

Article

Diet Composition and Trophic Niches of the Fish Community in Lake Balkhash

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Abstract

Lake Balkhash is a large endorheic lake experiencing ongoing hydrological and climatic variability. This study aimed to evaluate the species composition and structure of the forage base across three trophic levels—phytoplankton, zooplankton, and zoobenthos—and to analyze trophic interactions of fish communities, including non-native species, in order to assess the functioning of the food web in the western and eastern basins of the lake. A 2025 assessment revealed a structurally reorganized yet relatively stable ecosystem. Phytoplankton showed an increase in taxonomic richness, while zooplankton and zoobenthos demonstrated compositional restructuring with a greater representation of ecologically tolerant taxa. The presence of certain invertebrate taxa in both Lake Balkhash basins indicates persistent spatial heterogeneity of the ecosystem. Despite moderate ecological resilience, biodiversity has not yet returned to historically recorded peak levels. Trophic analysis of fish communities showed generally moderate niche overlap among benthivorous species with localized differentiation of resource use. Predatory fishes also exhibited moderate overlap: pikeperch (*Sander lucioperca*) maintained stable dietary patterns with partial overlap with Volga pikeperch (*Sander volgensis*), whereas snakehead (*Channa argus*) and asp (*Aspius aspius*) demonstrated clearer trophic segregation. Non-native species displayed relatively narrow trophic niches ($Bi < 0.30$), indicating summer feeding specialization.

Keywords: Lake Balkhash; trophic structure; niche overlap; phytoplankton; zoobenthos; benthivorous fish; predatory fish; ecological resilience; non-native species



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1. Introduction

The dynamics of forage organism communities (phytoplankton, zooplankton, and benthos) in lake ecosystems are influenced by a complex interplay of natural–climatic and anthropogenic factors [1]. Within these systems, these organisms constitute the trophic foundation that supports the functioning and productivity of higher-level consumers, particularly fish communities [2,3]. However, existing studies in this field are generally limited to the analysis of individual invertebrate groups or isolated components of fish food chains, lacking an integrated assessment of the entire forage base of the ecosystem [4–6].

Fish represent key functional components of lake food webs, occupying a wide spectrum of trophic niches and facilitating the transfer of matter and energy from basal resources to higher trophic levels of the ecosystem [7]. Understanding trophic relationships among

fish species, the nature of interspecific and intraspecific competition, as well as the composition and structure of the forage base, provides a scientific basis for the development of management measures aimed at conserving fish resources and, where necessary, improving ecosystem feeding conditions [8].

For Lake Balkhash (Kazakhstan), an ecosystem characterized by a long history of the formation and transformation of both invertebrate and fish communities, research in this field remains highly relevant under current environmental change driven by climatic factors, hydrological fluctuations, anthropogenic pollution, and shifting fishing pressure [9–11]. Large-scale introductions of forage invertebrates into Lake Balkhash during the 20th century contributed to increased fish productivity. However, subsequent interruptions and insufficient follow-up studies and management measures may have led to reduced taxonomic diversity and structural simplification of forage communities [12–14]. Stocking efforts in Eastern Balkhash with the polychaete *Nereis diversicolor* (O.F. Müller) and the bivalve *Abra ovata* (Philippi) have been reported by the Balkhash branch of the Research and Production Center for Fisheries [15]. Such transformations—manifested as both enrichment and regression of species diversity—can substantially influence the formation and functioning of fish trophic chains, ultimately affecting fish productivity, the structure of commercial stocks, and shifts in dominant species within the ichthyocenosis.

Monitoring changes in the species diversity of forage invertebrates allows for the assessment of competition intensity for food resources [16]. When competition for shared resources arises, spatial redistribution of organisms may occur, accompanied by altered habitat use and potential trophic niche overlap not previously observed within the community structure [17]. Given the large area of Lake Balkhash (16.4 thousand km²) and its pronounced spatial heterogeneity in physicochemical parameters—particularly salinity differences between the western and eastern basins—analysis of the forage base and fish trophic relationships is essential to identify inter-basin differences in dietary structure and food-web organization. The salinity of the lake increases sharply from west to east. In the western part of Lake Balkhash, mineralization values range from 680 to 2200 mg/dm³ (0.68–2.2 g/L), whereas in the eastern part they reach 4900–5600 mg/dm³ (4.9–5.6 g/L) [18].

In the present study, a comprehensive assessment of species composition and structure of the forage base was conducted across three trophic levels: phytoplankton, zooplankton, and zoobenthos. Based on these data, fish diets were analyzed, with particular attention to contemporary trophic linkages involving non-native species and the degree and nature of their competitive interactions. This integrative approach enabled evaluation of food-web functioning as a unified system and clarified the role of different forage components in maintaining the trophic structure of fish communities in the western and eastern parts of Lake Balkhash.

2. Materials and Methods

2.1. Study Area

Lake Balkhash is the 15th largest lake in Asia and is located in the arid zone of southeastern Kazakhstan [1,19]. Figure 1a illustrates the position of Lake Balkhash within the hydrological network of the Balkhash–Alakol Basin (Kazakhstan). According to data from the Balkhash meteorological station, the mean annual precipitation is 129.8 mm, and the mean annual air temperature is 5.9 °C. The lake is primarily fed by inflow from southern rivers, the most important of which are the Ili, Karatal, Aksu, and Lepsy rivers [20]. A pronounced west-to-east gradient in water mineralization is observed within the lake. Overall salinity remains relatively low: in the western basin, values range from 0.7 to 2.1 g/dm³, whereas in the eastern basin salinity gradually increases to 5.0 g/dm³ and, in some years, may reach 7.0 g/dm³ [21].

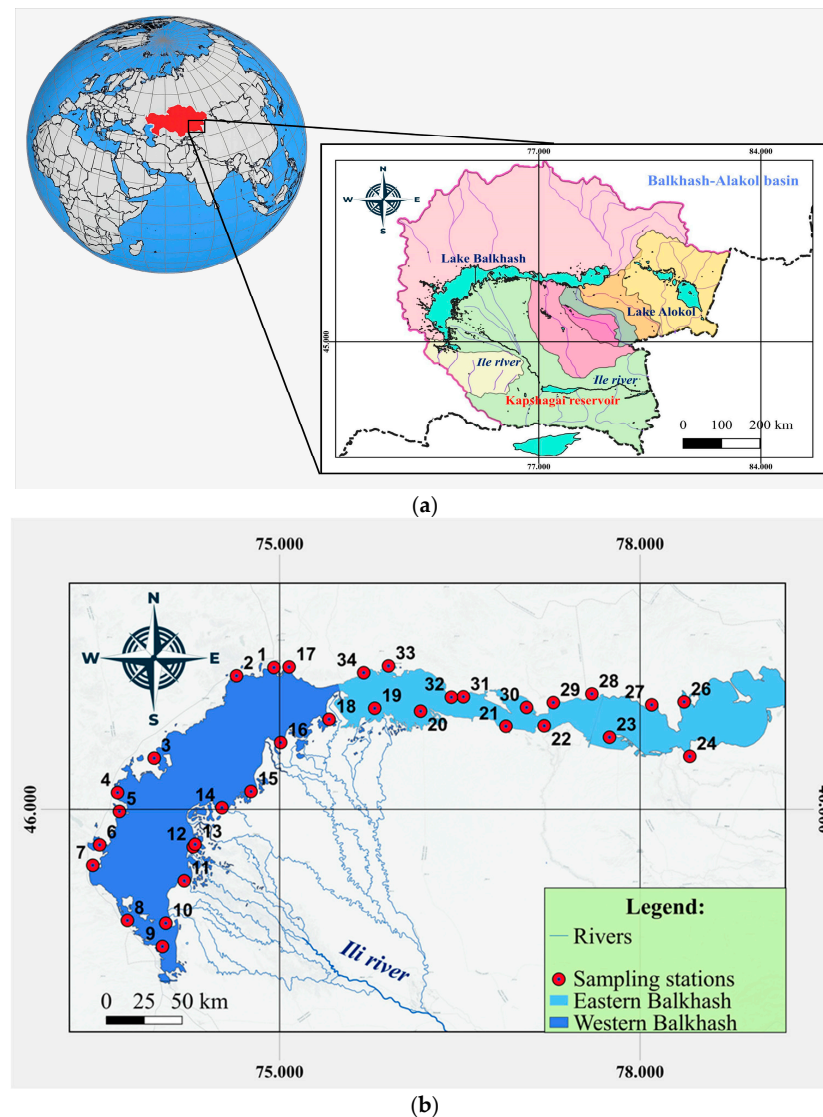


Figure 1. Geographic location of the study area within the Balkhash–Alakol Basin, Kazakhstan (a); sampling stations for the assessment of forage organism species composition and fish diet analysis in the eastern and western parts of Lake Balkhash (b).

Lake Balkhash represents a major fishery water body, supplying resources for both domestic consumption and export; in certain years, it accounts for approximately 25% of the total commercial fish catch in Kazakhstan [22].

2.2. Hydrochemical Analysis

Hydrochemical investigations included the determination of the gas regime, pH, organic matter content, ionic composition, and nutrient concentrations. Water samples were collected at all sampling stations using standard hydrochemical sampling procedures. Laboratory analyses were carried out using certified laboratory equipment in accordance with the requirements established for accredited laboratories [23–25].

2.3. Phytoplankton Sampling Method and Taxonomic Identification

Phytoplankton samples were processed according to established procedures described in the literature [26,27]. Phytoplankton were examined microscopically using a Primo Star microscope (Carl Zeiss, Jena, Germany) at magnifications of 40× and 100×. Taxonomic identification of planktonic algae was conducted using standard taxonomic keys and

identification manuals [28–33]. After collection, samples were stored in darkness for 3–4 days to allow sedimentation. Subsequently, the supernatant was carefully removed by siphoning through a fine-mesh sieve until the residual volume reached approximately 100 cm³. Before secondary sedimentation (2–3 days in darkness), samples were transferred into graduated cylinders. After settling, the volume was further concentrated to 5–10 cm³ by siphoning. The concentrates were then transferred into penicillin vials and fixed with one or two drops of 40% formaldehyde solution.

2.4. Zooplankton Sampling Method and Taxonomic Identification

A sampling of zooplankton was carried out simultaneously with the collection of hydrochemical samples at the same sampling sites. Zooplankton was collected using a Juday plankton net (mesh size 30 µm) by towing it from the bottom to the surface. The filtered water was transferred into 250 mL plastic containers and preserved with a 4% formaldehyde solution [26,27]. Zooplankton specimens were identified using standard taxonomic keys and species identification guides [34–41]. For the identification of various groups of planktonic invertebrates, both classical and modern identification keys were used. Rotifers (Rotifera) were identified using the key, which included morphological keys for genera and species of the USSR fauna [34]. General Cladocera representatives were identified using standard identification keys [36], while freshwater Cyclopoida were identified using appropriate taxonomic keys [37]. Freshwater Calanoida were identified using general identification keys [35] and a regional guide to the Calanoida fauna of Kazakhstan [38]. The families Chydoridae were identified using the keys [40], which included morphological identification tools for genera and species of the world fauna. The modern European identification key [41] provided morphological descriptions and reference tables for synonyms, distribution, and ecology of Cladocera and Copepoda (Calanoida, Cyclopoida). For the comprehensive identification of freshwater crustaceans, the key [42] intended for Russia and neighboring regions was used.

Planktonic animals were examined microscopically using an MBS-10M binocular stereomicroscope (Biomed, St. Petersburg, Russia) and a Primo Star microscope (Carl Zeiss, Jena, Germany) at magnifications of 40× and 100×. The collected samples were concentrated to a final volume of 150–400 cm³. After thorough homogenization, three sub-samples were withdrawn using a 1 mL pipette. In these subsamples, all individuals and 119 developmental stages of selected species (primarily the most abundant) were enumerated using a Bogorov counting chamber [43], which consists of a glass plate with interconnected channels separated by partitions. Subsequently, the sample was further concentrated to 125–150 cm³, and three additional subsamples were taken to count juvenile stages and rare species. This procedure was repeated once more after concentration to 50 cm³. The entire sample was examined to detect rare species that were not observed in previous subsamples.

