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Research article

Long-term study of the effects of river inflow on oxygen stratification and its consequences for selected abiotic and biotic factors in a deep reservoir

Ewa Szarek-Gwiazda *, Agnieszka Pociecha, Elżbieta Wilk-Woźniak

Institute of Nature Conservation, Polish Academy of Sciences, Adama Mickiewicza 33, 31-120, Krakow, Poland

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A B S T R A C T

One of the effects of climate change is an increase in extreme weather events, leading to more frequent droughts and floods, which alter river flow patterns and affect the distribution of dissolved oxygen (DO) in downstream reservoirs. Dissolved oxygen is crucial for biogeochemical cycles and aquatic communities. We investigated how fluctuations in river inflow and water exchange affect oxygen stratification in a submountain dam reservoir. We also assessed these effects on pH, changes in nutrients, chlorophyll *a*, and zooplankton density and composition. We analysed long-term (1994–2017) monitoring data from the deep Dobczyce Reservoir (southern Poland). We grouped the years in terms of DO concentrations in the metalimnion and hypolimnion. The results showed that the duration of oxygen stratification depends on the magnitude and timing of high inflows. Years with low summer inflows and limited mixing resulted in prolonged stratification lasting 3–4 months, with hypoxic conditions covering up to 83 % of the meta- and hypolimnion. Years with floods in May or September shortened stratification. In years with large summer inflows, oxygen stratification was strongly disturbed or not developed. In addition, years with high summer inflows showed higher concentrations of nutrients and chlorophyll *a* and greater zooplankton density dominated by opportunistic r-strategists (*Polyarthra vulgaris* and *Bosmina longirostris*). Water exchange rates were not accurate indicators of oxygen conditions. Thus, river flow variability plays a crucial role in shaping oxygen distribution, water quality and food web structure in deep submountain reservoirs.

1. Introduction

Dam reservoirs play an important role in the control and management of water resources. They serve many purposes, such as mitigating floods, securing water supplies, providing hydropower and many others. However, they also have negative impacts on the environment, e.g. dams disrupt the ecological connectivity of rivers, and water storage in artificial reservoirs affects the quantity, quality and timing of downstream flows (Lehner et al., 2011; Winton et al., 2019).

Global climate change is causing changes in precipitation, rising surface temperatures, more frequent floods and droughts, ice melt and reduced snow cover (IPCC, 2012; Nazari-Sharabian et al., 2018). These extreme weather events are expected to alter river flow patterns and impact downstream water infrastructure (Ehsani et al., 2017; Hayes et al., 2017). More frequent floods and droughts have a significant impact on reservoir ecosystems, especially on the change in thermal stratification (Wilk-Woźniak et al., 2021), which affects the distribution of Dissolved Oxygen (DO) in the water. DO is a crucial component of aquatic ecosystems that influences biota and biogeochemical processes (Davis, 1975). Its concentration in lakes and reservoirs depends on atmospheric diffusion, photosynthesis, respiration, decomposition of organic matter and chemical processes (Boehrer and Schultze, 2008; Detmer et al., 2022). In deep lakes and reservoirs, oxygen stratification is linked to thermal stratification and eutrophication (Boehrer and Schultze, 2008; Elçi, 2008; Zhang et al., 2015; Nazari-Sharabian et al., 2018). Thermal stratification creates a stable layer that limits mixing between surface and deep water. The deep hypolimnion becomes isolated and oxygen-depleted due to microbial respiration and the decomposition of organic matter (Boehrer and Schultze, 2008; Marcé and Armengol, 2010; Detmer et al., 2022). Higher water temperatures favour these processes and extend the periods of stratification (Wilk-Woźniak et al., 2021; Yaghouti et al., 2023). As a result, oxygen depletion in the deep-waters is increasingly observed worldwide as a direct consequence of climate change (Yaghouti et al., 2023; Woolway et al., 2021).

The pattern of oxygen stratification in dam reservoirs is influenced

* Corresponding author.
E-mail addresses: szarek@iop.krakow.pl (E. Szarek-Gwiazda), pociecha@iop.krakow.pl (A. Pociecha), wilk@iop.krakow.pl (E. Wilk-Woźniak).

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among other by size and morphometry (Detmer et al., 2022), climatic conditions (such as air temperature, wind, mixing) and hydrological variables (Elçi, 2008; Marcé and Armengol, 2010; Marcé et al., 2010; Zhang et al., 2015). Low inflows of the supporting river (summer droughts) lead to longer water residence times and more stable stratification (Darko et al., 2019). In contrast, high flow events can partially or completely disrupt stratification and markedly improve oxygen conditions in deep water (Szarek-Gwiazda et al., 2009; Marcé and Armengol, 2010; Marcé et al., 2010).

Climate change can intensify the eutrophication process through interactions between meteorological factors and nutrient availability (Whitehead et al., 2009) and increase the vulnerability of ecosystems (Dokulil and Teubner, 2011; Ostad-Ali-Askar et al., 2018), especially in agricultural areas with changing precipitation patterns (Dumitran et al., 2020). Hypoxia caused by stratification increases internal nutrient loading (Defeo et al., 2024). High runoff leaches nutrients from catchments (Banaduc et al., 2020; Dumitran et al., 2020).

Aquatic organisms are sensitive to conditions caused by stratification. Phytoplankton communities usually thrive in the warm epilimnion in summer when stratification is present. In eutrophic waters, summer phytoplankton consists of green algae and/or cyanobacteria (Wilk-Woźniak, 2009). Under mixed conditions or with strong currents, however, diatoms or chrysophytes grow rapidly. These groups benefit from the nutrient input and turbulent mixing (Wilk-Woźniak, 2009). Directly related to phytoplankton is the group of planktonic animals (zooplankton). Zooplankton reacts to changes in phytoplankton and to the stability or disturbance of the water, which is reflected in the dynamics, distribution, timing of life cycle events, abundance and community structure of zooplankton (Szarek-Gwiazda and Pociecha, 2024).

Adequate oxygen levels are essential for aquatic life, including fish, macroinvertebrates and zooplankton. Hypoxia causes stress, alters behaviour, inhibits feeding and growth and increases fish mortality (Doudoroff and Shumway, 1970; Bulbul Ali and Mishra, 2022). Well-oxygenated water supports the growth and reproduction of zooplankton (Banerjee et al., 2019; Karpowicz et al., 2020), although some species tolerate low oxygen concentrations relatively well (Karpowicz et al., 2020). Severe oxygen deficiency shifts zooplankton communities from large to small species and reduces biomass in anaerobic layers (Karpowicz et al., 2020). Sensitivity to low oxygen concentration varies between zooplankton species (Karpowicz et al., 2020) and fish (Doudoroff and Shumway, 1970; Bulbul Ali and Mishra, 2022).

Given these complex interactions, it is important to understand how river flow variability influenced by climate change affects oxygen stratification and the fundamental trophic level of plankton communities. Although numerous studies have examined either climate-induced thermal changes or the downstream effects of dams on rivers, relatively few have linked the hydrological aspect to the oxygen dynamics of reservoirs (Marcé and Armengol, 2010; Marcé et al., 2010).

Mountain and submountain reservoirs, which are characterised by highly fluctuating water discharges and great ecological and economic importance, provide an ideal setting for studying these effects. The rivers in the Carpathian region in southern Poland have a spring-summer flow regime (Materek, 2000; Pociask-Karteczka et al., 2003), but since 2000 climate change has led to more frequent extreme and irregular hydrological events, including prolonged droughts and intense rainfall, which alter river flows (Wilk-Woźniak et al., 2021). The changes in climate and river flows are expected to have a significant impact on the oxygen regime in the reservoirs of the mountain and submountain dam reservoirs, potentially affecting their function.

