

Article

The Structuring Effects of Salinity and Nutrient Status on Zooplankton Communities and Trophic Structure in Siberian Lakes

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Abstract: Many continental saline lakes are under the effects of salinity increase and anthropogenic eutrophication exacerbated by global change. The response of the food web to these drivers of change is not straightforward. To understand the consequences of salinity and eutrophication interactive effects on the food web, we studied the seasonal dynamics of zooplankton and phytoplankton and water quality parameters in 20 lakes of different salinity (from freshwater to hypersaline) and nutrient status (from oligotrophic to eutrophic) located in southern Siberia. We observed a pronounced bottom-up effect of nutrients, which induced an increase in the biomass of phytoplankton and zooplankton and a decline in water quality. A significant decrease in the species abundance of zooplankton was observed at a threshold salinity of 3 g L⁻¹ and the disappearance of fish at 10 g L⁻¹. The top-down effect induced by salinity manifested itself in an increase in the biomass of zooplankton with the disappearance of fish, and in the change of the size distribution of phytoplankton particles with an increase in the proportion of cladocerans in the zooplankton. Even though we observed that with the salinity increase the food web in saline lakes transformed from three-trophic to two-trophic without fish, we conclude that in the salinity range from 10 to 20–30 g L⁻¹ this transition in most cases will not increase the ability of zooplankton to control phytoplankton. Interactive effects of salinity and eutrophication strongly depend on the size and depth of the lake, as deep stratified lakes tend to have a better water quality with lower biomasses of both phyto- and zooplankton. Thus, the salinity per se is not the driver of the decline in water clarity or the uncontrolled development of phytoplankton. Moreover, for deep lakes, salinity may be a factor affecting the stability of stratification, which mitigates the consequences of eutrophication. Thus, small shallow lakes will be the most vulnerable to the joint effect of salinity increase and eutrophication with the degradation of ecosystem functioning and water quality at moderate salinities of 3–20 g L⁻¹.

Keywords: phytoplankton; eutrophication; zooplankton; top-down effects; saline lakes; bottom-up control; food web



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1. Introduction

Water level variability and related changes in salinity are often considered natural phenomena for saline lakes located in arid climates (e.g., [1]). Such water level and salinity changes can be either reversible and short-term (e.g., seasonal variations) or unidirectional and long-term (e.g., climate-induced trends) [2–5]. In response to these variations, changes in the biodiversity, structure, and complexity of the food web occur, associated with species-specific tolerance to salinity [6]. However, the occurrence and the rate of such variations

are greatly intensified by global change effects [7]. For example, it was predicted that for some regions of the globe (e.g., the Mediterranean region) climate change would lead to long-term water level decline and salinity increase in inland lakes [8].

The most pronounced effect of the salinity is on the presence of fish and the structure of the zooplankton community in a lake [9]. Zooplankton are of key importance in lakes and central in the lake food web, being sandwiched between the top-down regulators (fish) and bottom-up factors (phytoplankton). Therefore, they also provide information about the relative importance of top-down and bottom-up control and, ultimately, on the overall ecosystem functioning and response to environmental stressors of water quality and other ecosystem services [10]. Recent studies have shown a major shift in zooplankton community structure along a salinity gradient, often with drastic changes when certain salinity thresholds are reached—e.g., when fish disappear or at higher salinity above the limits of tolerance of *Daphnia* and other larger cladocerans [11].

Recently, lakes of different salinity located close to each other were used as natural laboratories to study the effect of variable salinity on the species and functional diversity of zooplankton [11–14]. These studies show a decrease in species diversity and predictable changes among the dominant zooplankton species with an increase in salinity. At the same time, the salinity-induced decrease in zooplankton diversity often occurs without a decrease in the total abundance and biomass and, hence, in the intensity of functioning of the ecosystem [15].

Presumably, changes in the zooplankton community associated with an increase in salinity may lead to a change in the ability of zooplankton to control the development of phytoplankton [16,17]. On the one hand, with the disappearance of planktivorous fish, an increase in the biomass of zooplankton and an increase in the grazing pressure on the phytoplankton can be predicted [18]. On the other hand, with an increase in salinity, large species of *Daphnia* and other filter feeders disappear from the ecosystem and the more selective copepods start to dominate [9]. Previous research showed that selective zooplankton species could stimulate the development of toxic cyanobacteria [19,20] or various filamentous phytoplankton [21,22], which can lead to a reduction in water quality.

Salinity is not the only factor that strongly affects the food web mostly via species abundance and composition. The bottom-up effect of anthropogenic eutrophication of inland waters promotes the uncontrolled development of algae and loss of water quality [23–25]. Thus, the effects of salinity and nutrient increase on the food web can be interactive, with consequences for the water quality that are difficult to predict.

Research on the dynamics of zooplankton and phytoplankton in lakes of different salinity and trophic status can help to understand the consequences of salinity and eutrophication interactive effects on the food web, which are also intensified by global change. Previously, we briefly described a series of lakes of different salinity (from freshwater to hypersaline) and nutrient status (from oligotrophic to eutrophic) located close to each other in southern Siberia [26]. In this paper, we analyse the results of seasonal observations of plankton and water quality parameters in these lakes in order to assess the response of the food web components to salinity and nutrient variations and estimate the relative importance of nutrient (bottom-up) and salinity (top-down) control of the food web. We tested the following hypotheses: (1) with a salinity increase, the length of the food web and the number of zooplankton species will decrease; (2) the effect of salinity on the composition and diversity of zooplankton will be nonlinear; (3) zooplankton will respond equally to top-down salinity related and bottom-up nutrient-related controls, while the control of phytoplankton by zooplankton will be less pronounced.

2. Materials and Methods

We studied inland lakes Tus, Slabitelnoe, Shunet, Krasnenkie-1, Krasnenkie-2, Uchum, Shira, Bele small, Dzhirim, Bele large, Utichye-3, Utichye-1, Vlasyevo, Sukhoye, Krasnenkoe, Chalaskol, Matarak, Itkul, Fyrkal, and Kiprino, located in the South of Siberia in the area with semi-arid climate (Figure 1).

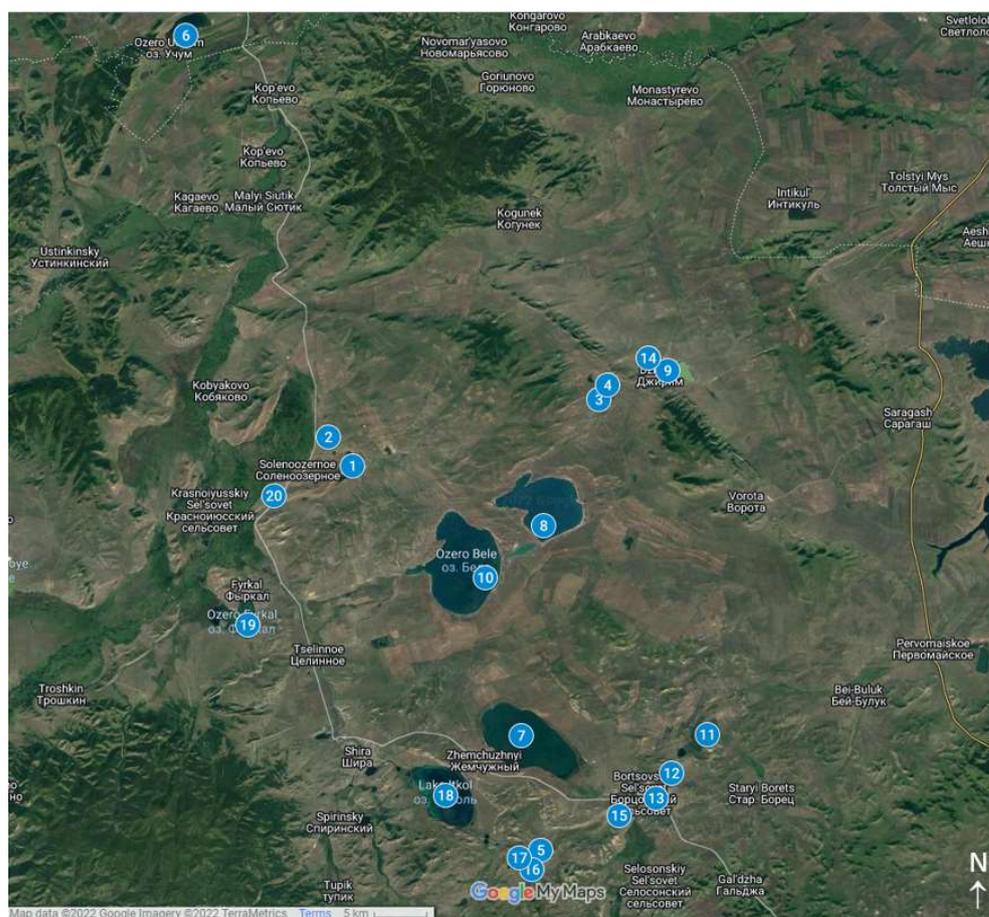


Figure 1. The map of the study lakes. Lakes are numbered from saline to freshwater (see Table 1). The map is available at <https://www.google.com/maps/d/edit?mid=1f3Aw36YdUF2WIF226jeXgJ1zS3cvhs7k&usp=sharing> (accessed on 29 April 2022).

Measurements of water column parameters and water and zooplankton sampling were performed on 17–21 July 2019 and 4–9 June, 17–20 August, and 12–14 October 2020. For small lakes, measurements and sampling were performed in the centre of the lake, which was determined visually from the map on the GPS navigator, for large lakes—at a distance of 1 km from the shore. The coordinates of sampling points and general description of lakes are presented in Table 1.

In each lake, we used a YSI Exo probe (YSI Inc., Yellow Springs, Ohio, OH, USA) to measure the vertical profiles of the temperature and specific electrical conductivity, which was used to calculate the total dissolve salts (TDS), the concentration of dissolved oxygen, redox potential, and pH. Additionally, with the submerged multichannel fluorometer FluoroProbe (bbe Moldaenke GmbH, Schwentingen, Germany), we measured vertical profiles of turbidity, coloured dissolved organic matter (CDOM, yellow substances (YS)), and fluorescence of photosynthetic pigments, which was automatically recalculated to the total concentration of chlorophyll *a* and the proportion of fluorescent signals related to the Chlorophyta (green algae), Bacillariophyta (diatom algae), Cryptophyta (cryptophytic algae) and Cyanobacteria.

Table 1. Characteristics of study lakes. S—lake area, $D_{\text{lake}}/D_{\text{sample}}$ —the depth of the lake at the sampling point/the depth of water sample used for analysis, Strat/ DO_{bott} —stratification pattern/the presence of oxygen near the bottom, ES—the dominant ecosystem services provided by the lake, TDS—the amount of total dissolved salts.

