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Hydrochemical gradients, aquatic biodiversity, and commercial fish dynamics in seven lakes of Burabay National Park, Kazakhstan

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ABSTRACT

Understanding how hydrochemical heterogeneity structures aquatic communities is essential for the ecological assessment and management of lake systems. This study evaluated hydrochemical differentiation and associated variation in zooplankton, macrozoobenthos, and fish assemblages across seven lakes of Burabay State National Natural Park, Northern Kazakhstan, using monitoring data collected during the open-water seasons of 2021–2025. The dataset comprised 214 hydrochemical samples, 215 zooplankton samples, 215 macrozoobenthos samples, 12,060 examined fish, and 126 gillnet deployments. Five-year mean lake-level pH ranged from 7.57 to 8.87, dissolved oxygen from 9.34 to 10.06 mg L^{-1}, and total dissolved solids (TDS) from 254 to 6,584 mg L^{-1}. TDS differed significantly among lakes ($p < 0.001$), forming a pronounced gradient from the lower-mineralization Borovoye and Shchuchye lakes through the intermediate Tekekol, Katarkol, and Bolshoe Chebachye lakes to the highly mineralized Maloe Chebachye and Zhukey lakes. The first two principal components explained 80.5% of the hydrochemical and biological variation and identified TDS, hardness, pH, and major-ion composition as the principal environmental gradient. Zooplankton richness ranged from 7 to 22 taxa and showed no significant interannual differences but was significantly lower in the higher-mineralization group than in the lower- and intermediate-mineralization groups. Macrozoobenthos richness ranged from 13 to 36 taxa and declined significantly in 2024–2025, although it did not differ significantly among mineralization groups. Fish richness remained comparatively stable among years and mineralization groups, whereas model-derived abundance and species dominance varied markedly among lakes and years. Exploratory Spearman analyses showed negative associations of zooplankton richness with pH, $Na^+ + K^+$, hardness, and Mg^{2+} and a positive association of macrozoobenthos richness with Ca^{2+}. Species-specific fish responses also differed along the hydrochemical gradient. Overall, the results revealed pronounced ecological differentiation among geographically proximate lakes and demonstrated that mineralization formed the principal environmental framework, while biological responses were modified by habitat characteristics, trophic interactions, lake morphometry, and fisheries-management history. These findings provide a regional baseline for integrated long-term monitoring, although temporal trends and environment–biota relationships require confirmation using balanced seasonal sampling and larger station-level and lake-year datasets.

Keywords: Lake ecosystems, Mineralization, Zooplankton, Macrozoobenthos; Fish assemblages, Hydrochemistry, Kazakhstan.
Article type: Research Article.

INTRODUCTION

Lakes are key components of the global water cycle and natural capital, playing an essential role in maintaining hydrological balance, regulating biogeochemical cycles, and supporting ecological resilience at the landscape level (Grande *et al.* 2023). Lake ecosystems store substantial volumes of freshwater, contribute to carbon sequestration, and exhibit high ecological complexity, making them critical components of natural capital at both

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global and regional scales (Grizzetti *et al.* 2019). From a socioeconomic perspective, lakes provide a wide range of ecosystem services, including water supply, fisheries production, recreation, flood regulation, and cultural and aesthetic benefits (Burkhard *et al.* 2012). At the same time, lake ecosystems are highly sensitive to climate change and anthropogenic pressure. Increasing water temperatures, shorter periods of vertical mixing, alterations in water balance, nutrient enrichment, and reduced river inflow may lead to oxygen depletion, eutrophication, increasing mineralization, and the degradation of aquatic habitats. The magnitude of these processes has been demonstrated in several lake systems worldwide. In Lake Tanganyika, climate warming and weakened vertical mixing reduced the area of oxygenated benthic habitat by 38%, accompanied by declines in fish and mollusc abundance (Cohen *et al.* 2016). In Lake Erie, a toxic cyanobacterial bloom in 2014 increased the microcystin concentration in drinking water to 2.5 μg L^{-1} and affected more than 400,000 consumers (Bullerjahn *et al.* 2016). The most extensive changes occurred in the Aral Sea, where the water level declined by 23 m, surface area decreased by 74%, water volume was reduced by 90%, and salinity increased from 10 to more than 100 g L^{-1} (Micklin, 2007). These examples demonstrate that alterations in hydrological and hydrochemical regimes can cause large-scale restructuring of food webs, biodiversity loss, and a decline in the resource value of lake ecosystems. Biological communities integrate environmental effects across different temporal and spatial scales, and their characteristics are therefore widely used to assess the ecological condition of aquatic ecosystems. Zooplankton responds relatively rapidly to changes in mineralization, nutrient concentrations, phytoplankton productivity, and predation pressure. Macrozoobenthos reflects longer-term changes at the water–sediment interface and is sensitive to oxygen availability, organic enrichment, substrate composition, and habitat stability. In addition, planktonic and benthic organisms constitute an essential component of the fish forage base and are directly related to lake fish productivity (Sánchez-Hernández *et al.* 2021). Fish communities are among the most informative biological components used to assess the ecological condition of lake ecosystems. Owing to their relatively long life cycles, trophic diversity, mobility, and dependence on habitat quality, fish integrate the cumulative effects of environmental stressors over time. Changes in species composition, abundance, age structure, dominance patterns, and the relative proportions of tolerant and sensitive species may reflect disruptions in oxygen conditions, changes in mineralization and trophic status, hydrological fluctuations, habitat degradation, and food-web restructuring. Accordingly, ichthyofauna can be used as a bioindicator of both short-term environmental disturbances and long-term ecosystem transformation (Pinna *et al.* 2023). Fish also represent an important resource component of aquatic ecosystems. The status of commercially important fish populations determines fisheries productivity, food provision, recreational value, and the sustainability of fisheries exploitation (Lynch *et al.* 2016). Assessments of the abundance, population structure, and dominance patterns of commercial ichthyofauna provide applied information for fisheries management, conservation planning, and the development of long-term monitoring programmes. Fish communities should therefore be considered both as biological indicators of ecological condition and as a key resource component determining the practical value of lake ecosystems (Dafforn *et al.* 2016; Schallenberg *et al.* 2018). However, indicators based on a single group of organisms may not fully reflect ecosystem condition under the simultaneous influence of multiple interacting stressors. Consequently, multi-component approaches combining fish, macroinvertebrate, and plankton community characteristics within unified assessment frameworks are increasingly being applied to freshwater ecosystem diagnostics. Systematic reviews have shown that integrating multiple biological components with hydrochemical and functional indicators provides a more reliable and sensitive means of detecting degradation processes than assessments based on a single taxonomic group (Biney *et al.* 2025; de Carvalho *et al.* 2025). The combined analysis of biotic, abiotic, and dynamic characteristics also makes it possible to evaluate ecosystem integrity and stability, as well as the potential risk of transitions to alternative ecological states (Huang *et al.* 2024). Recent studies have demonstrated close relationships between biotic indicators and abiotic environmental variables, including electrical conductivity, mineralization, nutrient concentrations, and dissolved oxygen. The spatiotemporal structure of aquatic communities is frequently governed by interacting trophic and hydrochemical gradients, highlighting the high indicator value of biological metrics for lake monitoring (Hui *et al.* 2024). For example, 232 phytoplankton taxa were identified in 25 lakes of the Songnen Plain in Northeastern China. At mineralization levels above 3,000 mg L^{-1}, cell density, genus richness, and the Shannon diversity index decreased significantly, while mineralization and alkalinity explained 10.7% of the variation in taxonomic composition. Approximately one-quarter of the recorded genera were tolerant of elevated salinity and alkalinity. In Lake Xinmiao, 146 phytoplankton species were recorded. From June to October, total dissolved solids increased from 219.17 to 363.33 mg L^{-1}, while the

