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Environmental Factors Affecting Distribution and Diversity of Phytoplankton in the Irkutsk Reservoir Ecosystem in June 2023

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Abstract: Studying correlations between phytoplankton communities and environmental factors is critical for understanding how aquatic ecosystems function. The high sensitivity of phytoplankton to changes in these factors makes it possible to control the state of the ecosystem of water bodies. Artificial lakes often demonstrate increased trophic status, inducing changes in phytoplankton structure. In this paper, we studied phytoplankton in June 2023 (hydrological spring) in two ecosystems, South Baikal and the Irkutsk Reservoir, that are connected by a water course but have different environmental parameters. The gradient of environmental parameters from the lake towards the reservoir revealed peculiarities in the distribution of some microalgae species. Microscopy and statistical analysis showed that water temperature was the most important factor affecting the structure of the communities. The warmer water of the reservoir, in contrast to the lake, demonstrated a twofold increase in species number, abundance, and biomass. Downstream from the reservoir, we observed a succession in the dominating Baikal species complex, its supplementation, and replacement with other species typical of the summer period and Baikal bays. The trophic status of the reservoir during the study may be described as oligotrophic, with local traits of mesotrophicity; its water refers to Class I and Class II and may be qualified as clean.

Keywords: Lake Baikal; Angara River; river regulation; microalgae; environmental parameters; water temperature

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1. Introduction

Reservoirs are artificial water bodies created by the construction of dams across a river or flooding of excavation pits.

As for the temperate and northern latitudes, most reservoirs are situated in Russia. They were created by the construction of hydroelectric dams across large rivers; the most investigated are reservoirs in the catchment area of the Volga [1–4], Yenisei [5,6], Ural [7], Ob [8,9], and Angara [10–13].

Reservoirs are located, as a rule, near human settlements and undergo anthropogenic stress [4,11]. In addition, regardless of latitude, river regulation induces a change in the hydrological regime and increases the risk of eutrophication. These changes are reflected in the species composition and abundance of phytoplankton [4]. The primary level of aquatic ecosystems is affected by increased concentrations of biogenic elements in reservoirs due to human activities [14,15]. For example, an increase in nutrient levels, such as total N and P in reservoirs during summer (or the dry season in the tropics), tends to shift phytoplankton species structure in favor of Cyanobacteria. Among Cyanobacteria, the growth of representatives of the genera *Aphanizomenon* Morren ex Bornet & Flahault, *Microcystis* Lemmermann, *Anabaena* Bory ex Bornet & Flahault, *Dolichospermum* (Ralfs ex Bornet & Flahault)

Wacklin, Hoffmann & Komárek, *Oscillatoria* Vaucher ex Gomont [4,16] is observed. Diatom algae, such as *Aulacoseira granulata* (Ehrenberg) Simonsen, in reservoirs in Vietnam [15], Cameroon [17], Nigeria [18], and Russia [4], and *Cyclotella meneghiniana* Kützing in some reservoirs in the Volga–Kama Cascade [4], are often considered eutrophication indicators.

Water quality in reservoirs depends on a complex of factors. One of them is rising water temperature [4,17–19]. In addition, northern reservoirs are affected by climatic changes that are more pronounced there than in the temperate latitudes [4,20,21]. The previously proposed hypothesis, according to which the ratio of illumination and biogenic elements affects the productivity of phytoplankton in lakes [22], is also valid for reservoirs. For example, water temperature, transparency, and concentration of nutrients (total N and P) were the main factors that affected the productivity and species composition of phytoplankton in reservoirs in Vietnam and Lebanon [15]. The importance of such factors as light availability has been demonstrated in reservoirs of the Volga–Kama Cascade in Russia [4]. High turbidity may also affect phytoplankton productivity [4,23].

Correlations between phytoplankton communities and environmental factors can have peculiarities in different reservoirs, and to reveal them is crucial for understanding how these artificial water bodies function.

The Irkutsk Reservoir is the first in a cascade of hydroelectric dams constructed across the Angara, which is the sole river flowing out of Lake Baikal. After 60 years of existence, the Irkutsk Reservoir became stable in many parameters: the shoreline was stabilized and a new main channel appeared, along which, up to the dam, Baikal water flows, undergoing some changes in the chemical and temperature regimes. The Irkutsk Reservoir serves as a water supply for Irkutsk and Shelekhov (more than 600 thousand residents); therefore, water quality monitoring is very important.

Previous water quality studies in the Irkutsk Reservoir showed that the trophic status of the reservoir has not changed over more than 50 years since its flooding (1956–1958) [11,13]. The composition of dominating species is basically much like that of the 1960s and 1980s, though the composition of the dominant and most abundant species was not always constant. The level of phytoplankton in spring directly depends, as earlier, on the productivity of diatom algae in Lake Baikal. On average, the phytoplankton biomass in the Irkutsk Reservoir during the growth period 2008 was within interannual fluctuations of the 1960s–1980s [11,24] and amounted to 510 $mg \cdot m^{-3}$ [13]. Water quality by indicator species (according to Pantle–Buck modified by [25] and by environmental and sanitary criteria [26,27]) corresponded to Class II (clean water) [13]. Only in small bays, it was slightly higher, varying between 1.3 and 1.5; however, these values remained within the range typical of Class II (clean water). The saprobic index 1.6 (moderately polluted water, Class III) was reported only for Kurma Bay in September. The concentrations of dissolved nutrients in the reservoir and bays were very low at that period [13].

The purpose of our study was to determine the distribution of phytoplankton species along the gradient of habitat parameters from South Baikal to the Irkutsk Reservoir, which is the sharpest in June, to identify key factors affecting the distribution of individual species, and to assess the status of the Irkutsk Reservoir ecosystem after a 15-year break of its research. We assume that the promotion of Baikal species in the reservoir is limited by the parameters of the habitat.

2. Site Description

The hydroelectric dam across the Angara River was constructed from 1950 to 1958, and the flooding of the Irkutsk Reservoir started in 1956. The project water level, 457.0 m, was achieved in 1960. The Irkutsk Reservoir is located 56 km from Lake Baikal within the city of Irkutsk. This is a low-head dam with a vertical drop of 28.6 m. The average multiannual Angara water discharge is 1915 $m^3 \cdot s^{-1}$ or 56 $km^3 \cdot year^{-1}$. The reservoir is shallow: the mean depth amounts to 13.6 m, and the maximum one at the dam does not exceed 35 m. The water surface area is 154 km^2. The width of the reservoir varies from

1 km at the source to 2.5 km at the dam. The area of the ex-Angara amounts to 28% from the area of the reservoir [28].

The Angara never ices over at the outflow from Lake Baikal and below the dam within the boundaries of Irkutsk; its temperature in winter is 0.3–1.7 °C. The ice cover lasts on average 145 days. The Irkutsk Reservoir is cold; in summer, water temperature runs up to 16 °C and 15.5–20.6 °C at the dam and in the bays, respectively [11]. Temperatures at the source are not stratified, and there is some heterogeneity of temperature in the horizontal direction and large temperature differences between the shore and the main channel. A zone of stagnant shore water and a zone of flowing Baikal water are clearly seen in the middle part of the reservoir [24].

The chemical composition of water in the Irkutsk Reservoir is under great influence from Lake Baikal, which refers to bicarbonate class calcium groups; it has a very low salt content (not over 100 mg·L^{-1}), low organic matter content, and high concentrations of dissolved oxygen. The mean concentrations in a 0–50 m layer of Lake Baikal are the following: dissolved phosphorous 21 ± 11 µm·L^{-1}, nitrate nitrogen 45 ± 19 µm·L^{-1}, and dissolved silica 2.16 µm·L^{-1} [29]. The quantity of nutrients in the Irkutsk Reservoir and bays is very low; e.g., the content of silicon during the open water period in June 2008 varied between 0.62 and 1 mg·L^{-1}, nitrate between 0.05 and 0.4 mg·L^{-1}, phosphate ions between 0.012 and 0.032 mg·L^{-1}, and dissolved oxygen within 10.88–12.82 mg·L^{-1}. Water quality indicator values, such as dissolved oxygen and ammonium ion concentrations, as well as biological oxygen, demand to allow the determination of the Irkutsk Reservoir water as clean to very clean (Class I and Class II) [13].

3. Materials and Methods

3.1. Sampling and Microscopy

Sampling was conducted in 22–26 June 2023, from the board of a research vessel "Papanin" at 9 stations in South Baikal and at 8 stations in the Irkutsk Reservoir, including bays (Figure 1, Table 1).