No.	Lake	Coordinate	S, km ²	$D_{\text{lake}}/D_{\text{sample}}$, m	Strat ¹ / DO_{bott} ²	ES ³	TDS, g L ⁻¹	Dry Residual, g L ⁻¹
1	Tus	54.739596°, 89.957181°	2.54	2.9/0.5–2.0	1 */2	2	38.73 ± 2.42	66.48 ± 3.15
2	Slabitelnoe	54.758119°, 89.926589°	0.16	1.1/0.5–1.0	1 */1	4	27.62 ± 1.43	43.75 ± 2.79
3	Krasnenkie-1	54.789130°, 90.309674°	0.61	1.4/0.5–1.0	0/2	4	21.89 ± 1.55	30.02 ± 2.60
4	Krasnenkie-2	54.801329°, 90.320764°	0.20	1.3/0.5–1.0	0/2	4	19.77 ± 1.60	27.24 ± 2.55
5	Shunet	54.419047°, 90.228202°	0.56	6.5/2.0	2/0	2	15.40 ± 0.71	20.80 ± 2.56
6	Uchum	55.094143°, 89.716882°	5.66	8.1/2.0	2/0	2	15.39 ± 0.56	19.96 ± 0.98
7	Shira	54.504697°, 90.201220°	39.13	24.2/2.0	2/0	1, 2	11.39 ± 0.14	17.35 ± 0.57
8	Bele small	54.682150°, 90.228909°	28.26	17.1/2.0	1/2	2	9.13 ± 0.10	12.52 ± 0.45
9	Dzhirim	54.810638°, 90.429847°	2.27	6.2/2.0	1/1	4	8.86 ± 0.04	10.18 ± 0.20
10	Bele large	54.642512°, 90.146674°	45.02	18.3/2.0	1/2	1, 2	6.04 ± 0.03	7.80 ± 0.26
11	Utichye-3	54.512453°, 90.463401°	1.67	6.4/2.0	1/1	3	4.82 ± 0.08	6.16 ± 0.62
12	Utichye-1	54.481329°, 90.414246°	0.41	1.8/1.0	1/1	4	4.30 ± 0.04	5.79 ± 0.24
13	Vlasyevo	54.457138°, 90.383218°	1.20	6.5/2.0	1/1	3	3.23 ± 0.05	3.27 ± 0.27
14	Sukhoye	54.823422°, 90.377964°	0.34	4.2/2.0	0/1	3, 4	1.77 ± 0.03	2.09 ± 0.15
15	Krasnenkoe	54.445164°, 90.337008°	0.14	1.3/0.5	0/2	4	1.60 ± 0.09	1.79 ± 0.15
16	Chalaskol	54.401568°, 90.213695°	0.34	2.7/1.0	0/2	3, 4	0.98 ± 0.01	1.12 ± 0.04
17	Matarak	54.406200°, 90.193142°	0.79	5.8/2.0	0/1	2, 3	0.84 ± 0.00	0.94 ± 0.06
18	Itkul	54.468351°, 90.110088°	20.51	9.6/2.0	1/1	1, 2	0.41 ± 0.01	0.57 ± 0.17
19	Fyrkal	54.602622°, 89.802478°	8.95	1.5/0.5–1.0	0/2	2, 3	0.30 ± 0.01	0.33 ± 0.04
20	Kiprino	54.710063°, 89.848019°	0.31	3.8/2.0	0/1	2	0.08 ± 0.01	0.15 ± 0.02

¹ 0—mixed, 1—seasonal stratification, 2—meromictic. *—reverse stratification with more saline and warm water near the bottom. ² 0—the permanent depletion of oxygen near bottom, 1—seasonal depletion of oxygen near bottom, 2—the permanently oxygenated water column. ³ 1—lake or part of the lake is a nature protected area, 2—lake is intensively used for seasonal (summer) recreation, 3—lake is used for fishing, 4—lake is used for cattle watering or cattle pens are located close to the lake.

The zooplankton in each lake were sampled by vertical tows from the bottom to the surface with the plankton net (mesh size 75 μm , mouth diameter 17 cm). Zooplankton samples were preserved in 70% ethanol. The samples were scanned at high resolution [27], and digital images of all animals belonging to Rotifera, Cladocera, Copepoda, and Anostraca were counted. Most Rotifera, Cladocera, and Anostraca were identified to the genus level and Copepoda to the order level. The biomass of zooplankton was calculated based on the linear size–weight regressions for different genera and orders [28–31].

From each lake, we also pumped 5 L of water from the epilimnion (the sampling depth is presented in Figure 1) for a series of analyses and measurements.

To analyse the total organic carbon content in seston, first, we filtered water through the 115 μm mesh and then through the glass fibre filters GF/F (Whatman), which were pre-combusted at 400 $^{\circ}\text{C}$ for 4 h. Filters were dried and later used to analyse the carbon content with a Flash EA 2000 NC Soil element analyser (ThermoFisher, Bremen, Germany) [32]. Previously we observed that for saline lakes, the organic carbon content in the analysis was elevated due to residuals of inorganic carbon after the evaporation of saline water from filters. Thus, we adjusted the data for saline lakes with the previously determined coefficient, which was proportional to the amount of inorganic carbon in the water [33].

For chemical analysis, 2 L of water filtered through the 115 μm mesh was frozen and analysed later in the analytical laboratory of the Institute of Biophysics SB RAS.

Chloride content was detected argentometrically. The Nessler method was used for ammonium nitrogen, nitrates were converted to nitrites by means of a cadmium column, and nitrite was determined by the colourimetric method after reacting with sulphanilamide and α -naphthylamine. Soluble reactive phosphorus was assessed using the ascorbic acid and ammonium molybdate method; total phosphorus was measured the same way after persulfate digestion of unfiltered samples. For sulphate estimation, samples were titrated with a BaCl_2 solution in the presence of nitrochromazo until the appearance of a blue colour [34,35]. The optical density of solutions was determined with a KFK-2MP spectrophotometer (Zagorsk Optical and Mechanical Plant, Russia). CO_3^{2-} and HCO_3^- were determined by titration with 0.1 N or 0.01 N HCl until pH 4.3. The pH was determined with a PB-11 pH-meter (Sartorius, Germany).

Total contents of elements (K, Na, Ca, Mg, S, B, Ba, Be, Bi, Ga, Ni, Pb, Fe, Mn, Mo, Cu, Co, Cd, Cr, Sr, Se, Sb, As, Al, Li, Ti, Tl, V, Zn) were determined with inductively coupled plasma optical emission spectrometry (ICP—OES) using an iCAP 6300 Duo spectrometer (Thermo Scientific, Cambridge, UK) [36]. Total solids (TS) were estimated in water samples after evaporation on a laboratory hot plate and drying at 105 $^{\circ}\text{C}$. A residue was measured on an analytical balance Pioneer 214C (Ohaus Corp., Pine Brook, NJ, USA) accurate to 0.0001 g.

To determine the size and number of phytoplankton organisms (considered particles) in the water, we used a FlowCam flow cytometer (FluidImaging Inc., Yarmouth, Maine, MA, USA) with a 50 μm capillary. From each water sample, 0.2 mL of water was run through the capillary at a flow rate of 0.04 mL per minute. The measurements were carried out in the trigger mode. In the trigger mode, the FlowCam captures images of particles when the fluorescent signal exceeds the threshold (400 nm) in at least one of the detection channels. The FlowCam was configured with an excitation 532 nm laser and two photodetectors detecting red (wavelength ≥ 650 nm, chlorophyll *a*) and orange (575 \pm 30 nm wavelength, phycoerythrin) fluorescence. The minimal size of captured images of particles was set at 2 μm . With the FlowCam, we analysed the abundance of particles, the area based average diameter, and the average aspect ratio of particles [37].

To elucidate the relationship between phytoplankton and zooplankton community structures and environmental factors, canonical correspondence analyses were performed with the vegan 2.5–7 package [38] for the R statistical programming language [39].

A preliminarily detrended correspondence analysis (DCA) of phytoplankton and zooplankton response variables revealed the largest gradient lengths of 1.09 SD and 4.51 SD, respectively. Therefore, redundancy analysis (RDA, linear ordination methods) was appropriate to test the relationship between phytoplankton and its explanatory variables,

while canonical correspondence analysis (CCA, unimodal type of ordination method) was selected to relate the zooplankton community structure and environmental factors (gradient > 4SD) [40].

A forward selection procedure, using the function *ordiR2step*, was performed to identify the best set of significant environmental variables ($p < 0.05$) explaining the variation in phytoplankton and zooplankton data. The significance of RDA and CCA models and canonical axis were tested using the Monte Carlo permutation test function *anova.cca* (999 permutations). The variance inflation factors VIF were examined to check superfluous variables. Only variables with $VIF < 10$ were retained. All variables were $\ln(x + 1)$ transformed to reduce distributional skewness prior to analysis [41].

In addition, to separately analyse the effect of salinity on the ecosystem properties of the study lakes, we classified lakes into 4 categories: freshwater (TDS < 0.5 g L⁻¹), moderately saline (TDS 0.5–3 g L⁻¹), brackish (TDS 3–10 g L⁻¹), and saline lakes (TDS > 10 g L⁻¹) [42]. To analyse the effect of top-down and bottom-up effects on the ecosystem properties of the study lakes, we classified lakes into fishless (0) and fish (1) lakes and elevated nutrient load (1) or not (0) lakes. The presence or absence of fish was determined based on literature data, personal communications of the locals or the presence of fishermen on the lake. The lake was categorized as an elevated nutrient load one when it was used for cattle watering or cattle pens were located close to the lake. On the sampling dates, lakes were also categorized as stratified (1) or not stratified (0) and oxygen-depleted near the bottom (1) or oxygen-rich (0). This classification was based on the vertical profiles of temperature and oxygen concentrations measured with YSI Exo.

To analyse the separate effects of salinity category (4 categories of lakes), nutrient load (1 or 0), season (4 months), fish presence (1 or 0), and stratification (1 or 0) on the characteristics of the lakes, we used factorial analysis of variances. Regression analysis was used to estimate correlations between various continuous variables. Statistical calculations were performed in STATISTICA 8.0.

3. Results

3.1. Physical and Chemical Characteristics of the Study Lakes

Among the study lakes, three were classified as freshwater (TDS < 0.5 g L⁻¹), four as moderately saline (TDS 0.5–3 g L⁻¹), six as brackish (TDS 3–10 g L⁻¹), and seven as saline lakes (TDS > 10 g L⁻¹) (Table 1, Appendix A, Table A1). The salinity of lakes was mostly determined by K, Na, Cl, Mg, and S (from 60% of the dry residuals in saline lakes up to 30% of dry residuals in freshwater lakes) (Appendix A, Table A1). The chemical type of water in moderately saline, brackish, and saline lakes was magnesium sulphate-chloride with some variability in ionic composition between lakes. Significant linear regression between the amount of the element in the dry residuals and the value of TDS was also observed for B, Bi, Ca, Ga, Li, Mn, and Sr. However, the total amount of these elements in the dry residuals was relatively low (from 0.5% of the dry residuals in saline lakes to 8% of dry residuals in freshwater lakes). The average content of CO₃ and HCO₃ in the water from freshwater lakes (17.7 ± 4.9 and 151.2 ± 25.5 mg L⁻¹) and moderately saline lakes (71.7 ± 9.4 and 485.2 ± 63.4 mg L⁻¹) was significantly lower than in brackish (143.2 ± 18.4 and 863.9 ± 75.1 mg L⁻¹) and saline lakes (166.5 ± 28.7 and 818.8 ± 72.5 mg L⁻¹). We did not detect any significant seasonal variability of TDS values and contents of elements in the study lakes ($p > 0.05$, ANOVA).

The lakes were variable in area (from 0.14 to 45.02 km²) and depth at the sampling points (from 1.1 to 24.2 m) (Table 1). Moderately saline lakes had the smallest areas and depths, but we did not detect any significant differences in these parameters between lakes from different salinity categories ($p > 0.05$, ANOVA).

Seasonal stratification of the water column in lakes depended on their depth. The average depth of mixed lakes (2.7 ± 0.6 m) was significantly lower than the depth of seasonally (7.8 ± 2.1 m) and permanently stratified (meromictic) (12.9 ± 5.7 m) lakes (Table 1). Seasonal stratification was also dependent on the salinity category ($p < 0.001$,

ANOVA) (Figure 2). Only 1 lake out of 7 freshwater and moderately saline lakes was seasonally stratified while 10 out of 13 brackish and saline lakes were stratified either seasonally or permanently.

