1.3	1.7
Ascomorpha ecaudis	1.1	1.1			0.1	
Ascomorpha ovalis			1.6	1.2	2.8 *	1.0
Brachionus angularis	2.2 *	0.1	4.2 *	4.9 *	1.2	0.4
Brachionus calyciflorus	0.3	1.3	0.2	1.6	0.7	1.7
Brachionus urceolaris						1.4
Conochilus unicornis	1.9	4.4 *	1.1	0.1	0.3	0.5
Conochilus natans	0.1	0.2	0.9	0.3		

Species	1986		2004		2013	
	S	Ν	S	Ν	S	Ν
Filinia terminalis	1.1	0.8	1.8	1.9	0.1	0.7
Filinia longiseta f. limnetica	0.1	0.1				0.5
Filinia longiseta f. longiseta			1.8		0.1	0.5
Filinia longiseta f. passa				1.8		
Kellicottia longispina	5.0 *	1.9	9.4 **	17.4 ***	2.1 *	1.7
Keratella cochlearis	65.9 ***	61.7 ***	24.9 ***	21.3 ***	28.4 ***	25.6 ***
Keratella cochlearis f. tecta			0.6	0.3	4.8 *	9.4 **
Keratella quadrata Lecane closterocerca	4.9 *	4.5 *	4.7 *	4.9 *	5.0 *	4.2 * 0.1
Notholca acuminata	0.1	0.2				
Pompholyx complanata			1.8	1.6		
Pompholyx sulcata	2.3 *	1.7				
Polyarthra dolichoptera	2.6 *	1.2	22.2 ***	12.8 ***	13.1 ***	6.6 **
Polyarthra maior			1.8	1.1	2.4 *	2.2 *
Polyarthra vulgaris	1.6	1.1			0.7	0.9
Synchaeta kitina Synchaeta oblonga	4.1 *	4.3 *	2.0	1.8		14.1 ***
Synchaeta longipes					0.7	0.2
Synchaeta tremula	0.6	0.2				
Synchaeta pectinata	0.7	0.3	2.0	1.7	3.3 *	1.6
Trichocerca cylindrica					4.0 *	1.9
Trichocerca capucina	0.4	0.1	0.9	0.9	1.7	1.8
Trichocerca					0.1	0.7
dixon-nuttalli						
Trichocerca pusilla					11.2 ***	8.7 **
Trichocerca similis	1.0	0.3	5.9 **	5.3 **	13.9 ***	9.7 **
Trichocerca stylata	0.5	0.1			0.3	1.1

Table 1. Cont.

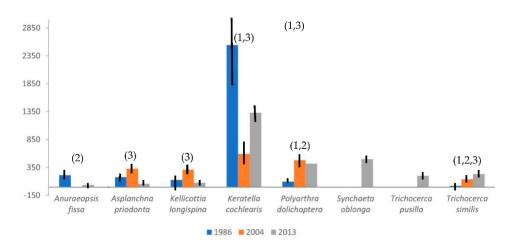


Figure 5. Variability (mean, standard deviation) of the abundance [indiv. L^{-1}] of dominant planktonic rotifer species in Lake Kortowskie. The significance of differences (p < 0.05) between years were indicated as follows: (1)–the difference between 1986/2004; (2)–the difference between 1986/2013; (3)–the difference between 2004/2013.