The aim of the study was to: (1) evaluate the effects of timing and magnitude of river inflow and water exchange rate on oxygen stratification in a submountain dam reservoir and (2) determine how these factors influence abiotic parameters (pH, nitrates NO_3^-, and total phosphorus P_{tot}) and biological indicators (phytoplankton activity via chlorophyll *a*, zooplankton density and dominant taxa). Nitrates and P_{tot} are of crucial importance for phytoplankton development. Their major source in Carpathian rivers is diffuse pollution, particularly leaching from soil during prolonged rainfall.

We hypothesis that drought (low river inflow) leads to stronger, longer-lasting stratification and severe hypolimnic oxygen depletion, along with internal nutrient loading and stress for aquatic organisms. Conversely, the timing and magnitude of high river inflow combined with higher water exchange rate, influence oxygen stratification patterns and help prevent extreme anoxia. High inflows also cause changes in nutrient concentrations and plankton growth. By analysing long-term data (1994–2017) and extreme events, we aim to clarify how climate-driven hydrology affects reservoir ecosystems. This knowledge is crucial for developing water management strategies in dam reservoirs to maintain water quality and ecological balance under changing climate conditions.

2. Materials and methods

2.1. Study area

The study was conducted in the Dobczyce dam reservoir (49° 52′ N, 20° 02′ E), a stratified submountain reservoir on the Raba River (southern Poland). It was formed by a dam built in 1986–1987. It primarily supplies Kraków (the second largest city in Poland) with drinking water. The catchment area of the River Raba above the reservoir covers an area of around 768 km^2, with mixed forested uplands and agricultural land. The Raba River contributes 88.6 % of the reservoir's inflow (Mazurkiewicz-Boroń, 2002; Wilk-Woźniak et al., 2021). It has a typical hydrological regime of the Carpathians, with high discharges due to snowmelt and rainfall in late spring and summer (Materek, 2000). At normal dam level (269.9 m asl), the reservoir covers 928 ha, holds 99.2 million m^3 of water, had an average depth of 11 m and a maximum depth of 27 m. Water exchange takes place on average three times a year, but varies from weeks during floods to more than six months during droughts (Amirowicz, 1998; Mazurkiewicz-Boroń, 2002; Szarek-Gwiazda et al., 2009). Morphologically, it consists of three parts: the Myślenicki Basin (56 %), the deep Dobczycki Basin near the dam (39 %), whose functioning is most similar to that of a lake, and the Wolnica Bay (5 %) with pond-like features (Godlewska et al., 2003). The Dobczycki Basin is dimictic, stratified in summer and is usually mixed twice a year in spring and autumn. The reservoir is categorized as meso-eutrophic and submontane (Wilk-Woźniak et al., 2009).

2.2. Methods

Data on the daily water inflow to the reservoir and the reservoir level on a given day from 1994 to 2017 (with the exception of 1999 and 2004) were provided by the Regional Water Management Authority in Kraków, Poland. Flow was defined as the volume of water passing through a specific cross-section of a watercourse per unit time, expressed in m^3/s. The water exchange rate was understood as the volume of annual water inflow, based on daily water inflow, into the reservoir divided by the average annual reservoir volume. The volume of the Dobczyce Reservoir was calculated using the method described by Amirowicz (1998). Data on physico-chemical and biological parameters were obtained from a monitoring programme carried out in the Dobczyce Reservoir from 1994 to 2017. The monitoring was conducted by the Freshwater Department of the Polish Academy of Sciences, which has been part of the Institute of Nature Conservation of the Polish Academy of Sciences since 2004. The authors participated in this programme. Samples were taken monthly from April to October in the central deep point of the reservoir (Fig. 1) at the following depths: 0, 2.5, 5, 7.5, 10, 12.5, 15, 20 m and 0.5 m above the bottom. In this study, the depths of 0–5 m were considered as epilimnion, 7.5–10 m as metalimnion and the layers ≥12.5 m to the bottom as hypolimnion. The study covered 21 years, excluding 1999, 2004 and 2005 due to missing data of the river flow or DO. Parameters

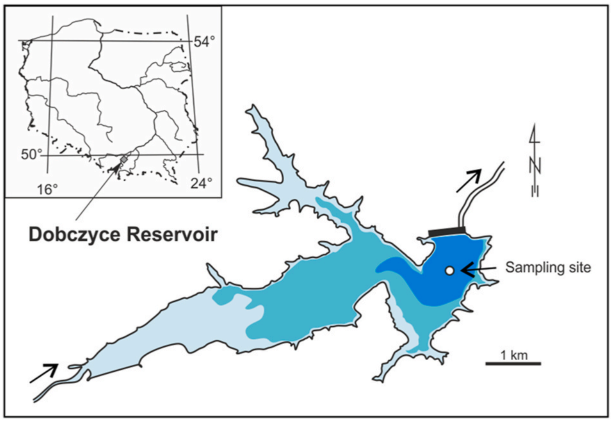

Fig. 1. Map of the Dobczyce reservoir and location of the sampling site.

analysed included: dissolved oxygen (DO), pH, nutrients (nitrates NO_3^-, total phosphorus P_{tot}), chlorophyll *a* and zooplankton density. Some data are missing for pH (October 2001), DO (April 2017), P_{tot} (1994–1996, 2000, September 2009, May 2013, 2014–2017) and chlorophyll *a* (May, September, October 2011, May 2015 and 2017).

For the analyses, we have chosen dissolved oxygen (DO) and pH, as they may determine the availability of nutrients (and other substances) and also affect the behaviour and physiology of living organisms. Nutrients were chosen because they are crucial for water eutrophication and fundamental to the development of primary producers. Among biotic parameters, primary producers (chlorophyll *a*) were chosen because they directly respond to the aforementioned abiotic factors and are essential for the life and development of other organisms. Zooplankton was selected due to its direct dependence on phytoplankton and the studied abiotic parameters (DO and pH). As a food source for fish, zooplankton is a very important part of the aquatic ecosystem.

The water pH value was measured in situ until 2005 using an Orion pH metre (Expandable Ion Analyser EA 940) and from 2005 using a WTW aparatus. Dissolved oxygen was determined using the Winkler method (APHA, 1992). Nitrates were analysed until 2005 using the hydrazine reduction method and since 2005 by ion chromatography (DIONEX ICS 1000 and IC DX 320, Dionex Corporation, Sunnyvale, USA) after filtration of the water samples through pore-sized syringe filters (Ministart RC 25, Sartorius Stedim Biotech GmbH, Germany). Comparative studies of these two methods showed negligible differences. Total phosphorus (P_{tot}) was analysed after mineralisation using the molybdenum blue method (APHA, 1992). Chlorophyll *a* was analysed using the ethanol method (Nusch, 1980).

The zooplankton samples for the taxonomic and quantitative analyses was collected at the same sampling site and time as water for the physico-chemical parameters and chlorophyll *a*. They were taken from three water layers: epilimnion, metalimnion and hypolimnion (up to a depth of 20 m) using a 5 L sampler. The total volume of samples at each depth was 15 L. Samples were concentrated using a plankton net (#50 μm) and treated with a 4 % formalin solution, after which subsamples were analysed under a microscope (magnification 40-400 ×) in 0.5 mL chambers. Taxonomic and numerical analyses of zooplankton were performed according to Starmach (1955), Hillbricht-Ilkowska and Patalas (1967), Szarek-Gwiazda and Pociecha (2024). The density of zooplankton was calculated using multiple counts (5 subsamples) and converted to ind/L.