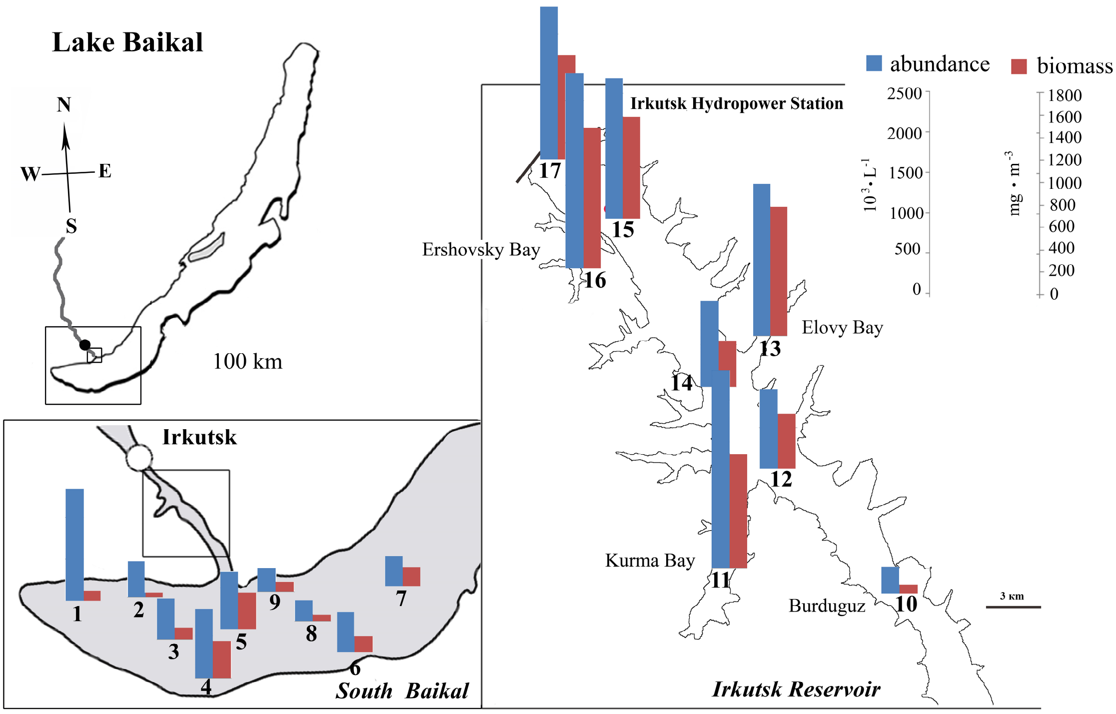

Figure 1. Distribution of quantity and biomass of phytoplankton in South Baikal and the Irkutsk Reservoir in June 2023 (scale of quantity and biomass values is the same in the left and right pictures).

Table 1. Sampling sites in South Baikal and the Irkutsk Reservoir and environmental parameters in June 2023 (for site numbers, see Figure 1).

Station Number	Station Name	Coordinates N/E	Max Depth, m	S, m	Water T, °C	pH	Si, $mg \cdot L^{-1}$	PO_4^{3-}, $mg \cdot L^{-1}$	NO_3^-, $mg \cdot L^{-1}$
1.	12 km from Kultuk	51° 40.578/ 103° 52.309	1250	22.0	4.51	7.18	0.52	0.022	0.41
2.	3 km from Marituy	51° 45.546/ 104° 13.222	1337	18.0	4.13	7.90	0.53	0.023	0.40
3.	Marituy-Solzan	51° 38.710/ 104° 13.715	1243	21.0	3.95	8.02	0.43	0.020	0.36
4.	3 km from Solzan	51° 31.428/ 104° 14.417	350	12.0	3.98	8.24	0.17	0.015	0.29
5.	Cape Tolsty-Snezhnaya River	51° 36.402/ 104° 44.147	1120	-	3.66	8.17	0.20	0.018	0.29
6.	3 km from Tankhoi	51° 35.440/ 105° 06.968	1402	10.0	3.76	8.06	0.40	0.018	0.34
7.	Cape Kadilny-Mishikha	51° 46.731/ 105° 22.528	1424	18.0	4.03	8.06	0.49	0.022	0.40
8.	Listvyanka-Tankhoi	51° 42.262/ 105° 00.720	700	17.0	4.02	8.04	0.50	0.023	0.40
9.	3 km from Listvyanka	51° 49.033/ 104° 54.616	1434	18.0	4.35	8.02	0.53	0.023	0.41
10.	Burduguz	52° 04.105/ 104° 59.451	15.5	-	5.33	8.10	0.56	0.019	0.37
11.	Kurma Bay	52° 06.845/ 104° 45.926	9.7	4.0	11.55	8.57	0.42	0.007	0.04
12.	center against Kurma Bay	52° 10.874/ 104 °47.935	17	5.0	7.66	8.27	0.52	0.016	0.22
13.	Elovy Bay	52° 09.906/ 104° 29.172	10	3.5	8.8	8.52	0.48	0.012	0.15
14.	center against Elovy Bay	52° 14.548/ 104° 45.243	25	-	8.63	8.29	0.52	0.015	0.24
15.	center against Ershovsky Bay	52° 21.511/ 104° 37.550	27	4.5	9.4	8.39	0.49	0.011	0.15
16.	Ershovsky Bay	52° 20.851/ 104° 34.439	16	3.0	9.9	8.42	0.40	0.011	0.12
17.	head water	52° 23.478/ 104° 33.722	25	3.5	9.53	8.48	0.47	0.010	0.11

Water transparency (S) was measured with a Secchi disc. Water samples were collected with a 5 L Niskin bottle (Volta, Moscow, Russia). Water temperature and pH were measured with a pH-410 field device (Aquilon, Moscow, Russia) at each sampling depth. Values from each depth were then averaged. Integrated samples (1.2 L) were obtained by integrating equal amounts of water (200 mL from each layer) collected from 0, 5, 10, 15, 20, and 25 m (stations 1–9), 0, 5, and 10 m (stations 10, 12, 14–17), or 0 and 5 m (stations 11, 13). An amount of 0.5 L of each integrated sample was frozen for hydrochemical analysis. For microscopy, 1.2 L of each integrated sample was filtered through 3 µm filters using a PVF-47/NB filtration system (BMT, Vladimir, Russia). Precipitate was collected and fixed with formaldehyde in a volume of 50 mL up to a final concentration of 3.7% (45 mL sample + 5 mL 37% formaldehyde) [30].

Microalgae cells were calculated according to Hensen [31] on lined cover slides using an Axiostar Plus microscope (Zeiss, Oberkochen, Germany) equipped with a TOUPCAM UA1000CA camera (ToupTek Photonics, Hangzhou, China). Cell biomass was measured by calculation via equating algae to certain geometric figures [32], applying an updated technique [33].

For scanning electron microscopy (SEM), 20 mL of each unfixed integrated sample was precipitated in the field with a syringe equipped with a special jet onto filters (diameter 13 mm, 0.8 μm pores) (Whatman Part of GE HealthCare, Chicago, IL, USA). Then, 20 mL of 70% ethanol was pumped through the filters, which were then stuck with double-sided tape onto SEM stubs and dried at normal temperature. Then, in the laboratory, they were coated with gold using an SCD vacuum evaporator (Blazers Union Ltd., Balzers, Liechtenstein) and analyzed using a Quanta 200 SEM (FEI Electron Optics B.V., Eindhoven, the Netherlands).

For determining species membership of diatoms and identifying silica-scaled chrysophytes, 30% hydrogen peroxide was added to the samples to remove organic matter. After that, the samples were heated in a thermostat at 85 °C for 2–3 h, rinsed, and transferred on SEM stubs and TEM grids covered with formvar. They were dried at normal temperature and analyzed using a Quanta 200 SEM (FEI Electron Optics B.V., Eindhoven, the Netherlands) and a Leo 906 E TEM (Zeiss, Germany), respectively.

Species indicator values and the Trophic State Index (Sap) were determined according to the following published techniques [26]: χ–0.0–xenosaprobionts; o-χ–0.6–oligo-xenosaprobionts; o–1.0–oligosaprobionts; o-β–1.4–oligo-beta-mesosaprobionts; β-o–1.6–beta-oligosparobionts; o-α–1.8–oligo-alpha-mesosaprobionts; β–2.0–beta-mesosaprobionts; β-α–2.4–beta-alpha-mesosaprobionts; α–3,0–alpha-mesosaprobionts; and α-p–3,6–alpha-poly–mesosaprobionts.

The identification of silica-scaled chrysophytes was conducted and reported in a separate paper [34].

3.2. Hydrochemistry

Frozen water samples were thawed at room temperature. The mineral forms of the biogenic elements were determined after filtration using membrane cellulose acetate filters with 0.45 μm pores (Vladisart, Vladimir, Russia).

The content of the biogenic elements was measured with a PE-5400VI spectrophotometer (ECROSKHIM Ltd., Moscow, Russia): nitrate was measured using salicylic sodium, detection limit 0.1 mg·L^{-1} [35]; silicon in the form of silicomolybdic heteropoly acid, detection limit 0.1 mg·L^{-1} [36]; and phosphates as phosphomolybdenum complex, detection limit 0.010 mg·L^{-1} [37].