2.5. Zoobenthos Sampling Method and Taxonomic Identification

Zoobenthos samples were collected using a Petersen grab with a sampling area of 0.025 m² [26]. The sediment was washed through a No. 23 millimetre mesh sieve until the fine sediment fractions were completely removed. Living organisms were manually picked from the sediment and placed into labeled glass containers, after which they were preserved in 4% formaldehyde solution. Organisms were identified and enumerated in the laboratory using an MBS-10M binocular stereomicroscope (Biomed, St. Petersburg, Russia) and a SOPTOP EX30 microscope (SOPTOP, Ningbo, China) at magnifications of 40× and 100×. Taxonomic keys appropriate for the respective groups and species were used [42,43]. Nekto-benthos material was collected using a bottom trawl with a mouth

opening of 0.75×0.35 m, towed over a distance of 10 m. Subsequent processing of these samples was conducted in the same manner as for the zoobenthos samples.

2.6. Fish Diet Sampling

Fish sampling and collection of dietary data were conducted across the western and eastern parts of Lake Balkhash. Figure 1 shows the sampling stations for non-native fish species, while the geographic coordinates of the stations are provided in Table 1.

Table 1. Geographic coordinates of sampling stations in the western and eastern parts of Lake Balkhash.

Western Balkhash			
1	Bertys Bay	46°48'46" N	74°57'09" E
2	Shubartyubek	46°45'57" N	74°38'29" E
3	Tasaral	46°17'43" N	73°57'21" E
4	Bolshoy Saryshagan	46°05'48" N	73°39'04" E
5	Priozersk	45°59'18" N	73°39'59" E
6	Kashkantenez	45°47'42" N	73°30'08" E
7	Karakamysh	45°40'36" N	73°26'42" E
8	Akkerme	45°21'20" N	73°44'00" E
9	Forest Islands	45°12'11" N	74°01'29" E
10	Ili River Mouth	45°20'22" N	74°03'10" E
11	Karauzyak	45°35'11" N	74°12'22" E
12	Проток Иир	45°46'59" N	74°16'52" E
13	Iir Channel	45°47'53" N	74°17'48" E
14	Maytan	46°00'35" N	74°31'12" E
15	Akhmetsuat	46°06'12" N	74°45'42" E
16	Tomar	46°23'04" N	75°00'31" E
17	Maly Saryshagan	46°48'58" N	75°04'44" E
Eastern Balkhash			
18	Orlinaya	46°31'02" N	75°24'41" E
19	Ultarakhty	46°34'50" N	75°47'29" E
20	Karabas	46°33'50" N	76°10'22" E
21	Shomyshkol	46°28'40" N	76°52'59" E
22	Karatal River Mouth	46°28'49" N	77°12'06" E
23	Karakol	46°24'54" N	77°44'43" E
24	Karashygan	46°18'19" N	78°24'48" E
25	Ayagoz River Mouth	46°39'34" N	79°13'45" E
26	Zhalanash	46°37'02" N	78°21'57" E
27	Tolepshapkan	46°36'01" N	78°05'47" E
28	Maykamysh	46°39'45" N	77°35'54" E
29	Balyktykol	46°36'48" N	77°16'39" E
30	Sarykamysh	46°35'07" N	77°03'17" E
31	Asambaykol	46°38'46" N	76°31'45" E
32	Tkshoky	46°38'38" N	76°25'45" E
33	Akzhaydak	46°49'19" N	75°54'22" E
34	Belen	46°47'00" N	75°41'59" E

Identification and quantitative assessment of forage organisms were performed using an MBS-10 binocular stereomicroscope, as well as MSKh-200 and MSKh-300 microscopes. Taxonomic identification and assignment of organisms to trophic groups were carried out according to standard identification keys for aquatic invertebrates [38–42].

Diet samples were collected from nine fish species during the summer period of 2025. Among them, four species were classified as non-predatory and five as predatory. The captured fish were assigned to the corresponding trophic groups (Table 2).

Table 2. Fish Species of Western and Eastern Balkhash Used for Diet Composition Analysis and Trophic Classification.

Species	Trophic Group	Number of Examined Specimens N (W/E)
<i>Cyprinus carpio</i> Linnaeus, 1758 ^a	Benthivore–omnivore	47/26
<i>Abramis brama</i> Linnaeus, 1758 ^a	Benthivore	39/37
<i>Rutilus caspicus</i> Yakovlev, 1870	Omnivore–benthoplanktivore	25/25
<i>Carassius gibelio</i> Bloch, 1782 ^a	Omnivore–benthivore	25/18
<i>Sander lucioperca</i> Linnaeus, 1758 ^a	Predator	55/42
<i>Sander volgensis</i> Gmelin, 1789	Predator	30/30
<i>Silurus glanis</i> Linnaeus, 1758	Predator	13/17
<i>Channa argus</i> Cantor, 1842	Predator	17/12
<i>Aspius aspius</i> Linnaeus, 1758 ^a	Predator	19/15

Note: Number of specimens examined for diet analysis in Western/Eastern Balkhash. ^a—Introduced species.

Prior to analysis, the captured fish specimens were measured for total length to the nearest 1 mm and weighed to the nearest 0.1 g. To determine the composition of the consumed food, stomachs were extracted. For this purpose, a longitudinal incision was made along the ventral side of the fish from the region immediately posterior to the gill isthmus to the anal fin. The digestive tract (esophagus, stomach, and intestine) was then separated from the other internal organs and preserved in 5% neutralized formalin for subsequent laboratory analysis [44].

Diet analysis was performed on individuals of different age classes and size groups within the studied fish species. The main biological parameters of the sampled specimens are presented in Table 3.

Table 3. Biological characteristics of fish species collected from the western and eastern parts of Lake Balkhash.

Species	Mean ± SD				Mean Age	
	l (mm)	Q (g)	l (mm)	Q (g)	Western Balkhash	Eastern Balkhash
	Western Balkhash		Eastern Balkhash			
<i>C. carpio</i>	309.3 ± 11.29	861.6 ± 101.3	296.9 ± 13.7	788.1 ± 83.6	5.1 ± 0.3	4.9 ± 0.3
<i>A. brama</i>	227.5 ± 6.35	219.2 ± 17.2	215.8 ± 4.4	210.5 ± 13.62	5.6 ± 0.3	5.3 ± 0.2
<i>R. caspicus</i>	157 ± 3	78.4 ± 4.6	159.3 ± 4.5	92.2 ± 7.6	3.6 ± 0.2	3.4 ± 0.2
<i>C. gibelio</i>	202.9 ± 4.58	273.2 ± 20.1	174.2 ± 6	191.8 ± 23.6	5.5 ± 0.2	4.1 ± 0.2
<i>S. lucioperca</i>	280.5 ± 9.6	342.9 ± 47.9	303.6 ± 9.1	389.2 ± 39.4	3.6 ± 0.2	4.2 ± 0.2
<i>S. volgensis</i>	191.8 ± 4.9	104.4 ± 6.9	222.5 ± 3.0	160.9 ± 6.5	4.1 ± 0.1	4.8 ± 0.1
<i>S. glanis</i>	592.7 ± 31.2	2504.7 ± 377.5	652.5 ± 28.5	2994.9 ± 366.5	4.6 ± 0.4	6.1 ± 0.4
<i>C. argus</i>	501.4 ± 11.42	1581.1 ± 104.02	492.4 ± 15.4	1618.3 ± 92.2	6.2 ± 0.3	5.8 ± 0.2
<i>A. aspius</i>	405.9 ± 7.39	1065.1 ± 57.3	294.3 ± 5.3	419.5 ± 22.1	7 ± 0.3	4 ± 0.2

2.7. Diet Analysis

To assess the degree of trophic similarity among the studied fish species, Pianka's niche overlap index was applied [40]. The value of Pianka's index ranges from 0 (no trophic niche overlap) to 1 (complete overlap), allowing quantitative evaluation of dietary similarity between species. The index values were interpreted as follows: $O_{jk} \geq 0.50$ was considered indicative of high trophic niche overlap and, consequently, a high potential for competitive interaction, whereas $O_{jk} < 0.50$ indicated low overlap. The index was calculated according to the standard formula described in [45,46].

$$O_{jk} = \frac{\sum_{i=1}^n P_{ij}P_{ik}}{\sqrt{\left(\sum_{i=1}^n P_{ij}^2\right) \left(\sum_{i=1}^n P_{ik}^2\right)}}$$

O_{jk} —niche overlap index between species j and k ; p_{ij} and p_{ik} —proportions of the i -th food item in the diets of species j and k , respectively; n —total number of food item categories considered in the analysis.

Trophic niche breadth was estimated using Levin's index [47]:

$$B_i = \frac{1}{(n-1)} \left(\frac{1}{\sum_j p_{ij}^2} - 1 \right)$$

The standardized niche breadth index (B_i) was used to quantify resource use, where p_{ij} represents the proportion of prey type j in the diet of predator i , and n denotes the total number of resource categories. The index ranges from 0 to 1, with values approaching zero indicating strong dietary specialization (consumption of a single resource), whereas values near one reflect a more generalized feeding strategy characterized by an even utilization of available resources. B_i values above 0.6 are interpreted as high niche breadth [48], values between 0.4 and 0.6 as moderate, and values below 0.4 as low [49].

Differences in dietary composition among species were assessed using the Bray–Curtis dissimilarity index [48]. The index ranges from 0 (identical diet composition) to 1 (completely distinct diets).

2.8. Statistical Analysis

Statistical analysis was conducted to compare mean values of the standardized niche breadth index (B_i) and Pianka's niche overlap index (O_{jk}) using one-way analysis of variance (ANOVA). The level of significance was set at $p < 0.05$ for all tests. ANOVA procedures were performed using IBM SPSS Statistics 22 and R software (version 4.5.3) [50,51].

Graphs illustrating the level of similarity in dietary components among fish species were generated using JASP software (version 0.18.3) [52].

Taxonomic similarity of phytoplankton, zooplankton, and zoobenthos was assessed using the Bray–Curtis index and calculated with PRIMER software (version 5) [53,54]. The dendrograms were automatically generated by the software.

3. Results

3.1. Hydrochemical Characteristics

In 2025, the water depth at the sampling stations in the western part of Lake Balkhash ranged from 1.4 to 7.7 m, whereas in the eastern part it varied from 3.0 to 5.3 m. Water transparency in the western basin ranged from 10 to 140 cm. Toward the eastern part of the lake, an increase in transparency was observed with increasing depth, varying from 40 to 350 cm.

During the study period, the water temperature in Lake Balkhash ranged between 23.2 and 26.5 °C. The average hydrochemical parameters of Lake Balkhash water are presented in Table 4.

Table 4. Hydrochemical parameters of Lake Balkhash water (summer 2025).

Lake Basin	pH	Dissolved Oxygen (mg/L)	Oxygen Saturation (%)	NH ₄ ⁺ (mg/L)	NO ₂ [−] (mg/L)	NO ₃ [−] (mg/L)	PO ₄ ^{3−} (mg/L)	Permanganate Oxidizability (mg O/L)	Mineralization (mg/L)
Western Balkhash	8.61 ± 0.05	8.04 ± 0.06	91.00 ± 2.00	0.04 ± 0.05	0.04 ± 0.03	0.45 ± 0.04	0.05 ± 0.07	5.30 ± 0.70	1727.00 ± 120.00
Eastern Balkhash	8.44 ± 0.05	8.48 ± 0.07	96.00 ± 2.00	0.06 ± 0.03	0.03 ± 0.04	0.27 ± 0.02	0.04 ± 0.02	10.10 ± 0.30	4068.00 ± 137.00

The pH values were 8.61 ± 0.05 in the western basin and 8.44 ± 0.05 in the eastern basin. The concentration of dissolved oxygen was slightly lower in the western part of the lake, reaching 8.04 ± 0.06 mg/L.