Pooling both sites, the annual mean abundance of Keratella cochlearis, the most abundant species in the lake studied, was the highest in 1986 at 2,542 indiv. L^{-1} (±687 SD) and the lowest in 2004 at 594 indiv. L^{-1} (±202 SD). In 2013, their annual mean abundance reached 1,333 indiv. L^{-1} (±170 SD). The values recorded in 1986 and 2013 were significantly higher (p < 0.05; Kruskal–Wallis test) than the mean abundance found in 2004. The percentage of *K. cochlearis* in the planktonic rotifer community also varied in the different years of the study and was estimated at approximately 60% in 1986, 20% in 2004, and more than 30% in 2013. In 2004, it was significantly lower (p < 0.001) than in 1986. Additionally, the proportion of the *tecta* form in the total abundance of the species K. *cochlearis* increased in 2013 from 2 to 22% in comparison with that in 2004. Unfortunately, incomplete data from 1986 on the abundance of the tecta form in the lake did not permit making further comparisons. The gradual increase of the importance of some species from the genus Trichocerca in Lake Kortowskie was noteworthy. In comparison with 1986, the annual mean abundance of *Trichocerca similis* increased reaching nearly 250 indiv. L^{-1} $(\pm 102 \text{ SD})$ in 2013. The values noted in the three years of the study differed significantly (p < 0.05; Kruskal–Wallis test). The share of this species in 2013 was 5% of the community, which was significantly higher (p < 0.001) than that in 1986 (0.5%). In 2013, Trichocerca *pusilla* was identified in the community at the annual mean abundance of 203 indiv. L^{-1} $(\pm 108 \text{ SD})$. The annual mean abundance of *Polyarthra dolichoptera* also increased throughout the study from approximately 100 (\pm 98 SD) to nearly 500 indiv. L⁻¹ (\pm 183 SD). The abundance of this species was significantly lower (p < 0.05; Kruskal–Wallis test) in 1986 than in 2004 or 2013, as was the percentage of *P. dolichoptera* in the community (p < 0.001), which increased from 2% in 1986 to nearly 20% in 2004, and 10% in 2013. A significant decrease (p < 0.05; Kruskal–Wallis test) was noted in the annual mean abundance of *Asplanchna* priodonta in 2013 in comparison to that in 1986 and 2004, and the percentage of this species in the community was significantly lower (p < 0.001) in 2013 (1%) than in 1986 (7%) and 2004 (10%).

The rotifer community species structure varied throughout the study period. Certain differences were also observed between the sites (Table 1).

In 1986, *K. cochlearis* was the eudominant species at both sites. The dominant species *Anuraeopsis fissa* was identified only at site N. In 2004, the eudominant zooplankton species were *K. cochlearis*, *P. dolichoptera*, *A. priodonta*, and *Kellicottia longispina*. The latter two species were eudominant only at site N, while they occurred as the dominant species at site S. *Trichocerca similis* was also a dominant species at both sampling sites. In 2013, *K. cochlearis* was again the eudominant at both sampling sites. The more abundant occurrence of the *tecta* form of *K. cochlearis*, as compared to that in 2004, was noteworthy, and it was a dominant species at site N. In turn, *T. similis*, *T. pusilla*, and *P. dolichoptera* were eudominant at site S and dominant at site N. Exceptionally, *Synchaeta oblonga* was noted in high abundance at the site N, where it was a eudominant species.

In 1986, 21 species were noted at site S and 22 species at site N, while in 2004 19 species were noted at each site, and in 2013 24 and 26 species were noted at the two sites, respectively (Table 1). Throughout the study period, the Shannon–Wiener index (H) based on rotifer abundance increased in Lake Kortowskie (Figure 6).

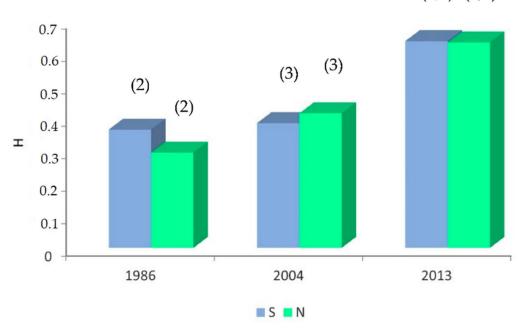


Figure 6. Temporal variability of the Shannon–Wiener index (H) based on rotifer abundance in Lake Kortowskie (S–the site in the southern basin of the lake, where the pipeline is located; N–the site in the northern basin of the lake). The significance of differences (p < 0.05) between years were indicated as follows: (2)–the difference between 1986/2013; (3)–the difference between 2004/2013. The differences between sites in the years analyzed were insignificant (p > 0.05).

In 1986, the H index was 0.36 at site S and 0.29 at site N, while these values in 2004 were 0.38 and 0.41, and in 2013 they were 0.64 and 0.63. The H index noted in the last year of the study was significantly higher (p < 0.05; Kruskal–Wallis test) than in the previous years. No significant differences were noted in the Shannon–Wiener index between the sites in given years (p > 0.05; Mann–Whitney U test).

Data on rotifer abundance and species composition were used to calculate rotifer indices and determine the trophic state of the lake (Table 2).

Table 2. Values of rotifer trophic state indices calculated with data from subsequent years of research (S-the site in the southern basin of the lake, where the pipeline is located; N-the site in the northern basin of the lake). Rotifer trophic state indices were based on rotifer numbers (Nr), total rotifer community biomass (Br), percentage of bacterivores in total rotifer numbers (Bac%), the ratio of biomass to numbers (B/N), the percentage of the *tecta* form in the population of *Keratella cochlearis* (Tecta%), and the contribution of species in the indicatory group numbers that indicate a high trophic state (Iht).