maximum concentrations of total nitrogen and total phosphorus reached 1.61 and 0.12 mg L^{-1}, respectively. In July and August, cyanobacteria accounted for up to 50% of total abundance. Mineralization, water temperature, total phosphorus, and five-day biochemical oxygen demand were identified as the main drivers of community variation (Huang *et al.* 2022). The first ordination axes explained 41.06% and 41.95% of the relationships between environmental factors and phytoplankton abundance and biomass, respectively. Similar patterns have been reported for macrozoobenthos in 11 lakes in Western Jilin Province. Among 1,259 examined individuals, 43 species were identified. Values of the macroinvertebrate multi-metric index of biotic integrity ranged from 0.11 to 0.86, and 35.7% of the investigated sites were classified as being in poor or very poor ecological condition (Ding *et al.* 2021). The lowest index values were recorded in lakes with the highest nitrogen and phosphorus concentrations. These findings indicate that individual components of aquatic communities may respond differently to mineralization, organic loading, and nutrient enrichment, which should be considered in integrated lake assessments. The practical applicability of integrated approaches has been demonstrated for Lake Baiyangdian in China. The developed assessment framework included 16 biological, hydrological, hydrochemical, and socio-ecological indicators (Zhao *et al.* 2025). The overall lake-health index was 55 out of 100, corresponding to a suboptimal condition, and 7 of the 9 surveyed stations were assigned to this category. The lowest scores were obtained for aquatic organisms, at 38.9 points, and the hydrological regime, at 44.7 points, confirming the need for the joint analysis of abiotic, biological, and ecosystem-service characteristics. For Kazakhstan and Central Asia, integrated lake assessment is particularly relevant because of the combination of high natural, recreational, and fisheries value with vulnerability to fluctuations in water availability, increasing mineralization, and declining water quality. Studies of Kazakhstani water bodies have confirmed the value of combining hydrochemical and biological indicators. In Lake Maybalyk, 97 microalgal taxa were identified, 71 of which had bioindicator significance (Tekebayeva *et al.* 2024). Across six lakes in Burabay National Park, 139 species of algae and cyanobacteria were recorded at 54 sampling stations, while mineralization and organic loading were identified as the principal factors differentiating phytoplankton communities (Barinova *et al.* 2023). In Lake Borovoe, 27 zooplankton species were recorded, with a mean abundance of 988.8×10^3 individuals m^{-3} and a biomass of 1.52 g m^{-3} (Mamilov *et al.* 2022). In the Alakol lake basin, fish distribution was found to be strongly associated with mineralization and water temperature. Despite these individual studies, Kazakhstan still has relatively few long-term investigations in which hydrochemical characteristics, zooplankton, macrozoobenthos, and quantitative ichthyofaunal indicators are assessed simultaneously across several lakes using a methodologically consistent framework. In particular, the relationships between gradients of mineralization and ionic composition, the diversity of lower trophic levels, and the abundance of commercially important fish species remain insufficiently understood. Furthermore, the interpretation of fish-community structure requires consideration not only of contemporary environmental conditions but also of the historical effects of stocking, acclimatization, and fisheries exploitation in individual lakes. The objective of the present study was therefore to provide an integrated assessment of aquatic ecosystems in Akmola Region, Kazakhstan, through the joint analysis of hydrochemical characteristics, zooplankton and macrozoobenthos biodiversity, ichthyofaunal species composition, and the abundance of commercially important fish species. Fish communities were considered both as bioindicators reflecting habitat condition, trophic status, and long-term ecosystem transformation and as a resource component characterizing the fisheries potential of the studied lakes.

MATERIALS AND METHODS

Study area and investigated lakes

The study was conducted in seven lakes located within and adjacent to the Burabay State National Natural Park, Akmola Region, Northern Kazakhstan: Bolshoe Chebachye, Maloe Chebachye, Borovoye, Shchuchye, Tekekol, Katarkol, and Zhukey. Six lakes are located within Burabay District, whereas Lake Zhukey is situated southeast of Kotyrkol Village in the neighbouring Birzhan Sal District. The study area has a sharply continental climate and is characterized by forest-steppe landscapes, pine and birch-aspen forests, steppe vegetation, wetlands, and areas subject to recreational use. The investigated lakes differ substantially in surface area, depth, shoreline configuration, hydrological conditions, and mineralization. Lake surface area ranged from 105 ± 2.7 ha in Tekekol to 1,704 ± 47.8 ha in Bolshoe Chebachye. Maximum depth varied from 4.42 ± 0.23 m in Borovoye to 26.40 ± 0.98 m in Bolshoe Chebachye, whereas mean depth ranged from 1.94 ± 0.04 m in Zhukey to 9.66 ± 0.10 m in Shchuchye. Bolshoe Chebachye was therefore the largest and deepest lake by maximum depth, while Shchuchye had the greatest mean depth. Tekekol was the smallest investigated water body, and Zhukey was the shallowest

according to mean depth. Lake surface area was estimated from satellite imagery, whereas maximum and mean depths were derived from field bathymetric measurements conducted along longitudinal and transverse transects at approximately 100-m intervals. Morphometric parameters were calculated following established limnological principles (Håkanson 1981). The values are presented as mean ± standard deviation for the 2021–2025 study period. The main geographical and morphometric characteristics of the lakes are summarized in Fig. 1 and Table 1.



Fig. 1. Location of the seven investigated lakes in Akmola Region, Kazakhstan.

Table 1. Coordinates and locations of the studied water bodies.

Water body	Location	Coordinates
Burabay District		
L. Bolshoe Chebachye	Borovoye Village	53.076638° N; 70.155808° E
L. Borovoye	Borovoye Village	53.075247° N; 70.277906° E
L. Katarkol	Kotyrkol Village	52.962233° N; 70.411317° E
L. Maloe Chebachye	Dorofeyevka Village	53.072192° N; 70.115217° E
L. Tekekol	4.8 km northwest of Borovoye Village	53.138628° N; 70.272072° E
L. Shchuchye	0.5 km northeast of Shchuchinsk Town	52.973903° N; 70.216131° E
Enbekshilder District		
L. Zhukey	9 km southeast of Kotyrkol Village	52.894075° N; 70.586792° E

Sampling design and monitoring effort

Field investigations were conducted during the open-water period from May to October in 2021–2025. A total of 20 permanent sampling stations were distributed among the seven lakes according to lake area, depth, shoreline configuration, habitat heterogeneity, and accessibility. Four stations were established in each of Lakes Bolshoe Chebachye, Maloe Chebachye, and Shchuchye, three in Lake Borovoye, two each in Lakes Katarkol and Zhukey, and one in Lake Tekekol. The stations represented the main littoral and open-water habitats of the investigated lakes. Hydrochemical, zooplankton, macrozoobenthos, and ichthyological surveys were conducted within the same monitoring network whenever habitat and logistical conditions permitted. Over the five-year study period, the dataset comprised 214 hydrochemical samples, 215 zooplankton samples, 215 macrozoobenthos samples, 12,060 individually examined fish, and 126 gillnet deployments. Sampling effort differed among years, with the most intensive hydrochemical and hydrobiological survey conducted in 2024. Annual monitoring effort is summarized in Table 2, while sampling dates, station coordinates, sampling depths, biological replicates, gillnet deployments, and net exposure periods are presented in Table 2. Because sampling effort was not uniform among years, raw annual taxonomic richness was used for descriptive characterization and was not interpreted independently as evidence of directional temporal change.

Hydrochemical measurements

Water sampling was conducted in accordance with GOST R 59024-2020 and the general requirements of ISO 5667-4:2016 [26] for lake-water sampling. Samples were collected from the surface water layer at the established monitoring stations. Where the monitoring design included vertical assessment, additional samples were collected from the near-bottom layer. Sampling was performed using clean equipment suitable for lake-water collection,

and the samples were transferred into pre-cleaned containers. Until laboratory analysis, the samples were stored and transported under cooled conditions at approximately 4 °C.

Table 2. Location and mean morphometric characteristics of the investigated lakes during 2021-2025.

Lake	Location	Number of points	Coordinates	Area (ha)	Maximum depth (m)	Mean depth (m)
Bolshoe Chebachye	Borovoye Village	4	53.076638 N; 70.155808 E	1704 ± 47.8	26.40 ± 0.98	6.06 ± 0.52
Maloe Chebachye	Dorofeyevka Village	4	53.072192 N; 70.115217 E	1592 ± 26.3	9.66 ± 0.10	4.78 ± 0.06
Borovoye	Borovoye Village	3	53.075247 N; 70.277906 E	932 ± 19.3	4.42 ± 0.23	2.40 ± 0.16
Shchuchye	Near Shchuchinsk	4	52.973903 N; 70.216131 E	1411 ± 22.5	21.32 ± 0.32	9.66 ± 0.10
Tekekol	Northwest of Borovoye Village	1	53.138628 N; 70.272072 E	105 ± 2.7	5.76 ± 0.13	2.68 ± 0.04
Katarkol	Kotyrkol Village	2	52.962233 N; 70.411317 E	486 ± 11.6	5.32 ± 0.10	2.52 ± 0.10
Zhukey	Southeast of Kotyrkol Village	2	52.894075 N; 70.586792 E	1614 ± 35.7	4.74 ± 0.12	1.94 ± 0.04

Water temperature, pH, and dissolved oxygen concentration were measured directly at the sampling stations using calibrated portable instruments. The equipment was calibrated according to the manufacturer's instructions before field measurements. The determination of pH and dissolved oxygen followed the general procedures of ISO 10523:2008 and ISO 5814:2012, respectively. The laboratory analytical programme included total dissolved solids, total hardness, free carbon dioxide, permanganate oxidizability, ammonium nitrogen, nitrite nitrogen, nitrate nitrogen, phosphate phosphorus, and the major cations and anions. Total dissolved solids were determined gravimetrically, total hardness by complexometric titration with EDTA, nutrient compounds by photometric methods, and permanganate oxidizability by titration. Major-ion concentrations were determined using the standardized analytical procedures adopted by the laboratory. During the five-year monitoring period, 214 hydrochemical samples, 215 zooplankton samples, and 215 macrozoobenthos samples were collected. In addition, 12,060 fish specimens were examined from 126 gillnet deployments. Sampling effort differed among years, with the largest number of hydrochemical and hydrobiological samples collected in 2024. The annual distribution of monitoring effort is presented in Table 3.