2.3. Statistics

The relationship between water exchange rate and DO concentration was calculated using Spearman's correlation coefficient. Non-parametric statistical methods were used in the study, as the Kolmogorov-Smirnov and Lilliefors tests confirmed non-normal distributions of the analysed parameters. For the meta- and hypolimnion from June to September (stratification period), we calculated the percentage of waters with DO concentrations: a) < 4 mg/L, b) 4–6 mg/L, c) 6–8 mg/L, d) > 8 mg/L. DO concentrations below 6 mg/L indicate hypoxic waters, while those below 4 mg/L indicate strongly hypoxic waters. These percentages provided insights into the overall distribution of oxygen concentrations during the stratification period. They were used to identify the years with similar DO concentrations through hierarchical cluster analysis. Euclidean distance and association within a group were used as clustering methods. Based on the obtained dendrogram of similarities, different year were categorized to groups. The differences in the values of the studied parameters (water exchange rate, pH, DO, NO_3^-, P_{tot}, chl *a*, zooplankton density - total and dominant taxa) between the groups obtained from the dendrogram of similarities were calculated using non-parametric Mann-Whitney U-tests. All statistical analyses were performed using STATISTICA (version 13.1).

3. Results

3.1. DO concentration

In April, May and October, the water was generally well oxygenated (median 9 mg/L) throughout the entire water column (Table S1, Fig. 2). Oxygen stratification was usually present from June to September. The epilimnion (0–5 m) remained well oxygenated throughout this period, with DO concentrations only occasionally falling below 5 mg DO/L at 5 m depth (August or September 1994, 2007, 2014, 2017). In contrast, the oxygenation of the meta- and hypolimnion varied from year to year. Hypoxic waters (<6 mg DO/L) accounted for 15–83 % and strongly hypoxic waters (<4 mg DO/L) for 5–67 % of meta- and hypolimnion (Fig. 2 – more detailed description below).

3.2. Oxygen stratification period (June–September)

3.2.1. DO and flow

To identify years with similar DO concentrations in the meta- and hypolimnion, we focused on the months June–September, when oxygen stratification typically occurs in the reservoir. In the hierarchical cluster analysis, five clusters of years were distinguished and the year 2010 was identified as an outlier due to its different DO patterns (Fig. 3). The proportion of strongly hypoxic waters (<4 mg DO/L) in the meta- and hypolimnion decrease between clusters in the following order: cluster 3 (63–67 %) > cluster 1 (50–58 %) > cluster 2 (39–50 %) > clusters 4, 6 (29–33 %) > cluster 5 (5–12 %) (Fig. 4). This was largely dependent on the magnitude and timing of the high flow. These clusters were grouped based on the long-term (1994–2017) median DO concentration (4.6 mg/L) in the meta- and hypolimnion as follows:

- **Group A** (clusters 3 and 1) – low median DO (below the long-term median). Strong oxygen stratification lasted 3–4 months (Table 1, Fig. 2). Hypoxic water (<6 mg DO/L: cluster 3, 75–83 %; cluster 1, 63–83 %) usually reached a depth of 7.5 m (occasionally 5 m), while strongly hypoxic water extended to 10 m (Fig. 2). The largest proportion of strongly hypoxic waters was found in cluster 3. Mean annual river inflows were usually low (Table 1). The exception was 2017 (11.8 m^3/s) due to high flow in September (Fig. 2). However, samples were collected before this event, so it was not reflected in the DO concentration. River flows above 50 m^3/s usually occurred in spring. Summer flows were usually low (mean 2.9 m^3/s), only sporadically exceeding 50 m^3/s, and had little effect on oxygen stratification (Table 1, Fig. 2).
- **Group B** (cluster 2) – average median DO (close to the long-term median). These years had average or high mean annual river flow (Table 1). High flow occurred in spring or summer, mainly in August (when stratification was already established), less frequently in June or July, and mainly affected the upper water layers (Table 1, Fig. 2).

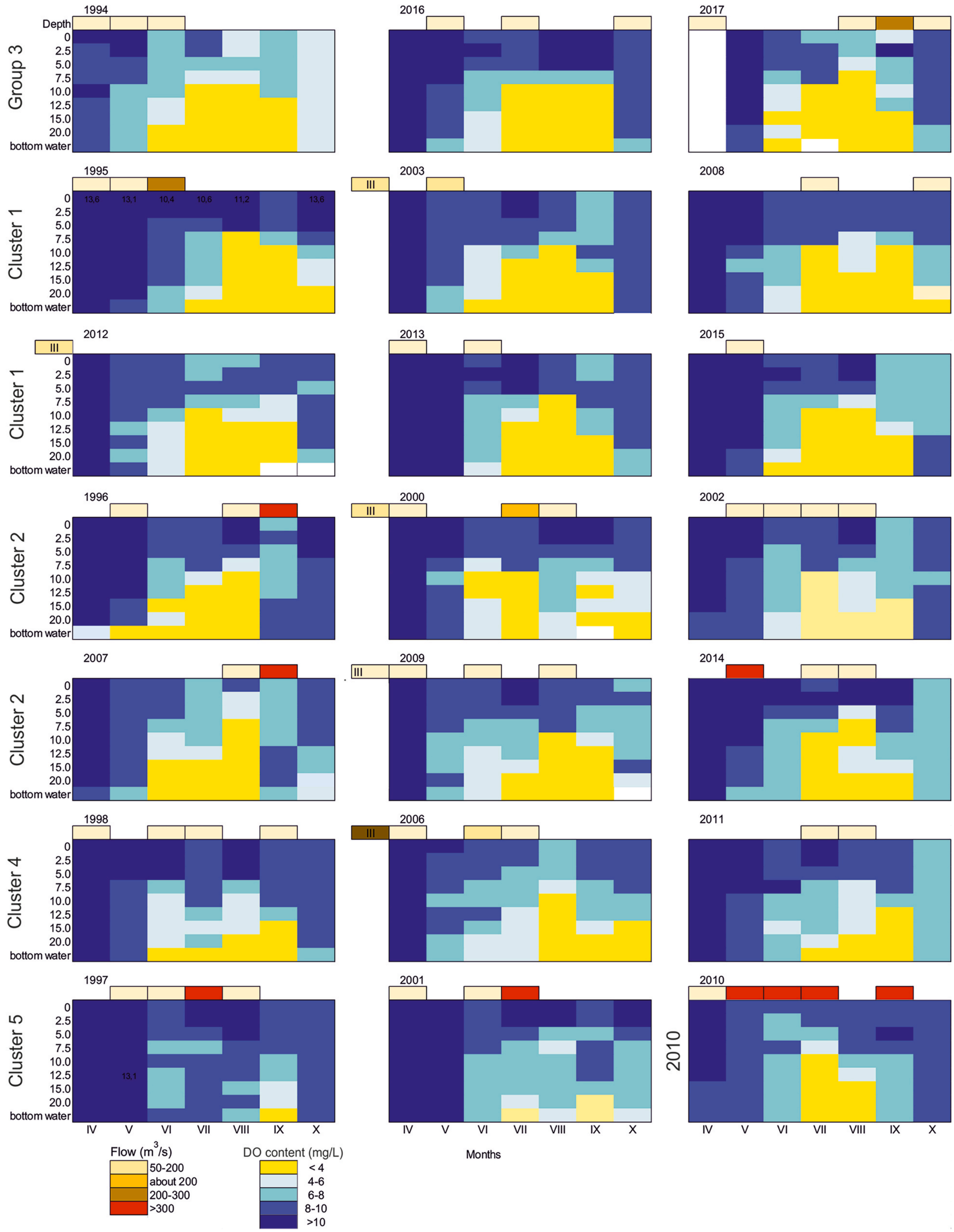

Fig. 2. Concentration of DO in the water of the reservoir between April–October 1994–2017 and high river flow (rectangular above the graph).

Some years experienced flooding in spring (May 2014) or autumn (September 1996, 2007), causing a later start or earlier end of oxygen stratification (Table 1, Fig. 2). Oxygen stratification showed a less regular pattern than in Group A (Fig. 2), although hypoxic and strongly hypoxic water occasionally reached similar depths. There was less hypoxic water (58–74 %) than in Group A, mainly due to an increase in water with DO concentrations of 4–6 mg/L and 6–8 mg/L (Fig. 4).