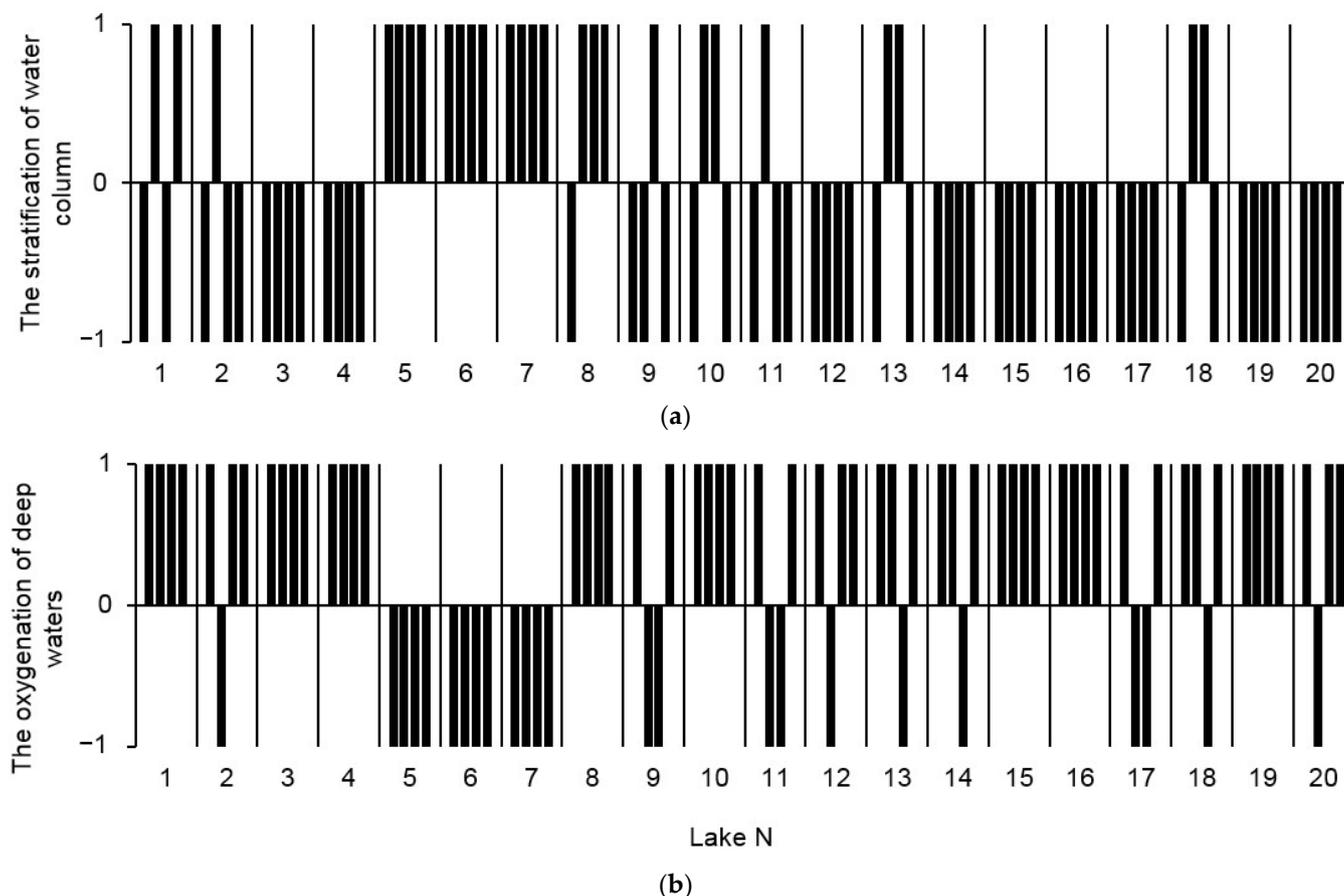


Figure 2. Seasonal dynamics (June, July, August, October) of the water column stratification (a): +1—stratified, −1—mixed, and deep water oxygenation (b): +1—O₂ present, −1—O₂ depleted, of study lakes. Lakes are numbered according to Table 1.

Seasonal stratification determined the presence of oxygen in the deep waters (Figure 2). Two-factorial ANOVA demonstrated the significant effect of stratification ($p < 0.001$) and the combined effect of stratification and months ($p = 0.018$) on oxygen depletion near the bottom. Almost all lakes were mixed and had an oxygenated water column except for the three meromictic lakes in June and October. In five stratified and four non-stratified lakes in July and in six stratified and three non-stratified lakes in August, oxygen near the bottom was depleted. In two stratified lakes and six mixed lakes, oxygen was present near the bottom on all sampling dates (Figure 2).

The correlation between the value of TDS and the concentrations of total phosphorus and forms of nitrogen, CDOM, and turbidity of water was insignificant (Table 2). At the same time, the effect of the salinity category on the concentrations of total phosphorus, CDOM, and turbidity of water was significant with the lowest values of P_{tot} , CDOM, and turbidity in freshwater lakes (Table 2). We also observed positive correlations between the concentration of the total phosphorus and CDOM ($p < 0.001$) and turbidity ($p = 0.012$).

Table 2. Average seasonal (June–October) water quality parameters (mean \pm SE) of study lakes.

Lake	P_{total} , mg L ⁻¹	P_{total} , mg L ⁻¹	N_{diss} , mg L ⁻¹	N_{diss} , mg L ⁻¹	Turbidity, FTU	Turbidity, FTU	CDOM, r.u.	CDOM, r.u.
Tus	0.097 \pm 0.029		0.22 \pm 0.13		2.7 \pm 0.6		2.87 \pm 0.17	
Slabitelnoe	0.076 \pm 0.024		0.12 \pm 0.02		3.9 \pm 1.2		6.61 \pm 0.49	
Krasnenkie-1	0.112 \pm 0.006		0.31 \pm 0.09		13.7 \pm 6.1		7.95 \pm 0.58	
Krasnenkie-2	0.148 \pm 0.017	0.078 \pm 0.010	0.37 \pm 0.15	0.25 \pm 0.04	10.3 \pm 2.9	5.4 \pm 1.2	7.26 \pm 0.52	4.56 \pm 0.49
Shunet	0.028 \pm 0.012		0.22 \pm 0.11		1.7 \pm 0.1		3.46 \pm 0.21	
Uchum	0.067 \pm 0.005		0.39 \pm 0.14		4.0 \pm 2.3		2.90 \pm 0.27	
Shira	0.018 \pm 0.005		0.13 \pm 0.05		1.8 \pm 0.5		0.83 \pm 0.06	
Bele small	0.019 \pm 0.008		0.09 \pm 0.03		2.5 \pm 0.6		0.26 \pm 0.04	
Dzhirim	0.835 \pm 0.078		0.26 \pm 0.09		30.1 \pm 10.2		11.39 \pm 1.10	
Bele large	0.009 \pm 0.001	0.519 \pm 0.173	0.15 \pm 0.02	0.26 \pm 0.06	2.1 \pm 0.5	13.2 \pm 4.8	0.37 \pm 0.04	5.35 \pm 1.09
Utichye-3	0.626 \pm 0.581		0.28 \pm 0.07		1.7 \pm 0.6		4.29 \pm 0.28	
Utichye-1	1.584 \pm 0.611		0.64 \pm 0.30		37.7 \pm 22.3		12.77 \pm 1.86	
Vlasyevo	0.038 \pm 0.003		0.16 \pm 0.05		4.9 \pm 0.8		3.03 \pm 0.33	
Sukhoye	0.580 \pm 0.089		0.26 \pm 0.05		69.1 \pm 28.4		12.43 \pm 0.99	
Krasnenkoe	0.211 \pm 0.136	0.227 \pm 0.066	0.22 \pm 0.03	0.20 \pm 0.02	6.5 \pm 2.7	23.7 \pm 9.4	5.47 \pm 0.61	7.09 \pm 1.09
Chalaskol	0.084 \pm 0.008		0.19 \pm 0.05		13.6 \pm 2.4		8.82 \pm 1.17	
Matarak	0.030 \pm 0.007		0.12 \pm 0.02		5.4 \pm 1.3		1.68 \pm 0.21	
Itkul	0.006 \pm 0.001		0.07 \pm 0.02		0.5 \pm 0.1		0.45 \pm 0.07	
Fyrkal	0.023 \pm 0.004	0.015 \pm 0.002	0.14 \pm 0.03	0.16 \pm 0.04	5.3 \pm 1.8	2.4 \pm 0.8	2.05 \pm 0.28	1.28 \pm 0.22
Kiprino	0.014 \pm 0.002		0.25 \pm 0.10		1.5 \pm 0.4		1.32 \pm 0.13	
The significance of the correlation ANOVA	$p = 0.30$	Current effect: F(3, 76) = 4.59, $p = 0.005$	$p = 0.72$	Current effect: F(3, 75) = 0.87, $p = 0.462$	$p = 0.25$	Current effect: F(3, 76) = 3.22, $p = 0.027$	$p = 0.76$	Current effect: F(3, 76) = 5.42, $p = 0.002$

P_{total} —the total concentration of phosphorus at the sampling depth, N_{diss} —the sum of NH_4 , NO_2 , and NO_3 at the sampling depth. CDOM—a yellow substances (coloured dissolved organic matter) measurement by FluoroProbe in relative units. Sampling depths are presented in Table 1.

The total concentrations of phosphorus, CDOM, and turbidity of water were strongly affected by the external nutrient load associated with the cattle watering or cattle pens located close to the lake (Table 3).

Table 3. The effect of nutrient load on the ecosystem parameters of study lakes.

Parameter	Lake Is Not Used for Cattle Watering or Cattle Pens Are Located Close to the Lake		Lake is Used for Cattle Watering or Cattle Pens Are Located Close to the Lake		The Significance of the Effect (One-Way ANOVA)
	Mean	SE	Mean	SE	
P _{total} , mg L ⁻¹	0.08	0.05	0.45	0.11	<i>p</i> < 0.001
Turbidity, FTU	2.84	0.35	23.10	5.60	<i>p</i> < 0.001
CDOM, r.u.	1.96	0.19	9.09	0.56	<i>p</i> < 0.001
The concentration of suspended particles in the epilimnion measured with FlowCam, particles mL ⁻¹	13 207	1 916	116 606	36 378	<i>p</i> < 0.001
The concentration of chlorophyll <i>a</i> in the epilimnion, µg L ⁻¹	7.98	1.31	43.39	10.82	<i>p</i> < 0.001
The content of organic carbon in seston, mg L ⁻¹	1.25	0.13	3.77	0.59	<i>p</i> < 0.001

P_{total}—the total concentration of phosphorus at the sampling depth, CDOM—a yellow substance (coloured dissolved organic matter) measurement by FluoroProbe in relative units, Mean—average value, SE—standard error.