Table 3. Summary of monitoring effort during 2021–2025.

Year	Hydrochemical samples	Zooplankton samples	Macrozoobenthos samples	Fish examined (individuals)	Gillnet deployments
2021	20	21	21	3,234	23
2022	20	20	20	2,821	23
2023	20	20	20	2,651	22
2024	140	140	140	1,858	40
2025	14	14	14	1,496	18
Total	214	215	215	12,060	126

Zooplankton sampling and analysis

Zooplankton samples were collected at the monitoring stations by filtering 100 L of surface lake water through an Apstein plankton net made of miller gauze No. 55 or No. 70. Sampling was performed following the general recommendations of EN 15110:2006 for zooplankton surveys in standing waters. Samples were immediately preserved with formaldehyde at a final concentration of 4%. In the laboratory, each sample was concentrated,

thoroughly mixed, and examined in quantitative subsamples under a light microscope. When organism density was low, the entire sample was analysed. Rotifers, cladocerans, and copepods were identified to the lowest practicable taxonomic level using standard identification keys (Kutikova 1970; Smith 2001; Korovchinsky 2004). Taxonomic richness was expressed as the number of recorded taxa per sample and per lake-year combination.
Where quantitative data were available, abundance was calculated relative to the original volume of filtered water and expressed as individuals per cubic metre. Biomass was expressed as grams per cubic metre using the laboratory procedure adopted for the corresponding taxonomic group.

Macrozoobenthos sampling and analysis
Macrozoobenthos was sampled using a Petersen grab with a capture area of 0.025 m². Each sample represented one grab collected at the corresponding monitoring station. Sampling-device selection and field procedures followed the general principles of ISO 10870:2012, and organisms were identified using standard taxonomic keys (Bogatov 1994). The collected sediment was washed through a sieve made of gauze No. 40. Retained organisms were manually separated from sediment and plant material, transferred into labelled containers, and preserved in 4% formaldehyde. In the laboratory, organisms were identified to the lowest practicable taxonomic level using standard identification keys. Taxonomic richness was expressed as the number of recorded taxa per sample and per lake-year combination. Where quantitative data were available, abundance and biomass were standardized to the sampled bottom area and expressed as individuals per square metre and grams per square metre, respectively.

Fish sampling and abundance estimation
Fish were sampled during 2021–2025 using passive gillnets with mesh sizes ranging from 20 to 70 mm. The nets were deployed at the established monitoring stations in representative littoral, sublittoral, and open-water habitats. The number and length of nets, mesh sizes, deployment coordinates and depths, and exposure durations were recorded for each survey and are provided in Tables 2-3. In total, 12,060 fish specimens were examined from 126 gillnet deployments. Fish were identified to species, and standard length and total body mass were recorded for each specimen following standard ichthyological procedures (Pravdin 1966). The total number of examined fish was not considered a direct measure of population abundance because gillnet catches depend on fishing effort, exposure duration, mesh-size selectivity, fish body size, species behaviour, and catchability. Fish measurements were performed following standard ichthyological procedure. Fish abundance was estimated using the correction-coefficient approach proposed by Kushnarenko & Lugarev (1980) and Sechin (1990) with species-specific swimming speeds obtained from Radakov & Protasov (1904).

$$N = \frac{Q \times S}{k},$$

where N is estimated fish abundance, Q is the number of fish recorded in control catches, S is lake area, and kkk is the combined correction coefficient:

$k = P \times K \times C,$

where P is the probability of encountering the fishing gear, K is the catchability coefficient, and C is the effective fishing area:

$C = V \times t \times g \times (2b + \pi Vt),$

where V is species-specific cruising speed, t is net exposure time, g is the number of nets, and b is net length. Values of P ranged from 0.020 to 0.028, and K was set to 0.5. Calculations were conducted separately by species, lake, and year. Because passive gillnets are species- and size-selective, the resulting values were treated as model-derived abundance estimates rather than absolute population sizes.

Statistical analysis
Hydrochemical variables were summarized for each lake and year and expressed as five-year means ± SD of annual values. Taxonomic richness of zooplankton, macrozoobenthos, and fish was calculated from the recorded taxon lists. Since annual sampling effort was not uniform, richness-based comparisons were considered exploratory. One-Way ANOVA was used to compare TDS among lakes and taxonomic richness among years and

mineralization groups. Based on five-year mean TDS, the lakes were classified into lower- (Borovoye and Shchuchye), intermediate- (Tekekol, Katarkol, and Bolshoe Chebachye), and higher-mineralization groups (Maloe Chebachye and Zhukey). Tukey's HSD test was used for pairwise comparisons at $p < 0.05$. The unavailable fish-richness value for Bolshoe Chebachye in 2023 was excluded. Principal component analysis was performed using standardized lake-level mean hydrochemical variables. Associations between hydrochemical characteristics and biological indicators were assessed using Spearman's rank correlations. Since these analyses included only seven lakes, interpretation focused on the direction and magnitude of associations. Model-derived fish abundance was compared descriptively among lakes, years, and species. All analyses and visualizations were performed in R.

RESULTS

Hydrochemical differentiation among the studied lakes

The seven studied lakes differed markedly in their hydrochemical characteristics. Mean pH ranged from 7.57 ± 0.27 in Borovoye to 8.87 ± 0.06 in Zhukey, whereas dissolved oxygen varied within a comparatively narrow range, from 9.34 ± 1.21 mg L^{-1} in Shchuchye to 10.06 ± 0.85 mg L^{-1} in Zhukey. Water hardness showed a substantially stronger spatial gradient, increasing from 2.42 ± 0.87 meq L^{-1} in Borovoye to 39.8 ± 1.4 meq L^{-1} in Zhukey. High hardness was also recorded in Maloe Chebachye (32.8 ± 1.2 meq L^{-1}). Permanganate oxidizability ranged from 6.73 ± 2.80 mg O_2 L^{-1} in Shchuchye to 32.46 ± 9.10 mg O_2 L^{-1} in Katarkol (Table 3).

Nutrient concentrations also differed among lakes. Ammonium nitrogen was highest in Maloe Chebachye (0.934 ± 0.770 mg L^{-1}), followed by Katarkol (0.642 ± 0.160 mg L^{-1}). Zhukey had the highest concentrations of nitrite nitrogen (0.0668 ± 0.0290 mg L^{-1}) and phosphate phosphorus (0.0718 ± 0.0220 mg L^{-1}), whereas nitrate nitrogen was highest in Shchuchye (1.18 ± 0.53 mg L^{-1}; Table 4). Total dissolved solids constituted the clearest hydrochemical gradient among the lakes. Across all lake–year combinations, TDS ranged from 234 mg L^{-1} in Borovoye to 7,675 mg L^{-1} in Zhukey. Five-year mean TDS was lowest in Borovoye (254 ± 21 mg L^{-1}) and Shchuchye (413 ± 53 mg L^{-1}).

Table 3. Mean general hydrochemical parameters of the investigated lakes during 2021–2025.

Lake	pH	CO_2 (mg L^{-1})	Dissolved O_2 (mg L^{-1})	Permanganate oxidizability (mg O_2 L^{-1})	Hardness (meq L^{-1})
Borovoye	7.574 ± 0.27	0.180 ± 0.000	9.734 ± 1.07	14.296 ± 4.35	2.42 ± 0.87
Shchuchye	8.174 ± 0.11	0.0022 ± 0.000	9.344 ± 1.21	6.732 ± 2.80	4.52 ± 1.25
Bolshoe Chebachye	8.258 ± 0.17	0.077 ± 0.027	10.042 ± 0.94	13.012 ± 2.99	13.4 ± 3.9
Maloe Chebachye	8.400 ± 0.19	0.120 ± 0.030	9.960 ± 0.18	12.388 ± 2.23	32.8 ± 1.2
Tekekol	8.680 ± 0.07	0.058 ± 0.002	9.444 ± 1.13	18.262 ± 5.20	7.52 ± 0.14
Zhukey	8.874 ± 0.06	0.198 ± 0.42	10.056 ± 0.85	21.300 ± 5.60	39.8 ± 1.4
Katarkol	8.646 ± 0.11	0.0705 ± 0.11	9.852 ± 1.08	32.460 ± 9.10	6.98 ± 0.18

Table 4. Mean nutrient concentrations in the investigated lakes during 2021–2025, mg L^{-1}.