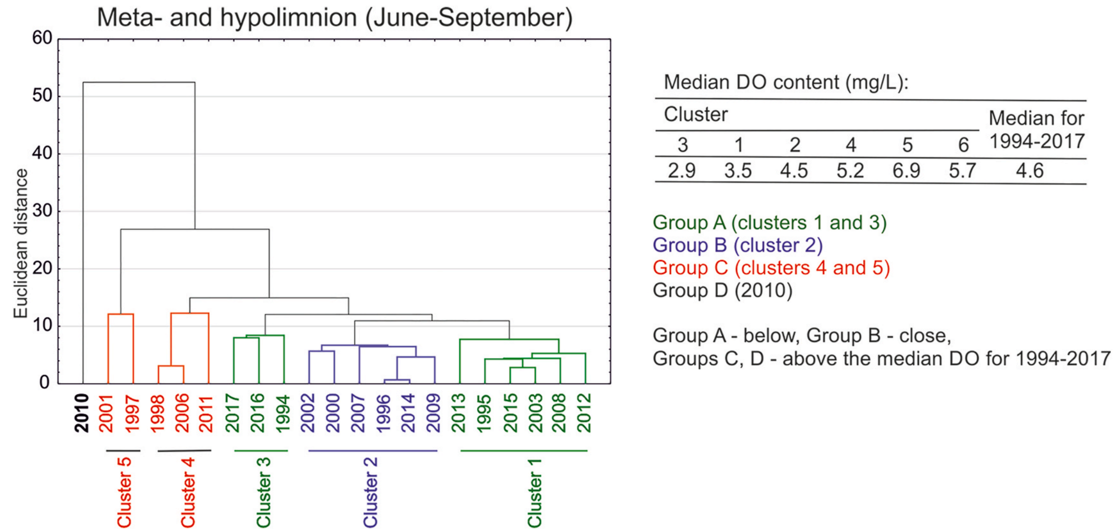

Fig. 3. Dendrogram of similarities for the percentage of DO content (<4 mg/L, 4–6 mg/L, 6–8 mg/L, >8 mg/L) in the meta- and hypolimnion during oxygen stratification (June–September 1994–2017).

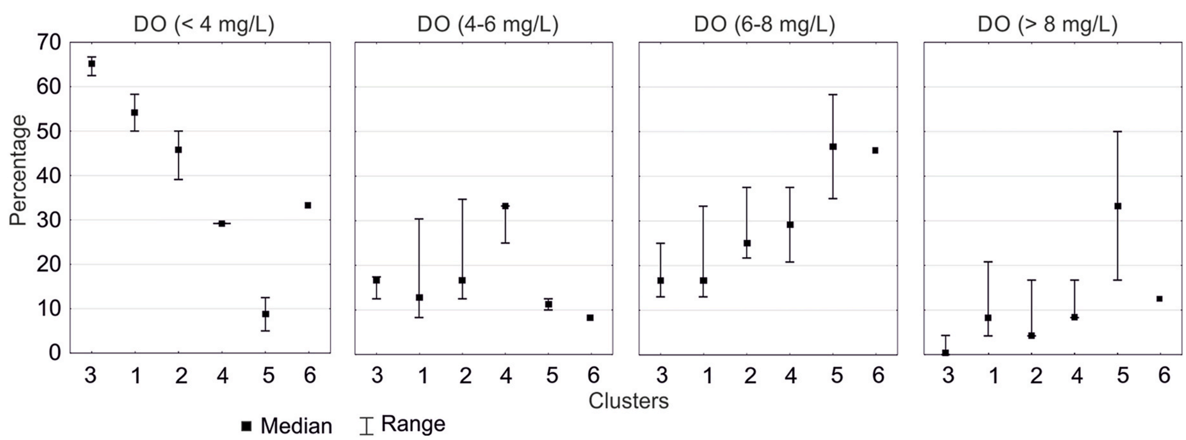

Fig. 4. Percentage of DO (medians) in the meta- and hypolimnion of the reservoir during oxygen stratification in different clusters.

- **Group C** (clusters 4 and 5) – high median DO (above the long-term median). Mean annual river flow in cluster 4 (7.7–12.3 m^3/s) was similar to cluster 3, while in cluster 5 it was higher (13.4–14.1 m^3/s) (Table 1). As in Group B, high flows occurred in spring and summer, but in summer they mainly took place in July (during the formation of stratification) and additionally in June or August (Table 1). In cluster 4, this resulted in weaker development of oxygen stratification in July, and often also in August, compared to groups A and B. Oxygen stratification was irregular: hypoxic water (<6 mg DO/L) still dominated the meta- and hypolimnion (54–63 %), but the proportion of strongly hypoxic water (<4 mg/L) was smaller, with such waters usually occurring below 15 m depth (Figs. 2 and 4). In cluster 5, a July flood prevented strong stratification. Consequently, the proportion of well-oxygenated water (6–8 and >8 mg DO/L) was the highest, and that of strongly hypoxic water was the lowest in this group (5–12 %) (Figs. 2 and 4). In the meta- and hypolimnion of Group C, significantly higher median DO and DO concentrations of 6–8 mg/L, and >8 mg/L, as well as significantly lower DO concentrations below 4 mg/L were observed compared to group A.
- **Group D** (cluster 6) – high median DO (above the long-term median). The outlier year 2010 experienced several floods. At the beginning of July strong oxygen stratification was observed, followed by a flood at the end of July and continued stratification in August. The proportion of both well and poorly oxygenated water was high (Figs. 2 and 4).

3.2.2. *Water exchange*

The average water exchange in the reservoir for the years 1994–2017 was 3.8 times/year (range 2.3–8.3 times/year) (Table 1). In Group A, water exchange rates were generally low, except in 2017 (cluster 3: 4.1 times/year) due to a peak discharge in September. In Group B water exchange rates were close to the long-term average, in Group C they fluctuated in cluster 4 and were high in cluster 5. In 2010 (Group D) it was very high (8.3 times/year) (Table 1).

The water exchange rates were significantly higher in Groups B and C than in Group A (Table 2). Considering all analysed years ($N = 21$), the water exchange rate showed a positive correlation with median DO ($r = 0.56$, $p < 0.05$) and the concentrations of 6–8 mg DO/L ($r = 0.54$, $p < 0.05$) and a negative correlation with the concentrations of <4 mg DO/L ($r = -0.54$, $p < 0.05$). However, no such relationship was observed in years with average or high median DO (Groups B, C, D; $n = 12$).

3.2.3. *Other abiotic and biotic parameters*

Other abiotic and biotic parameters were analysed in the epi-, meta- and hypolimnion (June–September 1994–2017) in relation to clusters distinguished by hierarchical cluster analysis.

Table 1
Total median DO concentrations in the meta- and hypolimnion of the reservoir during the stratification period (June–September) related to hydrological conditions which can influence oxygen stratification.

Cluster (Large group)	Median DO content (mg/L)	Mean annual river flow (m^3/s)	Water exchange (times/year)	Season with high flow	Maximum flow (m^3/s)*	Flood	Flood (m^3/s)
3 (A)	2.6–2.9	9.3–11.8	3.0–4.1	Spring, rarely summer or September	70.7–216.7		
1 (A)	2.6–4.4	6.0–9.5	2.3–3.2	Spring, rarely summer or September	38.1–212.0		
2 (B)	3.9–5.0	11.1–14.1	3.9–4.4	Spring and summer (always August)	81.6–187.7	May or September	284.2–510
4 (C)	5.7–6.9	7.7–12.3	2.8–4.1	Spring and summer (always July), rarely September	110–179.0		
5 (C)	6.8–7.9	13.4–14.1	4.3–4.7	Spring and summer	62.4–146.1	July	315–542
6 (D)	5.7	23.6	8.3	Spring and summer		May, June, July, September	363–710
Median for 1994–2017	4.6	11	3.8				

* Maximum flow from April to September.