Vaar	Cite	Rotifer Trophic State Indices						
Year	Site	Site Nr Br B/N Bac% Tect	Tecta%	Iht	Mean TSI _{ROT}			
1986 S N	S	53	61	33	63	58	-	53.6
	57	72	23	61	59	-	54.4	
2004 S N	54	58	42	45	50	-	49.8	
	52	53	51	48	51	-	51.0	
2013 S N	S	55	59	43	59	62	55	55.5
	Ν	54	55	51	59	60	56	55.8

(2,3) (2,3)

The mean values of rotifer trophic state indices calculated in 1986 and 2004 indicated that the lake was meso-eutrophic, while the mean index calculated in 2013 indicated it was eutrophic. Remarkably, the values of individual rotifer indicators calculated in 2013 showed little variation and almost all of them indicated that the sites studied were eutrophic. The exception was the ratio of planktonic rotifer biomass to number (B/N), which indicated that site S was mesotrophic, while site N was meso-eutrophic.

The rotifer indices calculated using the data from 2004 also indicated little variation. Most of these indices were indicative of a meso-eutrophic state, with the exception of the index based on rotifer biomass (Br) at site S, which was indicative of a eutrophic state, and the index based on the ratio of rotifer biomass to rotifer numbers (B/N), which was indicative of the lower mesotrophic state at site S. The greatest rotifer index variation was noted in the data from 1986. The indices based on the percentage of bacterivores in the rotifer community (Bac%) and the percentage of the *tecta* form in the population of *K. cochlearis* (Tecta%) were indicative of a eutrophic state at site S and a hypertrophic state at site N. Based on rotifer numbers (Nr), site S was classified as meso-eutrophic, and site N was classified as eutrophic. The index based on the ratio of planktonic rotifer community biomass to their numbers (B/N) was indicative of a mesotrophic state at site S.

Bottom water temperature was high in 1986, when the mean temperature reached 10.7 °C at site S and 8.8 °C at site N (Table 3). The bottom water temperature was lower at 7.9 and 7.2 (sites S and N, respectively) in 2004 and at 6.9 °C and 6.5 °C (sites S and N, respectively) in 2013. At the peak of summer stagnation (August) the water temperature near the bottom was also higher in 1986 than in 2004 and 2013.

Year	Site	Water Temperatu Bott	Water Temperature (°C) Near the Bottom	
		Mean	SD	in August
1007	S	10.7 *	2.9	13.0 **
1986	Ν	8.8 *	1.0	-
2004	S	7.9	1.6	7.1
	Ν	7.2	0.7	6.9
2013	S	6.9	0.7	6.9
	Ν	6.5	0.2	6.5

Table 3. Changes in water temperature in the years analyzed (May-October and during the stagnation peak). The data for 1986 were from Dunalska et al.* [20] and Lossow et al. ** [40]; S–the site in the southern basin of the lake, where the pipeline is located; N–the site in the northern basin of the lake.

4. Discussion

No significant differences in mean rotifer abundance or biomass were noted between the sites in the different years of the study. This means that regardless of the intensity of pipeline operation, discharging hypolimnion water from the deepest part of the southern basin did not affect local conditions, but had an impact on the entire lake ecosystem. This observation is consistent with the results of previous studies of the biocenosis of this lake [18,24,26]. The lack of significant temporal changes in rotifer abundance and biomass in Lake Kortowskie permitted concluding that this group was in a stable phase following fundamental restoration. The annual mean rotifer abundance ranged throughout the study period from 347 to 501 indiv. L^{-1} . The planktonic rotifer abundance values noted in Lake Kortowskie were similar to those observed in other lakes where restoration was conducted using various methods [11,12].