Lake	NH_4–N	NO_2–N	NO_3–N	PO_4–P
Borovoye	0.262 ± 0.070	0.0172 ± 0.006	0.730 ± 0.310	0.0334 ± 0.005
Shchuchye	0.100 ± 0.015	0.0054 ± 0.006	1.180 ± 0.530	0.0226 ± 0.002
Bolshoe Chebachye	0.192 ± 0.049	0.0080 ± 0.002	0.460 ± 0.170	0.0298 ± 0.008
Maloe Chebachye	0.934 ± 0.770	0.0106 ± 0.002	0.966 ± 0.710	0.0380 ± 0.007
Tekekol	0.260 ± 0.060	0.0136 ± 0.006	0.782 ± 0.300	0.0236 ± 0.006
Zhukey	0.226 ± 0.065	0.0668 ± 0.029	0.510 ± 0.260	0.0718 ± 0.022
Katarkol	0.642 ± 0.160	0.0158 ± 0.004	0.340 ± 0.100	0.0416 ± 0.015

Intermediate values were recorded in Tekekol (895 ± 62 mg L^{-1}), Katarkol (962 ± 39 mg L^{-1}), and Bolshoe Chebachye (1,130 ± 75 mg L^{-1}), whereas Maloe Chebachye (4,810 ± 267 mg L^{-1}) and Zhukey (6,584 ± 1,000 mg L^{-1}) represented the most highly mineralized systems. Mean TDS in Zhukey was approximately 26-fold higher than that in Borovoye (Table 5). TDS differed significantly among lakes (One-Way ANOVA, F (6, 28) = 200.98, $p < 0.001$). Tukey's HSD test identified Zhukey and Maloe Chebachye as distinct high-TDS groups. Bolshoe Chebachye occupied an intermediate position, whereas Borovoye had the lowest TDS. Shchuchye, Tekekol, and Katarkol formed partially overlapping intermediate-to-low groups (Fig. 2). Major-ion composition followed the overall TDS gradient. Borovoye and Shchuchye had comparatively low concentrations of $Na^+ + K^+$, Cl^-, Mg^{2+}, and SO_4^{2-}, with HCO_3^- representing the dominant measured anion by mass. In Maloe Chebachye and Zhukey,

elevated TDS was associated primarily with high concentrations of $Na^+ + K^+$, Cl^-, Mg^{2+}, and SO_4^{2-}. The relative ranking of the lakes by TDS remained generally consistent throughout 2021–2025.

Table 5. Five-year mean total dissolved solids and major-ion concentrations in the investigated lakes during 2021–2025 (mg L^{-1}). Values are mean ± SD of annual means, n = 5 years.

Lake	TDS	$Na^+ + K^+$	Ca^{2+}	Mg^{2+}	Cl^-	SO_4^{2-}	HCO_3^-
Borovoye	254.0 ± 20.9	15.8 ± 4.5	36.2 ± 7.1	11.8 ± 13.7	15.4 ± 3.6	20.8 ± 7.3	134.0 ± 9.5
Shchuchye	413.2 ± 52.8	49.2 ± 9.4	35.8 ± 8.4	28.6 ± 22.1	39.8 ± 3.3	62.0 ± 12.9	184.6 ± 35.0
Bolshoe Chebachye	1,130.4 ± 74.7	171.8 ± 24.4	51.4 ± 4.1	96.4 ± 28.5	174.2 ± 14.0	247.6 ± 54.5	349.8 ± 72.4
Maloe Chebachye	4,809.8 ± 267.2	1,045.6 ± 86.9	80.8 ± 19.2	427.6 ± 196.9	1,594.6 ± 349.3	1,165.6 ± 417.9	379.0 ± 180.3
Tekekol	895.0 ± 61.9	126.6 ± 8.7	32.2 ± 7.9	87.6 ± 36.2	79.2 ± 17.5	116.2 ± 17.4	321.2 ± 151.8
Zhukey	6,583.6 ± 999.5	1,568.2 ± 294.7	32.0 ± 4.5	464.0 ± 39.7	1,811.6 ± 409.1	1,748.2 ± 546.0	668.8 ± 125.9
Katarkol	962.2 ± 39.4	222.4 ± 118.3	37.6 ± 13.7	61.2 ± 10.3	106.2 ± 16.0	122.0 ± 13.0	385.4 ± 54.2

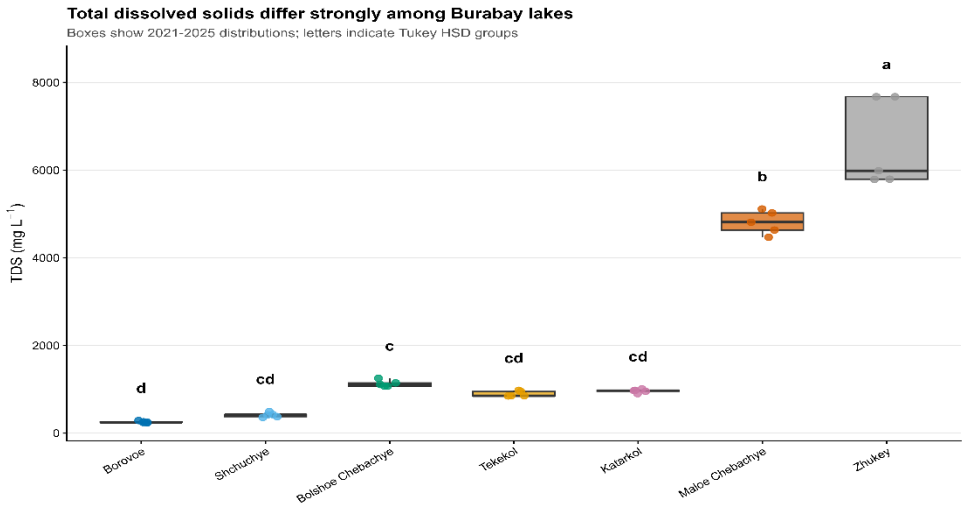


Fig. 2. Distribution of total dissolved solids (TDS) in the seven studied lakes during 2021–2025. Boxes represent interannual distributions, and different lowercase letters indicate significant differences among lakes according to Tukey HSD ($p < 0.05$).

Taxonomic richness of aquatic invertebrates

Observed zooplankton richness ranged from 7 to 22 taxa per lake–year combination. Mean richness across the seven lakes was 17.3 taxa in 2021, 16.4 in 2022, 16.0 in 2023, and 14.0 in both 2024 and 2025. Differences among years were not statistically significant (One-Way ANOVA, $F(4, 30) = 1.19$, $p = 0.337$), and all Tukey's HSD pairwise comparisons were non-significant ($p > 0.05$; Fig. 3A). Spatial variation was more pronounced than interannual variation. Shchuchye had the highest five-year mean zooplankton richness, with 20.2 taxa, whereas Zhukey had the lowest mean, with 11.2 taxa.

Zooplankton assemblages comprised Rotifera, Cladocera, and Copepoda. Shchuchye showed comparatively high richness of rotifers and cladocerans, whereas these groups were less diverse in Zhukey. Macrozoobenthos richness ranged from 13 to 36 taxa per lake–year combination. Mean richness decreased from 30.7 taxa in 2021 to 29.3 in 2022 and 27.0 in 2023, followed by a marked reduction to 18.6 taxa in both 2024 and 2025. The overall difference among years was significant (One-Way ANOVA, $F(4, 30) = 13.07$, $p < 0.001$). Tukey's HSD test showed that richness in 2024 and 2025 was significantly lower than in each of the years 2021–2023 ($p < 0.05$). No significant differences were found among 2021–2023 or between 2024 and 2025 (Fig. 3B). Bolshoe Chebachye had the highest five-year mean macrozoobenthos richness, with 28.0 taxa, followed by Katarkol with 27.0 taxa. Zhukey had the lowest mean richness, with 16.4 taxa. The lower richness recorded in 2024–2025 was accompanied by reduced representation of aquatic insects, particularly Odonata, Ephemeroptera, Hemiptera, and Trichoptera. In

contrast, broadly distributed taxa, including *Gammarus lacustris*, Chironomidae spp., gastropods, and leeches, occurred in several lakes and years.

Fish assemblage composition and model-derived abundance

Species composition and cumulative richness

The fish assemblages included representatives of Cyprinidae, Percidae, Esocidae, Coregonidae, and other taxonomic groups. Species recorded in multiple lakes or years included *Esox lucius*, *Rutilus rutilus*, *Perca fluviatilis*, *Tinca tinca*, *Cyprinus carpio*, *Carassius gibelio*, and *Abramis brama*. Additional cyprinid, coregonid, and predatory species occurred in individual lakes, resulting in marked spatial differences in assemblage composition. Cumulative fish species richness during 2021–2025 was highest in Maloe Chebachye, where 10 species were recorded. Bolshoe Chebachye supported nine species, Katarkol eight, Shchuchye seven, Borovoye six, Tekekol five, and Zhukey four species. Maloe and Bolshoe Chebachye therefore supported the most species-rich assemblages and included several species of fisheries importance. Borovoye, Shchuchye, and Katarkol contained mixed assemblages of cyprinids, percids, and predatory fishes, whereas Zhukey supported the lowest cumulative richness (Fig. 4).