Table 2
Differences in water exchange and DO concentration in the meta- and hypolimnion of the reservoir during oxygen stratification between Groups A-C (Mann-Whitney test, Z-value of statistics). The hydrologically different Group D was not included in the calculation.

Parameter	Groups	Z	N_1	N_2
Water exchange	A-B	−2,83**	9	6
	A-C	−2,07*	9	6
Median DO	A-B	−2,77**	9	6
	A-C	−2,93**	9	6
	B-C	−2,65**	6	6
<4 mg DO/L	A-B	3,06**	9	6
	A-C	2,93**	9	6
	B-C	2,65**	6	6
6–8 mg DO/L	A-C	−2,27*	9	6
>8 mg DO/L	A-C	−2,07*	8	6

*$p \leq 0.05$, **$p \leq 0.01$.

3.2.3.1. pH. The pH value of the water ranged from 4.2 to 9.3 (Table S1, Fig. 5). In summer, pH varied across oxygen-stratified layers. The largest vertical pH differences occurred in years with persistent oxygen stratification, while the smallest differences appeared in years with high summer water inflow and disrupted stratification (Fig. 5). Additionally, pH was highest in Group C with high summer inflow and the lowest in Group A with persistent stratification (Group C > Group B > Group A) (Tables S2 and S3, Fig. 5). In Groups B and C, the pH value was always neutral to slightly alkaline (pH > 6.7), while in Group A with long periods of strong oxygen stratification, a slightly acidic water reaction (pH < 5) was periodically present in the deeper layers (>20 m) of the reservoir.

3.2.3.2. Nutrients (nitrates, P_{tot}). The concentrations of NO_3^- in the reservoir water ranged from 5.3 to 11.1 mg/L (Fig. 5). They were significantly lower in all reservoir layers in hydrologically dry years than in years with high water inflow in both spring and summer (mainly in July) (Group A < Group C) (Table S2). In particular, the years with the most pronounced oxygen stratification had significantly lower NO_3^- concentrations than those of the other groups (cluster 3 < clusters 2, 4, 5, 1) (Table S3, Fig. 5). In contrast, high discharges and especially floods in summer caused a considerable increase in nitrate contents in the hypolimnion of the reservoir, up to ~11 mg/L in 2000 and 2001 (cluster 5 > clusters 1–4, 6). An exception was the year 2010 with several floods, but also with strong stratification in July and August, in which the hypolimnion water showed significantly lower NO_3 concentrations than in Groups B and C.

P_{tot} concentrations in the reservoir (no data for cluster 3) varied from undeterminate (nd) to 2.54 mg/L (Table S1, Fig. 5). The lowest P_{tot} concentrations (<10 μg/L) in the epilimnion and metalimnion were frequently found in the years of cluster 1 (64 % and 58 %, respectively), but also in cluster 4 (28 % and 17 %, respectively). P_{tot} concentrations in all reservoir layers were significantly lower in years with low water inflow and prolonged oxygen stratification (Group A < Groups B-D) (Table S2) and higher in years with higher water inflow in spring and summer (mainly in July) (Group C > Groups A, B and D), but especially in years with summer floods (cluster 5 > clusters 1, 2, 4, 6) (Tables S2 and S3, Fig. 5). An increase in the P_{tot} concentration in the hypolimnion periodically was observed in summer (e.g. up to 0.113 mg/L below a depth of 20 m in August 2002).

3.2.3.3. Chlorophyll a. The chl *a* content ranged from undetectable values to 45 μg/L (Table S1, Fig. 5). In the epilimnion, the chl *a* concentration was higher in years with high water inflow in spring and summer (and higher nutrient concentrations) (Group C > Groups A, B and D) (Table S2). In particular, it was higher in years with higher water inflow (but not flood) in summer (cluster 4 > clusters 1 and 2) (Table S3, Fig. 5). In the hypolimnion, the chl *a* content was higher both in years with strong oxygen stratification and with higher flow in summer comparing to other years (Group A, C > Group B).

3.2.3.4. Zooplankton. The zooplankton density varied in the studied layers: 180–420 ind/L (epilimnion), 180–210 ind/L (metalimnion) and 50–200 ind/L (hypolimnion). Higher zooplankton densities in the epilimnion occurred in years with increased river inflow and more disturbed stratification (Groups B and C > Group A; cluster 5 > clusters 1 and 3, cluster 2 > cluster 1) (Tables S2 and S4, Fig. 5), mainly due to significantly higher densities of *Polyarthra vulgaris* Carlin, 1943, juvenile stages of Copepoda and *Bosmina longirostris* (O.F. Müller, 1785) (Table S4, Fig. 6). In addition, higher densities of *Keratella cochlearis* (Gosse, 1851) were found in years with both well-developed (cluster 3) and severely disturbed stratification (cluster 5).

In the metalimnion, a higher density of zooplankton was found in years with high river inflow in spring and summer and higher DO content than in years with well-developed stratification (cluster 4 > cluster 3), which was primarily due to a higher proportion of juvenile stages of Copepoda (Tables S4 and 5, Fig. 6).

In the hypolimnion, a higher zooplankton density occurred in years with more oxygenated water (Group C > Groups A and B) (Table S2). This was associated with significantly higher densities of *Polyarthra vulgaris* (cluster 5 > clusters 2 and 3), *Daphnia cucullata* G.O. Sars, 1862 (cluster 5 > cluster 2), juvenile stages of Copepoda (clusters 4 and 5 > cluster 3), *Daphnia longispina* O.F. Müller, 1776, *Conochilus unicornis* Rousselet, 1892 (cluster 4 > clusters 2 and 3), and *Keratella quadrata* (Müller, 1786) (cluster 4 > cluster 2) (Table S4, Fig. 6).

