Hydrobiologia (2020) 847:1383–1398
https://doi.org/10.1007/s10750-020-04207-z

OPINION PAPER

Fluctuations in plankton community structure of endorheic soda lakes of southeastern Transbaikalia (Russia)

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Received: 21 June 2019 / Revised: 11 February 2020 / Accepted: 12 February 2020 / Published online: 20 February 2020

Abstract The aim of present research is to study the patterns of phyto- and zooplankton fluctuations in endorheic soda lakes (Uldz Gol-Torey Basin, southeastern Transbaikalia, Russia) under arid conditions because studied area is becoming increasingly arid. Plankton samples were collected in summer during time intervals with different lake water levels using standard hydrobiological methods. We detected four patterns of change in plankton communities with changing environmental conditions (increasing total dissolved solid, pH and temperature, and decreasing depth). The first pattern is characterized by a predominance of green algae, charophytes, diatoms and euglenophytes; the species composition and dominant zooplankton assemblage are the same in different years. The second pattern is characterized by a loss of cryptophyte and chrysophyte algae, a dominance of green and blue-green algae, a decrease in zooplankton species diversity, and an increased abundance of zooplankton, the dominant species are consistent over time. The third pattern exhibits marked decreases in phytoplankton diversity and density, a dominance of green algae and diatoms, a further decrease in the species richness of zooplankton, and increased abundance and biomass of some species. The fourth pattern is a marked by a reduction in plankton species diversity to a monospecific community.

Keywords Phytoplankton · Zooplankton · Fluctuations · Soda lakes · Uldz Gol-Torey Basin · Transbaikalia (Russia)

Handling editor: Judit Padisák

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Introduction

Continental salt lakes are special types of ecosystems that are extremely vulnerable to external factors, including climatic change (Williams, 2002). Even relatively small fluctuations in the most sensitive areas may result in significant and irreversible changes in their natural characteristics (Hammer, 1986). Saline lakes can be found on all continents and in most countries. Many of them are shallow and ephemeral in arid regions. They are characterized by high levels of conductivity, day–night temperature variation, turbidity, pH, alkalinity and total dissolved solids (TDS) (Sklyarov et al., 2011; Boros et al., 2014). Salt lakes are sensitive to changes in precipitation and strongly dependent on the hydrological budget. Water-level fluctuations in lakes, especially their extent, frequency and duration, are dominant forces controlling the functioning of these ecosystems (Leira &

Cantonati, 2008). Alternation of dry and wet seasons causes changes in the physical (water temperature, water level), and chemical (extensive seasonal and inter-annual variations in salinity and pH) characteristics of the lake and, as a consequence, considerable alterations in the biotic components (species composition, density) of the ecosystem (Comín et al., 1992; García et al., 1997; Gasse et al., 1997; Shadrin & Anufriieva, 2013). The ephemeral nature of many lake habitats leads to large and unpredictable fluctuations in salinity and to periodic drying out (Jeppesen et al., 2015).

The combination of sodium and carbonates results in alkaline conditions, and such systems are termed as "soda lakes". Brackish and saline alkaline lakes—"soda lakes"—have saline waters with sodium and carbonate species as the dominant ions and typically exceed a pH of 9 (Boros & Kolpakova, 2018). Carbonate (soda) lakes are athalassic origin and form in closed drainage basins exposed to high-evaporation rates. From the scientific point of view, saline–alkaline lakes are natural laboratories for adaptations of soda lake organisms to extreme environmental conditions. These lakes are inhabited by unique flora and fauna, which can tolerate these extreme environmental conditions (Pálffy et al., 2014). In this respect, studies of plankton communities (algae and invertebrates) playing a significant role both in the structural and functional integrity of saline lakes are especially actual (Ionescu et al., 1998; Ostroumov, 2003).