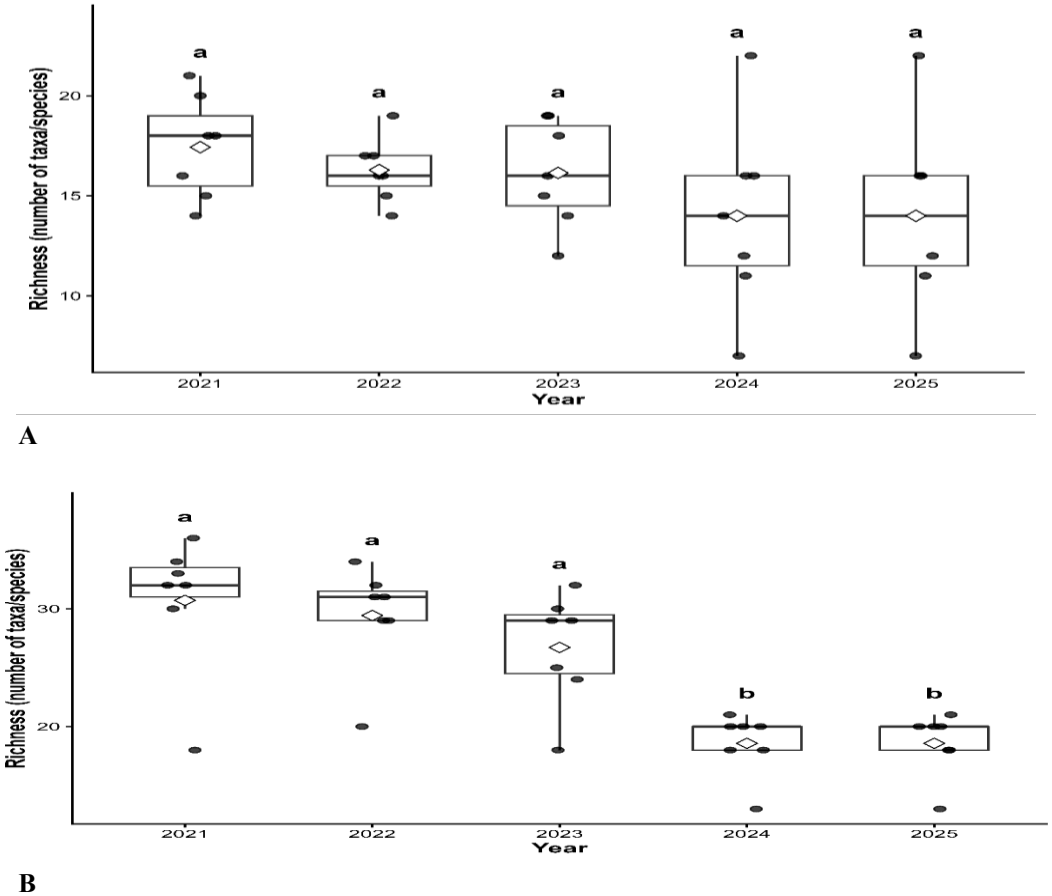


Fig. 3. Interannual variation in observed taxonomic richness of aquatic invertebrates across the seven studied lakes during 2021–2025: (A) zooplankton richness and (B) macrozoobenthos richness. Boxes represent the interquartile range, horizontal lines indicate medians, diamonds indicate means, and points represent individual lakes. Different lowercase letters indicate Tukey's HSD groups ($p < 0.05$).

Interannual variation in fish richness

Fish taxonomic richness remained comparatively stable across the studied lakes during 2021–2025. No significant differences were detected among years (One-Way ANOVA, $F(4, 29) = 0.12$, $p = 0.975$), and all Tukey's HSD pairwise comparisons were non-significant ($p > 0.05$; Fig. 5). The fish richness value for Bolshoe Chebachye in 2023 was unavailable and was excluded from the analysis.

Variation among lakes was more pronounced than variation among years. Maloe Chebachye and Bolshoe Chebachye supported up to nine species in individual years, whereas Zhukey generally supported only two to four

species. Thus, no system-wide interannual change in fish richness was detected, despite persistent spatial differences among the studied lakes.

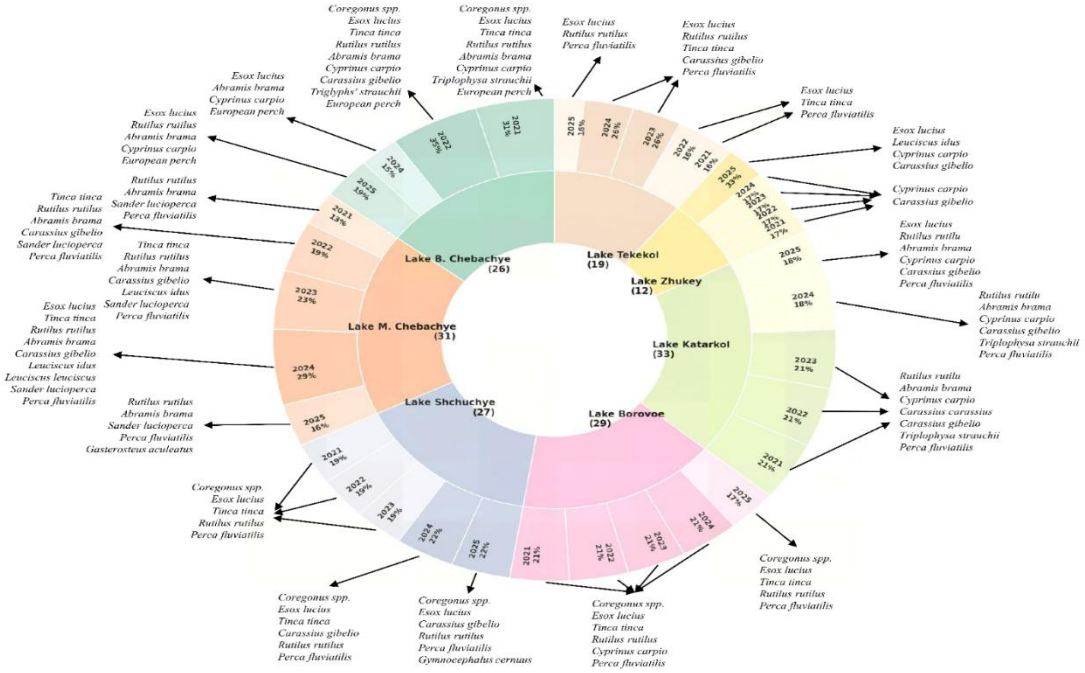


Fig. 4. Spatial and temporal variation in fish species composition across the seven studied lakes during 2021–2025. The inner ring indicates cumulative species richness in each lake, whereas the outer ring shows annual species occurrence records. Arrows link individual lake–year sectors to the corresponding lists of recorded fish species.

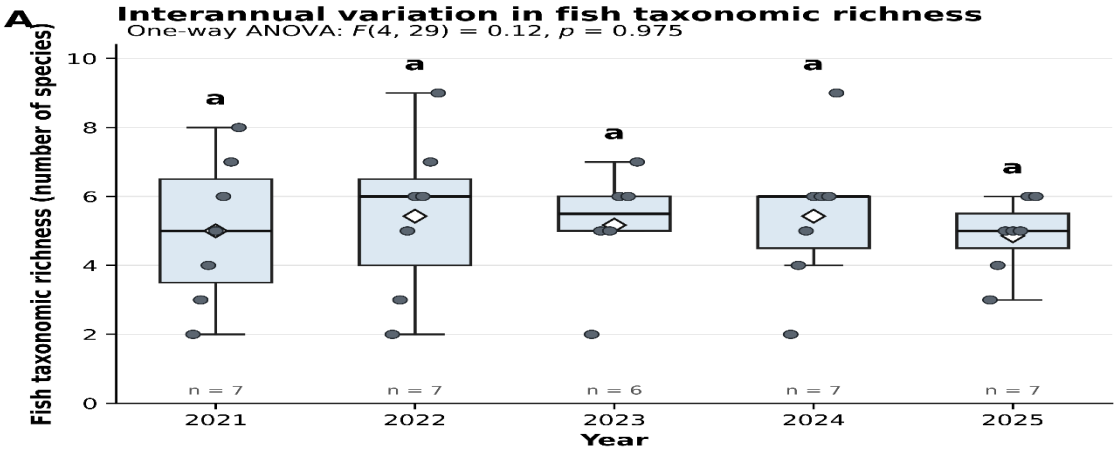


Fig. 5. Interannual variation in fish taxonomic richness across the seven studied lakes during 2021–2025. Boxes represent the interquartile range, horizontal lines indicate medians, diamonds indicate means, and points represent individual lakes. Identical lowercase letters indicate no significant differences among years according to Tukey's HSD test ($p > 0.05$). Sample sizes are shown below the boxes. The fish richness value for Bolshoe Chebachye in 2023 was unavailable and was excluded from the analysis.