In years with flood in summer and higher oxygen concentrations

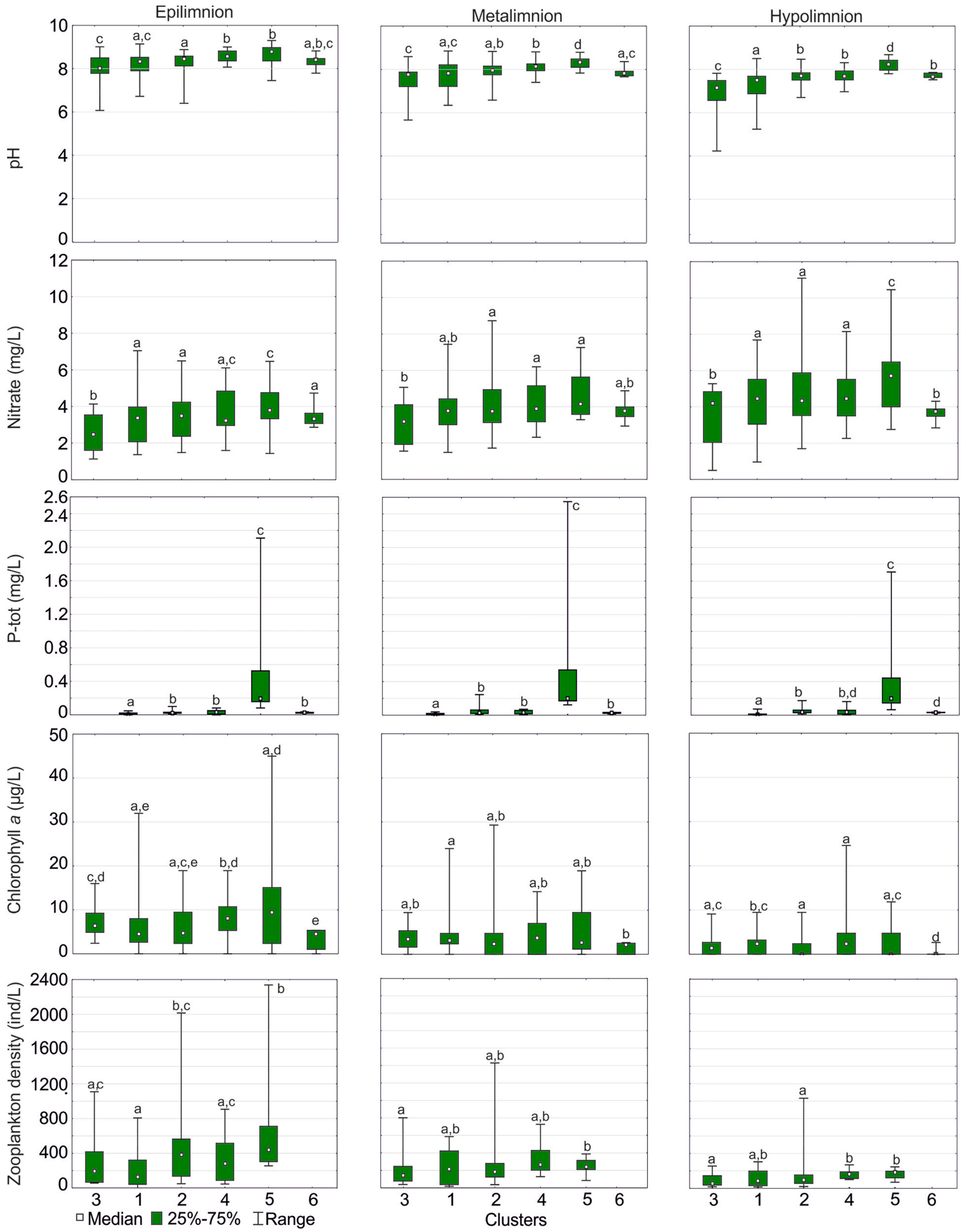

Fig. 5. Abiotic and biotic parameters in the reservoir during oxygen stratification in different clusters. Different letters indicate statistically significant differences between the clusters.

(cluster 5), zooplankton density was high in the epilimnion and hypolimnion. These layers were mainly dominated by r-strategists (e.g. *Pompholyx sulcata* Hudson, 1885, *Polyarthra vulgaris*, *Keratella cochlearis* (Rotifera), *Bosmina longirostris* (Cladocera) and numerous developmental stages of immature copepods (nauplius and copepodites) (Table S4).

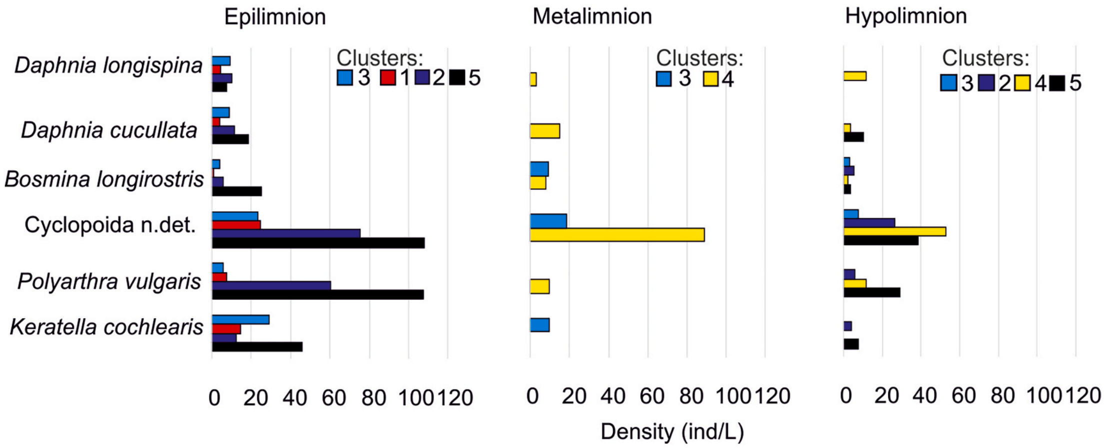

Fig. 6. Density of zooplankton in the selected clusters in the reservoir water during oxygen stratification.

4. Discussion

Our study focused on oxygen stratification in the deep dam reservoir and the interactions between selected abiotic and biotic factors. Previous studies showed that local climatic conditions and river inflows influenced various physical features of the studied reservoir, with the most important finding being that thermal stratification was extended as a result of these changes (Wilk-Woźniak et al., 2021). Therefore, we decided to conduct more in-depth analyses, which are important for the improved management of deep dam reservoirs affected by climate change.

The fate of river water flowing into deep dam reservoirs has been the subject of numerous studies (Cortés et al., 2014; Huang et al., 2019), including research on the Dobczyce Reservoir (Hachaj and Szlapa, 2017). During summer stratification in the Dobczyce Reservoir, the colder hypolimnion (approximately 10–14 °C) typically remains stable from spring to autumn (Bojarski et al., 2012; Hachaj and Szlapa, 2017). Water movement mainly occurs in the upper layer. The authors found that Raba River flows, the main source of water supply to the reservoir, of 2.03 m^3/s, typical for moderately dry periods, and 10.6 m^3/s, representing average flow, did not disrupt summer stratification. Moderately high flows of about 50 m^3/s, which occur after rainfall, generated strong currents visible throughout the reservoir, while flows exceeding 200 m^3/s, resulting from heavier rains, were strong enough to disturb the stratification. Flood flows, defined as those $\geq$300 m^3/s (Materek, 2000), completely disturbed summer stratification.

4.1. *Dissolved oxygen*

The results of our studies showed a strong relationship between river dynamics and oxygen stratification in the deep submountain dam reservoir. High water inflow in spring and low inflow in summer (mean 2.9 m^3/s) caused a long water residence time in the reservoir and limited water mixing in summer, which favoured pronounced oxygen stratification lasting for 3–4 months. As in other deep reservoirs (Zhang et al., 2015; Detmer et al., 2022), hypoxic water dominated the meta- and hypolimnion and occasionally reached shallower layers (5 m depth). This showed that low river inflow increases the risk of anoxia, which was also observed by Marcé and Armengol (2010). The deeper layers of the reservoir (meta- and hypolimnion), due to hypoxia, can be harmful to oxygen-sensitive organisms such as fish. Oxygen concentrations below 5–6 mg DO/L cause stress in fish, while concentrations below 2 mg DO/L can cause high mortality in freshwater fish (Doudoroff and Shumway, 1970). In severe hypoxia, oxygen-dependent organisms either die or migrate above the oxycline (Doudoroff and Shumway, 1970; Bulbul Ali and Mishra, 2022). Fish can migrate to epilimnion, which is well supplied with oxygen. However, these layers can become traps for fish, as they are more easily caught by birds that feed on them (Gwiazda, 2009). Another disadvantage in the upper layers can be high temperatures. For example, the lake trout (*Salmo trutta*) is a species adapted to cold, glacial or montane lakes. The lake trout was introduced by the Polish Angling Association to the Dobczyce Reservoir in the early 1980s. Due to the high summer temperatures above the thermocline and the low oxygen concentration below the thermocline, the lake trout did not manage to build up a population (pers. comm. A. Amirowicz). In addition, when the stratification is well developed, the warm layers of the epilimnion provide favourable conditions for the growth of cyanobacterial blooms, which can be toxic to fish and invertebrates. Fish protect themselves from high concentrations of cyanobacterial toxins in the lower layers, but if these lower layers are hypoxic and the toxins are present in the upper layers, then such an ecosystem also becomes a trap for fish.