Although soda lakes are widely distributed across the globe (Hammer, 1986), only a few have been studied. Soda lakes occur in Africa (the eastern Rift Valley), Canada (dry interior of the Province British Columbia and western provinces of Saskatchewan and Alberta), USA (North Basin), China (northern Tibet, Hebei), Mongolia (Uldz-Kerulen Basin), Europe (Carpathian Basin), Turkey (the Lake District in southwest), and are also a characteristic feature of the Russia (Transbaikalia, Western and Eastern Siberia). Onon-Borzya system of shallow lakes located in the southeastern Trans-Baikal region of Russia includes several hundred lakes. This area is characterized by aridity and an extremely continental climate; its waters exhibit high salt concentrations and alkaline environments (Sklyarov et al., 2011). This region is marked by variable hydrological processes over time and frequent changes in morphodynamic regimes (Bazhenova, 2013), which are subject to intra-century cycles of 27–35 years controlled by atmospheric humidification such that relatively wet, very cold periods alternate with dry, relatively warm periods (Obiazov, 2012). Terraces exposed through drying and beach ridges are prominent around the lakes; these are suggestive of recurring oscillations of climate and water availability in the territory. The bottoms of lakes are often flat basins with a limited catchment area and a saucer-shaped bottom topography (Kuklin et al., 2013). The Uldz Gol-Torey Basin is the largest closed drainage basin in the Onon-Borzya lake system. Lakes of this basin are very diverse in terms of chemical composition, while their TDS does not vary considerably (0.3–100 g l^{-1}), and pH ranges from 8.4 to 10.5. With increasing salinity, types of lacustrine waters change from hydrocarbonate–sulfate sodium to hydrocarbonate–chloride–sulfate sodium and then to hydrocarbonate–chloride sodium or from hydrocarbonate to hydrocarbonate–chloride and then to chloride–hydrocarbonate. Cationic composition changes from sodium–manganese to sodium (Sklyarov et al., 2011).

Since the 80s of the last century, long-term hydrobiological monitoring has been carried out on shallow soda lakes of the Uldz Gol-Torey Basin. Our main goal is to study the patterns of phyto- and zooplankton fluctuations in saline lakes under arid conditions. This work is important because these study area is becoming increasingly arid and this trend is expected to continue under current climate-change scenarios (Obiazov, 2012). The results of the present study will help predict changes in phyto- and zooplankton communities with further aridisation. We evaluated (i) if the variabilities under environmental and biological conditions during the period of drier climatic conditions, and if so at what scales, and (ii) to what extent these differences have an influence upon the plankton diversity structure.

Materials and methods

Study site

We conducted our studies during different water-level phases of the hydrological cycle, including years with high (1999 and 2003), intermediate (2007 and 2011) and low (2014 and 2016) lake levels. We investigated nine soda endorheic steppe lakes (Zun-Torey, Tsagan-

Nur, Bain-Tsagan, Bain-Bulak, Ukshinda, Bulun-Tsagan, Balyktui, Khadatui, Nizhnii Mukei) that were selected on the basis of their different areas and depths. The Zun-Torey Lake is the largest among them. In high water-fill years, it covers an area of 285 km^2; its maximum depth is 6.5 m. The area of other lakes does not exceed 12 km^2 during high stand periods. Whitish color of silt sediments found in the lake bed, together with hydrogen carbonate salts and suspension, impart a milk-white tint to the water. Water transparency is low, on average, about 0.5 m. The highest transparency (4.5 m) was observed in Bain-Tsagan Lake in high water-level years.

Zun-Torey, Bulun-Tsagan and Nizhnii Mukei are drying lakes, which completely dried in 2016–2018. Lakes Tsagan-Nor, Bain-Tsagan, Bain-Bulak, Ukshinda, Balyktui and Khadatui have permanent waters with highly variable water levels, but do not dry out completely (Bazarova et al., 2019) (Fig. 1).

The studied lakes can be divided into four groups according to salinity levels (Venice System, 1959): oligohaline (to 4 g l^{-1}), mesohaline (5–18 g l^{-1}), polyhaline (18–30 g l^{-1}), and hyperhaline (over 30 g l^{-1}). Over long-term periods, salinity varied within the ranges of the corresponding groups or surpassed their limits significantly. The lowest salinity was in the high water 1999. The salinity of the lakes depends not only on the water level of a particular water body, but also on the type of its feeding, as well as on morphometric features of the lake bottom (Zamana & Borzenko, 2010; Kuklin et al., 2013; Tsybekmitova & Belozertseva, 2014; Zamana & Vakhnina, 2014; Tsybekmitova, 2018). The main hydrochemical and morphometric characteristics of the studied lakes are described herein (Table 1).