Spatial and interannual variation in model-derived fish abundance

Model-derived fish abundance showed substantially greater interannual variability than taxonomic richness and varied markedly among lakes and species (Fig. 6). In Borovoye, total estimated abundance decreased from approximately 2.20 million individuals in 2021 to 1.32 million in 2025, primarily because of a decline in *R. rutilus*. Maloe Chebachye also showed an overall reduction in abundance, with a sharp decline in *R. rutilus* in 2024 accompanied by a pronounced increase in *P. fluviatilis*. Shchuchye maintained comparatively stable total abundance, although dominance shifted from *R. rutilus* toward *P. fluviatilis* and coregonids. In Katarkol, total estimated abundance increased during 2024–2025, whereas Tekekol generally had the lowest abundance estimates, except for a temporary increase in 2024. Zhukey exhibited the strongest interannual variation and was

dominated by *C. carpio* and *Carassius* spp. The estimated abundance of *Carassius* spp. increased from approximately 0.63 million individuals in 2021 to 2.27 million in 2023 and 2.52 million in 2024 before declining to approximately 1.40 million in 2025. *C. carpio* followed a similar pattern, increasing markedly in 2023–2024 and declining in 2025. The abundance data for Bolshoe Chebachye were discontinuous but indicated substantial changes in species contributions among the available years. Overall, the fish assemblages showed pronounced lake- and species-specific variation in estimated abundance and dominance structure.

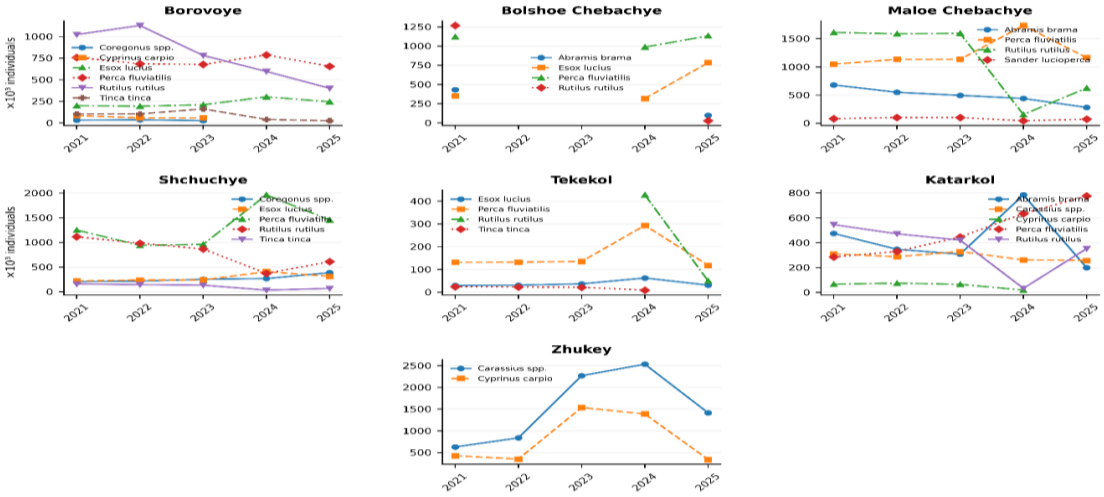


Fig. 6. Species-specific model-derived fish abundance in the seven studied lakes during 2021–2025, expressed as ×10³ individuals. Within each lake panel, colours, symbols, and line types identify individual fish species. Gaps indicate years without numerical abundance estimates. The y-axis scales differ among lakes.

Hydrochemical gradients and biological responses

Principal component analysis identified mineralization as the dominant hydrochemical gradient differentiating the seven studied lakes. The first two principal components explained 80.5% of the total variation, with PC_1 accounting for 63.4% and PC_2 for 17.1%. TDS, hardness, pH, $Na^+ + K^+$, Mg^{2+}, Cl^-, HCO_3^-, and SO_4^{2-} were oriented toward the positive side of PC_1, whereas zooplankton and macrozoobenthos richness were positioned predominantly in the opposite direction. Zhukey occupied the most positive position along the mineralization axis, consistent with its high TDS and major-ion concentrations. Maloe Chebachye was also positioned within the high-mineralization portion of the ordination but was separated from Zhukey along PC_2. Borovoye and Shchuchye occurred at the opposite end of PC_1, whereas Tekekol, Katarkol, and Bolshoe Chebachye occupied intermediate positions (Fig. 7).

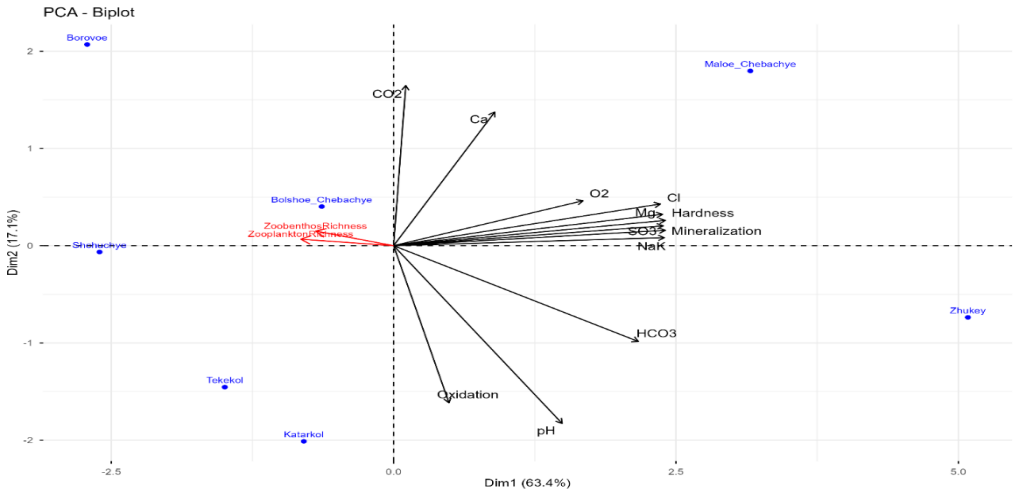


Fig. 7. PCA biplot showing relationships between hydrochemical variables and lake-level mean taxonomic richness of zooplankton and macrozoobenthos across the seven studied lakes during 2021–2025. Points represent individual lakes, and vectors represent hydrochemical and biological variables. PC_1 and PC_2 explained 63.4% and 17.1% of the total variation, respectively.

Species-specific model-derived fish abundance showed several strong lake-level associations with hydrochemical conditions (Fig. 8). *T. tinca* abundance was negatively associated with the principal mineralization variables, with Spearman's rank correlation coefficients ranging from −0.78 to −0.89. *C. lavaretus* abundance was negatively associated with pH, HCO_3^-, and $Na^+ + K^+$ (p = −0.77 to −0.87). *Carassius* spp. abundance was positively associated with both pH and permanganate oxidizability (p = 0.87), whereas *P. fluviatilis* abundance was negatively associated with permanganate oxidizability (p = −0.95) and pH (p = −0.76). Positive associations were also observed between *Abramis brama* abundance and Ca^{2+} (p = 0.87) and between *C. carpio* abundance and CO_2 (p = 0.77). Given the small number of lakes and the large number of pairwise comparisons, these associations were considered exploratory.

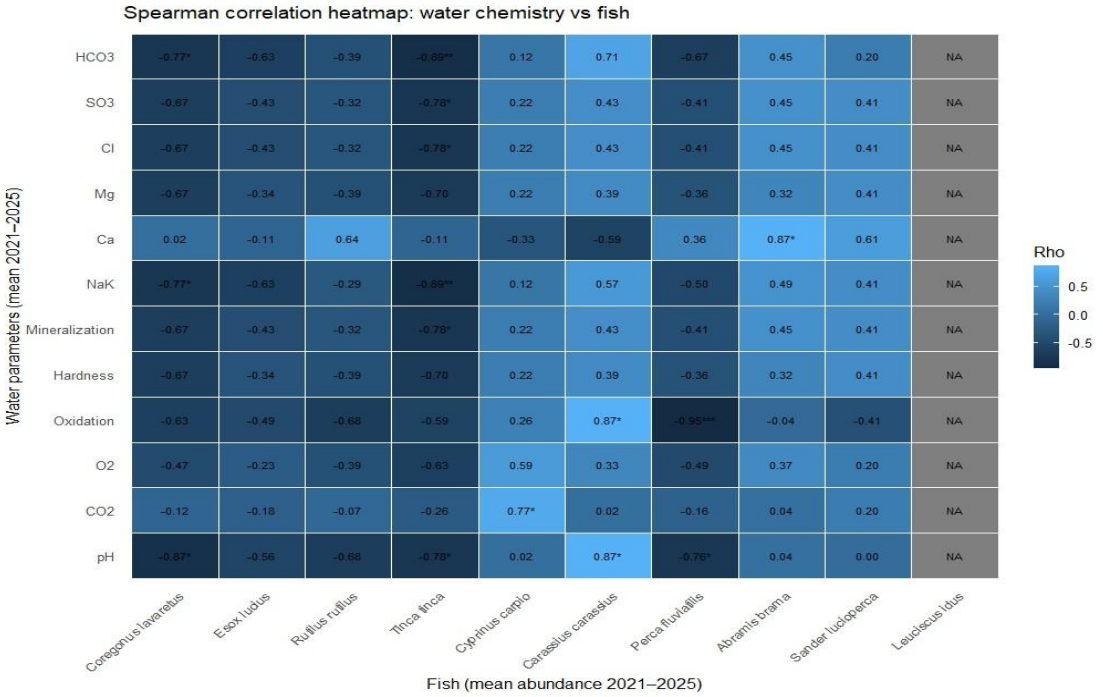


Fig. 8. Spearman correlation heatmap showing relationships between five-year lake-level means of hydrochemical variables and species-specific model-derived fish abundance across the seven studied lakes during 2021–2025. Cell values represent Spearman's rank correlation coefficients (ρ). Asterisks indicate nominal statistical significance (p < 0.05, *p < 0.01, and **p < 0.001), and NA indicates insufficient data for correlation analysis.