The concentrations of nutrients in the water did not exceed the regulatory standards established for fishery water bodies [23]. The spatial distribution of nutrient ions across the lake was relatively uniform. For example, nitrite concentrations in the western and eastern basins of Lake Balkhash were 0.04 ± 0.03 mg/L and 0.03 ± 0.04 mg/L, respectively.

The permanganate oxidizability increased from west to east. The average values of permanganate oxidizability were 5.30 ± 0.70 mg O/L in the western basin and 10.10 ± 0.30 mg O/L in the eastern basin.

A similar pattern was observed for water mineralization. In the western basin, the average mineralization was 1727.00 ± 120.00 mg/L, whereas significantly higher values were recorded in the eastern part of the lake, reaching 4068.00 ± 137.00 mg/L.

3.2. Phytoplankton

In 2025, a total of 148 phytoplankton taxa were recorded in Lake Balkhash, representing six divisions: Cyanobacteria, Bacillariophyta, Chlorophyta, Charophyta, Dinoflagellata, and Euglenophyta (Table 5). Overall, 110 taxa were identified in the western area and 112 in the eastern one, indicating comparable levels of species richness between the two areas.

Table 5. Frequency of Occurrence of Phytoplankton Representatives in Different Areas of Lake Balkhash in 2025.

Taxa	Area	
	Western Balkhash	Eastern Balkhash
Cyanobacteria		
<i>Merismopedia tenuissima</i> Lemm.	59	59
<i>M. minima</i> G. Beck.	18	53
<i>M. tranquilla</i> (Ehr.) Trevisan	24	6
<i>M. glauca</i> (Ehr.) Näeg.	12	6
<i>M. elegans</i> A.Br. ex Kütz.	6	
<i>Microcystis aeruginosa</i> Kütz. Emend. Elenk.	24	29
<i>M. pulvereae</i> f. <i>planctonica</i> (G. M. Smith) Elenk	6	
<i>M. pulvereae</i> (H.C.Wood) Forti	29	47
<i>Aphanocapsa holsatica</i> (Lemmerm.) G.Cronberg & Komárek	6	
<i>A. delicatissima</i> West & G. S. West		6
<i>A. incerta</i> (Lemmerm.) G. Cronberg & Komárek		6
<i>Anathece clathrata</i> (West & G. S. West) Komarek	12	41
<i>A. stagnina</i> (Spreng.) B. Peters.	6	
<i>Aphanizomenon flos aquae</i> Ralfs ex Bornet & Flahault	12	6
<i>Gloeocapsopsis magma</i> (Breb.) Komarek & Anagnostidis ex Komarek	35	18

Table 5. Cont.

Taxa	Area	
	Western Balkhash	Eastern Balkhash
<i>G. crepidinum</i> (Thuret) Geitler ex Komarek		12
<i>Chroococcus minutus</i> (Kütz.) Näg.	6	12
<i>Ch. minimus</i> (Keissler) Lemm.	6	6
<i>Ch. minor</i> (Kütz.) Näg.	24	6
<i>Ch. turgidus</i> (Kütz.) Näg.	6	12
<i>Gloeocapsa</i> sp.	35	18
<i>Limnococcus limneticus</i> (Lemm.) Komarkova, Jezberova, O. Komarek & Zapomelova	6	
<i>Coelosphaerium kuetzingianum</i> Näg.	41	24
<i>Snowella lacustris</i> (Chodat) Komarek & Hindak	59	94
<i>Gomphosphaeria aponina</i> Kütz.	6	65
<i>Chrysosporum bergii</i> (Ostenf.) E. Zapomelová, O. Skácelová		6
<i>Anabaena</i> sp.	6	
<i>Planktolyngbya contorta</i> (Lemm.) Anagnostidis & Komarek	6	18
<i>Phormidium</i> sp.	24	18
<i>Rhabdoderma lineare</i> Schmidle et Laut. emend Hollerb.		6
<i>Oscillatoria</i> sp.		6
<i>Lyngbya</i> sp.	6	
<i>Leptolyngbya tenuis</i> (Gomont) Anagnostidis & Komark.	6	
<i>Limnothrix planctonica</i> (Wołosz.) Meffert	6	
<i>Spirulina laxa</i> G.M.Sm.	12	6
<i>S. tenuissima</i> Kütz. ex De Toni	6	
<i>Spirulina</i> sp.		6
Total: 37	30	27
Bacillariophyta		
<i>Amphora ovalis</i> Kütz	24	41
<i>Amphora</i> sp.		12
<i>Halamphora coffeiformis</i> (C.Ag.) Mereschk.	12	
<i>Stephanocyclus meneghinianus</i> (Kütz.) Kulikovskiy	12	18
<i>Planothidium lanceolatum</i> (Breb. ex Kütz.) Lange Bertalot	6	12
<i>Pantocsekiella kuetzingiana</i> (Thwaites) K. T. Kiss & E.Acs		12
<i>Lindavia comta</i> (Kütz.) T.Nakov & al.	41	65
<i>Lineaperpetua lacustris</i> (Grunow) P.Yu, Q. M.You, Kociolek & Wang		6
<i>Coscinodiscus</i> sp.		6
<i>Cocconeis pediculus</i> (Ehr.)	18	24
<i>C. placentula</i> (Ehr.)	6	18
<i>Caloneis amphisbaena</i> (Bory) Cl.	12	24
<i>C. westii</i> (W.Sm.) Hend.		6
<i>Cymbella cymbiformis</i> C.Ag.	6	12
<i>C. turgidula</i> Grun.	6	
<i>C. parva</i> (W. Sm.) Cl.	12	6
<i>C. turgida</i> (Greg.) Gl.	6	
<i>C. cistula</i> (Ehr.) Kirch.	12	6
<i>C. ventricosa</i> Kütz.	6	6
<i>Cymbella</i> sp.		6
<i>Brebissonia lanceolata</i> (C. Ag.) R.K.Mahoney & Reimer	12	6
<i>Hantzschia amphioxys</i> (Ehr.) Grun.		6
<i>Cymbopleura naviculiformis</i> (Auerswald ex Heiberg) Krammer	6	
<i>Encyonema leibleinii</i> (C.Ag.) W.J.Silva, R.Jahn, T.A.V.Ludw., & M.Menez.	6	
<i>Campylodiscus noricus</i> Ehr. Ex Kütz.		12
<i>C. clypeus</i> Ehr.	6	6
<i>Gomphonema lanceolatum</i> C. Ag.		18
<i>Gomphonema acuminatum</i> Ehr.	6	

Table 5. Cont.

Taxa	Area	
	Western Balkhash	Eastern Balkhash
<i>Gomphonema</i> sp.	12	6
<i>Gomphonella olivacea</i> (Hornem.) Rabenh.		18
<i>Gyrosigma acuminatum</i> (Kütz.) Rabenh.	12	
<i>Epithemia sorex</i> Kütz.	12	6
<i>E. adnata</i> (Kütz.) Breb.	12	18
<i>E. argus</i> (Ehr.) Kütz.	18	6
<i>E. gibba</i> (Ehr.) Kütz.	12	12
<i>Rhopalodia gibba</i> var. <i>ventricosa</i> (Ehr.) Grun.	6	6
<i>Pinnularia interrupta</i> W. Sm.	12	
<i>Pinnularia viridis</i> (Nitzsch.) Ehr.	12	12
<i>Pinnularia</i> sp.	6	6
<i>Diatoma vulgare</i> Bory	12	6
<i>D. elongatum</i> (Lyngb.) C. Ag.		12
<i>Diatoma</i> sp.		12
<i>Diploneis ovalis</i> (Hilse) Cl.	12	6
<i>D. smithii</i> (Breb.) Cl.		6
<i>Fragilaria capucina</i> Desm.	12	29
<i>F. crotonensis</i> Kitt.		6
<i>Fragilaria</i> sp.	12	12
<i>Fragilariforma virescens</i> (Ralfs) D.M.Williams & Round	6	6
<i>Aneumastus tusculus</i> (Ehr.) D.G.Mann & Stickle		6
<i>Hippodonta hungarica</i> (Grun.) Lange Bert., Metz. & Witk.		6
<i>Navicula cryptocephala</i> Kütz.	12	6
<i>N. tripunctata</i> (O.F.Müll.) Bory		6
<i>N. lanceolata</i> (Ag.) Kütz.	6	
<i>N. radiosa</i> (Ehr.) Kütz.	12	
<i>N. gregaria</i> Donk.	6	6
<i>Navicula</i> sp.	24	24
<i>Craticula cuspidata</i> (Kütz.) D.G.Mann	12	6
<i>Placoneis gastrum</i> (Ehr.) Mereschk.		18
<i>Tryblionella angustata</i> W.Sm.	12	
<i>Tryblionella hungarica</i> (Grun.) Frenguelli		6
<i>T. punctata</i> W.Sm.	6	
<i>Nitzschia acicularis</i> (Kütz.) W.Sm.	6	6
<i>N. amphibia</i> Grun.		6
<i>N. gracilis</i> Hantz.	24	12
<i>N. gracilis</i> var. <i>capitata</i> (Greg.) Grun.		6
<i>N. linearis</i> W.Sm.	12	
<i>Nitzschia sigmoidea</i> (Nitzsch) W.Sm.	6	
<i>Nitzschia</i> sp.	12	12
<i>Neidium</i> sp.		18
<i>Ulnaria ulna</i> (Nitzsch) Compere	53	12
<i>Rhoicosphenia abbreviata</i> (C.Ag.) Lange Bertalot	12	
<i>Surirella librile</i> (Ehr.) Ehr.		12
<i>Surirella ovalis</i> Bréb.	6	
<i>Cymatopleura elliptica</i> W.Sm.	6	
<i>Mastogloia braunii</i> Grun.	18	12
<i>M. baltica</i> Grun.	12	
Total: 76	53	59
Charophyta		
<i>Cosmarium</i> sp.	6	
<i>Elakatothrix lacustris</i> Korsch.	12	6
<i>Mougeotia</i> sp.	18	12
Total: 3	3	2

Table 5. Cont.

Taxa	Area	
	Western Balkhash	Eastern Balkhash
Chlorophyta		
<i>Ankistrodesmus</i> sp.		6
<i>Chlamydomonas</i> sp.		6
<i>Crucigenia fenestrata</i> (Schmidle) Schmidle	6	
<i>Crucigenia quadrata</i> Morren	12	
<i>Dictyosphaerium ehrenbergianum</i> Näg.		18
<i>Kirchneriella lunaris</i> (Kirch.) Möbius		18
<i>Lagerheimia geneviensis</i> Chod.	6	
<i>Monoraphidium griffithii</i> (Berk.) Komark. Legn.	6	6
<i>Monoraphidium contortum</i> (Thuret) Komark. Legn.	6	12
<i>Mucidosphaerium pulchellum</i> (H.C.Wood) C.Bock	6	47
<i>Neglectella solitaria</i> (Wittr.) Stenclová & Kaštovský		12
<i>Oocystis borgei</i> J.W.Snow		12
<i>Oocystis lacustris</i> Chod.	35	53
<i>Oocystis parva</i> W. West.		12
<i>Oocystis</i> sp.	6	6
<i>Planctonema lauterbornii</i> Schmidle	12	6
<i>Pseudopediastrum boryanum</i> (Turpin) E.Hegewald	6	6
<i>Scenedesmus quadricauda</i> (Turp.) Breb.	6	6
<i>Tetraedron minimum</i> (A.Br.) Hansg.	24	24
<i>Ulothrix</i> sp.		6
<i>Ulothrix zonata</i> (F.Weber & Mohr) Kütz.	6	6
Total: 21	13	18
Dinoflagellata		
<i>Ceratium hirundinella</i> (O.F. M.) Dujardin	6	
<i>Glenodinium gymnadinium</i> Penard.	6	
<i>Glenodinium</i> sp.	53	18
<i>Gymnodinium</i> sp.	12	12
<i>Parvodinium umbonatum</i> (F.Stein) Carty	18	6
<i>Peridinium</i> sp.	41	24
Total:6	6	4
Euglenophyta		
<i>Trachelomonas</i> sp.	59	29
<i>Euglena viridis</i> Ehr.	12	
<i>Euglena</i> sp.	6	
<i>Lepocinclis</i> sp.	6	6
<i>Phacus</i> sp.	6	
Total: 5	5	2
Total: 148	110	112

Note. Empty cells indicate that the respective taxon was absent at the corresponding site. They do not represent missing data.