Sampling and analysis

Plankton samples were collected in July to August, when the water had reached its maximum annual temperature. Samples were obtained from both nearshore and deep water of the lakes. For

Fig. 1 Location map of soda lakes in the Uldz Gol-Torey Basin (Transbaikalia, Russia)

Table 1 Geographical position (GPS), depth (*H*), transparency (TR), water temperature (*T*), total dissolved solids (TDS), pH for the soda lakes in the Uldz Gol-Torey Basin (Russia)

Lake (code)/GPS	Lake level	Sampling, *H* (m, min–max)	TR (m, min–max)	*T* (°C, min–max)	TDS ($g\ l^{-1}$)	pH
Lake group A						
Bain-Bulak (4)	High	2.2–6.2	0.6–1.0	17.1–20.5	0.7	8.5
50° 22′ 33″ N, 114° 48′ 80″ E	Intermediate	3.4–3.5	0.5	19.8–21.5	1.8	9.0
	Low	1.3–3.1	0.3	23.0–24.2	2.7	9.2
Balyktui (7)	High	3.0–6.0	1.0	19.3–19.5	0.9	8.5
50° 24′ 55″ N, 114° 42′ 43″ E	Intermediate	2.0–3.0	1.0	21.6–22.1	1.2	–
	Low	1.5–3.5	1.2	22.5–24.6	3.7	9.3
Khadatui (8)	High	3.1–6.5	0.8	19.5	2.1	–
50° 23′ 9″ N, 114° 46′ 49″ E	Intermediate	1.8–3.4	0.4–0.5	21.3–23.4	2.6	–
	Low	2.0	0.2	25.2	3.4	9.5
Lake group B						
Tsagan-Nor (2)	High	1.5–7.8	1.4–1.5	17.8–19.8	2.1–2.7	8.9
50° 11′ 59″ N, 114° 59′ 36″ E	Intermediate	2.2–6.0	2.2–2.5	22.6–22.9	4.4	9.1
	Low	0.5–4.1	4.0	23.1–25.3	6.4–7.1	9.6–9.8
Bain-Tsagan (3)	High	6.0–11.0	3.7–4.5	18.8–21.5	2.1	9.1
50° 20′ 00″ N, 115° 06′ 28″ E	Intermediate	7.8–9.0	1.5–2.5	21.6–23.5	4.1–4.4	9.3–9.4
	Low	2.1–7.1	0.8–0.9	21.2–25.2	6.2–6.4	9.6–9.7
Ukshinda (5)	High	3.3–7.8	1.0	21.3	2.0	8.9
50° 20′ 29″ N, 114° 50′ 0″ E	Intermediate	4.5–5	0.7–0.8	21.2–22.1	4.3–4.8	9.3
	Low	3.7	0.7	23.4–24.7	7.8	9.6
Lake group C						
Zun-Torey (1)	High	1.5–6.5	0.5	20.4–23.4	2.1	9
50°4′ 31″ N, 115° 48′ 46″ E	Intermediate	1.6–1.7	0.3	19.5–25.2	8.1	9.4
	Low	0.1–1.5	0.1–0.3	21.4–26.4	14.3–20.9	9.4–9.9
Lake group D						
Bulun-Tsagan (6)	High	1.9–5.6	1.1–1.7	19.2–23.1	2.6	9.0
50° 6′ 44″ N, 115° 6′ 35″ E	Intermediate	0.6	0.6	22.4	18.1	9.4
	Low	0.4	0.4	28.5	58.1	10.3
Nizhnii Mukei (9)	High	3.8	2.0	19.1	17.0	9.2
49° 58′ 16″ N, 115° 17′ 7″ E	Intermediate	1.1	0.3	24.6	59.1	9.6
	Low	0.2–0.6	0.2	28.8	81.4	10.1

- no data

phytoplankton, samples were collected from two or three layers (the surface layer, the Secchi depth, and the benthic layer) with a Patalas bathometer (PB-6, Borok, Russia). The samples were fixed with 4% formalin solution. The sedimentation method was used to concentrate phytoplankton. Cell calculation was made in a counting plate (0.01 ml volume) using the Hansen method (Sadchikov, 2003). Biomass was determined based on the volume of individual algae cells or colonies and their geometric figures. The specific weight was taken equal to one unit (Sadchikov, 2003). We used the taxonomic database of algae (Guiry & Guiry, 2020) for the valid names of species.