3.3. Statistical Analysis

Exploratory analyses of community composition were performed using vegan v.2.5-6 [38]. For exploratory analyses, the phytoplankton species abundance and biomass data were transformed with the Hellinger procedure [39] and subjected to principal component analysis (PCA). Linear regression of explanatory variables was performed using the envfit function of the vegan package, followed by an adjustment of permutation-based regression *p*-values using the Holm procedure. Environmental factors having an adjusted *p*-value threshold below 0.05 were drawn on the ordination plane.

One-way ANOVA and Kruskal–Wallis statistical tests were used to examine the impact of independent factor variables on the continuous environmental variables and summary numerical values associated with the microeukaryotic community profiles. The *p*-values were adjusted using the false discovery rate (FDR) procedure. Both raw and adjusted *p*-values were reported. R package ggpubr [40] was used to visualize the group-wise distribution of environmental data.

Environmental factors and summarized numerical values of biomass and abundance of phytoplankton were analyzed for collinearity. Pearson correlation coefficients and their *p*-values were computed for each pair of explanatory variables using R packages rcorr and Hmisc. The correlation matrix was visualized with R package rcorr using hierarchical clustering to group variables. Next, data on biomass and abundance of phytoplankton were excluded from the analysis, and variables were centered and scaled to have zero means and standard deviations of one. This standardized environmental matrix was used for the constrained ordination of phytoplankton species abundance using redundancy analysis (RDA). Both forward selection and backward elimination approaches were tested to produce a model.

4. Results

4.1. Species Composition

In total, 99 phytoplankton species from 7 systematic ranks, such as Chrysophyta (42), Bacillariophyta (20), Chlorophyta (16), Cyanobacteria (10), Cryptophyta (5), Dinophyta (5), and Haptophyta (1) (Table 2), were detected at the stations in South Baikal and the Irkutsk Reservoir.

Table 2. Distribution of phytoplankton species in South Baikal and the Irkutsk Reservoir in June 2023, with their ecological and geographical characteristics. "+"—the presence of this species.

Species	Sap	Station Number																
		South Baikal									Irkutsk Reservoir							
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Cyanobacteria																		
Cyanodictyon planctonicum Mayer		+	+	+			+		+						+	+		
Gomphosphaeria aponina Kützing	o													+				
Limnococcus limneticus (Lemmermann) Komárková, Jezberová, Komárek & Zapomelová								+			+							
Lyngbya sp.					+													
Merismopedia tenuissima Lemmermann	β-α						+		+									
Microcystis sp.		+		+		+			+	+		+		+		+	+	
Pseudanabaena galeata Böcher	α					+			+		+				+		+	
Romeria sp.												+				+	+	
Synechocystis limnetica Popovskaja	o			+		+		+	+		+	+			+	+	+	
Spirulina minima var. *baicalia* Kobanova										+								+
Cryptophyta																		
Cryptomonas gracilis Skuja	o			+				+										
C. ovata Ehrenberg	β-α				+									+	+			
Komma caudata (Geitler) Hill	β	+		+		+								+			+	
Rhodomonas lens Pascher & Ruttner												+	+	+	+	+	+	+
R. pusilla (Bachmann) Javornický	β-o	+	+	+	+	+	+	+	+	+	+	+			+			+
Dinophyta																		
Apocalathium baicalense (Kisselev & Zvetkov) Craveiro, Daugbjerg, Moestrup & Calado	o													+				
Dinophyta sp.								+				+		+	+	+	+	+
Glenodinium sp.			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Gymnodinium baicalense Antipova	o	+						+									+	
G. helveticum (Penard) Takano & Horiguchi														+			+	
Haptophyta																		
Chrysochromulina parva Lackey		+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+

Table 2. *Cont.*

Species	Sap	Station Number																
		South Baikal									Irkutsk Reservoir							
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Chrysophyta																		
Chrysococcus rufescens Klebs	o-β				+							+	+	+				
Chrysolykos planctonicus Mack	o											+			+	+		
Chrysosphaera melosirae (Meyer) Bourrelly						+												
Chrysosphaerella baicalensis Popovskaya		+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+
C. brevispina Korshikov			+			+				+	+	+	+		+	+	+	+
C. coronacircumspina Wujek & Kristiansen												+					+	
Dinobryon bavaricum Imhof	o											+						
D. cylindricum Imhof	o-β	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
D. divergens Imhof	o-α				+						+		+		+			
D. korshikovii Matvienko ex Kapustin		+	+	+	+								+	+			+	
D. sertularia Ehrenberg	o-α											+	+	+	+			
D. sociale (Ehrenberg) Ehrenberg	β			+			+					+	+	+	+	+	+	+
D. suecicum Lemmermann	o	+	+	+	+	+					+	+	+	+	+	+	+	+
Kephyrion littorale Lund							+											
Paraphysomonas bandaiensis Takahashi												+						
Paraphysomonas sp. 1														+				
Paraphysomonas sp. 2												+						
Spiniferomonas abrupta Nielsen												+	+		+			+
S. bourrellyi Takahashi									+			+		+	+			+
S. cornuta Balonov															+			
S. silverensis Nicholls												+	+		+	+		
S. triangularis Siver												+			+			
S. trioralis Takahashi			+			+					+	+	+	+	+	+	+	+
S. trioralis f. *cuspidata* Balonov		+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+
Mallomonas acaroides Perty	o-α											+		+	+		+	
M. alpina Pascher & Ruttner		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
M. crassisquama (Asmund) Fott												+	+	+	+	+	+	+
M. elongata Reverdin												+						
M. grachevii Bessudova											+	+			+			
M. punctifera Korshikov	o-β											+	+	+				
M. striata var. *getseniae* Voloshko																+		
M. striata Asmund															+		+	
M. tonsurata Teiling	o-α														+			
M. trummensis Cronberg												+						
M. vannigera Asmund	o-α	+	+	+	+	+					+	+			+			+
Mallomonas sp.															+		+	
Synura echinulata Korshikov	o-β											+						
S. cf. *glabra* (Korshikov) Škaloud & Kynclová											+	+	+	+	+	+	+	+
S. punctulosa Balonov												+					+	+
S. spinosa f. *longispina* Petersen & Hansen															+			
Synura sp. 1														+				+
Synura sp. 2											+	+	+	+	+	+	+	+
Bacillariophyta																		
Asterionella formosa Hassall												+	+	+	+	+	+	+
Aulacoseira baicalensis (Meyer) Simonsen	χ	+	+	+	+	+	+	+	+	+	+		+					
A. granulata (Ehrenberg) Simonsen	β-α													+				
A. islandica (Müller) Simonsen	o-χ	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
A. ambigua (Grunow) Simonsen	o-β												+					+
Crateriportula inconspicua (Makarova & Pomazkina) Flower & Hakansson																		
Cyclostephanos dubius (Hustedt) Round	o-β											+	+	+	+	+	+	
Discostella pseudostelligera (Hustedt) Houk & Klee												+	+	+	+	+	+	+
Fragilaria radians (Kützing) Williams & Round	o	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

Table 2. *Cont.*

Species	Sap	Station Number																
		South Baikal									Irkutsk Reservoir							
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Nitzschia graciliformis Lange-Bertalot & Simonsen emend Genkal & Popovskaya	o	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Stephanodiscus meyeri Genkal & Popovskaya										+		+	+	+	+	+	+	+
S. minutulus (Kützing) Cleve & Möller	o-β				+						+	+	+	+	+	+	+	+
Lindavia costata (Loginova, Lupikina & Khursevich) Nakov, Guillory, Julius, Theriot & Alverson														+				
L. minuta (Skvortzov) Nakov *et al.*	o	+	+	+	+	+	+	+	+	+				+		+	+	+
Fragilaria capucina Desmazières	o										+		+		+			
Hannaea baicalensis Genkal, Popovskaya & Kulikovskiy	o										+	+						
Tabellaria flocculosa (Roth) Kützing	o-α													+			+	+
Ulnaria acus (Kützing) Aboal	β	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
U. ulna (Nitzsch) Compère	o-α						+					+			+	+	+	+
Urosolenia eriensis (Smith) Round & Crawford												+	+	+			+	+
Chlorophyta																		
Ankistrodesmus arcuatus Korshikov	β	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+
Chlorella vulgaris Beijerinck			+	+		+	+	+		+	+	+	+	+		+		
Chlamydomonas proboscigera var. *conferta* (Korshikov) Ettl			+															
Coelastrum pseudomicroporum Korshikov	β							+		+								
Desmodesmus communis (Hegewald) Hegewald	β-o									+		+	+	+			+	
Elakatothrix genevensis (Reverdin) Hindák	o-α		+		+			+	+	+	+	+		+		+	+	+
Koliella longiseta (Vischer) Hindák	β											+			+	+	+	
K. variabilis (Nygaard) Hindák		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Mucidosphaerium pulchellum (Wood) Bock, Proschold & Krienitz	β	+	+		+				+		+		+					+
Monoraphidium contortum (Thuret) Komárková-Legnerová	β		+	+	+		+		+	+		+	+	+	+	+	+	+
M. griffithii (Berkeley) Komárková-Legnerová	β	+	+	+	+	+	+	+	+		+	+	+		+	+	+	+
M. minutum (Nägeli) Komárková-Legnerová	β	+		+	+			+	+					+		+		
Mychonastes homosphaera (Skuja) Kalina & Puncochárová	α	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Scenedesmus ecornis (Ehrenberg) Chodat	o-β								+	+								
Sphaerocystis planctonica (Korshikov) Bourrelly						+			+									
S. schroeteri Chodat	β-o											+		+				
Total number of species	49	26	27	29	28	27	24	26	29	26	32	59	41	50	53	42	49	42
Station number		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
		South Baikal									Irkutsk Reservoir							

Note: Green color shows the species that were found in the Irkutsk Reservoir but were absent from South Baikal at the moment of the study.