3.2. Food Web Components

3.2.1. Phytoplankton

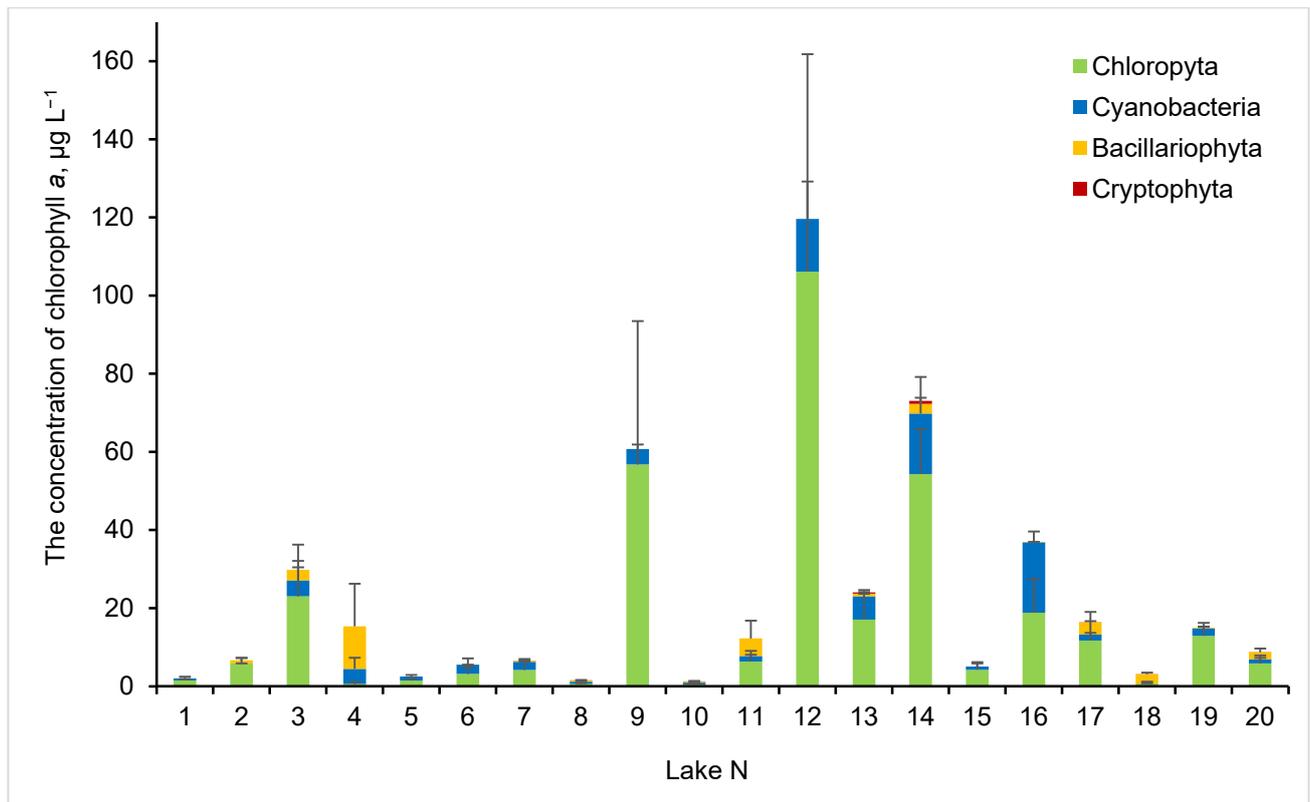
The chlorophyll *a* concentration and other parameters proportional to the abundance of phytoplankton (the organic carbon content in seston and the abundance of particles) (Figure 3b) varied across lakes (Figure 3a).

The correlations between values of parameters related to phytoplankton abundance and TDS were insignificant. Moreover, we did not detect any effect of season or salinity category on these parameters. The values of parameters related to phytoplankton abundance were strongly determined by the nutrient status, presumably associated with cattle watering or cattle pens located close to the lake (Table 3). The correlations between the values of parameters related to phytoplankton abundance and the values of other water quality parameters such as CDOM and turbidity were significant (*p* < 0.05, correlation analysis).

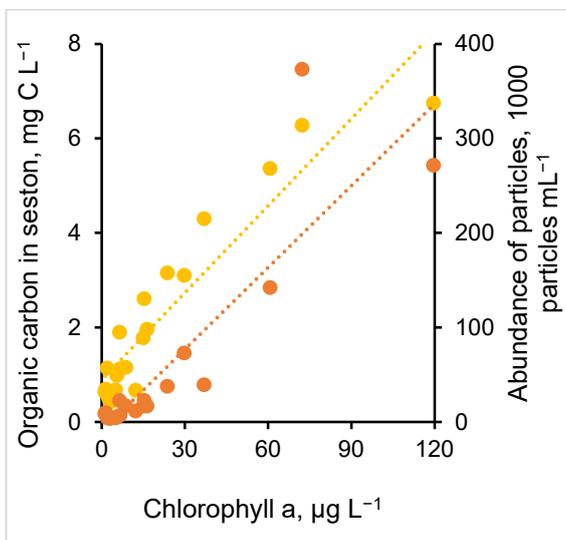
The effect of the stratification of the water column on the phytoplankton abundance was also significant with higher values in non-stratified lakes ($30.9 \pm 6.8 \mu\text{g Chl } a \text{ L}^{-1}$, $2.9 \pm 0.4 \text{ mg C L}^{-1}$, $76210 \pm 22470 \text{ particles mL}^{-1}$) compared with stratified lakes ($3.9 \pm 0.8 \mu\text{g Chl } a \text{ L}^{-1}$, $1.1 \pm 0.2 \text{ mg C L}^{-1}$, $9614 \pm 2311 \text{ particles mL}^{-1}$).

The phytoplankton in all lakes was dominated by Chlorophyta (green algae) (Figure 3c). The proportions of Chlorophyta, Bacillariophyta (diatom algae), Cryptophyta and Cyanobacteria, were independent of the season and nutrient load. The effect of the salinity category on the taxonomic composition of phytoplankton was significant for diatoms and cyanobacteria (Figure 3) (*p* < 0.05, ANOVA). The highest proportion of diatom algae (up to 30%) was observed in freshwater lakes, declining (7–12%) with the salinity increase. By contrast, the proportion of cyanobacteria was the lowest in freshwater lakes (8%), increasing (to 21–28%) with the increase in salinity.

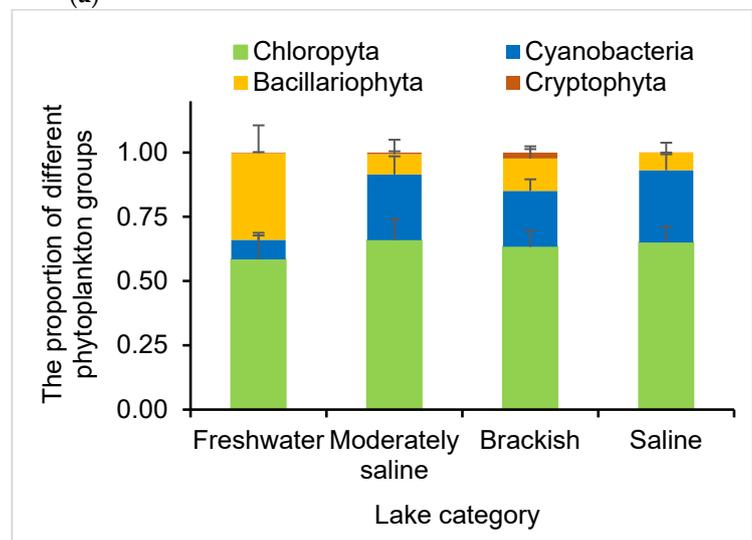
Phytoplankton response variables included in the RDA analysis were concentrations of chlorophyll *a* of four phytoplankton classes (Chlorophyta, Bacillariophyta, Cryptophyta and Cyanobacteria) and two morphological characteristics of phytoplankton particles—diameter and aspect ratio.



(a)



(b)



(c)

Figure 3. The abundances of phytoplankton expressed in chlorophyll *a* in the epilimnion of study lakes (a), the correlations between parameters related to phytoplankton abundance (b), and proportions of different phytoplankton groups in lakes of different salinity categories (c). Lakes are numbered according to Table 1.

The forward selection procedure indicated that yellow substance (YS), fish presence, percentage of cladoceran biomass in total zooplankton biomass, and temperature were significant environmental factors affecting phytoplankton community structure (Table 4). RDA model was statistically significant ($F = 6.62$, p -value < 0.001) and explained 26.1% of the variance in phytoplankton data. The first RDA axis explained 17.0% of the variance and the second RDA axis explained 5.3% of the variance (Figure 4).

Table 4. Phytoplankton classes and morphological characteristics as response variables explained by the environmental factors selected in RDA with the *forward selection* procedure. Statistics: *p*-value, F-test, R^2 -adjusted, and VIF.

Classes/Morphological Characteristics	Description	VIF	R^2 adj	F	Pr(>F)
<i>Chlorophyta</i>	Concentration of chlorophyll <i>a</i> (Chl <i>a</i>) of Green algae				
<i>Cyanobacteria</i>	Chl <i>a</i> of Cyanobacteria				
<i>Bacillariophyta (Diatoms)</i>	Chl <i>a</i> of Diatoms				
<i>Cryptophyta</i>	Chl <i>a</i> of Cryptomonads				
Diameter	Mean particle diameter				
Aspect ratio	Ratio of minimal to maximal Ferret diameter				
Selected predictors	Description	VIF	R^2 adj	F	Pr(>F)
Yellow substance	Coloured dissolved organic matter, detected at 370/680 nm excitation-emission wavelengths	1.3	0.13	12.64	0.002
Fish	Presence/absence of fish	1.4	0.18	5.71	0.002
Clad/Zooplankton	Ratio of cladoceran biomass to total zooplankton biomass	1.2	0.20	3.20	0.018
Temp	Temperature	1.0	0.22	3.00	0.016

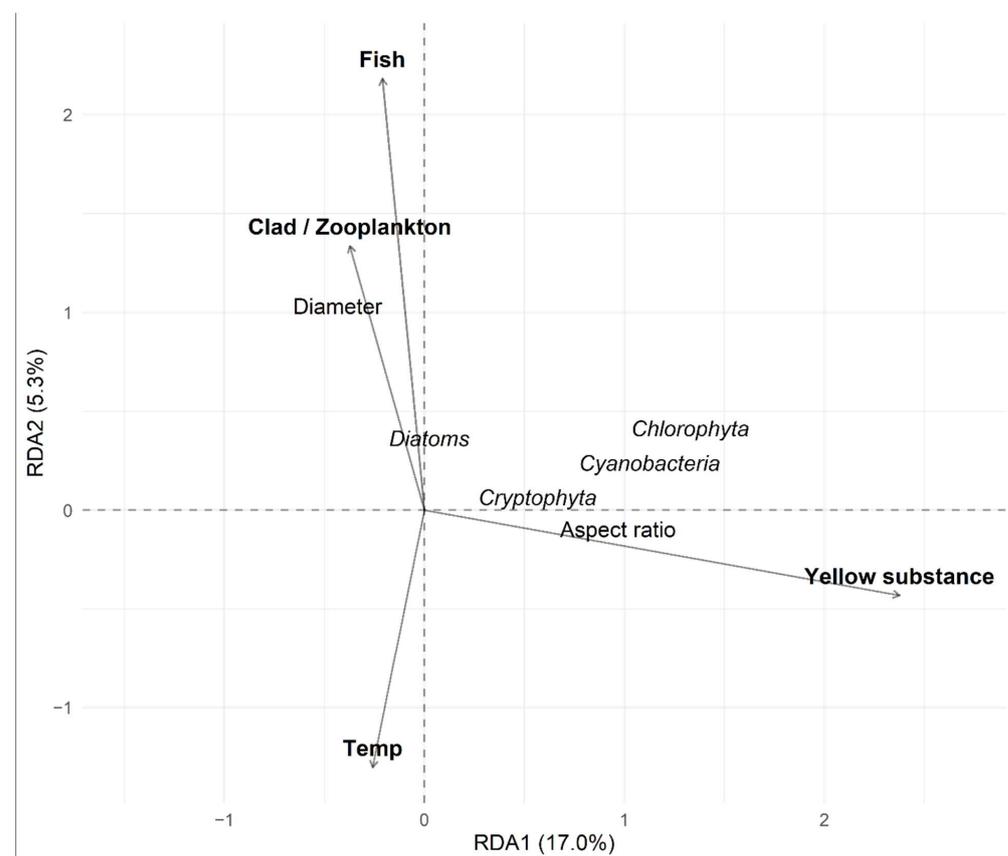


Figure 4. Redundancy analysis (RDA) ordination diagram showing the relationships between the chlorophyll *a* concentrations of the phytoplankton classes and morphological characteristics and the environmental variables. See Table 4 for phytoplankton classes and variable abbreviations.