For aquatic invertebrates, the Spearman correlation coefficients were consistent with the principal mineralization gradient. Zooplankton richness was negatively associated with pH (p = −0.79), $Na^+ + K^+$ (p = −0.75), hardness (p = −0.71), and Mg^{2+} (p = −0.71). Macrozoobenthos richness showed a positive association with Ca^{2+} (p = 0.76). These relationships indicated a stronger correspondence between mineralization and zooplankton richness than between mineralization and macrozoobenthos richness. Taxonomic richness was also compared among the three descriptive mineralization groups (Fig. 9). Zooplankton richness differed significantly among the groups (One-Way ANOVA, $F(2, 32) = 10.03$, $p < 0.001$). Mean richness was 18.1 taxa in the lower-mineralization group, 16.0 taxa in the intermediate, and 12.3 taxa in the higher one. Tukey's HSD test showed that zooplankton richness was significantly lower in the higher-mineralization group than in both the lower ($p < 0.001$) and intermediate (p = 0.012) ones. The lower and intermediate groups did not differ significantly (p = 0.203). Macrozoobenthos richness did not differ significantly among the mineralization groups [$F(2, 32) = 2.32$, p = 0.114]. Mean richness was 25.6 taxa in the lower, 26.7 taxa in the intermediate, and 21.2 taxa in the higher groups. Fish richness also showed no significant differences among the mineralization groups ($F(2, 31) = 1.66$, p = 0.206). Mean richness was 5.6 species in the lower, 5.5 species in the intermediate, and 4.3 species in the higher groups. Although Zhukey combined high mineralization with low fish richness, Maloe Chebachye retained the highest cumulative fish species richness despite belonging to the same hydrochemical group. Fish assemblage structure therefore differed substantially between lakes with similarly high TDS. Overall, mineralization constituted the principal hydrochemical axis differentiating the studied lakes. The clearest associated biological pattern was observed for zooplankton richness, which decreased toward the high-mineralization end of the gradient. Macrozoobenthos and

fish richness showed greater overlap among the mineralization groups, whereas fish assemblages were differentiated more strongly by species composition, abundance, and dominance structure than by total taxonomic richness.

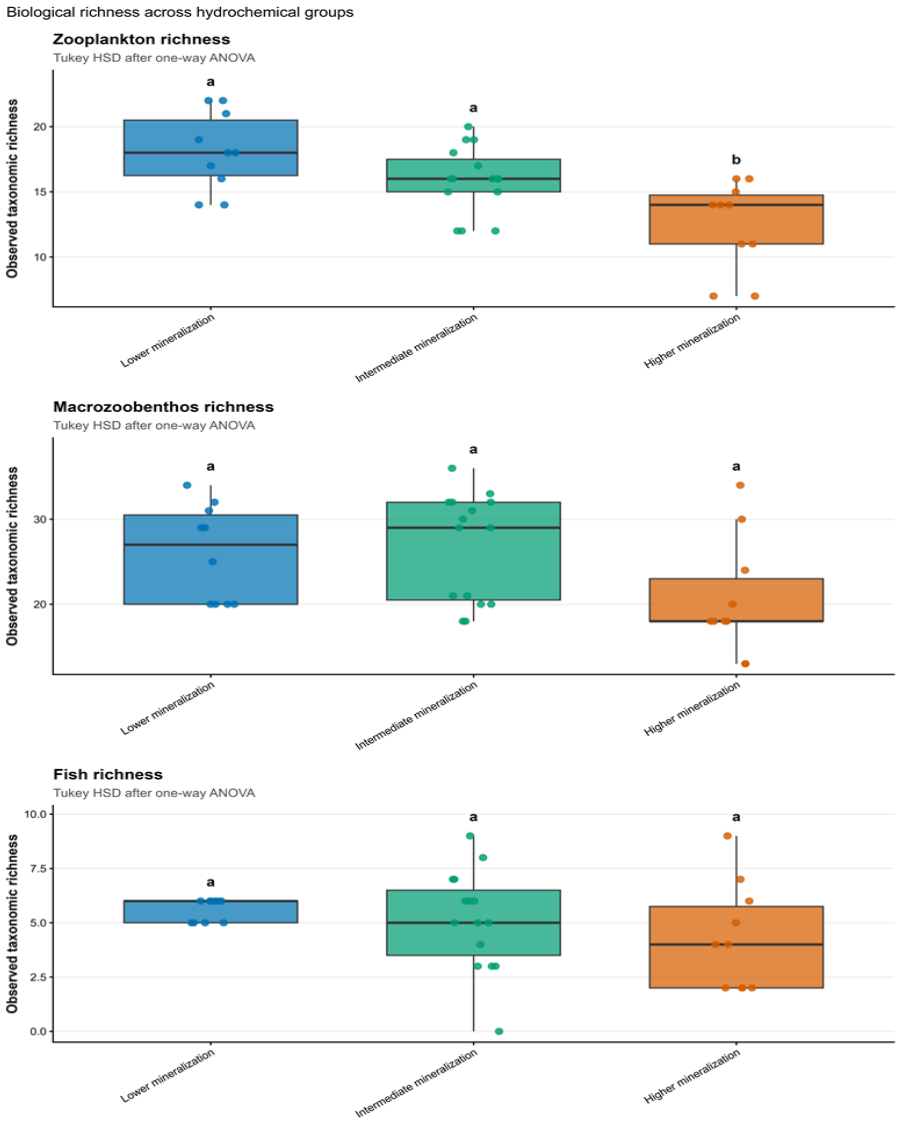


Fig. 9. Observed taxonomic richness across the lower-, intermediate-, and higher-mineralization lake groups for (A) zooplankton, (B) macrozoobenthos, and (C) fish. Boxes represent the interquartile range, horizontal lines indicate medians, and points represent individual lake–year values. Different lowercase letters indicate significant differences among mineralization groups according to Tukey's HSD test ($p < 0.05$); identical letters indicate no significant difference.

DISCUSSION

The results demonstrate that the ecological differentiation of the studied lakes was driven primarily by persistent spatial variation in hydrochemical conditions, whereas biological responses differed among organism groups and levels of community organization. Zooplankton richness was most clearly associated with the mineralization gradient, macrozoobenthos showed a stronger temporal change, and fish assemblages varied mainly in abundance and dominance structure rather than in total species richness. These contrasting responses support the use of integrated hydrochemical, biological, habitat, and fisheries indicators, since no single parameter can reliably distinguish natural lake-specific variability from ecological degradation under interacting pressures such as salinization, eutrophication, climate change, habitat modification, and resource use (Zhao *et al.* 2025; Jeppesen *et al.* 2015). The consistent separation of the lakes along the principal mineralization axis and the generally stable ranking of their TDS values during 2021–2025 suggest strong control by lake-specific characteristics. Catchment geology, basin morphology, hydrological connectivity, groundwater inputs, water residence time, and the balance