The number of species in the Irkutsk Reservoir was two times higher than in South Baikal (59 versus 29). The species diversity at the South Baikal stations varied from 26 to 29 species. The very first station of the reservoir (St. 10, Burduguz) showed an increase in the species diversity up to 32 species. Downstream of the reservoir, the species diversity was considerably higher (up to 59 species in Kurma Bay) (St. 11). The increase in species diversity was accounted for by Chrysophyta from the genera *Synura* and *Spiniferomonas* and small-size centric Bacillariophyta, such as *Cyclostephanos dubius*, *Discostella pseudostelligera*, and *Stephanodiscus minutulus*. The species composition of phytoplankton in the bays and in the central part of the reservoir was generally similar (see Table 2).

The saprobity is known for 49 species from the 99 found in the study area (see Table 2). They refer to three main self-purification zones: xenosaprobic (absolutely clean), oligosaprobic (almost clean), and mesosaprobic (temperately polluted with two β and α subzones). Among the indicator organisms found, o and β-saprobionts ranged from 27 to 20%, respectively, o-β-saprobionts amounted up to 14%, o-α-saprobionts up to 16%, β-o-saprobionts up to 6%, β-α-saprobionts up to 6%, α-bionts up to 4%, and β-α, χ-o, and χ-bionts up to 2%. As one can see, the species list in the reservoir was supplemented at the expense of o–1.0–oligosaprobionts (six species) and o-β–1.4–oligo-beta-mesosaprobionts (five species).

The Trophic State Index generally ranged by all stations between 0.9 and 1.4; it varied between 1.1 and 1.4 in South Baikal and between 0.9 and 1.2 in the Irkutsk Reservoir, including bays. The Trophic State Index values were 1.0 in all bays of the reservoir. The mean Trophic State Indexes were 1.2 and 1.0 in South Baikal and the Irkutsk Reservoir, respectively.

4.2. Abundance of Phytoplankton and Dominant Species

When moving from South Baikal to the Irkutsk Reservoir, the total abundance and biomass of phytoplankton increased (Figure 1), and the dominant species changed (Figures 2 and 3); they had features in the distribution by station (Figure 4).

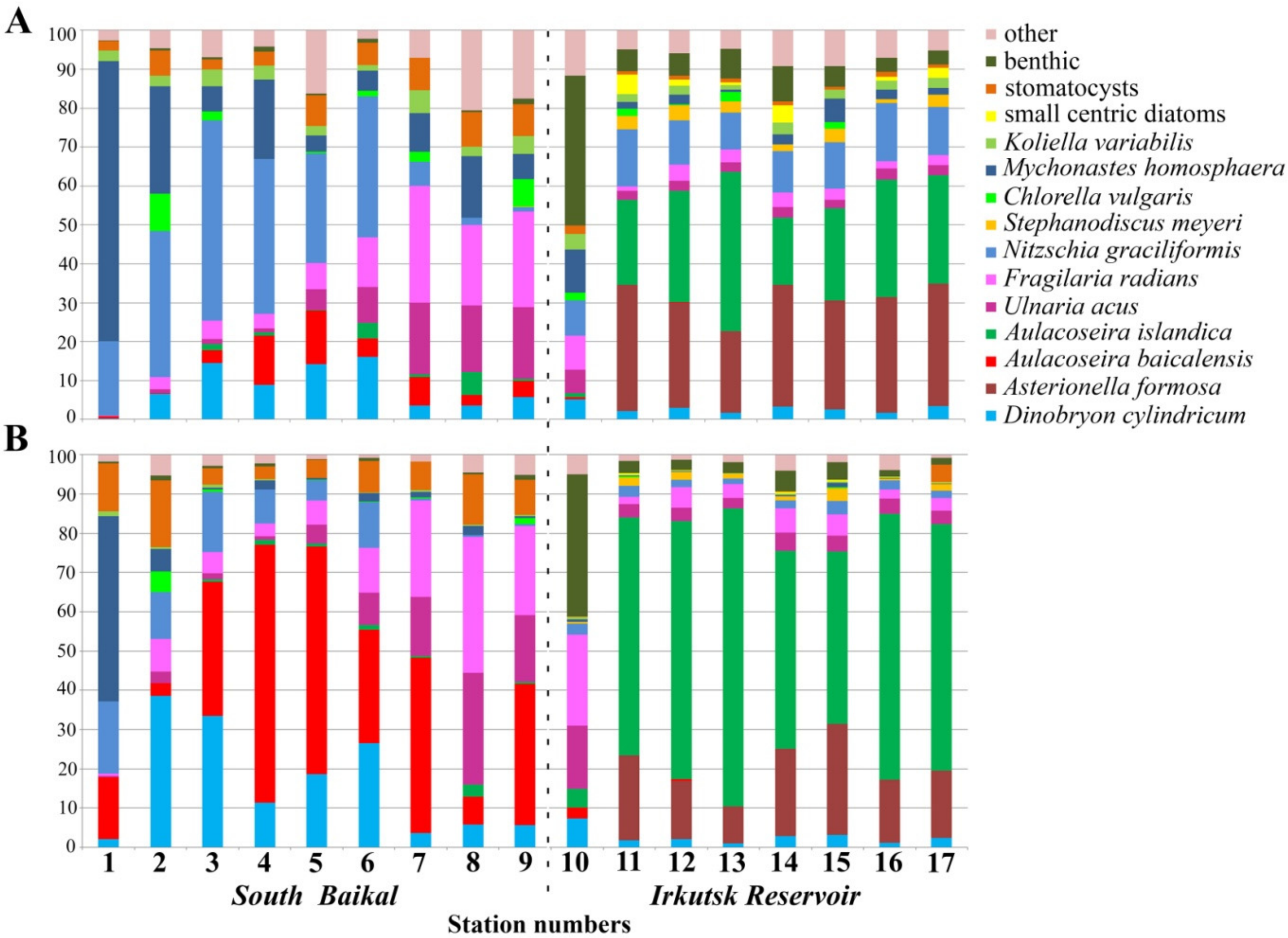

Figure 2. Percentage ratio by quantity (**A**) and biomass (**B**) of phytoplankton species in South Baikal and in the Irkutsk Reservoir in June 2023 (for station number, see Table 1 and Figure 1).