Very high to extremely high variability of rotifer abundance and biomass was found in 1986 and 2004. This indicated that the biocenosis was more destabilized in these years. A higher withdrawal rate may cause periodical decreases in zooplankton abundance and biomass. The scope of the pipeline is to drain bottom waters and higher water layers and to discharge them outside the lake ecosystem into the recipient river. Living organisms are discharged along with the water. Widuto [24] observed decreased zooplankton abundance during summer stagnation at site S and the disappearance of zooplankton from the bottom waters at a water withdrawal rate of 180 L^{-1} . Waligóra [41] estimated that in 1986 the total rotifer biomass withdrawn through the pipeline was 380 kg annually. All of the above might explain the considerable rotifer variability in 1986. Seasonal variations in occurrence of A. priodonta also affected zooplankton biomass in 1986 and 2004. At lower withdrawal rates, increase in zooplankton abundance is expected because of reduced zooplankton removal by the pipeline and improved environmental conditions. An indirect effect of hypolimnetic withdrawal is an increased zooplankton vertical range of occurrence because oxygen conditions are improved in deeper water layers at site S [26]. The removal of hypolimnetic waters increases the depth of higher strata that are well-oxygenated. Besides, at lower withdrawal rates, there was found to be slower oxygen depletion in the upper hypolimnion at the start of summer stagnation [20]. In 2004 and 2013, the rate of hypolimnion waters removal was the same, but in 2004 rotifer variability was higher, probably because of pipeline operation resumption and biocenosis destabilization. Further studies are needed to assess the effect of seasonal fluctuations in pipeline operation and the effects of these fluctuations on temporary environmental conditions and the vertical distribution of zooplankton.

Much about the impact of restoration on zooplankton could be determined by comparing the pre-restoration zooplankton data with results obtained in subsequent years of research. Unfortunately, the only data available from the pre-restoration period are unreliable. A quantitative study of zooplankton was performed with a 100 μ m plankton net [42], which did not retain smaller rotifer species. The results of this study estimated the abundance of planktonic rotifers at similar values to those noted in the years included in the present study. However, because the selectivity of the plankton net used at that time was lower, presumably the actual abundance of planktonic rotifers in the period prior to restoration was substantially higher compared to the values recorded in later years.

In Lake Kortowskie, some differences among years were observed in both the domination structure and mean abundance of the most important rotifer species. *Keratella cochlearis* was the main component of the planktonic rotifer community. In subsequent years, a successive decrease in the percentage share of this species in overall rotifer abundance and in the mean abundance of *K. cochlearis* was noted in the lake. Simultaneously, data from 2004 and 2013 indicated a significant increase in the numerical share of the *tecta* form of this species in its overall abundance. *Keratella cochlearis* is a cosmopolitan, eurytopic species [43] that occurs commonly in various types of lakes, including in the northern hemisphere both in America [44] and in Europe [45–47]. *Keratella cochlearis* exhibits a strong dependence on phosphorous availability [27]. The *tecta* form of this species is also found in nearly all areas globally [43]. According to Tausz et al. [44], *K. c. f. tecta* exhibits a high affinity with eutrophic indicator variables including turbidity, total nitrogen, total phosphorus, and chlorophyll-*a*. The co-occurrence of *K. cochlearis* and the *tecta* form was evidence that the lake was eutrophic, while the increasing share of the *tecta* form indicated that the water quality in Lake Kortowskie was deteriorating.

In 2004, the mean *K. cochlearis* abundance in Lake Kortowskie was significantly lower than in 1989 and 2013, while, simultaneously, *P. dolichoptera*, *K. longispina*, and *A. priodonta* increased in abundance. This indicated a temporary improvement in water quality in 2004. This was the year that followed the years when the pipeline was not in operation. Water quality assessment conducted in 2003 indicated highly advanced eutrophication as was confirmed by, inter alia, excessive oxygenation of the upper water layers, complete oxygen depletion at depths as shallow as 6m, and high concentrations of chlorophyll *a* in surface water layers [40]. The pipeline was put back into operation in 2004, which could have caused significant changes in the biocenosis. It seems that the effects of resuming pipeline operation could be compared to those that occur in lakes at the initial stages of restoration. As Nürnberg [5] demonstrated, the results of restoration through hypolimnetic withdrawal are most apparent in the first years following the initiation of

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the treatment, when water quality improves. One indication of positive changes after the resumption of restoration in Lake Kortowskie could have been the decrease in 2004 in the abundance of *K. cochlearis*, which exhibits high affinity to water phosphorus compound content. Moreover, decreases in the mean abundance of *K. cochlearis* or *A. fissa*, which are species considered to be detritophages [48], were accompanied in this year by increases in the mean abundance of *P. dolichoptera* and of *K. longispina*, which are phytophages [48]. These changes in the quantitative ratios of the zooplankton structure indicated the positive reaction of the biocenosis to the resumption of pipeline operation. Food resources available to zooplankton undergo qualitative changes in composition as the trophic state changes. During progressing eutrophication, bacterial production increases in response to nutrient availability, while the availability of edible phytoplankton decreases [49,50]. Restoration measures can cause the opposite situation. Krienitz et al. [51] reported an increased share of edible phytoplankton species in the total phytoplankton as a result of restoration. In zooplankton communities, an increase in the share of phytophages can then be expected, as was observed in the planktonic rotifer community in Lake Kortowskie in 2004.