No taxa exhibited 100% occurrence in both areas. The highest frequency of occurrence was recorded for *Snowella lacustris* (59% in the western area and 94% in the eastern area). Widely distributed taxa ($\geq 50\%$ occurrence in at least one area) included *Ulnaria ulna* (53% in the western area), *Lindavia comta* (41% and 65% in the western and eastern areas, respectively), *Oocystis lacustris* (35% and 53%), *Gomphosphaeria aponina* (65% in the eastern area), *Glenodinium* sp. (53% in the western area), *Trachelomonas* sp. (59% and 29%), and *Mucidosphaerium pulchellum* (47% in both areas, according to the table data). These taxa consistently showed high frequencies of occurrence within their respective areas. The majority of the recorded taxa (over 60%) occurred at frequencies of 6–24% and can therefore be classified as rare or locally distributed. This group includes numerous representatives

of the genera *Navicula*, *Nitzschia*, *Cymbella*, and *Pinnularia*, as well as several green algae and dinoflagellates.

In terms of taxonomic composition, Bacillariophyta exhibited the highest diversity (76 taxa in the western area and 59 in the eastern area). Cyanobacteria comprised 37 and 27 taxa, respectively; Chlorophyta comprised 21 and 18 taxa; Charophyta comprised 3 and 2 taxa; Dinoflagellata comprised 6 and 4 taxa; and Euglenophyta comprised 5 and 2 taxa.

Overall, the phytoplankton communities of the western and eastern areas were characterized by similar species richness, the absence of taxa with ubiquitous (100%) occurrence, and a predominance of species with low frequencies of occurrence, reflecting spatial heterogeneity in community structure.

The dendrogram illustrates the very high similarity in phytoplankton species composition among 38 sites in Lake Balkhash, with all branches representing $\geq 90\%$ similarity (Figure 2).

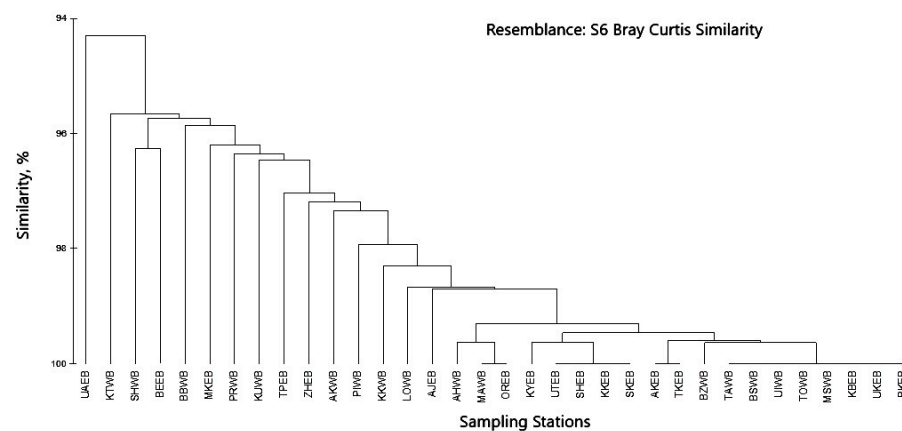


Figure 2. Dendrogram of the Bray–Curtis similarity of the species composition of Phytoplankton in Different Areas of Lake Balkhash in 2025. Abbreviations: BS-WB—B. Saryshagan, PR-WB—Priozersk, KK-WB—Kashkanteniz, AK-WB—Akkerme, LO-WB—Les. Ostr. (Forest Island), UI-WB—Mouth of Ile River, KU-WB—Karauzyak, PI-WB—Protok Iir (Iir Channel), AH-WB—Akhmetsuat, BZ-WB—Bozarat, MS-WB—Maly Saryshagan, UTEB—Ultrakhty, KBEB—Karabas, SHEB—Shomyshkol, UAEB—Ustye r. Ayagoz, ZHEB—Zhalanash, TPEB—Tolepshapkan, AJEB—Akzhaydak, MKEB—Maykamys, AKEB—Asambaykol, TKEB—Tkshoky.

Freshwater and slightly brackish sites (e.g., BB-WB—Bukhta B, ST-WB—Shubartyubek, TS-WB—Tasaral) form distinct clusters, indicating nearly identical species composition.

Transitional sites (e.g., MS-WB—Maly Saryshagan, OLEB—Orlinaya, UTEB—Ultrakhty) link several clusters, also demonstrating very high similarity. Highly saline or more isolated sites (e.g., ZHEB—Zhalanash, KGBE—Karashygan, TPEB—Tolepshapkan) form separate branches, yet still maintain $\geq 90\%$ similarity, reflecting unique but closely related communities.

Overall, the dendrogram indicates that all studied sites of Lake Balkhash share a very high degree of similarity in phytoplankton composition, highlighting the dominance of similar species throughout the water body.

3.3. Zooplankton

In 2025, a total of 56 zooplankton taxa were recorded in Lake Balkhash, including Rotifera, Cladocera, and Copepoda (Table 6). In the western area, 39 taxa were recorded, and in the eastern area, 36 taxa, indicating comparable species richness across the two areas. No taxa were observed with 100% occurrence in both areas. The highest frequencies were recorded for *Arctodiaptomus salinus* and *Mesocyclops leuckarti* (94–100%), *Diaphanosoma lacustris* (82–88%), and *Thermocyclops crassus* (82–88%). *Daphnia* (*Daphnia*) *galeata* occurred

at 47% in the eastern area, while *Harpacticoida* gen. sp. appeared in 29% of samples in both areas. Rotifers, such as *Euchlanis dilatata dilatata*, *Habrotrocha bidens*, and *Trichotria pocillum pocillum*, were recorded at intermediate frequencies (12–18%).

Table 6. Frequency of Occurrence of Zooplankton Representatives in Different Areas of Lake Balkhash in 2025.

Taxa	Area	
	Western Balkhash	Eastern Balkhash
Rotifera		
<i>Anuraeopsis fissa fissa</i> Gosse	12	
<i>Brachionus plicatilis longicornis</i> Fadeev	6	18
<i>Brachionus p. plicatilis</i> Muller		6
<i>B. quadridentatus melheni</i> Barrois et Daday		6
<i>B. q. ancylognathus</i> Schmarda	12	
<i>B. q. hyphalmyros</i> Tschugunoff		6
<i>Dissotrocha aculeata</i> Ehrenberg	6	
<i>Eosphora najas</i> Ehrenberg		6
<i>E. ehrenbergi</i> Weber	6	
<i>Euchlanis pyriformis</i> Gosse	12	6
<i>E. dilatata dilatata</i> Leydig	18	18
<i>E. deflexa deflexa</i> Gosse	12	
<i>Habrotrocha bidens</i> Gosse	18	6
<i>Hexarthra oxyuris</i> Zernov		24
<i>Keratella cochlearis cochlearis</i> Gosse	12	18
<i>K. q. quadrata</i> Muller		6
<i>Lecane (Monostyla) lunaris</i> Ehrenberg		6
<i>L. luna presumta</i> Ahlstrom		6
<i>L.l. luna</i> Muller	6	6
<i>Notholca acuminata acuminata</i> Ehrenberg	6	
<i>N. cyrtopus</i> Gosse		12
<i>N. pseudocerberus</i> Beauchamp	6	
<i>Polyarthra major</i> Burckhardt	12	
<i>P. remata</i> Skorikov	6	
<i>Synchaeta oblonga</i> Ehrenberg		6
<i>S. pectinata</i> Ehrenberg	12	
<i>Testudinella patina patina</i> Hermann	6	
<i>Trichocerca pusilla</i> Lauterborn	6	
<i>Trichotria pocillum pocillum</i> Muller	6	6
<i>T. truncata truncate</i> Whit	6	
Total: 30	20	17
Cladocera		
<i>Acroperus costata</i> Sars	6	

Table 6. Cont.

Taxa	Area	
	Western Balkhash	Eastern Balkhash
<i>A. harpae</i> Baird	6	
<i>Alona affinis</i> Leydig		6
<i>A. costata</i> Sars		12
<i>A. guttata</i> Sars	12	12
<i>A. rectangula</i> Sars	35	24
<i>Bosmina (Bosmina) longirostris</i> Muller	12	
<i>Ceriodaphnia laticaudata</i> Muller		6
<i>Chydorus sphaericus</i> Muller	18	12
<i>Daphnia (Daphnia) galeata</i> Sars	6	47
<i>Diaphanosoma lacustris</i> Korinek	82	88
<i>Ilyocryptus agilis</i> Kurz	6	
<i>Leptodora kindtii</i> Focke		6
<i>Polyphemus pediculus</i> Linne		6
<i>Sida crystallina</i> Muller	6	
Total: 15	10	10
Copepoda		
<i>Acanthocyclops venustus</i> Norman et Scott	6	
<i>Arctodiaptomus salinus</i> Daday	94	100
<i>Cyclops vicinus</i> Uljanin	12	
<i>Erqasilus</i> gen. sp.	6	18
<i>Eucyclops denticulatus</i> Graeter		6
<i>Eucyclops macrurus</i> Sars		6
<i>Harpacticoida</i> gen. sp.	29	29
<i>Mesocyclops leuckarti</i> Claus	94	100
<i>Paracyclops fimbriatus</i> Fischer	12	6
<i>Thermocyclops crassus</i> Fischer	82	88
<i>T. taihokuensis</i> Harada	18	12
Total: 11	9	9
Total: 56	39	36

Note. Empty cells indicate that the respective taxon was absent at the corresponding site. They do not represent missing data.

Most taxa, including *Anuraeopsis fissa fissa*, *Brachionus plicatilis*, *Eosphora najas*, *Keratella cochlearis*, *Acroperus costata*, *Chydorus sphaericus*, *Bosmina longirostris*, and others, were observed rarely, with frequencies of 6–18%, indicating localized occurrence.

Overall, the zooplankton of Lake Balkhash in 2025 exhibited similar species richness in both areas, absence of taxa with ubiquitous occurrence, and a predominance of taxa with low frequency, reflecting spatial heterogeneity in the community.

The dendrogram reveals very high similarity in zooplankton species composition among 38 sampling stations in Lake Balkhash, with all clusters exhibiting Bray–Curtis similarity values above 90% (Figure 3). Several sites, such as UAEB, KTWB, and SHWB,

form tight clusters reflecting nearly identical species assemblages. Transitional stations (e.g., AHEB, MAVB, OREB) link clusters while maintaining similarity above 90%. Even the most distinct stations display similarity close to or exceeding 90%, indicating a largely homogeneous zooplankton community across the lake. Overall, the dendrogram highlights strong spatial uniformity in zooplankton species composition, suggesting widespread distribution of similar species throughout Lake Balkhash.