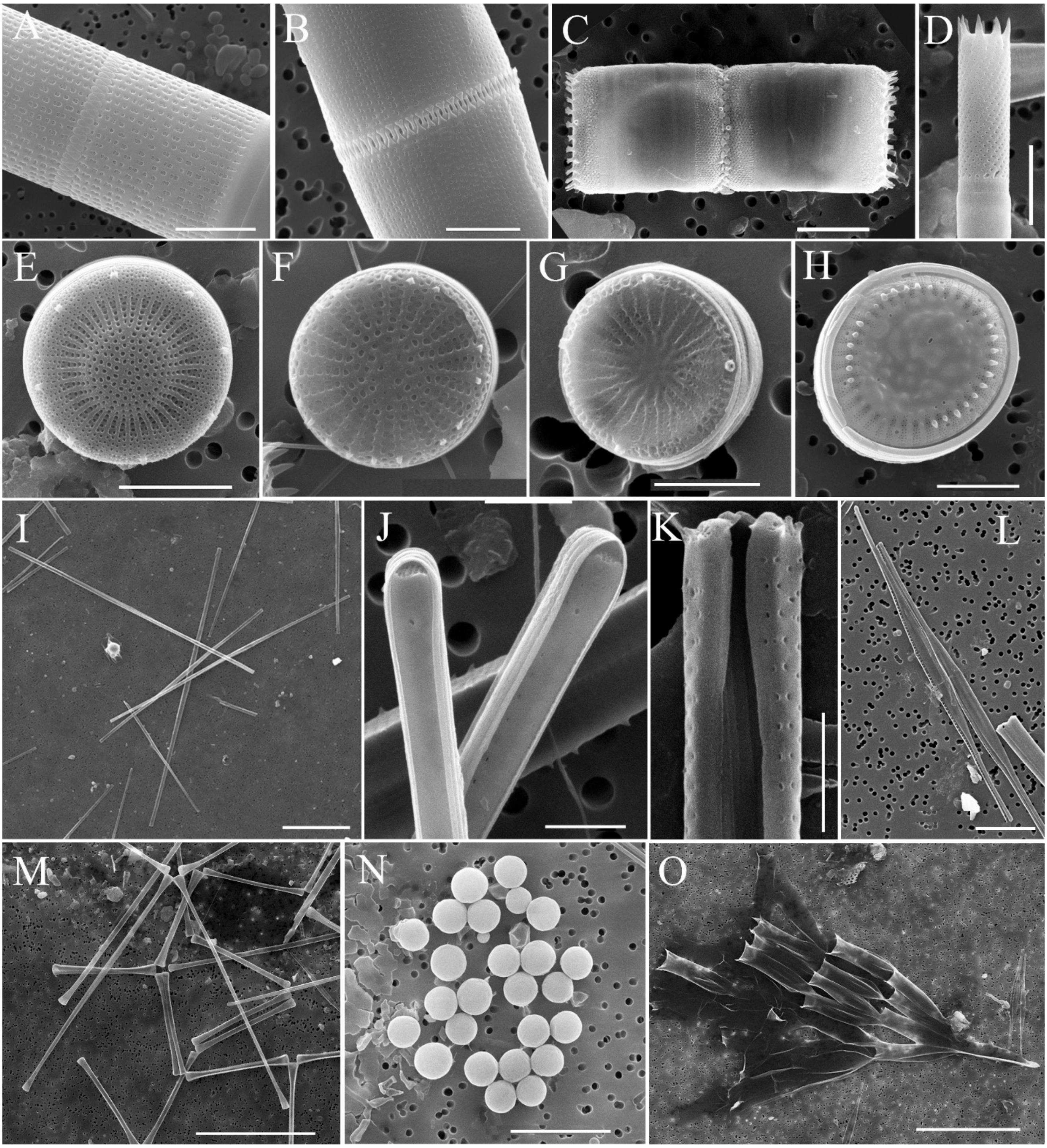

Figure 3. Dominant phytoplankton species from South Baikal and the Irkutsk Reservoir. SEM: (**A**) *Aulacoseira baicalensis*; (**B**) *Aulacoseira islandica*; (**C**) *Stephanodiscus meyeri*; (**D**) *Aulacoseira ambigua*; (**E**) *Cyclostephanos dubius*; (**F**) *Stephanodiscus minutulus*; (**G**) *Discostella pseudostelligera*; (**H**) *Lindavia minuta*; (**I**) *Fragilaria radians/Ulnaria acus*; (**J**) *Ulnaria acus*; (**K**) *Fragilaria radians*; (**L**) *Nitzschia graciliformis*; (**M**) *Asterionella formosa*; (**N**) cf. *Mychonastes homosphaera*; (**O**) *Dinobryon cylindricum*. Scale bars: (**A**–**E**,**H**)—5 μm; (**C**,**J**,**K**)—2 μm; (**I**,**M**,**O**)—50 μm; (**L**,**N**)—10 μm.

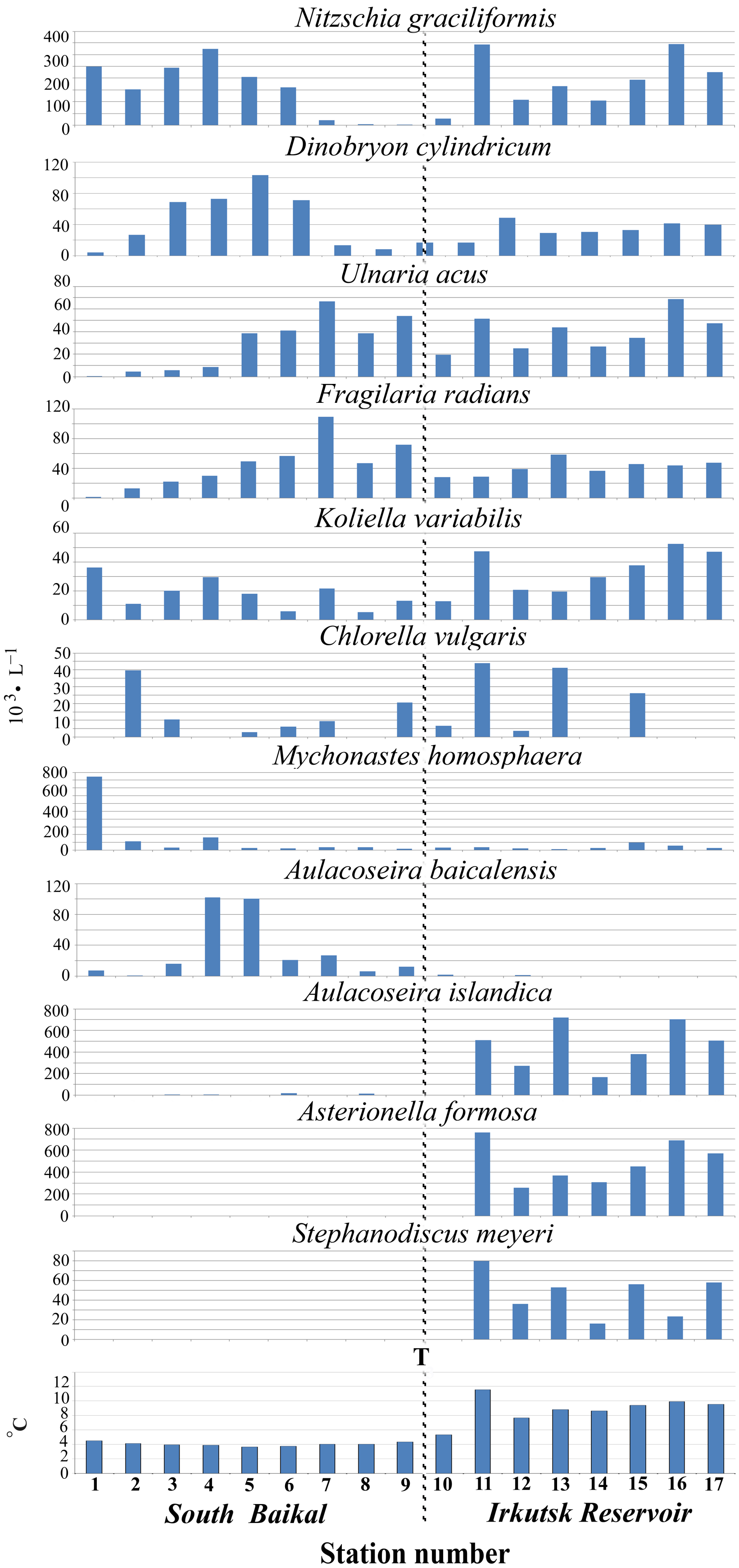

Figure 4. Distribution of water temperature and dominant species by stations.

The total abundance and biomass at the South Baikal stations varied between 255 and 1333 thousand cells·L^{-1} and between 61 and 473 mg·m^{-3}, respectively (see Figure 1). The highest values of phytoplankton abundance, up to 946 thousand cells·L^{-1}, were recorded at St. 1 (12 km from Kultuk), where small-size Chlorophyta *Mychonastes homosphaera* was abundant. At all other South Baikal stations, Bacillariophyta, such as *Nitzschia graciliformis*, *Fragilaria radians*, *Ulnaria acus*, and *Aulacoseira baicalensis*, were the most abundant. However, the quantity values of these species varied from station to station. For example, *A. baicalensis* had the maximum quantity of 102 thousand cells·L^{-1} at St. 4 (3 km from Solzan) and the minimum quantity of 0.6 thousand cells·L^{-1} at St. 2 (3 km from Maritui). The maximum quantity of *Nitzschia graciliformis*, 323 thousand cells·L^{-1}, was also recorded at St. 4 (3 km from Solzan), while the minimum quantity of this species, 3 thousand cells/L, was recorded at St. 9 (3 km from Listvyanka). A significant contribution to the abundance of phytoplankton in South Baikal was made by chrysophyte *Dinobryon cylindricum*, with its 103 thousand cells·L^{-1} recorded at St. 5 (Tolstoy-Snezhnaya) (see Figure 2).

The total abundance and biomass of phytoplankton cells in the Irkutsk Reservoir ranged between 960 and 2350 thousand cells/L^{-1} and between 544 and 1679 mg/m^{-3}, respectively (see Figure 1). The most abundant were Bacillariophyta *A. islandica* (up to 720 thousand cells·L^{-1}), despite its modest growth in South Baikal (only up to 13 thousand cells·L^{-1} at St. 8 Listvyanka-Tankhoi), and *Asterionella formosa* (up to 762 thousand cells·L^{-1}), which did not occur in South Baikal at all. The quantity values of *Nitzschia graciliformis* were similar, though they were slightly higher in the reservoir (up to 345 thousand cells·L^{-1} at St. 16 Ershovsky Bay) than in South Baikal (up to 323 thousand cells·L^{-1} at St. 4 (3 km from Solzan)). Bacillariophyta such as *Stephanodiscus meyeri* (up to 79 thousand cells·L^{-1} at St. 11 Kurma Bay) were found in Lake Baikal only once at the station 3 km from Listvyanka. *D. cylindricum*, which reached 63 thousand cells·L^{-1} at the upstream side (St. 17), and Chlorophyta, such as *Koliella variabilis* (up to 52 thousand cells·L^{-1} in Ershovsky Bay) (St. 16), were subdominant.