Zooplankton samples were obtained using a Juday net (mesh size of 0.064 mm), with a single sampling pass from the lake bed to the surface in the case of deep waters. Shallow waters were filtered through a hydrobiological scoop net (mesh size of 0.094 mm). The samples were preserved in a 4% formalin solution following standard routine and counted in the Bogorov and Kolkwitz chambers (Kiselev, 1969). The biomass of zooplankters was calculated using the regression equations of the body length to the wet weight (Ruttner-Kolisko, 1977; Balushkina & Vinberg, 1979).

Standard techniques were employed to collect and process the plankton samples. Laboratory analyses were conducted in the Laboratory of Aquatic Ecosystems of the Institute of Natural Resources, Ecology and Cryology of the Siberian Branch of Russian Academy of Sciences (Chita, Russia).

Abiotic factors (TDS, pH, water temperature) were measured at the same time as hydrobiological sampling using a multiparameter portable water-quality test system (Aquaread GPS-AQVAMETER, Great Britain). Water transparency and depth were determined with a standard Secchi disk.

Statistical analysis

Data analysis of variance was performed using the XLSTAT. We performed redundancy analysis (RDA) for the lake groups and environmental variables using the pooled data of the samplings. Multivariate data were standardized and analyses were performed using the R program (Dalgaard, 2008).

Results

Environmental parameters

The RDA performed with RDA divided the studied lakes into four lake groups (Fig. 2; Table 1).

Lake group *A* consisted of oligohaline lakes (such as Bain-Bulak, Balyktui, Khadatui) for which the hydrochemical status did not change with decreasing water level. TDS ranged from 0.7–2.1 to 2.7–3.7 g l^{-1}, pH ranged from 8.5 to 9.2–9.5 and water temperature ranged from 17.1–20.5 to 22.5–25.2°C.

Lakes of the group *B* including Tsagan-Nor, Bain-Tsagan, Ukshinda exhibited a change in water type from oligohaline (2.0–2.7 g l^{-1}) to mesohaline (6.2–7.8 g l^{-1}) during drier. pH value changed from 8.9–9.1 to 9.6–9.8, temperature ranged from 17.8–21.5 to 21.2–25.3°C.

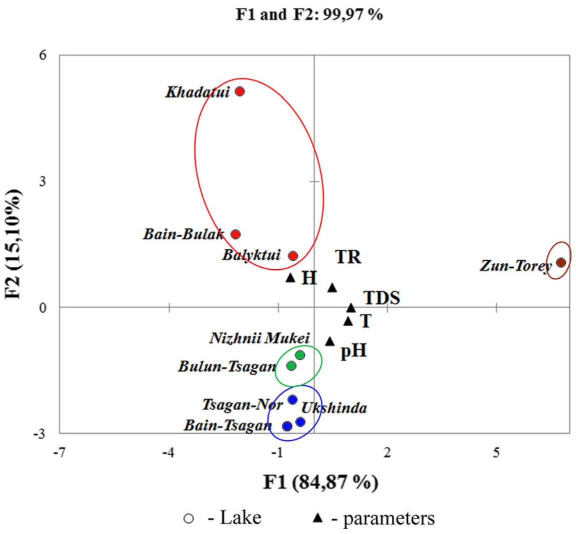

Fig. 2 RDA biplots of ordination between soda lakes of the Uldz Gol-Torey Basin and environmental variables. Red Lake group A, blue Lake group B, brown Lake group C, green Lake group D

In Lake Zun-Torey (group *C*), the salinity increased from oligohaline (2.1 g l^{-1}) to polyhaline (14.3–20.9 g l^{-1}) levels during transitions from high to low water levels. In the high water years (1999 and 2003), pH was 9 and water temperature was 20.4–23.4°C and in low water years (2014 and 2016) pH and temperature increased to 9.4–9.9 and 21.4–26.4°C.