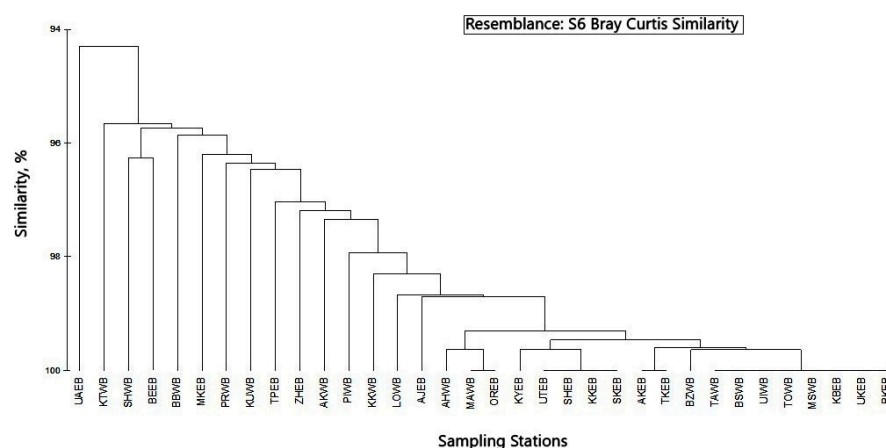


Figure 3. Dendrogram of the Bray–Curtis similarity of the species composition of Zooplankton in Different Areas of Lake Balkhash in 2025. Abbreviations: BBWB—Berty Bay, SHWB—Shubartyubek, TAWB—Tasaral, BSWB—B. Saryshagan, PRWB—Priozersk, KTWB—Kashkanteniz, KKWB—Karakamyss, AKWB—Akkermé, LOWB—Forest Islands, UIWB—Mouth of the Ile River, KUWB—Karauzyak, PIWB—Ir Channel, MAWB—Maytan, AHWB—Akhmet Suat, BZWB—Bozaral, TOWB—Tomar, MSWB—Small Saryshagan, OREB—Orlinaya, UTEB—Ultrakty, KBEB—Karabas, SHEB—Shomyshkol, UKEB—Mouth of the Karatal River, KKEB—Karakol, UAEB—Mouth of the Ayagoz River, ZHEB—Zhalanash, KYEB—Karashigan, TPEB—Tolepshapkan, AJEB—Akzhaydak, BKEB—Balyktikol, MKEB—Maykamys, SKEB—Sarykamys, BEEB—Belen, AKEB—Asambaykol, TKEB—Tkshoky.

3.4. Zoobenthos

In 2025, a total of 15 zoobenthos taxa were recorded in Lake Balkhash, including representatives of Mollusca, Vermes, Crustacea, and Chironomidae (Table 7). In the western area, 10 taxa were recorded, and in the eastern area, 12 taxa were recorded, indicating comparable species richness between the two areas.

Table 7. Frequency of Occurrence of Zoobenthos Representatives in Different Areas of Lake Balkhash in 2025.

Taxa	Area	
	Western Balkhash	Eastern Balkhash
Mollusca		
<i>Monodacna colorata</i> (Eichwald, 1838)	29	
<i>Lymnaea ovata</i> (Draparnaud, 1805)		6
Total: 2	1	1
Vermes		
<i>Oligochaeta</i> gen.sp.	82	35
<i>Hypania invalida</i> Grube, 1860	35	12
<i>Hypaniolla kowalevskii</i> (Grimm, 1877)	24	6
Total: 3	3	3

Table 7. Cont.

Taxa	Area	
	Western Balkhash	Eastern Balkhash
Crustasea		
<i>Corophium curvispinum</i> (Sars, 1895)	41	12
<i>Niphargoides robustoides</i> Sars, 1894	6	35
<i>Gammarus lacustris</i> G.O.Sars, 1863	18	
<i>Paramysis ullskyi</i> Czerniavsky, 1882		6
Total: 4	3	3
Chironomidae		
<i>Harnischia fuscimanus</i> (Kieffer, 1921)	41	
<i>Chironomus</i> gr. <i>plumosus</i> (Linnaeus, 1758)	12	47
<i>Glyptotendipes gripekoveni</i> (Kieffer, 1913)		12
<i>Tanypus punctipennis</i> (Meigen, 1818)	6	18
<i>Tabanus</i> sp.		6
<i>Chrysops</i> sp.		6
Total: 6	3	5
Total: 15	10	12

Note. Empty cells indicate that the respective taxon was absent at the corresponding site. They do not represent missing data.

No taxa were observed with 100% occurrence in both areas. Among the most frequently recorded taxa were *Oligochaeta* gen. sp. (82% in the western area, 35% in the eastern area), *Corophium curvispinum* (41% in the western area), and *Chironomus* gr. *plumosus* (12% in the western area, 47% in the eastern area). *Hypania invalida* occurred at 35% and 12% in the western and eastern areas, respectively, while *Harnischia fuscimanus* was recorded at 41% in the western area.

Other taxa, including *Monodacna colorata*, *Lymnaea ovata*, *Hypaniolla kowalevskii*, *Gammarus lacustris*, *Niphargoides robustoides*, *Paramysis ullskyi*, *Tanypus punctipennis*, and Tabanidae (*Tabanus* and *Chrysops*), were recorded at low frequencies (6–24%), indicating localized occurrence.

Overall, the zoobenthos community in Lake Balkhash in 2025 exhibited similar species richness in both areas, the absence of taxa with ubiquitous occurrence, and a predominance of taxa with low frequency, reflecting spatial heterogeneity in benthic communities (Figure 4).

The dendrogram based on Bray–Curtis similarity shows a high degree of resemblance in zoobenthos species composition among the 38 sampling stations of Lake Balkhash (Figure 4). All stations cluster at similarity levels above 90%, indicating low spatial variability in benthic community structure across the lake.

Several stations form very tight clusters, reflecting nearly identical zoobenthic assemblages and minimal differences in species composition. Transitional stations connect the main clusters while still maintaining similarity values above 90%, suggesting gradual spatial changes rather than distinct ecological boundaries.

Even the most dissimilar stations exhibit similarity values close to 90%, confirming the overall homogeneity of the zoobenthos community. In general, the dendrogram highlights strong spatial uniformity and a widespread distribution of similar benthic species throughout Lake Balkhash.

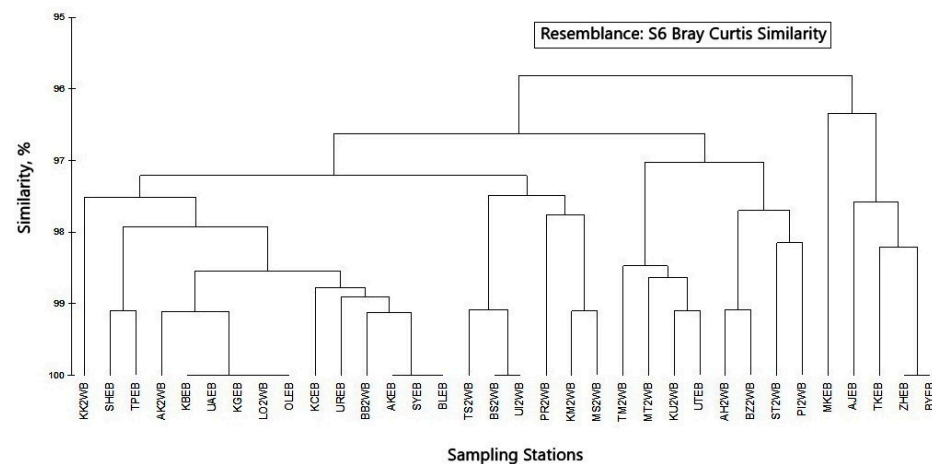


Figure 4. Dendrogram of the Bray–Curtis similarity of the species composition of Zoobenthos in Different Areas of Lake Balkhash in 2025. Abbreviations: ST-WB—Shubartyubek, TS-WB—Tasaral, BS-WB—B. Saryshagan, PR-WB—Priozersk, KK-WB—Kashkanteniz, KM-WB—Karakamis, AK-WB—Akkerme, LO-WB—Les. Ostr. (Forest Island), UI-WB—Mouth of Ile River, KU-WB—Karaulyak, PI-WB—Protok Iir (Iir Channel), MT-WB—Maytan, AH-WB—Akhmetsuat, BZ-WB—Bozaral, TM-WB—Tomar, MS-WB—Maly Saryshagan, OLEB—Orlinaya, UTEB—Ultrakhty, KBEB—Karabas, SHEB—Shomyshkol, UREB—Ustye r. Karatal, KCEB—Karakol, UAEB—Ustye r. Ayagoz, ZHEB—Zhalanash, KGEB—Karashygan, TPEB—Tolepshapkan, AJEB—Akzhaydak, BYEB—Balyktykol, MKEB—Maykamys, SYEB—Sarykamys, BLEB—Belen, AKEB—Asambaykol, TKEB—Tkshoky.

3.5. Diet Analysis

3.5.1. Diet Composition of Benthivorous Fish Species

The diet of benthivorous fish species in Lake Balkhash differed quantitatively between the western and eastern basins: 18 food components were identified in the western part and 16 in the eastern part. The proportional contribution of individual food items varied depending on the species considered. Figure 5 presents the composition of dietary components of benthivorous (“non-predatory”) fish species.

The diet of common carp (*C. carpio*) in the western part of Lake Balkhash consisted primarily of mollusks (30.71%), detritus (15.03%), macrophytes (13.57%), chironomid larvae (8.93%), insect larvae (5.99%), mysids (3.23%), gammarids (1.71%), and unidentified digested remains (16.50%). Other food components each accounted for less than 1% of the total diet composition.

The diet of roach (*R. caspicus*) was dominated by macrophytes (66.04%), followed by mysids (12.16%), corophiids (5.38%), chironomid larvae (10.31%), and detritus (5.70%).

In crucian carp (*C. gibelio*), the diet consisted almost entirely of plant material (97.51%). The occurrence of zooplankton (1.81%), chironomid larvae (0.55%), and fish eggs (0.13%) was minimal and may be considered incidental for this species.

The diet of common bream (*A. brama*) included six principal components: corophiids (33.76%), mysids (24.87%), mollusks (18.09%), detritus (11.82%), oligochaetes (9.18%), and macrophytes (2.28%).

In the eastern part of Lake Balkhash, the diet of common carp (*C. carpio*) showed an increased contribution of plant material (57.4%), followed by detritus (16.54%), chironomid larvae, algae (4.63%), mysids (2.58%), and corophiids. Digested remains accounted for 6.38%, while mayflies, caddisflies, ostracods, and periphyton each contributed less than 1%.

In roach (*R. caspicus*), the proportion of plant material in the eastern basin (37.91%) was lower than in the western part. Mysids comprised 25.35% of the diet, cestodes 19.29%, and chironomid larvae 14.17%, whereas the remaining components were present in minor proportions.