However, spring and summer water flows greatly influenced oxygen stratification in the reservoir. High summer flows, during the period of stratification formation or occurrence, were particularly important, as they provided well-oxygenated water to the reservoir (median ~10 mg DO/L, Szarek-Gwiazda and Gwiazda, 2022). The greatest impact was caused by high flows (>50 m^3/s) in July during the formation of oxygen stratification (and additionally in June or August), resulted in weaker oxygen stratification and a lower percentage of strongly hypoxic water (<4 mg DO/L, only 29 %). Floods in July (>300 m^3/s, Materek, 2000) prevented the development of strong oxygen stratification, which led to the best overall water oxygenation. Flood events typically increase and homogenise DO content throughout the water column of dam reservoirs (Marcé and Armengol, 2010; Marcé et al., 2010). Moderate to heavy rainfall also cools the surface water, increasing its density and encouraging water mixing in reservoirs (Liu et al., 2020). High flows (>50 m^3/s) in August, which improved oxygenation mainly in the upper water layers during the period of oxygen stratification, had a slightly lesser effect than those in July. Only a high flow (~200 m^3/s), observed once at the turn of July and August 2000, strongly disrupted the oxygen stratification and increased DO concentrations in the reservoir water column. Floods in spring (May) and autumn (September) had less effect on reducing hypoxia in the metalimnion and hypolimnion compared to July floods. They shortened the period of oxygen stratification, but stratification still remained well developed. In Groups B and C, oxygen stratification patterns were usually irregular, influenced by high flows or by artificial forcing or inhibition of flow as a result of human decisions in managing the reservoir fill level.

The rate of water exchange in the reservoirs depends on annual river inflow. In the Dobczyce Reservoir (1994–2017), it ranged from 2.3 to 8.3 times/year. Lower water exchange rates were associated with a high percentage of strongly hypoxic waters (<4 mg DO/L) in the meta- and hypolimnion during 3–4 months strong oxygen stratification. In contrast, higher water exchange rates were related to better water oxygenation, indicated by higher median DO and concentrations of 6–8 mg DO/L. However, this relationship was inconsistent in years with average or high mean annual water flows (Groups B–D). For example, years with floods had high water exchange rates (4.4–4.7 times per year), but spring and autumn floods affected stratification differently from July floods, as discussed earlier. Additionally, low water exchange rates were observed both in years with well-developed oxygen stratification, and in years with weaker stratification. In 2011 (Group C), low exchange rates coincided with an autumn drought in the Raba River (Kholiavchuk and Cebulska, 2021), although high summer inflows strongly influenced oxygen stratification. Therefore, the water exchange rate alone is not an accurate indicator of oxygen conditions without considering hydrological patterns.

To summarize, in years with low inflow in summer, strong oxygen stratification develops, covering large parts of the meta- and hypolimnion. Due to the low oxygen concentration, these parts do not provide a sufficient habitat for aquatic organisms (Kragh et al., 2020). In other years, a different pattern of oxygen stratification developed, depending on the magnitude and time of the inflow.

4.2. Other abiotic and biotic parameters during the stratification period

The thermal stratification period is very important for deep lakes and reservoirs. Many lakes exhibit vertical stratification of water masses for extended periods, and density differences promote the development of chemical gradients that significantly affect lake organisms (Boehrer and Schultze, 2008).

The Carpathian reservoirs and rivers generally have neutral to slightly alkaline pH (Szarek-Gwiazda and Mazurkiewicz-Boroń, 2010; Romanescu et al., 2016), influenced by geological, climatic-hydrological, and biological factors (Mazurkiewicz-Boroń, 2002). We found that water pH in the reservoir (Group C > Group B > Group A) varied between the studied years depending on water flow and oxygen stratification. The lowest pH values in the water column occurred in hydrologically dry years with low inflow and strong oxygen stratification (Group A). They were the highest in years with high spring and summer inflow (Group C), especially with flood in July (cluster 5), when the Raba River supplied water with pH 6.9–9.4 (median pH 7.7–8.0, Szarek-Gwiazda and Gwiazda, 2022). Reservoir water pH is usually higher and more uniform throughout the water column during floods (Faithful and Griffiths, 2000; Szarek-Gwiazda et al., 2009). Additionally, pH values varied across the oxygen-stratified layers typical of deep reservoirs (Szarek-Gwiazda, 2013), with the greatest pH drop in years with prolonged strong stratification (Group A). Higher pH in the epilimnion is caused by photosynthesis consuming CO_2, while lower pH in the deeper hypolimnion (below 15 m) results from respiration and organic matter decomposition (Boehrer and Schultze, 2008). Water pH influences both abiotic (Kleeberg and Schubert, 2000; Søndergaard et al., 2001; Zhang et al., 2014) and biotic parameters (Chakraborty et al., 2021) in aquatic ecosystems. Changes in pH affect the availability of nutrients and trace metals, which may impact the physiology of phytoplankton species, influencing cell morphology, biomass, and species composition (Chakraborty et al., 2021). Variations in water pH significantly influence zooplankton density in the epilimnion of the Dobczyce Reservoir (Szarek-Gwiazda and Pociecha, 2024) and also in other dam reservoirs in Europe (Muñoz-Colmenares et al., 2021).

Nitrates in Carpathian rivers originated mainly from diffuse sources. Consequently, the highest nitrate concentrations in the Raba River were recorded in hydrologically wet years, when they leached from the agricultural catchment during prolonged rainfall, and the lowest in hydrologically dry years (range 1.0–9.4 mg/L; Szarek-Gwiazda and Gwiazda, 2022). Similarly, in the Dobczyce Reservoir, we observed significantly lower nitrate concentrations in hydrologically dry years with higher nitrates inflow mainly in spring, compared to years when it occurred in both spring and summer (July, and additionally June or August) (Group A < Group C). Nitrate concentrations increased in the hypolimnion during summer floods (Group C –cluster 5) because floodwater from the Raba River are rich in nutrients (Godlewska et al., 2003; Szarek-Gwiazda et al., 2010). Increased nitrogen leaching from agricultural catchments enhances the risk of eutrophication downstream, especially when nitrogen limits algal growth (Dumitran et al., 2020). Although nitrates rarely limit algal growth in Carpathian reservoirs, they can favour the development or even bloom of certain algal and cyanobacterial species, e.g. *Woronichinia naegeliana* (Wilk-Woźniak and Mazurkiewicz-Boroń, 2003).

The highest P_{tot} concentrations in the reservoir water also occurred in years with high inflows during spring and summer (July, and additionally June or August) (Group C > Groups A, B and D), especially these with a July flood, highlighting the role of diffuse sources in phosphorus enrichment. This is consistent with the earlier study by Szarek-Gwiazda and Gwiazda (2022), which indicated significantly higher P_{tot} concentrations in the Raba River water in hydrologically average and wet years compared to hydrologically dry years (range 0.001–1.916 mg/L). Flood–related increases in P_{tot} concentrations have also been reported in other reservoirs (Tüzün and İnce, 2006; Dumitran et al., 2020). Occasionally, low P_{tot} contents (<10 μg/L) appeared in the epilimnion during these periods, indicating phosphorus uptake by primary producers. Moreover, high pH and good water oxygenation favour the sedimentation of dissolved phosphate via co-precipitation with calcium carbonate or formation and adsorption by iron hydroxides (Kleeberg and Schubert, 2000). Conversely, the lowest P_{tot} concentrations in the water column were found in hydrologically dry years with limited external phosphorus input and strong oxygen stratification (Group A < Groups B–D). Phosphorus delivered in spring was used by primary producers during the growing season. Spring algal blooms or mass development, common in this reservoir (Mazurkiewicz-Boroń, 2002), likely caused a decrease in P_{tot} concentration (<10 μg/L, up to 64 % of cases) in the epilimnion, which limits algal growth (Vollenweider, 1976). Although phosphorus is generally limiting for algal growth (Grossman and Aksoy, 2015), we found that this phenomenon mainly occurred in hydrologically dry years.