The composition of the dominant species in South Baikal and the Irkutsk Reservoir was simultaneously similar and different (Figure 2A). The most abundant in South Baikal were diatoms *Nitzscia graciliformis*, *Fragilaria radians*, *Ulnaria acus*, *Aulacoseira baicalensis*, chrysophycean *Dinobryon cylindricum*, and green alga *Mychonastes homosphaera*, while diatoms *Asterionella formosa*, *Aulacoseira islandica*, and *Nitzscia gracilliformis* prevailed in the reservoir (Figure 3). Large-size species contributed to the phytoplankton biomass most of all (Figure 2B). In the lake, these were *A. baicalensis*, *F. radians*, *U. acus*, and *D. cylindricum*, while they were *A. islandica* and *A. formosa* in the reservoir. We have to note that the phytoplankton structure at St. 10, located first downstream of the reservoir, had traits of "Baikal" phytoplankton of that period, with the presence of *A. baicalensis*, which was further replaced by *A. islandica*.

4.3. Peculiarities of Phytoplankton in the Bays of the Irkutsk Reservoir

The phytoplankton in the bays of the reservoir (St. 11, 13, and 16) had high species diversity (47–59) (Table 2) and high quantitative values (Figure 1). A higher content of benthic species was also recorded. Species such as *Asterionella formosa*, *A. islandica*, and *Nitzschia graciliformis* had their maximum quantity in the bays of the reservoir (Figure 4). Bacillariophyta *Stephanodiscus meyeri*, Chrysophyta *Dinobryon cylindricum*, as well as Chlorophyta *Koliella variabilis* and small species *Chlorella vulgaris* and *Mychonastes homosphaera*, acted as subdominants.

In the most species-rich Kurma Bay (St. 11), as in the central part of the reservoir, Bacillariophyta *A. formosa* (761 thousand cells·L^{-1}), *A. islandica* (511 thousand cells·L^{-1}), and *Nitzschia graciliformis* (342 thousand cells·L^{-1}) were the most abundant. The maximum abundance among the other studied stations was reached by the rare species *Stephanodiscus meyeri* (79 thousand cells·L^{-1}), typical of the summer plankton of Lake Baikal. During the study, the species was almost absent from South Baikal (Figure 4). The largest numbers of Chrysophyta and Chlorophyta species were also recorded there, but their quantitative values were not high. Chlorophyta was dominated by *Koliella variabilis* (47 thousand cells·L^{-1}) and *Chlorella vulgaris*, which forms its maximum abundance there only (44 thousand cells·L^{-1}). The maximum abundance and biomass of phytoplankton, 2350 thousand cells·L^{-1} and 1369 mg·m^{-3}, respectively, were noted in Kurma Bay (St. 11).

Fifty species were detected in Elovy Bay (St. 13). *Asterionella formosa* (370 thousand cells·L^{-1}) and *A. islandica* were the most abundant at the station, reaching the maximum quantity among other stations (720 thousand cells·L^{-1}). The total phytoplankton abundance and biomass were high: 1803 thousand cells·L^{-1} and 1537 mg·m^{-3}, respectively.

Forty-eight species were found in Ershovsky Bay (St. 16). Bacillariophyta *Asterionella formosa* (690 thousand cells·L^{-1}), *A. islandica* (702 thousand cells·L^{-1}), and *Nitzschia graciliformis* (344 thousand cells·L^{-1}) were the most abundant at the station. Chlorophyta *Koliella variabilis* (52 thousand cells·L^{-1}) reached the maximum abundance among the other stations in Ershovsky Bay. The total phytoplankton abundance in Ershovsky Bay was also high, up to 2334 thousand cells·L^{-1}, while the biomass had a maximum value of 1675 mg·m^{-3}.

4.4. Analysis of Factors Affecting the Species Structure of Phytoplankton Communities

As we can see from Table 1, during the transition from South Baikal to the Irkutsk Reservoir, there is a significant decrease in transparency and nutrient concentrations, while water temperature and pH increase. To determine the key factors affecting the structure of phytoplankton communities during the study, a statistical analysis of the data was performed. As revealed by PCA, phytoplankton communities can be split into two robust groups (Figure 5).

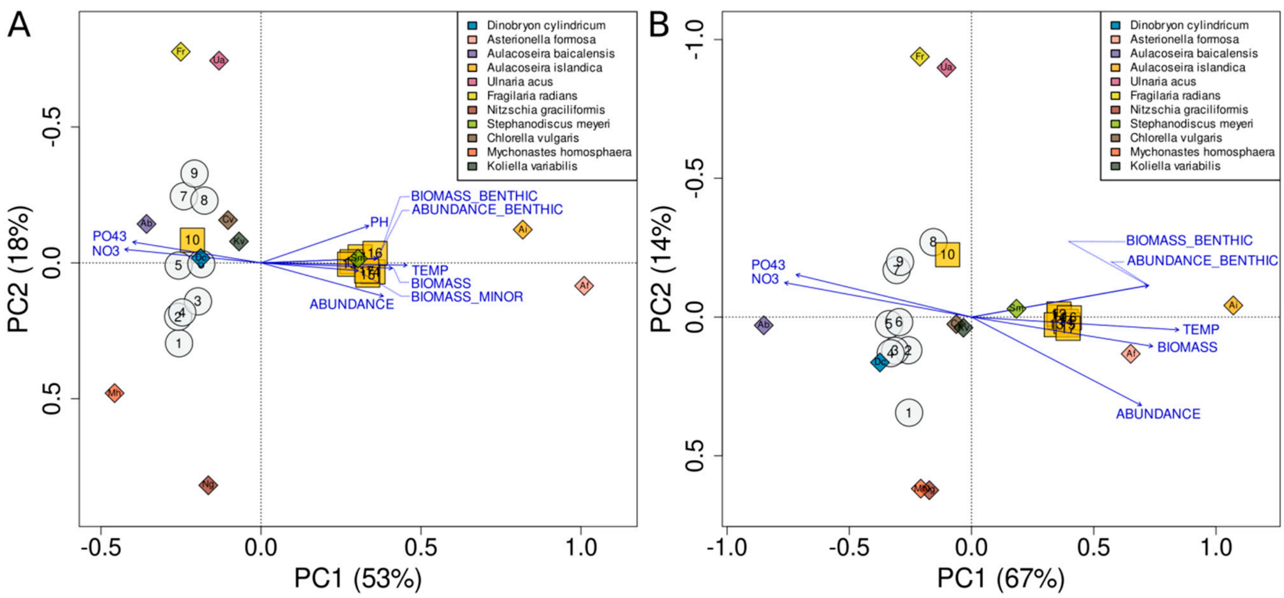

Figure 5. Exploratory analysis of phytoplankton species community profiles. (**A**)—PCA of species abundance. (**B**)—PCA of species biomass. Gray circles—sampling sites in the south basin of Lake Baikal. Yellow squares—sampling sites across the Irkutsk water reservoir. Diamonds—dominant phytoplankton species. Blue arrows—linear regression of explanatory variables, showing the direction and range of their impact.

Both species abundance and biomass profiles generate similar ordinations. Sampling site St. 10 (Burduguz) is closer to the Lake Baikal community profiles. The rest of the Irkutsk water reservoir profiles are very similar to each other. Thus, the phytoplankton community profiles were divided into two categories according to PCA: lake (sampling sites 1–9) together with St. 10 and reservoir (sampling sites 11–17). One-way ANOVA was used to examine the environmental variables, which are different between these two groups of sampling sites (Table 3, Figure 6).