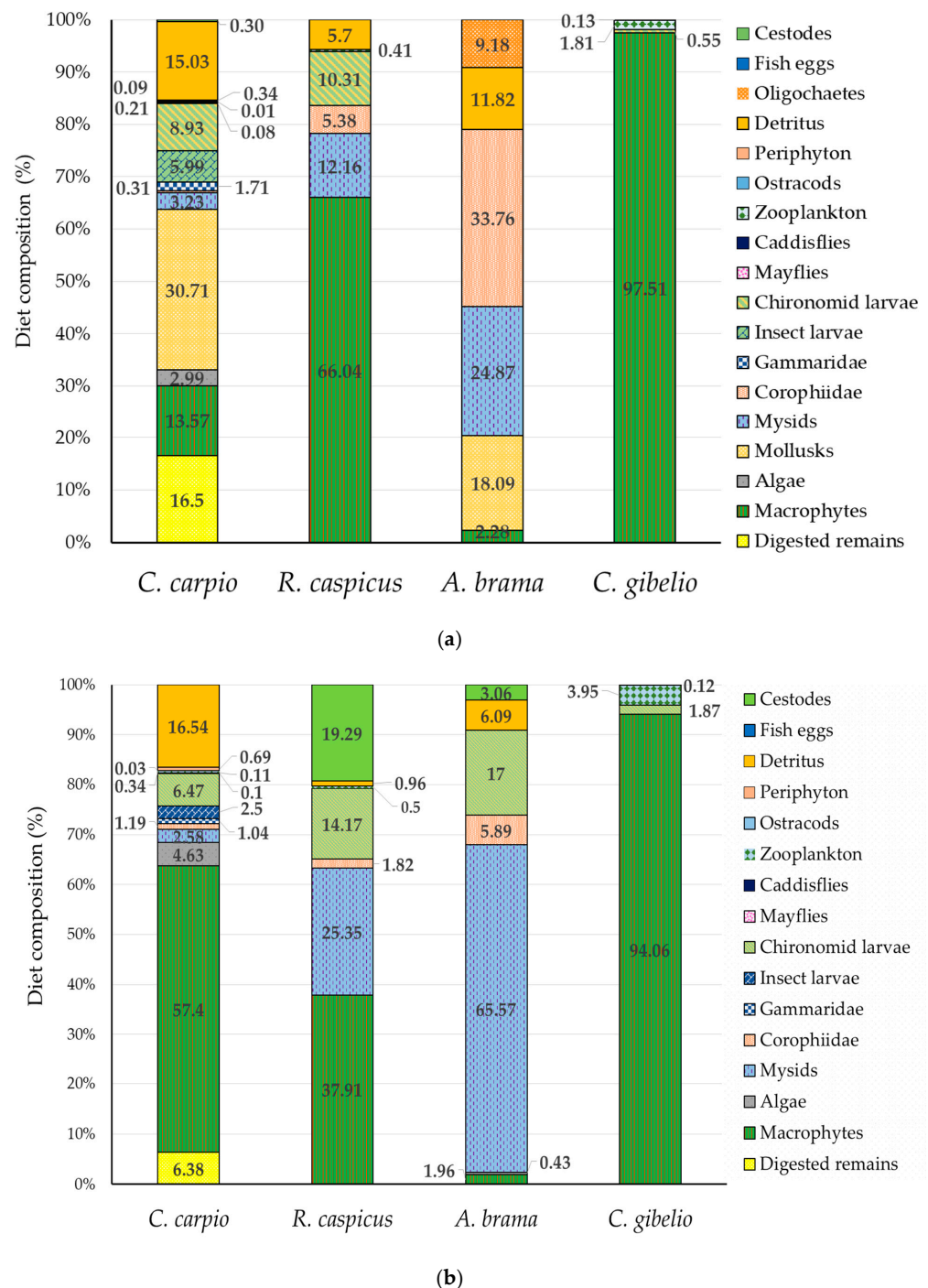


Figure 5. Diet composition of benthivorous fish species from the western part (a) and eastern part (b) of Lake Balkhash.

The diet of crucian carp (*C. gibelio*) remained dominated by higher aquatic vegetation (94.06%), with smaller contributions from zooplankton (3.95%), chironomid larvae (1.87%), and fish eggs (0.13%). In common bream (*A. brama*), mysids represented approximately 65.57% of the diet. In the eastern basin, bream also consumed chironomid larvae (17%), detritus (6.09%), corophiids (5.89%), and cestodes (3.05%).

Interspecific comparison using the Bray–Curtis index revealed differences in the consumption of dietary components among species (Table 7).

The diet of crucian carp (*C. carassius*) remained dominated by higher aquatic vegetation (94.06%), with smaller contributions from zooplankton (3.95%), chironomid larvae (1.87%),

and fish eggs (0.13%). In common bream (*A. brama*), mysids represented approximately 65.57% of the diet. In the eastern basin, bream also consumed chironomid larvae (17%), detritus (6.09%), corophiids (5.89%), and cestodes (3.06%).

Interspecific comparison using the Bray–Curtis index revealed differences in the consumption of dietary components among species (Table 8).

Table 8. Bray–Curtis (BC) dissimilarity among benthivorous species in Lake Balkhash.

Species	<i>C. carpio</i>	<i>R. caspicus</i>	<i>A. brama</i>	<i>C. gibelio</i>
Western Balkhash				
<i>C. carpio</i>	X	0.68	0.64	0.86
<i>R. caspicus</i>	0.68	X	0.74	0.33
<i>A. brama</i>	0.64	0.74	X	0.98
<i>C. gibelio</i>	0.86	0.33	0.98	X
Eastern Balkhash				
<i>C. carpio</i>	X	0.51	0.81	0.40
<i>R. caspicus</i>	0.51	X	0.71	0.60
<i>A. brama</i>	0.81	0.53	X	0.96
<i>C. gibelio</i>	0.40	0.60	0.96	X

Moderate trophic similarity among benthivorous fish species from the western part of Lake Balkhash was observed between roach and crucian carp (BC = 0.33), common carp and common bream (BC = 0.64), and common carp and roach (BC = 0.68). Pronounced differences in dietary composition (BC > 0.70) were recorded for crucian carp and common carp, common bream and roach, common carp and crucian carp, as well as common bream and crucian carp.

In the eastern part of Lake Balkhash, trophic similarity among benthivorous fish species remained generally moderate; however, marked dietary differentiation was observed for common bream compared to the other species.

3.5.2. Diet Composition of Predatory Fish Species

The diet of predatory fish species in Lake Balkhash is characterized by a mixed trophic structure. Digested remains of animal origin were detected in the stomach contents of all examined predatory species, indicating pronounced ichthyophagy and the consumption of other macrozoobenthic organisms.

The most diverse diet was recorded in pikeperch (*S. lucioperca*) from the western part of the lake, where 10 food components were identified. The diet was dominated by digested fish remains (39.2%), reflecting a high degree of specialization toward piscivory. Substantial proportions were also represented by roach (*R. caspicus*) (19.05%), crucian carp (*Carassius* spp.) (17.3%), common bream (*A. brama*) (9.53%), and freshwater shrimp remains (7.72%). Figure 6 shows the composition of dietary components of predatory fish species in Lake Balkhash.

The diet of Volga pikeperch (*S. volgensis*), a closely related species to pikeperch, was dominated by freshwater shrimp (37.6%), mysids (23.6%), and unidentified fish remains (20.04%). The diet of this species comprised six food components in total.

In asp (*A. aspius*), only four dietary components were recorded, with digested fish remains (37.46%) and mysids (35.15%) constituting the largest proportions. Common bream (*A. brama*) and roach (*R. caspicus*) were also identified in the diet. The consumption of bream and roach appears consistent with their ecological characteristics, as these species inhabit

not only near-bottom layers but also actively migrate within the pelagic zone, particularly during early ontogenetic stages.

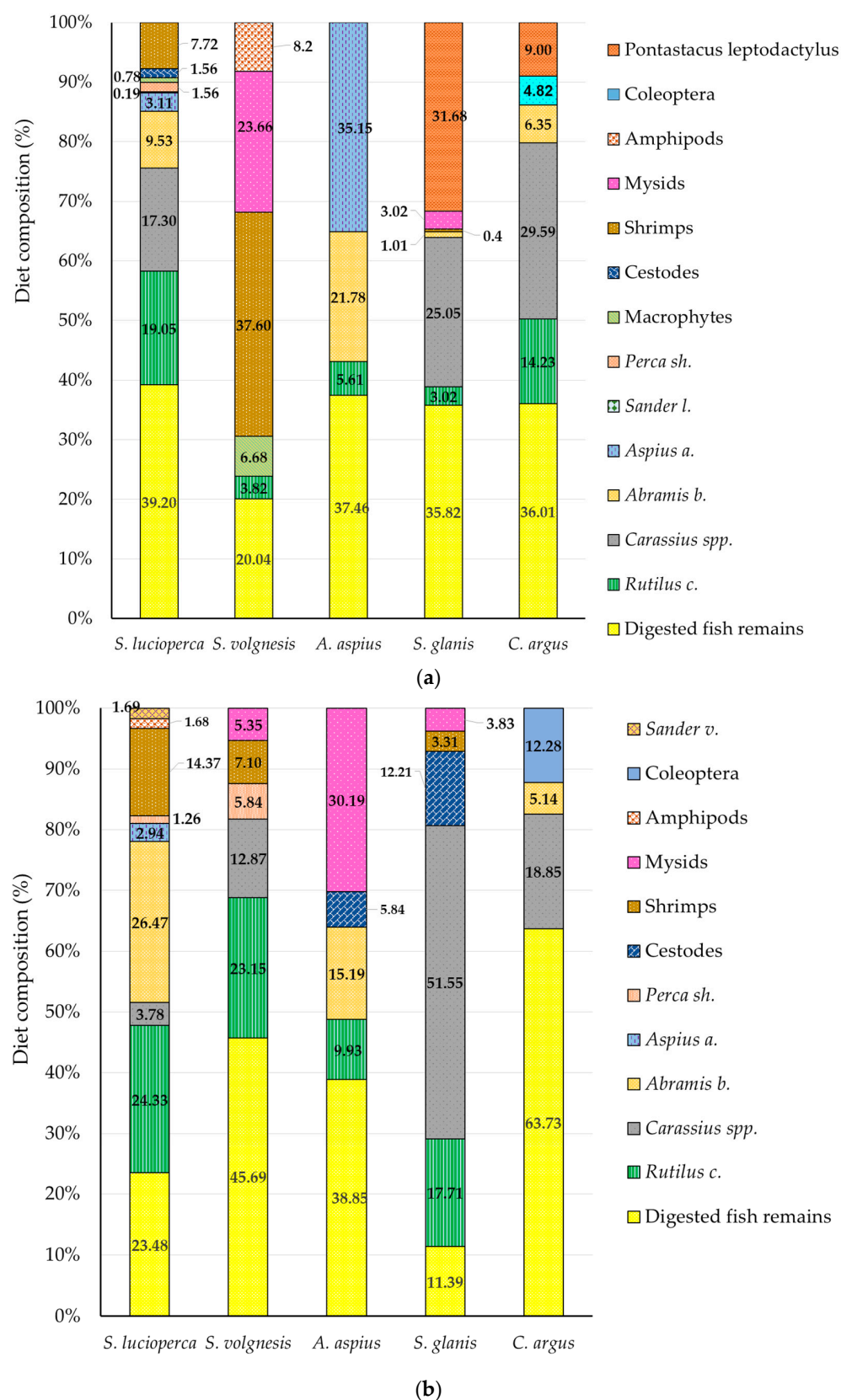


Figure 6. Diet composition of predatory fish species from the western part (a) and eastern part (b) of Lake Balkhash.

In the diets of wels catfish (*S. glanis*) and snakehead (*C. argus*), remains of pikeperch accounted for 31.68% and 9%, respectively, while crucian carp represented 25.05% and 29.59%. Roach consumption was higher in snakehead (14.23%) compared to catfish (3.02%).

Significant dietary differences among predatory fish species from the western part of Lake Balkhash were observed between snakehead and pikeperch (BC = 0.76), Volga pikeperch and asp (BC = 0.76), and catfish and snakehead (BC = 0.74). The greatest dietary similarity was recorded between snakehead and both asp and catfish (BC = 0.26). Figure 7 illustrates trophic similarities and differences among predatory fish species based on Bray–Curtis index calculations.