between inflow and evaporation probably contributed to the persistence of these differences. Consequently, highly mineralized lakes should not automatically be regarded as degraded forms of lower-mineralization systems. Their ecological condition must be evaluated relative to their natural hydrochemical type and should account for ionic composition, alkalinity, hardness, nutrient availability, and organic loading in addition to TDS. Freshwater salinization is increasingly recognized as a multidimensional process, since individual ions have different physiological and ecological effects and can interact with eutrophication and other environmental stressors (Herbert *et al.* 2015; Kaushal *et al.* 2018; Cunado *et al.* 2023). The comparatively similar mean dissolved-oxygen concentrations among lakes should not be interpreted as evidence of uniformly favourable oxygen conditions. Annual or whole-water-column averages may conceal short-term and near-bottom hypoxia during thermal stratification, under ice cover, or periods of intensive organic-matter decomposition. Such events may be particularly important in deeper lakes and can affect nutrient release from sediments, benthic invertebrates, fish recruitment, and overwinter survival. Climate-related changes in thermal structure may further prolong stratification and restrict oxygen renewal in bottom waters (Woolway *et al.* 2020; Jane *et al.* 2021). Therefore, the ecological significance of oxygen conditions depends on their vertical and seasonal dynamics rather than on mean concentrations alone. Zooplankton displayed the clearest biological response to the combined mineralization–alkalinity gradient. Its lower richness in the higher-mineralization group and its position opposite TDS, hardness, pH, and major-ion variables in the PCA are consistent with environmental filtering of sensitive freshwater taxa. Elevated ionic concentrations can impose osmoregulatory stress, alter food-web interactions, and reduce the suitability of habitats for salt-sensitive rotifers, cladocerans, and copepods. Experimental and field studies have similarly shown that salinization can reduce zooplankton abundance, biomass, body size, taxonomic richness, and functional diversity, although the magnitude of the response differs among taxonomic groups and ionic compositions (Van de Meutter *et al.* 2008; Hintz & Relyea 2019). Nevertheless, the contrasting biological characteristics of Maloe Chebachye and Zhukey show that TDS alone cannot explain community diversity. Despite both lakes belonging to the higher-mineralization group, they differed substantially in biological richness and fish assemblage composition. This divergence suggests that mineralization interacted with lake depth, nutrient and organic-matter availability, habitat heterogeneity, food resources, hydrological conditions, and predation pressure. Because pH, hardness, TDS, and major-ion concentrations covaried along the same ordination axis, the negative association between zooplankton richness and pH is more appropriately interpreted as a response to the broader saline–alkaline environment than as an isolated pH effect. The absence of significant interannual differences in zooplankton richness does not necessarily indicate complete ecological stability. Taxonomic richness can remain relatively constant while assemblages undergo substantial changes in abundance, biomass, body-size distribution, taxonomic identity, feeding strategy, and functional composition. Replacement of sensitive taxa by tolerant forms may therefore simplify food-web structure without producing an immediate decrease in the total number of recorded taxa. Functional traits and quantitative community characteristics may consequently provide earlier or more sensitive evidence of ecological change than richness alone (McGill *et al.* 2006; Barnett *et al.* 2007; Litchman *et al.* 2013). Macrozoobenthos exhibited a different response pattern. Its marked reduction in richness during 2024–2025, combined with the absence of a significant difference among mineralization groups, suggests that the recent temporal decline cannot be attributed solely to the spatial TDS gradient. The reduced representation of Odonata, Ephemeroptera, Hemiptera, and Trichoptera may reflect changes in near-bottom oxygen conditions, sediment quality, organic deposition, macrophyte cover, substrate heterogeneity, water level, or shoreline disturbance. These factors directly affect benthic habitat availability and may operate independently of, or interact with, water-column mineralization. The persistence of broadly tolerant taxa, including chironomids, gastropods, leeches, and *Gammarus lacustris*, is also consistent with combined chemical and habitat filtering. The positive association between macrozoobenthos richness and Ca^{2+} may reflect the importance of calcium for calcifying organisms and overall ionic balance. However, calcium also covaries with hardness, catchment lithology, buffering capacity, and sediment mineralogy; therefore, the observed relationship probably represents a broader geological and habitat context rather than a direct effect of calcium alone. Studies of freshwater and saline inland waters similarly indicate that benthic assemblages are jointly structured by salinity, nutrients, depth, vegetation, sediment characteristics, oxygen conditions, and habitat quality (James *et al.* 2003; Ding *et al.* 2021). Fish assemblages showed weaker correspondence with the overall mineralization gradient than zooplankton. Fish species richness remained comparatively stable among years and mineralization groups, whereas model-derived abundance and dominance structure changed considerably. This divergence indicates that

richness alone is insufficient for evaluating fish-community dynamics. The loss or reduction of one dominant species may be compensated numerically by another species without changing total richness, even though trophic structure, productivity, recruitment, and ecosystem functioning are substantially altered. The species-specific correlations further suggest that fish responses to hydrochemical conditions were ecologically differentiated. The negative relationships of *Tinca tinca* and *Coregonus lavaretus* with mineralization-related variables are consistent with their association with comparatively fresh or less alkaline conditions. Conversely, the positive relationships of *Carassius* spp. with pH and permanganate oxidizability may reflect the tolerance of crucian carp to chemically variable, productive, and organically enriched waters.

The negative association of *Perca fluviatilis* with permanganate oxidizability may indicate less favourable conditions under elevated organic loading. Associations involving *Abramis brama*, *Cyprinus carpio*, calcium, and CO_2 may similarly reflect combinations of productivity, habitat conditions, and lake type rather than direct effects of individual chemical variables. Since these correlations were based on only seven lake-level observations and numerous pairwise comparisons, they should be regarded as exploratory ecological patterns rather than evidence of causal relationships. Fish assemblages integrate environmental conditions over relatively long periods and are additionally influenced by spawning habitat, food availability, winter oxygen conditions, recruitment success, fishing pressure, stocking, and historical introductions. Their ecological status should therefore be evaluated using species composition, trophic and reproductive guilds, size and age structure, recruitment, biomass, and the proportions of native, introduced, tolerant, and sensitive species. The comparatively high cumulative richness of Maloe Chebachye despite its elevated mineralization reinforces the importance of habitat characteristics and fisheries-management history in modifying the expected effects of water chemistry. Historical introductions and continued stocking may obscure relationships between contemporary hydrochemical conditions and fish-community structure. Research in the Alakol lake system has likewise shown that present fish distributions reflect interactions among mineralization, temperature, hydrological connectivity, and historical species introductions. The pronounced changes in model-derived abundance observed in several of the studied lakes may therefore reflect both ecological processes and management interventions. These estimates are most informative for relative comparisons, since they remain sensitive to fish movement, encounter probability, catchability, mesh selectivity, effective fishing area, and net exposure. Their interpretation should be supported by standardized numerical and biomass catch per unit effort, population age and size structure, recruitment data, harvest statistics, and stocking records. Habitat-oriented management may provide more sustainable fish-population responses than repeated stocking alone (Cowx 2002).

The combined results indicate that ecological assessment and management should be adapted to the natural hydrochemical type of each lake. Lower-, intermediate-, and higher-mineralization systems should not be evaluated against a single reference condition. Instead, lake-specific baselines should distinguish persistent natural mineralization from directional changes associated with declining inflow, enhanced evaporation, nutrient enrichment, organic pollution, or shoreline disturbance. This interpretation is consistent with regional studies showing that salinity and organic pollution structure aquatic communities in the Burabay Lake system and that combined hydrochemical and biological assessments provide more informative conclusions than individual indicator groups (Barinova *et al.* 2023; Tekebayeva *et al.* 2024). Interpretation of temporal patterns was limited by unequal annual sampling effort, the use of raw richness values, missing observations, and the small number of lake-level data points available for multivariate and correlation analyses.

The use of five-year means also emphasized persistent spatial differences while reducing information on seasonal and interannual variability. These limitations restrict causal inference but do not negate the pronounced hydrochemical differentiation among the lakes or the contrasting responses of zooplankton, macrozoobenthos, and fish. Future monitoring should employ balanced seasonal sampling at fixed stations and retain data at the station–date and lake–year levels. Comparisons of taxonomic richness should be standardized by sampling effort and completeness, while hierarchical or mixed-effects models could account for repeated observations within lakes. Biological monitoring should incorporate abundance, biomass, body-size distributions, functional traits, and community composition. Environmental monitoring should additionally include vertical temperature and dissolved-oxygen profiles, water levels, sediment characteristics, macrophyte cover, shoreline pressures, and fisheries-management records. Such an integrated design would improve the distinction between natural lake-specific variability and directional ecological change and would provide a stronger basis for lake-specific conservation and management decisions.

CONCLUSION

The five-year assessment revealed pronounced and persistent hydrochemical differentiation among the seven studied lakes, with mineralization, hardness, pH, and major-ion composition forming the principal environmental gradient. Biological responses to this gradient differed among organism groups. Zooplankton richness showed the clearest relationship with hydrochemical conditions and was significantly lower in the higher-mineralization lake group. Macrozoobenthos richness did not differ significantly among mineralization groups but declined markedly during 2024–2025, indicating the probable importance of temporal changes in habitat, sediment, and near-bottom conditions. Fish taxonomic richness remained comparatively stable, whereas model-derived abundance and species dominance varied substantially among lakes and years. The contrasting biological characteristics of lakes with similarly high TDS demonstrate that mineralization alone does not determine aquatic-community structure. The observed patterns reflected the combined influence of ionic composition, nutrient and organic-matter conditions, lake morphometry, habitat characteristics, trophic interactions, hydrological regime, stocking history, and fisheries pressure. Consequently, lake condition should be evaluated relative to lake-specific hydrochemical and ecological baselines using an integrated set of water-quality, biological, habitat, and fisheries indicators. Model-derived fish abundance estimates are most appropriate for relative comparisons and should be interpreted together with standardized numerical and biomass CPUE, population structure, recruitment, harvest, and stocking data. Future research should employ fixed monitoring stations, standardized seasonal surveys, and balanced annual sampling effort. Taxonomic richness should be complemented by standardized measurements of abundance, biomass, body-size distribution, functional composition, and fish CPUE. Retaining observations at the station–date and lake–year levels and analysing them using mixed-effects and multivariate approaches would improve the assessment of spatial and temporal variability. Integration of biological observations with water-level dynamics, vertical temperature and dissolved-oxygen profiles, sediment and habitat characteristics, shoreline pressures, and fisheries-management records will provide a stronger basis for distinguishing natural ecosystem variability from climatic and anthropogenic change and for developing lake-specific conservation and management strategies.

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