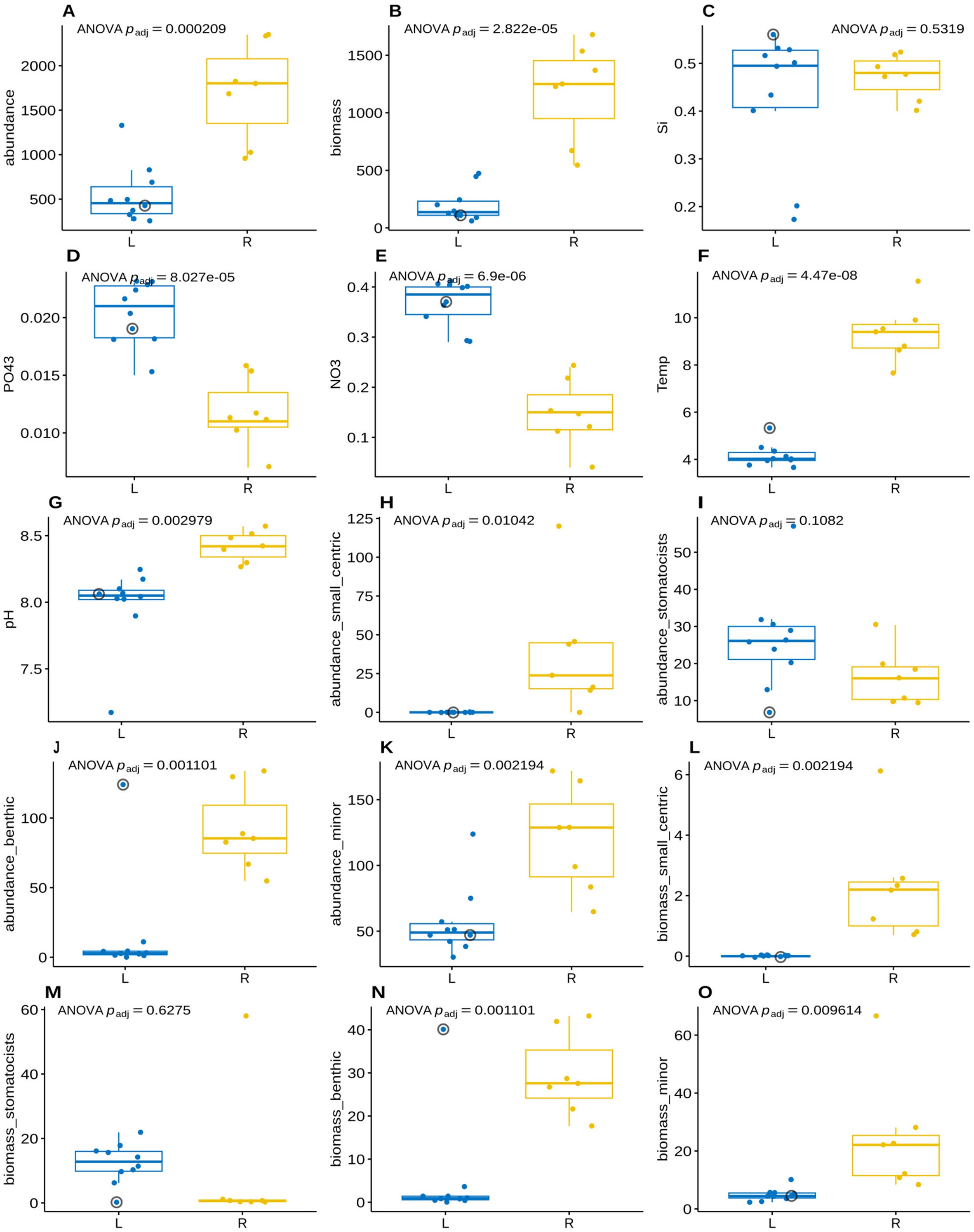

Figure 6. One-way ANOVA of environmental variables for L (Lake Baikal) and R (Irkutsk Reservoir) sampling sites. Station 10 (Burduguz) is circled.

Table 3. One-way ANOVA computed for environmental and summary numerical variables.

	ANOVA			Kruskal–Wallis		
	p	p_{adj}	P_{adj} **Sign**	p	p_{adj}	P_{adj} **Sign**
	Physical and chemical environmental variables					
Si	5.0×10^{-1}	5.3×10^{-1}		7.0×10^{-1}	7.0×10^{-1}	
$PO_4{}^{3-}$	2.1×10^{-5}	8.0×10^{-5}	***	1.0×10^{-3}	2.1×10^{-3}	**
$NO_3{}^{-}$	9.2×10^{-7}	6.9×10^{-6}	***	6.0×10^{-4}	1.9×10^{-3}	**
Temperature	3.0×10^{-9}	4.5×10^{-8}	***	6.4×10^{-4}	1.9×10^{-3}	**
pH	2.0×10^{-3}	3.0×10^{-3}	**	6.3×10^{-4}	1.9×10^{-3}	**
	Summary numerical variables					
Total phytoplankton abundance	7.0×10^{-5}	2.1×10^{-4}	***	1.3×10^{-3}	2.1×10^{-3}	**
Total phytoplankton biomass	5.6×10^{-6}	2.8×10^{-5}	***	6.4×10^{-4}	1.9×10^{-3}	**
Abundance of small centric diatoms	8.3×10^{-3}	1.0×10^{-2}	*	1.3×10^{-3}	2.1×10^{-3}	**
Abundance of stomatocists	9.4×10^{-2}	1.1×10^{-1}		7.1×10^{-2}	7.6×10^{-2}	.
Abundance of benthic diatoms	5.1×10^{-4}	1.1×10^{-3}	**	3.4×10^{-3}	4.3×10^{-3}	**
Abundance of minor species	1.2×10^{-3}	2.2×10^{-3}	**	2.5×10^{-3}	3.7×10^{-3}	**
Biomass of small centric diatoms	1.3×10^{-3}	2.2×10^{-3}	**	1.3×10^{-4}	1.9×10^{-3}	**
Biomass of stomatocists	6.3×10^{-1}	6.3×10^{-1}		6.3×10^{-2}	7.3×10^{-2}	.
Biomass of benthic diatoms	5.1×10^{-4}	1.1×10^{-3}	**	3.4×10^{-3}	4.3×10^{-3}	**
Biomass of minor species	7.1×10^{-3}	9.6×10^{-3}	**	9.1×10^{-4}	2.1×10^{-3}	**

Column legend: ANOVA/Kruskal–Wallis p-values: p—p-value | p_{adj}—FDR-adjusted p-value | p_{adj} sign—the adjusted p-value significance code: *** $\leq$ 0.001; 0.001 $\leq$ ** $\leq$ 0.01; 0.01 $\leq$ * $\leq$ 0.05; 0.05 $\leq$. $\leq$ 0.1.

Phosphate (Figure 6D) and nitrate (Figure 6E) anion concentrations were greater in the Lake Baikal sites. This fact obviously correlates with higher values of temperature (Figure 6F), total phytoplankton abundance (Figure 6A), and biomass (Figure 6B) in the reservoir sites. The abundance and biomass of small centric diatoms (Figure 6H,L), benthic diatoms (Figure 6J,N), and minor species (Figure 6K,O) were also higher in the reservoir sampling sites.

Importantly, phosphate and nitrate anion concentrations have strong positive correlations, while both anions negatively correlate with water temperature, phytoplankton abundance, and biomass (Figure 7A). The constrained ordination by RDA generated a model with the single explanatory parameter “temperature” using both forward selection and backward elimination approaches of choosing variables. In this model, temperature alone explained 44% out of 50% of the adjusted total variation in the species abundance matrix. The RDA ordination pattern (Figure 7B) is very similar with that of unconstrained PCA (Figure 5).

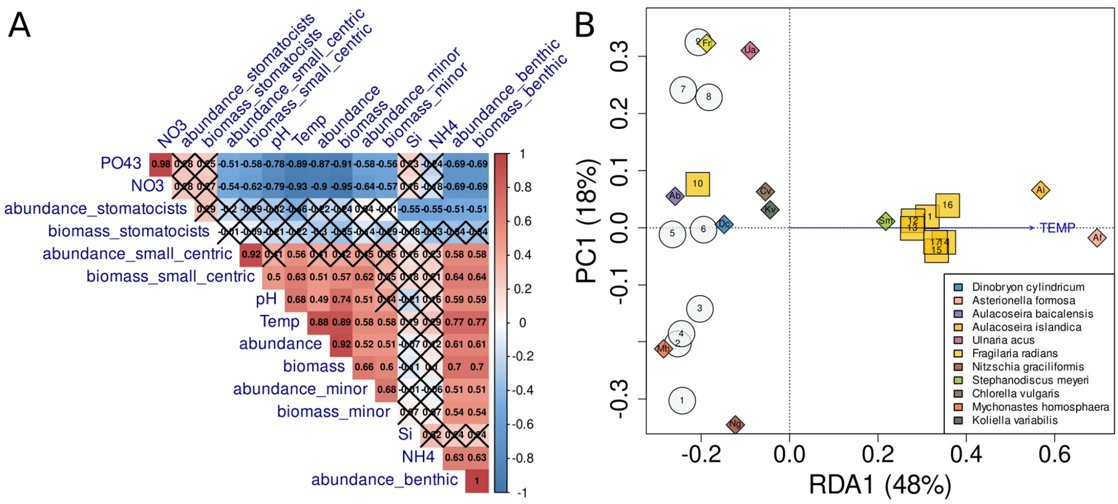

Figure 7. (**A**)—Analysis of correlation of environmental parameters. Numerical values are Pearson correlation coefficients with the color legend on the right. Crossed cells are non-significant correlations

(p > 0.05). (**B**)—Constrained ordination of the phytoplankton community profiles using redundancy analysis. Gray circles—sampling sites in the south basin of Lake Baikal. Yellow squares—sampling sites across the Irkutsk Reservoir. Diamonds—dominant phytoplankton species. Blue arrow—explanatory variable, used in the model.