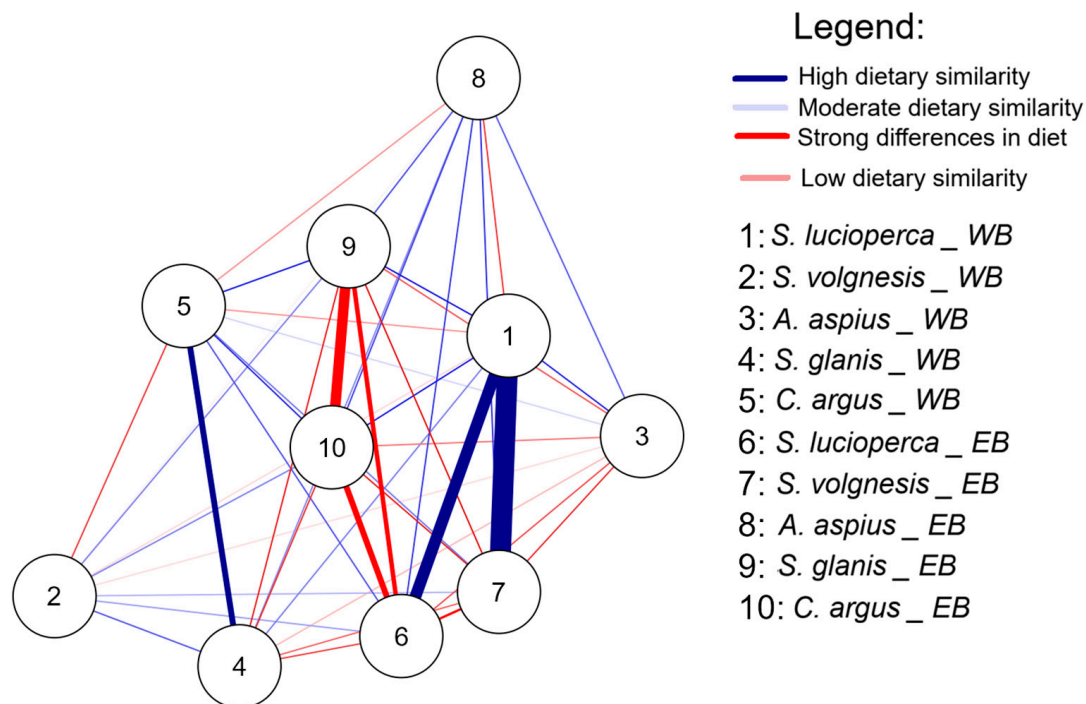


Figure 7. Similarities and differences in dietary components of predatory fish species in Lake Balkhash: _WB (Western Balkhash), _EB (Eastern Balkhash).

The diet of predatory fish in the eastern part of Lake Balkhash shows similarities in the consumption of certain components recorded in the western basin. For example, pikeperch (*S. lucioperca*) consumed up to 10 food components, with roach, common bream, freshwater shrimp, and digested fish remains forming the bulk of the diet. The contribution of bream and roach increased to 26.47% and 24.33%, respectively.

In Volga pikeperch (*S. volgnensis*), digested fish remains accounted for 45.69% of the diet. Other components were more evenly distributed, including roach (23.15%), crucian carp (12.87%), freshwater shrimp (7.1%), and mysids (5.35%). Notably, unlike other predatory species, the diet of *S. volgnensis* included the endemic Balkhash perch (*Perca schrenkii* Kessler, 1874). The population of this endemic species has declined markedly following the introduction and subsequent expansion of predatory fish, accompanied by a reduction in the proportion of native ichthyofauna. Its occurrence in the diet of Volga pikeperch may therefore represent an additional trophic pressure on the endemic component of the ichthyocenosis.

Crucian carp constituted the dominant prey item in the diet of wels catfish (*S. glanis*), accounting for 51.55%, while other components were relatively evenly distributed. As a benthic predator, catfish likely consumes crucian carp due to its high abundance in bottom habitats and spatial overlap in these biotopes.

In snakehead (*C. argus*), digested fish remains predominated (63.73%). Aquatic beetles (Coleoptera) contributed 12.28%, while crucian carp (18.85%) and bream (5.14%) were recorded in smaller proportions.

Dietary similarities and differences for both basins of Lake Balkhash are presented in Figure 7.

The highest trophic similarity was identified between pikeperch (*S. lucioperca*) inhabiting the two basins of the lake, which is expected for the same species ($BC \leq 0.30$). In addition, the closely related Volga pikeperch (*S. volgensis*) from the eastern basin exhibited dietary similarity with pikeperch from the western basin, suggesting partial trophic niche overlap.

In the eastern part of Lake Balkhash, moderate trophic similarity (BC within intermediate values) was observed among most of the studied species. An exception was recorded for snakehead (*C. argus*) and asp (*A. aspius*), which demonstrated pronounced differences in dietary composition ($BC \geq 0.70$), indicating trophic differentiation and reduced niche overlap between these species.

3.5.3. Assessment of Trophic Niche Breadth

The diversity of dietary components identified in this study indicates varying degrees of trophic specialization among the examined fish species of Lake Balkhash. Calculation of trophic niche breadth indices enabled an integrated assessment of the feeding strategies of introduced species within this ecosystem. Table 9 presents the niche breadth index values for species inhabiting the western and eastern parts of Lake Balkhash.

Table 9. Levin's niche breadth index values for fish species of Lake Balkhash.

Species	Western Balkhash	Eastern Balkhash	<i>p</i> -Value
<i>C. carpio</i>	0.27	0.11	0.19
<i>A. brama</i>	0.20	0.08	0.14
<i>R. caspicus</i>	0.07	0.18	0.12
<i>C. gibelio</i>	0.00	0.01	0.005
<i>S. lucioperca</i>	0.29	0.35	0.32
<i>S. volgnesis</i>	0.27	0.22	0.24
<i>S. glanis</i>	0.19	0.19	0.19
<i>C. argus</i>	0.23	0.11	0.17
<i>A. aspius</i>	0.17	0.24	0.20

Note: Differences among groups were tested using one-way ANOVA followed by Tukey's HSD post hoc test ($\alpha = 0.05$).

The values of Levin's niche breadth index for the studied fish species did not exceed $Bi < 0.30$, allowing the introduced species of Lake Balkhash to be classified as trophically narrow specialists. These results are consistent with the analysis of dietary composition presented in Section 3.5.2 and further confirm the identified patterns of trophic specialization.

No substantial differences in niche breadth were detected among most species, likely reflecting their taxonomic relatedness and the consumption of similar dominant food components. An exception was observed for crucian carp, for which no significant variation between basins was recorded, as its diet was largely restricted to macrophytes. Pikeperch exhibited the most diverse diet, with slightly higher niche breadth values (although still $Bi < 0.30$) due to the consumption of approximately 9–10 food components.

The predominance of a limited number of dominant prey groups may entail ecological risks, including increased sensitivity to environmental fluctuations, reduced capacity

for trophic switching, and intensified interspecific competition. It should be noted that the present dietary analysis is based primarily on summer data, which constrains the interpretation of trophic patterns. Seasonal variation in resource availability and trophic interactions may alter the spectrum of consumed prey and allow partial substitution among food items. Therefore, further multi-seasonal studies are recommended to provide a more comprehensive assessment of trophic niche breadth and plasticity in the studied species.

3.5.4. Assessment of Niche Overlap Using Pianka's Index

Analysis of niche overlap among benthivorous fish species in the western part of Lake Balkhash (Table 10) revealed the presence of interspecific competition. A particularly high level of overlap was recorded between crucian carp and roach ($O_{jk} = 0.97$), indicating pronounced competition for shared food resources. For the remaining species pairs, trophic overlap was moderate and did not exceed Pianka's index values of $O_{jk} \leq 0.46$.

Table 10. Pianka's niche overlap index values (O_{jk}) for benthivorous fish species in Lake Balkhash.

Species	<i>C. carpio</i>	<i>R. caspicus</i>	<i>A. brama</i>	<i>C. gibelio</i>
Western Balkhash				
<i>C. carpio</i>	X	0.46	0.42	0.35
<i>R. caspicus</i>	0.46	X	0.21	0.05
<i>A. brama</i>	0.42	0.21	X	0.97
<i>C. gibelio</i>	0.35	0.05	0.97	X
Eastern Balkhash				
<i>C. carpio</i>	X	0.12	0.76	0.95
<i>R. caspicus</i>	0.12	X	0.58	0.03
<i>A. brama</i>	0.76	0.58	X	0.74
<i>C. gibelio</i>	0.95	0.03	0.74	X

It is likely that in the western basin of Lake Balkhash, the relatively narrow trophic specialization of the studied species, combined with sufficient availability of food resources during the summer period, provided favorable feeding conditions. This may have contributed to a reduction in the overall intensity of interspecific competition for dietary resources.

In the eastern part of Lake Balkhash, interspecific competition increased among all examined benthivorous fish species. The highest trophic overlap was observed between roach and common carp ($O_{jk} = 0.76$), crucian carp and common carp ($O_{jk} = 0.95$), and crucian carp and roach ($O_{jk} = 0.74$). Competition involving common bream was generally moderate or minimal when compared with other species, except for roach ($O_{jk} = 0.58$). Notably, trophic overlap between common carp and common bream remained low ($O_{jk} = 0.12$), although competition between carp and other species was more pronounced.

The observed competitive patterns in the eastern basin, particularly among crucian carp, common carp, and roach, are likely associated with the seasonal abundance of macrophytes and mysids. In contrast, common bream appears to engage less frequently in direct competitive interactions with common carp due to its substantial consumption of mysids and chironomid larvae, and comparatively lower reliance on macrophytes.

Competition among predatory fish species in the western part of Lake Balkhash was recorded among four species (Table 11). Competitive pressure exerted by Volga pikeperch was comparatively weaker. Strong niche overlap was identified between snakehead and pikeperch ($O_{jk} = 0.92$), as well as between snakehead and wels catfish ($O_{jk} = 0.87$). The

consumption of crucian carp (*Carassius* spp.) as a major prey item by both catfish (*S. glanis*) and snakehead (*C. argus*) suggests the formation of potential competitive interactions between these species. At the same time, the absence of roach (*R. caspicus*) in the diet of snakehead is noteworthy, despite the similarity of their occupied habitats.

Table 11. Pianka's niche overlap index values (O_{jk}) for predatory fish species in Lake Balkhash.

Species	<i>S. lucioperca</i>	<i>S. volgnesis</i>	<i>S. glanis</i>	<i>C. argus</i>	<i>A. aspius</i>
Western Balkhash					
<i>S. lucioperca</i>	X	0.47	0.72	0.92	0.69
<i>S. volgnesis</i>	0.47	X	0.30	0.31	0.28
<i>S. glanis</i>	0.72	0.30	X	0.87	0.45
<i>C. argus</i>	0.92	0.31	0.87	X	0.56
<i>A. aspius</i>	0.69	0.28	0.45	0.56	X
Eastern Balkhash					
<i>S. lucioperca</i>	X	0.73	0.36	0.55	0.65
<i>S. volgnesis</i>	0.73	X	0.53	0.56	0.76
<i>S. glanis</i>	0.36	0.53	X	0.44	0.27
<i>C. argus</i>	0.55	0.56	0.44	X	0.71
<i>A. aspius</i>	0.65	0.76	0.27	0.71	X

This pattern may reflect reduced availability of roach due to intensive predation by other piscivorous species, thereby limiting its inclusion in the snakehead diet. Consequently, snakehead appears to shift toward more accessible prey items, indicating a degree of trophic plasticity under conditions of interspecific competition.

In contrast to the western basin of Lake Balkhash, the eastern part exhibited increased trophic competition involving pikeperch, with overlap values of $O_{jk} = 0.73$ in relation to one species and $O_{jk} = 0.76$ in relation to asp. At the same time, trophic overlap between pikeperch and asp also increased ($O_{jk} = 0.65$). In other species pairs, competition remained moderate compared with the aforementioned groups.