YS was strongly correlated with the first axis, whereas fish, clad/zooplankton, and temperature were related to the second axis. YS and associated nutrient load was the most important environmental gradient affecting phytoplankton abundance. Biomasses of green

algae and cyanobacteria were positively correlated with YS. Diatoms and Cryptophyta were found at moderate YS values. Morphological characteristics of algae were determined by temperature and YS. Large cell algae were more frequent in lakes with lower temperatures, a high percentage of small Cladocera in total zooplankton, and fish presence. Small and round cells were generally more abundant at a higher level of YS and at moderate temperatures.

3.2.2. Zooplankton and Fish

The number of fishless lakes increased as the salinity increased. All saline lakes (TDS > 10 g L⁻¹) were fishless, while 25% of brackish lakes, 50% of moderately saline lakes, and 100% of freshwater lakes were with fish. The biomass of pelagic zooplankton varied across lakes (Figure 5a). The proportion of Cladocera biomass in the zooplankton biomass was maximal in freshwater lakes (ca. 30%) and decreased with the salinity increase. Almost 100% of Cladocera biomass in freshwater lakes was represented by the small (<1 mm) *Bosmina* sp., *Chydorus* sp., *Daphnia* sp., and *Ceriodaphnia* sp. In moderately saline and brackish lakes, the proportion of large-bodied cladocerans represented by *Daphnia magna* and *Moina mongolica* was relatively high. At all salinities, lakes were dominated by Copepoda (>60% of the zooplankton biomass). The proportion of cyclopoid copepods was maximal in freshwater lakes (ca. 60%) and declined almost to zero (<1%) in saline lakes. In contrast, the biomass of calanoid copepods increased from ca. 1% in freshwater lakes to almost 70% in saline lakes. Nauplii of Copepoda accounted for 3–5% of zooplankton biomass (Figure 5b). The biomass of pelagic zooplankton was significantly higher in fishless or non-stratified or nutrient-rich lakes (ANOVA, $p < 0.0001$) (Figure 6).

The total number of pelagic zooplankton species decreased with the salinity increase (Figure 7a). The most pronounced effect of the salinity on the number of species was observed for Cladocera, with the highest number of species in freshwater lakes and only one species in saline lakes (Figure 7b).

We detected broad salinity tolerance in many zooplankton species (Figure 8). However, when we used the abundance threshold (>1% of biomass), we observed clear salinity preferences of different zooplankton species. Among Rotifera, the high abundance of *Asplanchna* sp. was observed in freshwater, moderately saline, and brackish lakes, *Keratella* sp.—in moderately saline lakes, and *Brachionus* sp.—in brackish and saline lakes. Among Cladocera, *Bosmina*, *Ceriodaphnia*, and *Chydorus* species were abundant in freshwater lakes, *Daphnia* sp.—in moderately saline lakes, specifically, *Daphnia magna*—in brackish lakes and *Moina mongolica*—in saline lakes. Among Copepoda, *Cyclopoida* were abundant in freshwater and moderately saline lakes, *Calanoida*—in lakes with salinities up to 30 g L⁻¹, *Harpacticoida*—in lakes with salinities >30 g L⁻¹. Among Anostraca, *Artemia* was abundant in Lake Tus with the highest salinity, around 40 g L⁻¹.

The forward selection procedure identified total dissolved salts (TDS), total phosphorus, mineral nitrogen, the total count of particles measured by FlowCam, fish, maximum depth of the lake, and YS as significant explanatory variables for the abundance of zooplankton species with 38.6% variation captured in CCA (first axis: 19.9%, second axis 6.6%) (Table 5, Figure 9). The CCA model was statistically significant ($F = 5.61$, p -value < 0.001).

TDS and fish were the most important predictors in zooplankton community composition on the CCA first axis. The variance along the CCA second axis was mostly explained by the nutrients N-min, P-tot, and concentration of particles. The freshwater zooplankton community was located on the right side of the diagram and included the majority of cladoceran species: *Daphnia longispina*, *Ceriodaphnia* sp., *Diaphanosoma* sp., *Alona* sp., *Chydorus* sp., and *Leptodora kindtii*. Rotifers of the genera *Keratella* and *Filinia* also preferred waters with low TDS. Calanoida, Harpacticoida, cladoceran species *Moina mongolica*, and rotifers *Brachionus plicatilis* and *Hexarthra* sp. were observed in the left part of the diagram, associated with higher TDS. *Artemia* sp. was the species found at the highest salinity. The second axis represents a gradient of nutrient concentration affecting zooplankton species composition. *Daphnia magna* and *D. longispina* showed a higher correlation with phosphorus compared to other cladoceran species.

To demonstrate interactions between the two structuring factors, nutrient load and salinity, and the components of lake ecosystems we constructed a simplified diagram (Figure 10). This diagram reflects major correlations between measured parameters and significant effects observed in our study.

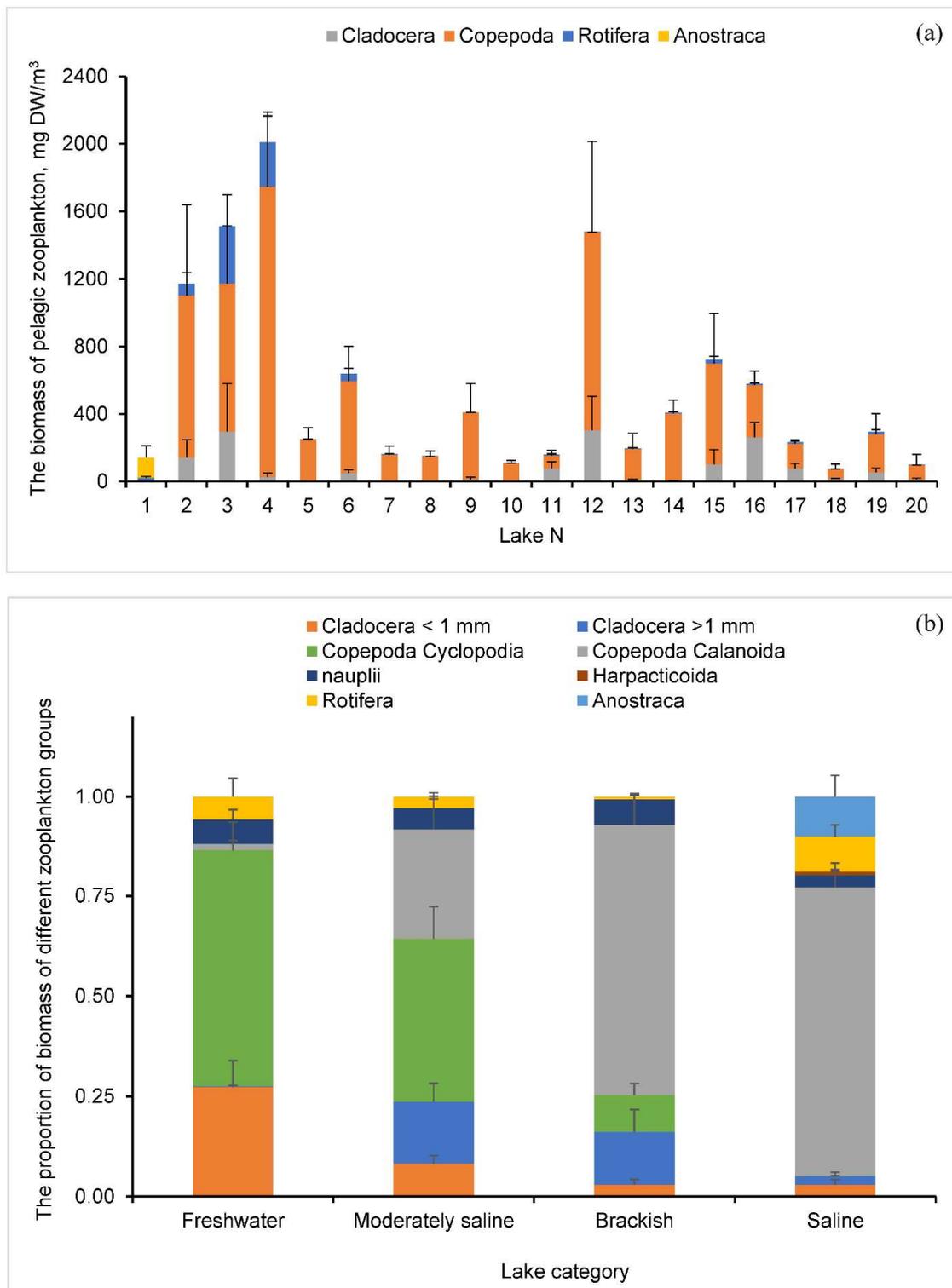


Figure 5. The average seasonal biomass of major zooplankton groups in study lakes (a) and the proportions of biomass of different groups in lakes of different salinity categories (b). Lakes are numbered according to Table 1.

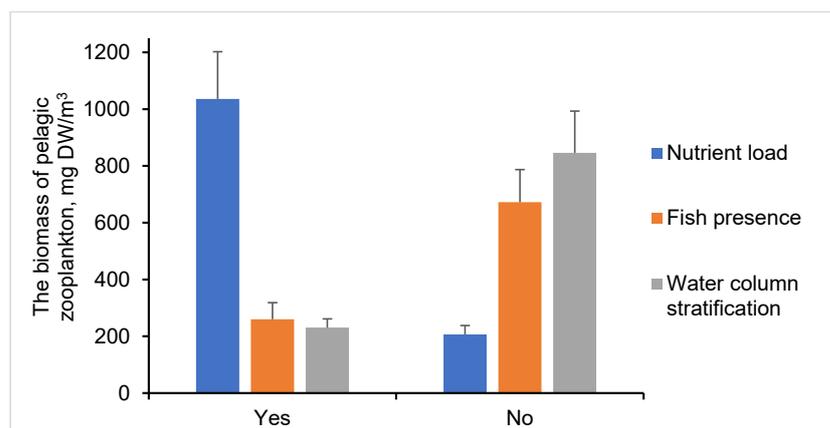


Figure 6. The effects of nutrient load, water column stratification, and fish presence on the biomass of pelagic zooplankton in study lakes.