5. Discussion

In Lake Baikal, June is considered hydrological spring [41]. Both microscopic [42,43] as well as high throughput sequencing methods [44] demonstrated that the phytoplankton community at that period considerably differed from that of July, i.e., hydrological summer.

One of the factors determining the phytoplankton species composition in the Irkutsk Reservoir is Lake Baikal being a source of the Angara Rivers, across which the hydroelectric dam forming the reservoir was constructed. The Irkutsk Reservoir is an impoundment on-stream artificial lake with a predominance of hydraulic currents [27]. This explains the dominance of "Baikal" species, that is, species typical of Lake Baikal and its bays in spring and summer, in the phytoplankton of the Irkutsk Reservoir during the study. Thus, the species list for the Irkutsk Reservoir compared to South Baikal included small centric Bacillariophyta, such as *Cyclostephanos dubius*, *Discostella pseudostelligera*, and *Stephanodiscus minutulus*, typical of summer Baikal phytoplankton in July. When moving to the Irkutsk Reservoir, the taxa diversity of silica-scaled chrysophytes increased with the emergence of species of the genera *Synura* and *Spiniferomonas*, which are usual in the summer phytoplankton of Lake Baikal [45]. *Stephanodiscus meyeri*, typical of summer phytoplankton in Lake Baikal, reached the maximum quantity (79 thousand cells·L^{-1}). At the same time, the species was almost absent from the stations in South Baikal (Figure 4).

Temperature was one of the factors differentiating the South Baikal and Irkutsk Reservoir communities. Changes in species composition, abundance, and biomass followed the water temperature gradient. The redundancy analysis yielded a model with temperature being the single explanatory variable (Figure 7B), explaining more than 40% of the variation in species abundance. At the same time, temperature strongly positively correlated with the abundance and biomass of phytoplankton, while it was negatively correlated with concentrations of phosphate and nitrate anions (Figure 7A). These results highlight that we cannot determine the causal effects of one explanatory variable to another. However, in our settings, it seems reasonable to suggest that the temperature of water is the main factor influencing the community's trophic state. The ANOVA results also bring evidence of enrichment of phytoplankton species composition in minor and centric species when getting into warmer waters of the reservoir (see Figure 6). At the same time, species having different temperature preferences occurred in the study area (see Figure 4). A bright example of psychrophilic Baikal species that diminish their abundance or stop their growth entirely in the warmer waters of the Irkutsk Reservoir is *Aulacoseira baicalensis*, which is endemic to Lake Baikal. This species is known to reach its maximum quantity (400–600 thousand cells·L^{-1}) at water temperatures of 1–3 °C, while the maximum temperature value when the species is still detectable in the lake is 8 °C [46]. According to Table 2 and Figure 4, the species was present at St. 10 at 5.33 °C and at St. 12 at 7.66 °C; it did not occur at any other stations in the Irkutsk Reservoir, where higher temperatures were recorded. The related *Aulacoseira islandica* seems to compete with *A. baicalensis* for nutrient sources, since it occurred in South Baikal as single cells but was vegetating more actively in the Irkutsk Reservoir; however, it is considered a psychrophilic species, being the most abundant in Lake Baikal under the ice in April (up to 1–7 mln cells·L^{-1}) [46] (Figure 4).

A distribution pattern by stations similar to that of *A. islandica* was observed in two diatoms, *Stephanodiscus meyeri* and *Asterionella formosa*, which differ in ecology. *S. meyeri* inhabits Baikal from February to July, giving a high abundance at a wide temperature range of 0.2–10 °C. *A. formosa* is a more thermophilic species, typical for Baikal bays, actively vegetating at 8–19 °C [46].

The diatoms *Nitzschia graciliformis* and chrysophyte *Dinobryon cylindricum* and green *Koliella variabilis* were also among tolerant species inhabiting both waters of the lake and the reservoir with stable abundance.

The dominant phytoplankton complex of the Irkutsk Reservoir differs from that of tropical reservoirs. As has been evidenced earlier [11], the cold oligotrophic waters of Lake Baikal limit in spring the growth of Cyanobacteria, which is typical, during almost all seasons, of many tropical reservoirs, such as, e.g., the Hongmen Reservoir in Vietnam [15], the Ufiobodo and Ebonyi Reservoirs in Nigeria [18], and the Korhogo Reservoir in Côte d'Ivoire [18]. However, the phytoplankton species composition in the Irkutsk Reservoir has common traits with the northern reservoirs of the Volga–Kama Cascade [4]. For example, *A. islandica* dominating in the Irkutsk Reservoir was also a part of the vernal phytoplankton in almost all reservoirs of the Volga–Kama Cascade [4]. At the same time, there are no data about the dominance of *Nitzschia graciliformis* and *Asterionella formosa* in those reservoirs.

The species composition in the Irkutsk Reservoir was also notable in June 2023 for the predominance of Chrysophyta by the richness of species. Electron microscopy revealed species of silica-scaled chrysophytes on the basis of the ultrastructure of their siliceous scales. They were the core of the diversity of Chrysophyta (31 species in total) [34]. Also, we may note a certain increase in species diversity of the genus *Dinobryon* compared to data from 2012 [13], when there were only three species on the list. Our study supplemented the species list of this genus up to seven species (see Table 2). A dominance of species of the genus *Dinobryon* and silica-scaled chrysophytes of the genera *Mallomonas* and *Synura* as a component of phytoplankton functional groups had been earlier reported for the Tuyen Lam Reservoir in Vietnam during the rainy season [15].

The comparison of the species composition with earlier studies showed that the main core of the dominant species remained. Baikal waters also affected the phytoplankton of the Irkutsk Reservoir, despite its more active growth and higher species diversity. For example, *Nitzschia graciliformis*, dominating in South Baikal, was also playing a leading role in phytoplankton in the Irkutsk Reservoir. Nonetheless, the higher temperature values induced the growth of species more typical of summer, such as *Asterionella formosa*. The quantitative values did not exceed those obtained previously [11,13].

The water quality assessment conducted using indicator organisms showed that in June 2023, the waters of the Irkutsk Reservoir could be referred by their trophic status to Class II and qualified as clean. Thus, the phytoplankton biomass did not exceed on average 2 $g \cdot m^{-3}$ during the study; therefore, the reservoir may be described as oligotrophic, with some mesotrophic traits [47–49].

The water quality evaluation conducted at the lower reaches of the Irkutsk Reservoir using Pantle–Buck's indicator organisms modified by Sladečeck and in accordance with the environmental and sanitary classification [24–26] allows referring waters of the reservoir to Class II (clean water). Altogether, we may state that the Trophic State Index of the Irkutsk Reservoir in June 2023 correlates with previous data [13].

6. Conclusions

Compared to Lake Baikal, the Irkutsk Reservoir in June 2023 was notable for a twofold increase in species diversity, total phytoplankton abundance, and total phytoplankton biomass, inducing, highly likely, a reliable decrease in nutrient (PO_4^{3-} and NO_3^-) concentrations. The diversity of phytoplankton species was under a considerable influence of water temperature, limiting, on one hand, the expansion of psychrophilic Baikal species (*Aulacoseira baicalensis*) into the reservoir, but favoring, on the other hand, the growth of a broader spectrum of species typical, mostly, of the next summer phytoplankton of the lake. These include *Nitzschia graciliformis*, which is not dominant in other reservoirs of the world, and *Asterionella formosa*, which is a common representative of the phytoplankton in reservoirs [50–52]. The role of blue-green algae was minor. Since water temperature is the main environmental factor affecting the distribution and diversity of phytoplankton in the Irkutsk Reservoir ecosystem, its significant rise in summer and on the global time scale may cause a considerable restructuring of the phytoplankton communities of the reservoir and deterioration of water quality. An opposite scenario is also possible, i.e., an expansion of Baikal endemics downstream of the Angara and their dispersal into other reservoirs of the Angara Cascade in early spring at low water temperatures.

Studying the relationships between phytoplankton communities and environmental factors is critical to understanding how aquatic ecosystems function. The high sensitivity of phytoplankton to changes in these factors makes it possible to control the state of the ecosystem of water bodies.

Author Contributions: A.F., scanning electron microscopy, literature search, interpretation of the results, writing of the first version of the manuscript; Y.G., statistical analysis; L.T., A.F. and V.B., light microscopy, counting of the phytoplankton, determination of diatoms' proportion in the abundance and biomass of phytoplankton; A.B., electron microscopy, identification of scaled chrysophytes, literature search, writing; M.S., hydrochemical analysis; A.M., D.H., M.N. and I.M., sampling, measurements during field work, preparation of samples for laboratory research; Y.L., writing—review and editing. All authors have read and agreed to the published version of the manuscript.

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