4. Discussion

The comparative analysis of phytoplankton, zooplankton, and zoobenthos communities suggests that Lake Balkhash is currently undergoing a phase of structural reorganization driven by ongoing hydrological and climatic variability. The observed patterns indicate increasing biodiversity among primary producers and relative stabilization at higher trophic levels, reflecting a complex ecosystem response to long-term environmental fluctuations [55,56].

Phytoplankton diversity has increased markedly over the past two decades. In 2004, 91 species were recorded, with Chlorophyta dominating in the western area and Bacillariophyta forming the basis of diversity in the eastern area [18]. By 2025, total richness had risen to 148 taxa, with a more balanced distribution between the two areas. Diatoms became the most diverse division, while cyanobacteria continued to play a significant ecological role. Notably, *Snowella lacustris* remained one of the most widespread taxa across both periods, whereas species such as *Lindavia comta*, *Ulnaria ulna*, and *Oocystis lacustris* became more prominent in 2025.

Despite the substantial increase in taxonomic richness, the absence of taxa with ubiquitous occurrence and the predominance of low-frequency species indicate persistent spatial

heterogeneity within the lake. These patterns likely reflect the influence of strong environmental gradients between the western and eastern basins, including differences in salinity, hydrological connectivity, and nutrient availability. The observed diversification of phytoplankton communities may therefore be associated with improved hydrological conditions in recent years, while basin-scale environmental contrasts continue to structure community composition.

In contrast to phytoplankton, zooplankton communities demonstrate relatively stable species richness but noticeable internal restructuring. The total number of taxa remained similar between 2021–2023 (59 taxa) and 2025 (56 taxa), although the relative contribution of major groups changed [55]. In particular, the proportional contribution of Rotifera declined, whereas Cladocera and Copepoda increased. Core taxa such as *Arctodiaptomus salinus*, *Mesocyclops leuckarti*, *Thermocyclops crassus*, *Diaphanosoma lacustris*, and *Daphnia galeata* remained persistent and exhibited high frequencies in 2025, indicating a relatively stable functional core of the zooplankton community.

The decline in rotifer diversity together with the increased importance of crustacean taxa may reflect shifts in trophic structure, salinity conditions, or hydrological stability. Such changes are consistent with the general tendency for larger crustacean zooplankton to dominate under conditions of improved water balance and reduced environmental instability. As in phytoplankton communities, none of the zooplankton taxa demonstrated complete ubiquity across the lake, further emphasizing spatial patchiness as a persistent ecological feature.

Long-term zoobenthos data (1975–2024) clearly demonstrate the sensitivity of benthic communities to hydrological fluctuations. Periods of minimal diversity, such as the 7–9 taxa recorded during the 1990s, coincided with declining water levels and increased evaporation. In contrast, the peak recorded in 2021 (35 taxa) corresponded to improved water balance within the basin [56]. In 2025, 15 taxa were recorded, representing an intermediate level of diversity.

The continued prominence of tolerant taxa such as *Hypania invalida* and the *Chironomus plumosus* group indicates that benthic communities still experience certain environmental constraints, although present conditions appear considerably more favorable than during previous periods of hydrological stress. Comparable species richness between the western and eastern areas, together with the absence of ubiquitous taxa, further supports the conclusion that spatial heterogeneity remains a fundamental characteristic of the benthic community structure.

Taken together, these results indicate that Lake Balkhash is currently experiencing a gradual process of ecological restructuring rather than a simple linear recovery. The pronounced increase in phytoplankton diversity likely reflects improved hydrological inputs and the expansion of available ecological niches. In contrast, zooplankton and zoobenthos communities appear to respond primarily through structural reorganization and stabilization of functionally important taxa rather than through a direct increase in overall species richness.

The persistence of spatial heterogeneity across all trophic levels suggests that hydrological and physicochemical gradients between the western and eastern basins remain key drivers of ecosystem organization. These gradients, which are strongly influenced by variations in inflow from the Ili River and regional climatic conditions, continue to shape the distribution and interactions of aquatic communities within the lake.

Overall, the 2025 data do not indicate a complete ecological recovery to historical maxima but rather reflect the establishment of a relatively stable and moderately resilient ecosystem state shaped by long-term variability in water balance and climate-related pressures.

Prior to the implementation of acclimatization measures, the ichthyofauna of Lake Balkhash consisted predominantly of Balkhash perch (*Perca schrenkii* Kessler, 1874), Balkhash marinka (*Schizothorax argentatus* Kessler, 1874), Ili marinka (*Schizothorax pseudak-saiensis* Herzenstein, 1889), and spotted loach (*Triplophysa strauchii* (Kessler, 1874)). At that time, the trophic network was characterized by relatively simple interactions and a low level of food competition. Stability within the fish community was largely maintained through trophic interactions between the dominant predator—Balkhash perch—and its prey, primarily juveniles of native fish species inhabiting the middle reaches of tributary rivers [49].

A major transformation of trophic relationships began following the introduction of pikeperch and several invertebrate species in 1958 [13], which resulted in the restructuring of food chains and increased interspecific interactions. Analyses of pikeperch feeding ecology revealed pronounced dietary shifts during the process of naturalization, reflecting a redistribution of predation pressure on native species [57,58]. For example, in 1963, Balkhash perch comprised 45–73% of the pikeperch diet. Subsequently, during 1964–1969, a sharp decline in marinka abundance was recorded, likely associated with intensified predation by pikeperch [59].

Competition for food resources has been documented among benthivorous fish species, particularly between common carp and bream exploiting similar benthic prey [60]. At the same time, pronounced qualitative and quantitative differences in zoobenthos structure have been identified between the western and eastern basins of the lake. In the western basin, carp exhibits a mixed feeding strategy involving zoobenthos, macrophytes, and detritus, with molluscs dominating the diet (20–95% of total volume). In contrast, amphipods (Corophiidae) and insect larvae, mainly chironomids, predominate in carp diets in the eastern basin [59].

Similar trophic spectra of benthivorous fish have been reported in other lakes and reservoirs of Kazakhstan as well as in hydrologically comparable ecosystems outside the region [61–63]. Lake Balkhash and the Alakol lake system are frequently considered ecological analogs [64]. Comparable feeding patterns among carp, roach, and bream have also been documented in Kapshagay Reservoir [65].

Analysis of trophic niche overlap among benthivorous fish in the western basin of Lake Balkhash indicates the presence of interspecific competition, although its overall intensity remains moderate. The most pronounced overlap was observed between crucian carp and roach ($O_{jk} = 0.97$), suggesting a high potential for competitive interactions. For other species pairs, Pianka's index did not exceed 0.46, indicating relatively limited trophic similarity. Such patterns may be associated with trophic specialization and the relatively high availability of food resources during the summer period.

In the eastern basin, trophic overlap among benthivorous fish species appears to be higher. The greatest similarity was observed among crucian carp, common carp, and roach, suggesting increased competition for available resources. In contrast, bream demonstrated relatively low overlap with most species, except for moderate similarity with roach. This trophic differentiation may be explained by the stronger reliance of bream on mysids and chironomid larvae, which reduces competition for macrophyte resources.

The feeding ecology of predatory fish species—including pikeperch, snakehead, asp, wels catfish, and Volga pikeperch—is strongly influenced by habitat structure, prey availability, and ontogenetic behavioral traits. Spatial niche differentiation among predators appears to reduce direct competition: asp typically occupies surface waters, pikeperch deeper zones, wels catfish benthic habitats, and snakehead vegetated shallow areas [66]. Ontogenetic development is known to influence feeding strategies in fish through changes in morphology, prey capture ability, and energetic requirements. In the present study,

ontogenetic effects on the consumption of specific dietary components were observed in predatory species such as *Sander lucioperca* and *Aspius aspius*. Differences in diet composition were detected among individuals of different age groups inhabiting the western and eastern basins of Lake Balkhash. For instance, pike-perch from the western basin (mean age 3.6 ± 0.2 years) consumed approximately ten dietary components. Their diet was dominated by digested fish remains (about 40%), while other prey items included roach, crucian carp, bream, and shrimp. In contrast, individuals from the eastern basin (mean age 4.2 ± 0.2 years) consumed largely similar prey categories, but the proportion of crucian carp was lower (3.78%), and the share of digested fish remains reached 23.48%, which is nearly two times lower than in the western basin.

Age-related differences in diet composition were also observed in asp. Individuals from the western and eastern parts of the lake (7 ± 0.3 and 4 ± 0.2 years, respectively) exhibited notable differences in feeding patterns. In the eastern basin, the diet included significant proportions of mysids (30.19%) and cestodes (5.84%). In contrast, in the western basin the diet was dominated by fish prey, and cases of cannibalism involving juvenile conspecifics were recorded (35.15%).

Overall, these results suggest that ontogenetic variation contributes to shifts in trophic resource use in predatory fish species. Changes in age structure appear to influence the composition of consumed prey and may result in size-dependent trophic strategies within the fish community of Lake Balkhash.

In the western basin of Lake Balkhash, the most pronounced trophic overlap occurs among *C. argus*, *S. lucioperca*, and *S. glanis*, whereas *S. volgensis* demonstrates relatively distinct feeding preferences. In the eastern basin, niche overlap increases among pike-perch, snakehead, and *A. aspius*, while trophic relationships among other species combinations indicate the persistence of competitive interactions.

5. Conclusions

1. The 2025 assessment of phytoplankton, zooplankton, and zoobenthos communities in Lake Balkhash indicates a structurally reorganized yet relatively stable ecosystem under ongoing hydrological and climatic variability. Phytoplankton exhibited a substantial increase in taxonomic richness, whereas zooplankton and zoobenthos showed compositional restructuring with increased contributions of ecologically tolerant taxa. The absence of ubiquitous species and the predominance of low-frequency taxa across all trophic groups reflect persistent spatial heterogeneity. Overall, the lake demonstrates moderate ecological resilience but has not fully recovered to historical maximum diversity levels.

2. Benthivorous fish species in Lake Balkhash are characterized predominantly by a moderate degree of trophic similarity, with certain species pairs exhibiting pronounced trophic differentiation. In the western basin, a mosaic pattern of niche overlap is observed, where some species show partial overlap in resource use, whereas others display substantial differences in diet composition.

In the eastern basin, trophic similarity generally remains moderate; however, common bream (*A. brama*) demonstrates a more distinct trophic position compared with other benthivorous species.

3. Predatory fish species of Lake Balkhash also exhibit overall moderate trophic similarity, while maintaining intraspecific dietary stability in pikeperch (*S. lucioperca*). Partial niche overlap is observed between pikeperch and Volga pikeperch (*Sander volgensis*), whereas snakehead (*C. argus*) and asp (*A. aspius*) show marked trophic differentiation, indicating the development of distinct feeding strategies.

4. Introduced fish species are characterized by narrow trophic niche breadth ($Bi < 0.30$), reflecting pronounced dietary specialization. No substantial interspecific differences were

detected, except for pikeperch, which exhibited a slightly broader range of consumed prey items. These findings suggest limited trophic plasticity during the summer period and highlight the need for multi-seasonal studies to achieve a more comprehensive evaluation of their ecological strategies.

5. In the western basin, trophic overlap among species is maintained, with the strongest overlap observed between crucian carp and roach. In the eastern basin, dietary similarity generally increases, while bream retains a relatively distinct trophic position. Among predatory species, the greatest niche overlap in the western basin occurs between snakehead, pikeperch, and catfish, whereas in the eastern basin trophic similarity increases between pikeperch, snakehead, and asp. Overall, the trophic relationships indicate the persistence of competitive interactions among species.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d18040201/s1>.

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Conflicts of Interest: Fisheries Research and Production Center LLP refers to a research institute, although its name may resemble that of a company. It is not a commercial entity, and it has no commercial interest in the results of this study. Therefore, there are no conflicts of interest to declare.

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