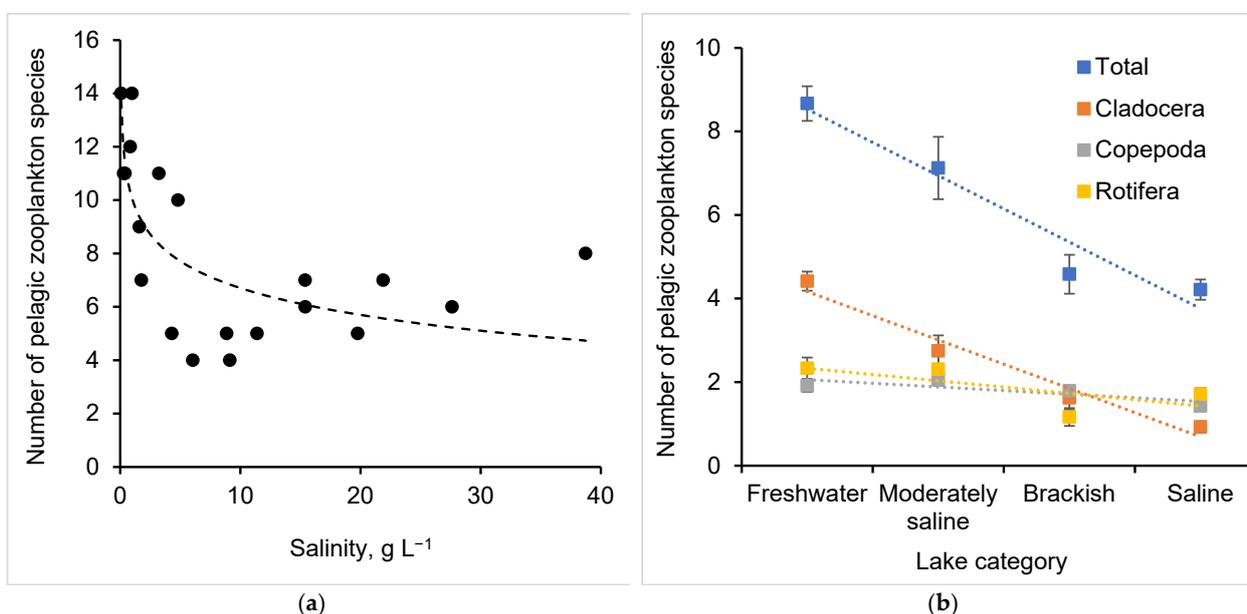


Figure 7. The effects of salinity (a) and lake category (b) on the total number of pelagic zooplankton species.

Table 5. Zooplankton groups/species explained by the environmental factors selected in CCA with the forward selection procedure. Statistics: p-value, F-test, R²-adjusted, and VIF.

Taxon, Short Name	Description
Calanoida	<i>Arctodiaptomus salinus</i> , Calanoind copepod species
Cyclopoida	Cyclopoid copepod species
<i>Brachionus</i> sp.	<i>Brachionus plicatilis</i> , <i>Brachionus</i> sp.
<i>Moina</i>	<i>Moina mongolica</i> .
<i>D. magna</i>	<i>Daphnia magna</i>
<i>Daphnia</i> sp.	<i>Daphnia longispina</i> , <i>Daphnia</i> sp.
<i>Bosmina</i>	<i>Bosmina</i> spp.
<i>Asplanchna</i>	<i>Asplanchna</i> sp.
<i>Ceriodaphnia</i>	<i>Ceriodaphnia</i> sp.
<i>Keratella</i>	<i>Keratella quadrata</i> , <i>Keratella cochlearis</i> , <i>Keratella testudo</i>
<i>Harpacticoida</i>	Harpacticoid copepod species

Table 5. Cont.

Taxon, Short Name		Description			
<i>Chydorus</i>		<i>Chydorus</i> sp.			
<i>Diaphanosoma</i>		<i>Diaphanosoma</i> sp.			
<i>Hexarthra</i>		<i>Hexarthra</i> sp.			
<i>Filinia</i>		<i>Filinia</i> sp.			
<i>Alona</i>		<i>Alona</i> sp.			
<i>L. kindtii</i>		<i>Leptodora kindtii</i>			
<i>Artemia</i>		<i>Artemia</i> sp.			
Selected predictors	Description	VIF	R2.adj	F	Pr(>F)
TDS	Total dissolved salts	3.5	0.18	18.74	0.002
P-tot	Total phosphorus	2.5	0.22	4.17	0.004
N-min	Mineral forms of nitrogen	1.6	0.24	3.88	0.014
Particles tot	Total count of particles measured by FlowCam	6.7	0.26	2.53	0.008
Fish	Presence/absence of fish	4.6	0.27	2.55	0.008
Depth	Maximum depth of lake	4.7	0.29	2.68	0.014
Yellow substance	Coloured dissolved organic matter, detected at 370/680 nm excitation-emission wavelengths	6.5	0.31	3.25	0.002

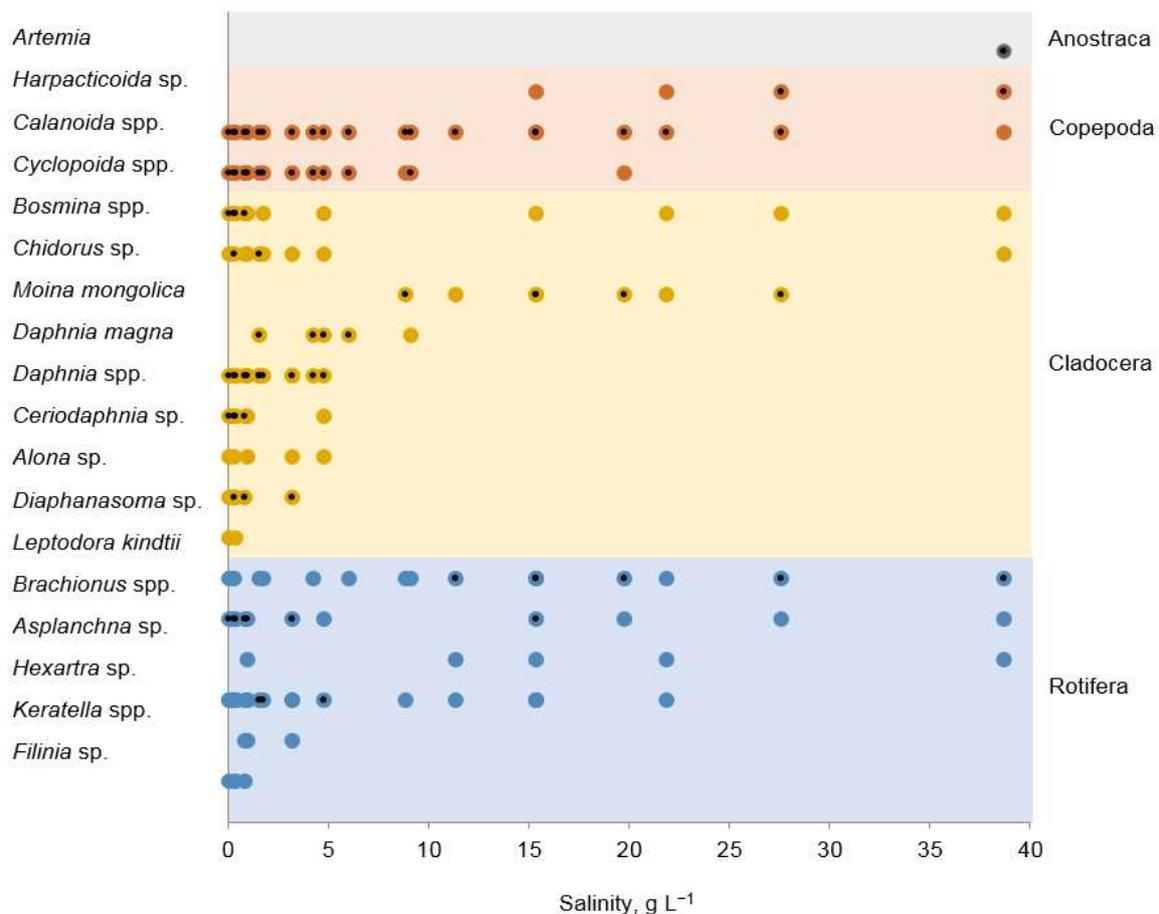


Figure 8. The effect of salinity on the occurrence and abundance of different zooplankton species in study lakes. Black dots indicate that the biomass of this species was >1% of the total biomass of pelagic zooplankton in the lake at least on one sampling date.

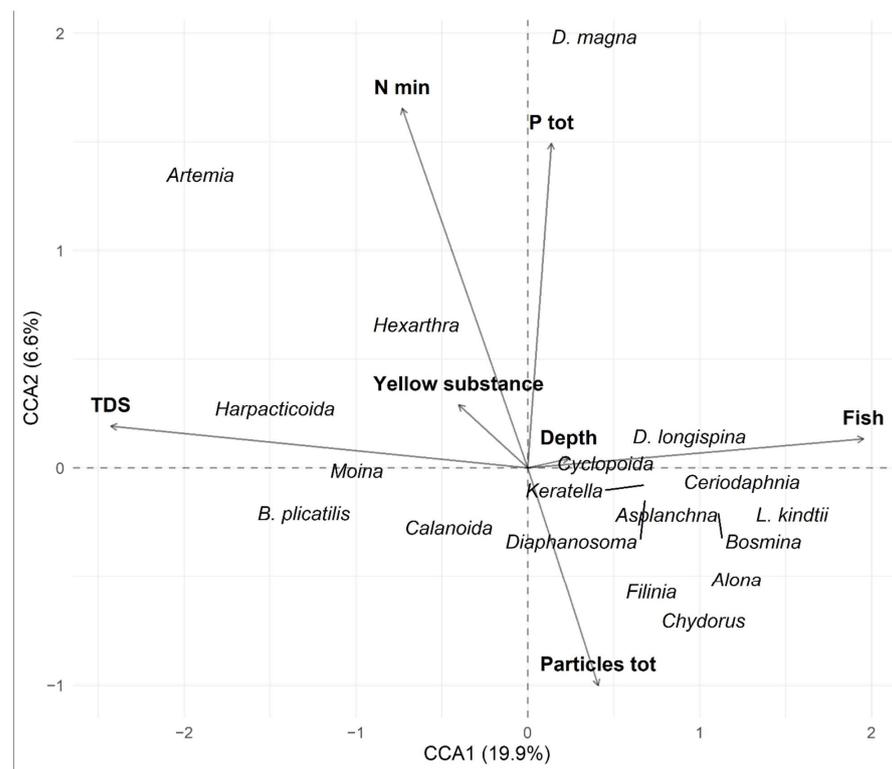


Figure 9. Canonical correspondence analysis (CCA) ordination diagram of the zooplankton species and the environmental variables. See Table 2 for species and variable abbreviations.

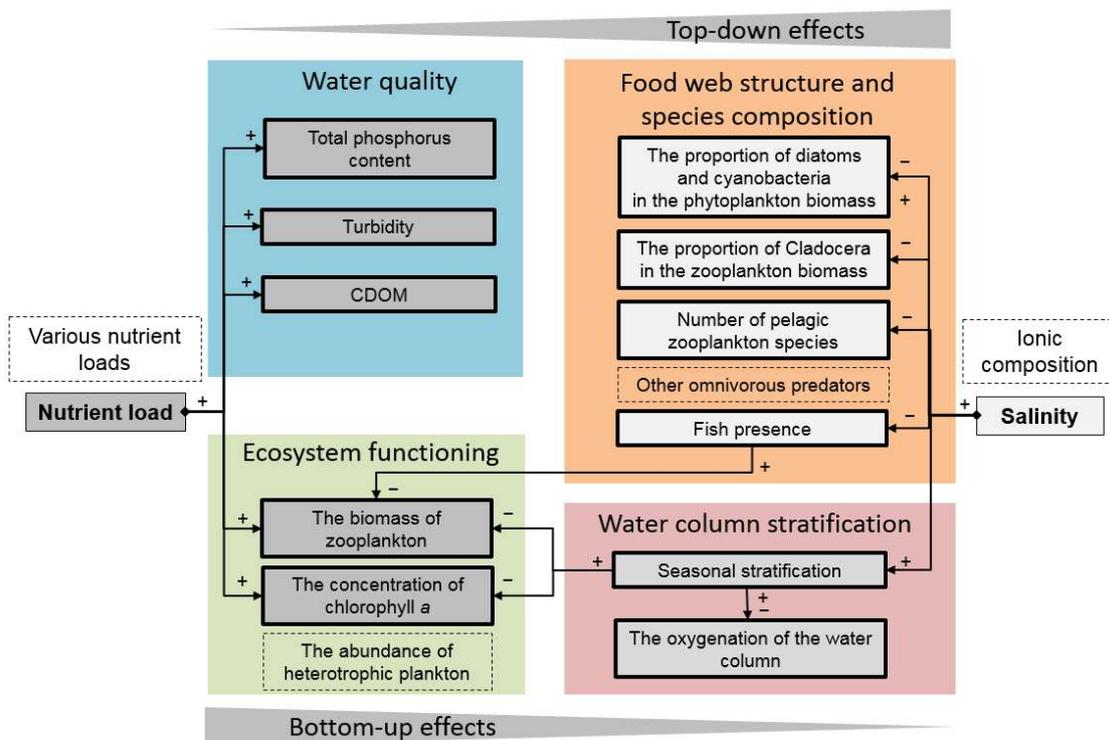


Figure 10. Scheme of detected interactions between two structuring factors (nutrient status and salinity) and ecosystem parameters of a number of lakes in southern Siberia. + —there is a positive correlation between parameters or significant effect of the factor, + —there is a negative correlation between parameters or significant effect of the factor. Boxes with dotted lines—important factors and ecosystem parameters not accounted for in this study (see discussion for details).