During the stratification, an increase in reductive conditions and a decrease in pH due to the decomposition of organic material in the water-sediment system facilitate the release of phosphates and ammonia from the sediments (internal input), a well-known process in lakes (Søndergaard et al., 2001; Kleeberg and Schubert, 2000; Kowalczewska-Madura et al., 2022; Defeo et al., 2024). The release of soluble phosphorus from redox-sensitive iron forms in the sediment (Søndergaard et al., 2001; Defeo et al., 2024) in this reservoir is favoured by DO concentrations below 3 mg/L in bottom water (Szarek-Gwiazda, 2013), which usually occurred in clusters 1–4 and occasionally in clusters 5–6. A decrease in pH below 5, occasionally observed in cluster 3, causes the release of carbonate-bound P (Søndergaard et al., 2001). The release of phosphorus from bottom sediments is responsible for cyanobacterial blooms in summer (Mazurkiewicz-Boroń, 2002; Kowalczewska-Madura et al., 2022). A decrease in DO (<1 mg/L) and pH (≤6) (mainly Group A), favours the release of ammonium into the overlying water (Zhang et al., 2014). Nutrients released into the hypolimnetic waters during stratification by these and other processes (Søndergaard et al., 2001) are generally unavailable to phytoplankton, as only motile organisms (for phytoplankton, e.g. dinophytes, euglenophytes, cryptophytes) can inhabit the thermocline and benefit from the advantages of both the epilimnion and hypolimnion (Boehrer and Schultze, 2008). Therefore, if stratification is present, the released phosphorus remains largely trapped in the deep layers of the reservoir until autumn mixing (Wilk-Woźniak et al., 2021). In other years, particularly Group C, disturbance of stratification by higher flows favours the upward transport of nutrients and increases their availability to algae.

The results of our studies showed that the highest phytoplankton production (chl *a* concentration) in the epilimnion was in years with high water inflow in spring and summer and with strongly disturbed stratification (Group C) compared to the other years. Such conditions favoured the development of species of strategy type C (competitors) or R (ruderal), which reproduce rapidly, allowing rapid and abundant development of phytoplankton communities in a short time after a flood or high tide (Godlewska et al., 2003; Wilk-Woźniak, 2009). However, in the years with low water inflow (Group A - cluster 1), chlorophyll *a* concentrations in the epilimnion remained at a low level despite occasional algal blooms due to limited phosphorus availability (see P_{tot}). The extremely wet conditions of 2010 (water exchange 8.3 times/year) were not suitable for the development of algae, as expressed by the chlorophyll *a* content in the water. This could be related to the increase in suspended solids added with the flood, which reduces the availability of light and is not conducive to algal growth (Bilotta and Brazier, 2008).

Zooplankton density was influenced by both river flow and DO concentration. Higher zooplankton densities occurred in years with high spring and summer flows or summer floods (Group C), which improved meta- and hypolimnion oxygenation and increased pH, concentrations of nutrient and chlorophyll *a*. Zooplankton generally prefer well-oxygenated water, as low DO reduces their abundance and biodiversity (Banerjee et al., 2019). Anoxia and oxidative stress affect zooplankton by reducing their anaerobic respiration and hindering their reproduction, development, migration, and energy budget. These factors may also have further consequences for population and community dynamics (Frederick et al., 2025). In waterbodies with oxic hypolimnetic water, zooplankton exhibit diel vertical migration, moving to the dark hypolimnion during the day to escape fish predation or ultraviolet radiation in the epilimnion (Doubek et al., 2018). However, the physiologically stressful conditions of anoxic hypolimnia may force zooplankton to remain in the epilimnion. However, Karpowicz et al. (2020) found that some zooplankton species in lakes, such as *Bosmina berolinensis* Imhof, 1888, tolerate anoxia. In general, our results are consistent with those of Banerjee et al. (2019), who identified DO, nitrates, phosphates, pH and dissolved solids as key factors in zooplankton variation.

Further, during summer floods, which improved water oxygenation (Group C - cluster 5), the density of rotifers increased, especially in the epilimnion, while large cladocerans and copepods were eliminated. This phenomenon was also observed by Godlewska et al. (2003). This is because such conditions favoured small, opportunistic rotifers (r-strategists) such as *Polyarthra vulgaris* and small cladocerans such as *Bosmina longirostris*. These r-strategists are mainly found in unstable conditions such as lotic habitats with high currents and suspended organic matter (Pociecha and Wilk-Woźniak, 2005, 2006).

High inflows in spring and summer (Group C - cluster 4) favoured large zooplankton species such as *Daphnia longispina*, probably due to increased DO concentration, high food availability (phytoplankton) and lower fish predation in moderately turbid waters. Other large zooplankton species such as *Cyclops strenuus* Fischer, 1851 and *Mesocyclops leuckartii* (Claus, 1857) favoured a less disturbed environment (K-type strategy). K – strategists prefer a stable environment with slow-flowing or stagnant waters with good food availability (Pociecha and Wilk-Woźniak, 2005, 2006). Overall, the zooplankton density in the different years reflected the fluctuations in water flow dynamics and DO concentration in the reservoir.

5. Conclusions

Long-term studies carried out at the deep, submountain Dobczyce Reservoir (southern Poland) showed that hydrological variability, especially river inflow, plays a key role in shaping the oxygen stratification as well as selected physico-chemical and biological parameters of the reservoir. Low river inflows in summer and low water exchange rates led to strong and persistent oxygen stratification lasting 3–4 months, resulting in extensive zones of hypoxia and even anoxia in the lower layers of the reservoir, similarly to lakes.

The meta- and hypolimnion were better oxygenated in years with high spring and summer flow. Average water oxygenation occurred in years with spring and autumn floods, which shortened the period of oxygen stratification, as well as in years with high flow in August, which disturbed the upper water layers. Higher DO concentrations in these layers was observed in years with high inflows in July and also in June or August, during the formation of oxygen stratification. Flooding in July prevented the development of strong oxygen stratification.

Nutrient dynamics were closely linked to hydrological conditions. Higher river inflows increased the input of nitrate and P_{tot}, mainly from diffuse sources in the catchment, which led to increased nutrient concentrations in the reservoir. In years characterized by high river flow and better oxygenation of the water, we observed an increase in zooplankton density, especially in the epilimnion and hypolimnion. The dominant species were opportunistic r-strategists: *Polyarthra vulgaris* and *Bosmina longirostris*. These conditions favoured both rotifers and small cladocerans, while large cladocerans and copepods preferred more stable, less disturbed habitats. The timing and magnitude of river flow, together with the availability of oxygen, nutrients and chl *a*, were key factors influencing zooplankton community dynamics.

The study demonstrates the strong dependence of reservoir ecosystem functioning on hydrological variability. Low flows, as projected in climate change scenarios, can increase the risk of hypoxia, reduce the availability of habitats for aquatic organisms and increase eutrophication. Conversely, episodic high flows may be beneficial for oxygen supply, but can also transport significant amounts of nutrients that impair algal development. These findings highlight the importance of integrated catchment and reservoir management that considers both hydrological and ecological processes to maintain water quality and ecosystem health in submountain dam reservoirs.

CRediT authorship contribution statement

Ewa Szarek-Gwiazda: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Agnieszka Pociecha:** Writing – review & editing, Writing – original draft, Methodology, Investigation. **Elżbieta Wilk-Woźniak:** Writing – review & editing, Writing – original draft, Methodology, Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.127742.

Data availability

The authors do not have permission to share data.

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