Over the years studied, a successive increase in rotifer species diversity was observed. In 2013, the Shannon–Wiener species diversity index was significantly higher than in previous years. This change could have resulted from the effects of restoration, i.e., increased temperatures in deeper water layers and the range of oxygen content in the water column, and changes in the water withdrawal rate through the pipeline. Increased water temperature was noted in 1986, when the water withdrawal rate was maximal. The bottom water temperature decreased in 2004 and 2013, when the water withdrawal rate was three times lower. At higher withdrawal rates, the temperature of the hypolimnion in Lake Kortowskie increased substantially, which caused increased bottom sediment oxygen consumption, and, consequently, oxygen depletion. Lower withdrawal rates permitted achieving a more balanced increase in temperature and an increased range of the occurrence of oxygen [20,52]. Moderately increasing deeper water layer temperatures and improving oxygenation facilitate the expansion of the zone with favorable conditions for zooplankton development. This can also lead to a reduction in the level of competition for resources and, consequently, increased species diversity in the biocenosis. Additionally, lower withdrawal rates limit the suctioning out of individuals from the ecosystem. This could explain the significant increase in species diversity recorded in 2013, when the water withdrawal rate through the pipeline was three times lower than in 1986. This effect might not have been apparent in 2004, when pipeline operation was resumed following its shutdown, because increased zooplankton diversity is not achieved in lakes during the initial restoration period, but it is noted later [53]. One of the limitations in estimating the effect of hypolimnion water withdrawal on rotifer diversity in the present study is the lack of the assessment of other factors that could have affected species diversity. Unfortunately, archival physicochemical data for 1986 are not available. Therefore, we emphasize the need for further research to evaluate this effect. The significant increase in zooplankton species diversity in Lake Kortowskie should be viewed unambiguously as a positive, long-term effect of the restoration conducted. This effect is desirable and is reported for lakes in which restoration has been successful regardless of the water restoration method applied [12,13,53].

The trophic state assessment of Lake Kortowskie based on zooplankton indicated progressive eutrophication. The lake was meso-eutrophic in 1986 and 2004 and eutrophic in 2013. The results we obtained corresponded well with changes in physico-chemical and biological parameters in Lake Kortowskie observed over the years by other researchers. Based on the physico-chemical properties of lake water in 1986, Lossow et al. [40] determined the lake condition to be moderately eutrophic. However, from the mid-1990s, the lake entered an advanced eutrophic state. Phytoplankton study also indicated deteriorating water quality. In the 1987–1990 period, cyanobacteria dominance increased in lake waters while studies from 1999–2000 showed increased total phytoplankton biomass [54]. Ecological status assessments of Lake Kortowskie based on phytoplankton indicated poor water quality in 1987–1990 and bad water quality in 1999 and 2011 [21].

The deteriorating water quality in Lake Kortowskie is the result of the disadvantageous hydrological balance of the lake that stems from the limited, variable water inflow from the Kortówka River (primary tributary) [40]. When the pipeline is operating passively, water withdrawal is limited. Currently, it is only periodically possible for the pipeline to operate at the maximum withdrawal rate of 80 L s⁻¹ [22]. However, with recently observed climate change and resulting increased rainstorms, it is predicted that the efficiency of hypolimnetic withdrawal in Lake Kortowskie will improve [55]. Torrential rains occur in summer, which is when the pipeline is in operation. This should facilitate maintenance of a sufficient level of efficient pipeline operation. Simultaneously, a sufficient level does not necessarily mean high efficiency, which can also be disadvantageous. Studies of lakes restored with this method indicate that if hypolimnetic withdrawal is too vigorous, the temperature rises and light conditions in the deeper water layers improve, which also improves conditions for phytoplankton development. This, in turn, can lead to algal blooms and deteriorating lake water quality. Moreover, intense hypolimnetic discharge leads to the risk of premature destratification and the shortening of the time in which nutrients are exported from the hypolimnion, which also affects lake water quality negatively [5]. Global climate change and its effects, including projected water level fluctuations in lakes, should prompt us to reconsider water body management with a particular focus on restored lakes [56]. The impact of climate change on the effects of lake restoration with passive hypolimnetic withdrawal is an issue that currently requires much more detailed research.

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