4. Discussion

4.1. Physico-Chemical and Ecological Characteristics of Study Lakes

Salinity did not affect directly such water quality parameters as turbidity, CDOM, the amount of total phosphorus, and inorganic nitrogen. However, salinity was a factor that was significant for the seasonal stratification of the water column in the study lakes. In turn, the stratification of the water column affected the depletion of oxygen near the bottom. Salinity is a factor that controls water density and one of the factors that promote permanent stratification of the water column in lakes (meromixis) [43]. In such lakes, oxygen is absent in deep waters during the entire period of permanent stratification. Three out of twenty lakes that we studied are meromictic lakes with the year-round depletion of oxygen near the bottom [44,45]. We also observed summer depletion of oxygen in the hypolimnion in several saline lakes with seasonal stratification. The solubility of oxygen in water decreases as salinity increases [46]. In addition, salinity can contribute to the growth of the stability of the seasonal stratification of the water column. These factors may indirectly contribute to the likelihood of oxygen depletion during summer stratification. However, the summer depletion of oxygen near the bottom was not solely related to the water column stratification. We also observed very low oxygen content in two shallow but phosphorus-rich lakes (Utichye-1 and Sykhoye) and two deeper, although still not stably stratified at the sampling dates, lakes (Matarak and Kiprino). The local stability of the water column, turbidity, and intensity of organic matter decomposition near the bottom are the processes determining the oxygen content. Thus, the lake depth, weather, and climate effects [47], nutrient status and biochemical processes may be more important drivers of oxygen depletion in deep waters. The dynamics and temporal and spatial fluctuations of oxygen in near-bottom waters and underlying processes may be the subject of further detailed research.

Parameters related to water quality (turbidity, total phosphorus, CDOM) were correlated with a qualitatively estimated increased nutrient load associated with the livestock watering, intensive cattle grazing in the catchment area, and the location of livestock pens and farms near the lake. In our lakes, CDOM was a very good predictor of total phosphorus content, which supported the previously observed link between CDOM values and water quality [48]. It is well known that in lakes located near livestock grazing and watering sites, the phosphorus content increases and the water quality decreases (e.g., [49]). High phosphorus content leads to an increase in water turbidity, consistent with a well-established relationship between phosphorus content in a water body and water quality (e.g., [50]). The study lakes have other external nutrient sources, e.g., agriculture, precipitation, groundwater, etc. However, our qualitative estimate of the increased nutrient load seems to be a good predictor of quantitatively estimated nutrient content and water quality parameters. Other external nutrient sources may result in different amounts and proportions of phosphorus and nitrogen in lake water. Thus, the developed conceptual model may be different with other external nutrient sources.

In our study, the lakes with high phosphorus content and low water quality parameters were mainly represented by small lakes of various salinity (from 1 to 30 g L⁻¹). None of the freshwater lakes that we studied could be classified as a lake with low water quality. We can assume that freshwater in a region with many saline lakes is considered a valuable resource and such lakes are used for recreation or environmental protection (one of the study lakes is part of a national reserve). At the same time, small saline lakes are not considered places with high recreational or nature protection values and are used for livestock watering or wastewater discharge. In this context, salinity can be considered as a factor that indirectly stimulates the deterioration of water quality, by reducing the value of the lake and increasing the nutrient load.

Based on our results we propose the scenario of the response of lakes to salinity and nutrient effects. With the salinity increase, the stability of seasonal water column stratification will increase followed by more frequent events of oxygen depletion in deep waters. In addition, salinity might indirectly stimulate the increased nutrient load, as the

local community will consider moderately saline and brackish lakes less valuable. The increased nutrient load will affect phosphorus content and related water quality parameters such as water turbidity and CDOM.

4.2. Food Web Structure and Interactions

Our first hypothesis, consistent with many studies on saline lakes in different regions of the world [11–14], was confirmed. The number of pelagic zooplankton species decreased with the salinity increase. We also observed a classical quick decline in diversity of freshwater species at salinity below 3 g L^{-1} and minimal diversity of zooplankton at the narrow salinity range between 5 and 10 g L^{-1} [51,52]. Thus, our results support the well-established fact of the minimum macro zooplankton diversity at critical salinity of $8\text{--}10 \text{ g L}^{-1}$ is related to the physiology and mechanisms of osmoregulation [53]. At the same time, the zooplankton species diversity was similar at a salinity range of $15\text{--}40 \text{ g L}^{-1}$. This observation partly coincides with the results by Lin et al. [11].

Even though the first hypothesis is not novel, as it was tested in other saline lakes, it is still important to test it in different systems of lakes, which are located in different climates and geographic zones. Now that we confirmed that our system of lakes is representative enough to study the effect of salinity on the food web structure, we can use it for further related studies to compare with other regions of the globe.

For the fish, which is the top component of the aquatic food web, salinity is a critical factor. When the threshold salinity is exceeded, the food web is shortened because fish is eliminated. In the study of a group of lakes of different salinity in Tibet, the critical salinity for the presence of fish in the ecosystem was 10 g L^{-1} [9]. This value corresponds to the results of our observations. Of the lakes that we studied, there is evidence of the presence of gibel carp *Carassius gibelio* in Lake Shira, with higher salinity (ca. 15 g L^{-1}). However, fish in this lake was observed only at the confluence of a freshwater river [54]. The salinity threshold for the presence of fish is geographically and ion-specific. In many regions with coastal lakes and brackish lagoons, sea species can inhabit saline lakes at higher salinity thresholds (e.g., [55]). There are published data about natural fish populations even in Asian continental saline lakes that can survive much higher salinity (e.g., ca. 20 g L^{-1} in Mongolian lakes [56]; up to 50 g L^{-1} in China and Mongolia [57]). So, even though in several systems of continental saline lakes located in the arid climate zone in Eurasia (our study, [9]) the salinity $> 10 \text{ g L}^{-1}$ was critical for the high abundance of diverse fishes, this value cannot be considered a universal threshold.

Even though our estimate of the presence of fish in the lakes was indirect, we can speculate about the diversity and abundance of fish in the system of our lakes. There are very few scientific investigations of fish communities in most of the study lakes. The fish communities of larger freshwater lakes (Fyrkal and Itkul) and nearly freshwater Lake Matarak are quite diverse with reported *Esox lucius* Linnaeus, 1758 (pike), *Perca fluviatilis* Linnaeus, 1758 (perch), *Coregonus peled* Gmelin, 1788 (peled, in lake Itkul), *Carassius auratus* Gibelio (Prussian carp), and other species; so all types of carnivorous, planktivorous and omnivorous fish species are present in these lakes [58,59]. As was predicted by general ecological considerations, Cladocera in these lakes were mostly represented by the small-sized *Bosmina*, *Chydorus*, and *Daphnia*. Smaller freshwater Lake Kiprino and small moderately saline and brackish Lakes Sukhoye, Krasnenkoe, Chalaskol, Utichye-3, and Vlasyevo are inhabited by omnivorous *Carassius*. Large saline Lake Bele was numerously stocked with various fish species including salmon [60] but regular observations demonstrated that the most common species are perch, peled, and Prussian carp. At the same time, we did not know the biomass of different fish species. Thus, it is impossible to quantify the fish effect. However, as we observed the striking difference between the biomasses of zooplankton in fish and fishless lakes, we were able to use the indirect estimate of fish presence as the structuring factor. It is clear that to move further, from qualitative to quantitative estimates, the composition, biomass, and diet of fish in these lakes need to be studied.

In the present study, we did not take into account the occurrence and abundance of the large benthic-planktonic species *Gammarus lacustris*. It was demonstrated before that in saline lakes Shira and Shunet, *Gammarus* can be considered as a component of the pelagic plankton community [61], and, based on fatty acid analysis, some zooplankton can be included in its diet [62]. *Gammarus* was visually abundant but not sampled and quantified in lakes with a salinity range from 4 to 15 g L⁻¹ (Lakes Shunet, Uchum, Shira, Bele small, Dzhirim, Bele large, Utichye-3, Utichye-1). Amphipods, as a top predator, may be an important factor in structuring the zooplankton community in lakes with different salinity [63–65], which was not taken into account in our study. This is an open window to extend this study and explore the effect of *Gammarus* on the food web.

In accordance with our second hypothesis, we detected several salinity thresholds with related changes in the species and taxonomic composition of plankton. For phytoplankton, a decrease in the proportion of diatoms and an increase in the proportion of cyanobacteria was observed with salinity above 1 g L⁻¹. For zooplankton, we detected (a) a decrease in the proportion of the biomass of Cladocera and an increase in the proportion of the biomass of Rotifera at salinity above 10 g L⁻¹; (b) among Cladocera, the large-bodied *Daphnia magna* was abundant at the narrow salinity range of 3–10 g L⁻¹; (c) the salinity resistant *Moina mongolica* was the only dominant Cladocera species in the salinity range of 10–30 g L⁻¹; (d) *Artemia* was present at a salinity of 40 g L⁻¹.

Not only the overall TDS value but also the chemical composition of water is an important but not adequately studied factor affecting zooplankton composition and food web structure [17]. We can discuss the subtle effects of variable ionic composition even in our system of geographically close lakes. For example, Lake Dzhirim has an intermediate TDS value between Lakes Bele large and Bele small. However, while the ionic content of Lakes Bele is rather shifted towards magnesium and sulphate, Lake Dzirim water is richer in sodium chloride. As a result, the species composition and food web in Lake Dzirim (the absence of fish, the dominance of Calanoids and *Moina mongolica*) is more pronouncedly structured by salinity compared with Lake Bele small (the presence of fish, *Daphnia magna* presence), with higher TDS but lower nitrogen and chloride. There are other differences between these two lakes as well (size, depth, nutrient status). Thus, we should keep in mind that ionic composition is also an important factor, and more detailed studies are needed to reveal these effects.

Previously, Lin et al. [11] proposed a conceptual model of salinity-related changes in the taxonomic structure of the zooplankton community. This model is very simplified and represents the change of zooplankton taxonomic structure with salinity increase as a sequence of Copepods and small cladocerans–Large cladocerans–*Artemia*. Recently, Zsuga et al. [14] described changes in zooplankton taxonomic composition observed in 23 small saline lakes in Kazakhstan. They observed patterns in species composition change that were similar to our observations. However, an important difference between their study and ours is that they did not study seasonal dynamics; all the lakes in their sample are small non-stratified lakes; salinity was the only major structuring factor.

In the current study, we sampled lakes in a relatively small range of salinities. When lakes with salinity >100 g L⁻¹ are included in such comparative studies, the patterns of a reduction in the species composition and changes in the food web with an increase in salinity are more obvious [66,67]. However, the key changes in the structure of the food web associated with the disappearance of fish and the change of dominant groups of zooplankton that may contribute to the loss of control over the phytoplankton community from the top [68] occur in the salinity range below 50 g L⁻¹. Thus, a detailed examination of a number of lakes with salinities varying within a narrow range carried out in the current study is of considerable interest.

The most significant result is related to the third hypothesis, where we assessed the response of zooplankton to top-down and bottom-up control, as well as salinity-related changes in the ability of zooplankton to control the biomass and species composition of phytoplankton. We revealed two major patterns. An increase in the nutrient status (bottom-

up control) affects the increase in the biomass of both phytoplankton and zooplankton and the decline in water quality parameters. Under the effect of salinity, we mostly observed structural shifts associated with the disappearance of fish and changes in proportions of different taxonomic groups in phytoplankton and zooplankton. The components of the food web (phytoplankton, zooplankton, and fish) mutually influence each other. Modification of the “top-down” effect in the fish-zooplankton pair under the salinity increase is manifested as an increase in the biomass of zooplankton with the disappearance of fish, and in the zoo- and phytoplankton pair as an increase in the average diameter of phytoplankton particles when zooplankton are dominated by the less selective and small Cladocera grazers.

A number of studies showed that selective zooplankton species can shift the phytoplankton community towards toxic cyanobacteria [19,20] or filamentous phytoplankton [21,22]. In our study, we observed changes in the size distribution of phytoplankton particles that can be attributed to the non-selective feeding of cladocerans on smaller particles. However, we did not observe a top-down effect related to a decrease in the phytoplankton abundance with the zooplankton increase. It was proposed and repeatedly demonstrated before that large filter feeder species are able to control the development of phytoplankton abundance (e.g., [69,70]). In our study, we did not observe this effect. One of the possible reasons is the effect of *Gammarus*, which can be a top predator in the moderately saline and brackish lakes. There are other possible modification factors. For example, inorganic suspended particles can be a significant inhibitory factor for filter-feeding zooplankton (e.g., cladocerans) (e.g., [71]). We did not estimate the abundance or presence of such particles. The turbidity of water is the only measure of water clarity in our study. As lakes are usually sampled on calm days, the resuspension of water and the presence of inorganic suspended particles may remain unnoticed. We focused on pelagic communities; thus, we assume that near shore resuspension of sediments and the presence of fine suspended particles in the water is not the major structuring factor in our system. Yet, for small shallow lakes during windy days, it can be a significant but unaccounted factor.

Similar to many other researchers (e.g., [11–14]), we focused on the algae–zooplankton–fish trophic cascade. However, the heterotrophic plankton, primarily composed of bacteria, can also be an important food source for Rotifera and Cladocera in the trophic web. Many of the study lakes are eutrophic or hypertrophic; thus, the high importance of heterotrophic bacterioplankton in the planktonic trophic web can be assumed. For example, it was demonstrated that in one of the study lakes, Lake Shira, the production of heterotrophic bacteria might exceed the total photosynthesis of phytoplankton [72], and the diet of dominant zooplankton species included heterotrophic bacteria [73]. We measured organic carbon in seston collected by GF/F filters. Thus, we assume that part of the bacterioplankton mixed with seston was also included in the analyses. As we observed a positive correlation between organic carbon in seston and chlorophyll a abundance, we assume that the contribution of bacteria to total organic carbon in our samples was not considerable. However, we estimated the seston abundance only in the epilimnion. The heterotrophic plankton can be distributed in the water column with higher concentrations at a certain patch or depth [74–76]. More detailed studies are needed to characterize the potential bottom-up effect of the heterotrophic microplankton on the planktonic food web.

Our results demonstrated that zooplankton are indeed sandwiched between bottom-up and top-down control. We observed that phyto- and zooplankton biomasses were primarily controlled by nutrient load (bottom-up control). At the same time, we found almost no significant differences between phytoplankton communities in different lakes that could be associated with zooplankton species composition. We already mentioned several reasons that should be taken into account in further studies. In addition, we can expect that cascade effects in ecosystems can be detected based on the dynamic characteristics of interacting populations [77]. Thus, more frequent sampling or multiyear sampling in lakes with different salinity will reveal top-down effects of zooplankton on phytoplankton under the structuring effect of salinity. The alternative approach is to use controlled mesocosm experiments [78].

5. Conclusions

Saline lakes located in arid climates are influenced by various anthropogenic drivers of change. For many of the small and medium saline lakes in the vast Eurasian steppe belt, the increase in nutrient load with the increase in salinity can be predicted. With the salinity increase and the transition of lakes from freshwater to the moderately saline or brackish category, the ecosystem value related to the presence of freshwater will decrease. Thus, such lakes will be more frequently used as wastewater collectors or places for cattle watering and pasture. The salinity increase will also reduce fish diversity and, at some regional specific critical salinities, will transform many of the ecosystems from three-trophic level, with fish–zooplankton–phytoplankton, to two-trophic-level systems without fish. However, in the salinity range from 10 to 20–30 g L⁻¹, this decline in fish diversity and, probably, abundance will not necessarily increase the ability of zooplankton to control phytoplankton, as natural or invasive euryhaline fish species or other omnivores such as gammarids may still partially control zooplankton. These effects will also strongly depend on the size and depth of the lake. Deep seasonally or permanently stratified lakes will tend to have a better water quality with lower biomasses of both phyto- and zooplankton. Thus, the effect of salinity per se is not the driver of water quality decline in terms of water clarity and uncontrolled development of phytoplankton. Such factors as physical characteristics of the lake (size and depth) and nutrient load have strong interactive effects with salinity. Moreover, for deep lakes, salinity may be a factor affecting the stability of stratification, which mitigates the consequences of eutrophication. The most vulnerable lakes to the joint effects of salinity increase and nutrient load are small shallow lakes, which will experience degradation of ecosystem functioning and water quality at moderate salinities in the range of 3–20 g L⁻¹.

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Appendix A

Table A1. The major chemical components of water in the study lakes. Lake categories: F—freshwater, MS—moderately saline, B—brackish, S—saline.

Lake Category	Lake	The Concentration of the Element or Compound (Mean ± SE), mg L ⁻¹							
		K	Mg	Na	S	Cl	SO ₄	CO ₃	HCO ₃
S	Tus	174.5 ± 20.1	5017.9 ± 477.1	12,887.9 ± 1714.8	7119.2 ± 588.8	14,826.8 ± 1493.7	20,580.2 ± 994.0	146.6 ± 32.0	867.0 ± 122.6
	Slabitelnoe	101.1 ± 12.6	1627.9 ± 168.8	11,262.8 ± 668.4	6454.4 ± 442.7	4813.4 ± 490.0	14,115.0 ± 2130.5	246.7 ± 39.6	951.9 ± 98.8
	Krasnenkie-1	38.1 ± 4.3	598.6 ± 67.3	8795.6 ± 973.9	4714.7 ± 478.2	3633.0 ± 450.8	12,222.2 ± 1116.9	36.6 ± 13.5	551.5 ± 71.1
	Krasnenkie-2	71.1 ± 7.9	593.0 ± 61.0	8780.9 ± 1087.8	5229.3 ± 632.3	1398.3 ± 80.9	12,804.3 ± 1094.2	108.9 ± 17.4	716.2 ± 71.9
	Shunet	34.1 ± 3.1	1898.5 ± 246.2	4006.4 ± 376.2	2376.4 ± 126.9	4294.5 ± 558.1	4687.5 ± 616.6	23.6 ± 7.2	547.5 ± 122.4
	Uchum	41.4 ± 1.2	249.8 ± 16.3	6052.9 ± 396.8	2981.1 ± 72.2	2105.3 ± 79.0	5945.0 ± 936.9	464.6 ± 49.6	1464.3 ± 257.1
	Shira	35.3 ± 0.6	1148.0 ± 61.5	3272.3 ± 50.5	2552.4 ± 114.2	1939.7 ± 48.9	4612.5 ± 1019.9	138.5 ± 22.3	633.0 ± 76.0
B	Bele small	46.2 ± 2.6	842.2 ± 49.7	2609.0 ± 71.8	1919.0 ± 21.7	1255.3 ± 58.5	4502.5 ± 918.9	227.1 ± 47.3	1168.4 ± 282.8
	Dzhirim	20.0 ± 3.0	211.6 ± 11.7	3021.9 ± 185.9	1029.0 ± 56.2	2012.5 ± 69.1	2466.7 ± 66.7	179.6 ± 19.9	1187.1 ± 186.3
	Bele large	34.4 ± 4.9	575.5 ± 74.9	1747.2 ± 248.9	1277.9 ± 225.5	802.4 ± 31.1	4200.2 ± 562.0	139.5 ± 25.6	647.3 ± 78.4
	Utichye-3	28.2 ± 5.2	392.8 ± 58.7	993.6 ± 6.3	536.4 ± 134.3	805.0 ± 175.0	1630.0 ± 130.0	57.6 ± 33.6	898.8 ± 449.9
	Utichye-1	34.6 ± 3.1	417.1 ± 31.6	1157.3 ± 128.4	597.2 ± 87.9	735.0 ± 105.3	1282.3 ± 351.2	139.5 ± 50.9	1171.2 ± 241.3
	Vlasyevo	26.7 ± 5.0	302.5 ± 39.9	629.1 ± 83.6	338.9 ± 41.0	414.2 ± 69.4	980.0 ± 101.0	123.9 ± 7.0	636.0 ± 67.0
MS	Sukhoye	9.3 ± 0.7	48.5 ± 2.8	551.6 ± 20.6	156.6 ± 7.7	117.8 ± 18.4	409.5 ± 48.5	92.3 ± 16.3	833.6 ± 70.0
	Krasnenkoe	19.2 ± 2.1	102.1 ± 5.5	353.1 ± 30.2	165.6 ± 15.5	228.7 ± 32.1	469.3 ± 41.6	98.2 ± 23.8	192.0 ± 76.4
	Chalaskol	14.1 ± 0.8	94.8 ± 3.9	168.7 ± 2.7	87.1 ± 10.5	59.3 ± 9.6	302.8 ± 44.2	66.3 ± 21.2	455.3 ± 59.2
	Matarak	8.7 ± 0.2	87.3 ± 1.9	153.5 ± 3.5	72.7 ± 5.9	44.3 ± 5.0	172.5 ± 48.8	35.7 ± 4.7	411.4 ± 63.8
F	Itkul	4.7 ± 0.8	57.9 ± 12.3	74.8 ± 34.3	50.6 ± 28.0	43.4 ± 13.9	160.5 ± 65.2	21.8 ± 9.3	230.7 ± 6.7
	Fyrkal	1.8 ± 0.2	42.9 ± 4.5	34.2 ± 7.5	17.6 ± 5.6	14.6 ± 2.5	25.4 ± 1.9	25.5 ± 9.1	171.3 ± 36.4
	Kiprino	0.4 ± 0.1	6.3 ± 0.7	32.1 ± 14.2	14.7 ± 5.5	18.3 ± 2.8	44.2 ± 20.2	11.6 ± 7.6	47.4 ± 5.9
	Correlation with dry residual	R ² = 0.82 <i>p</i> < 0.001	R ² = 0.71 <i>p</i> < 0.001	R ² = 0.87 <i>p</i> < 0.001	R ² = 0.88 <i>p</i> < 0.001	R ² = 0.80 <i>p</i> < 0.001	R ² = 0.90 <i>p</i> < 0.001	R ² = 0.08 <i>p</i> = 0.017	R ² = 0.09 <i>p</i> = 0.010

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