In the *D*-group lakes, Bulun-Tsagan and Nizhnii Mukei the water salinity changed from oligo-, mesohaline (2.6–17.0 g l^{-1}) to hyperhaline (58.1–81.4 g l^{-1}). In low lake water levels pH and water temperature were highest (10.1–10.3 and 28.5–28.8°C respectively) compared to other studied lakes.

Species diversity of plankton communities

Phytoplankton consisted of 81 algal taxa ranked below the genus level, representing the divisions Cyanobacteria (12 taxon), Bacillariophyta (18), Cryptophyta (1), Dinophyta (1), Chrysophyta (2), Charophyta (5), Chlorophyta (39), and Euglenophyta (3). The largest contributions to phytoplankton diversity were made by green algae, diatoms and cyanobacteria, which together accounted for 86% of the total number of phytoplankton species. The species richness of zooplankton consisted of 51 taxa ranked below the genus level, including 19 species and subspecies of Rotifera, 16 species of Copepoda, 15 species of Cladocera, and 1 species of Anostraca (Table 2).

Fluctuations in plankton community diversity structure

We documented four patterns (I–IV) of plankton community change (in species diversity, abundance and biomass) with changing environmental conditions (increasing TDS, pH and temperature, and decreasing depth) (Fig. 3; Table 3).

Pattern *I* was observed for the lake group A and characterized by a predominance of green algae, charophytes, diatoms and euglenophytes. Mean abundance and mean biomass decreased from 1036.8 to 32–476 × 10^3 cells l^{-1} and from 1996.7 to 2.5–324.6 mg m^{-3}, respectively. The species composition of zooplankton decreased (from 7–20 to 5–11 species). Mean values of abundance and biomass both decreased and increased. Dominant assemblage was consistent through time.

The changes in the plankton community (pattern *II* for the lakes group B) involved a loss of cryptophyte and chrysophyte algae, a dominance of green and blue-green algae, and both increase or decrease of species diversity and abundance of phytoplankton. In zooplankton, species richness decreased (from 8–12 to 5–7 species) and density of zooplankton increased (from 42.6–263.8 × 10^3 ind. m^{-3} and 1.8–6.7 g m^{-3} to 176.3–323.2 × 10^3 ind. m^{-3} and 5.4–11.0 g m^{-3}), the dominant species were the same in different years.

Lake Zun-Torey (group *C*) exhibited pattern *III* community changes: decreases in quantitative phytoplankton indicators (from 96 to 32–38.3 × 10^3 cells l^{-1} and from 65.5 to 7.8 mg m^{-3}), a predominance of green algae and diatoms, a further decrease in the species richness of zooplankton (from 16 to 4 species), and an increase in the total abundance (from 51.3 to 378.8 × 10^3 ind. m^{-3}) and biomass (from 1.6 to 17.5 g m^{-3}) due to increase of some species (such as *Moina brachiata* (Jurine, 1820) and *Metadiaptomus asiaticus* (Uljanin, 1875)) density.

Pattern *IV* (for D-group lakes) was characterized by the species diversity of the plankton communities was reduced to a monospecific community. Either algae or invertebrates were abundant in briny waters. In particular, in Lake Nizhny Mukei in 2011, only *Brachionus plicatilis* Müller, 1786 was recorded in zooplankton; in 2014, there was a benthic alga *Ulnaria ulna* (Nitzsch) Compère and Anostraca. In addition, either algae or invertebrates were abundant in brine waters. In Lake Bulun-Tsagan (2014), there was a massive bloom of cyanobacteria (20,575.2 × 103 cells l^{-1} and 952.4 mg m^{-3}), in Lake Nizhny Mukei (2011), the rotifer abundance abruptly grew (11,733.3 × 103 ind. m^{-3} and 8.21 g m^{-3}).

Discussion

Soda lake ecosystems are characterized by high variability in abiotic and biotic parameters. Changes in the species composition, density and biomass are strongly related to changes in the physical and chemical characteristics of the water, driven in turn by climatic fluctuations (Comín et al., 1992). The salinity of a lake that undergoes strong inter-annual variations is associated not only with the meteorological conditions occurring over the catchment but also with changes in water level and the type of water input as well as the morphometric features of the lake bottom (Reati et al., 1997; Bazarova et al., 2019), lake geology (Simon et al., 2011), and geomorphology (Williams, 2002). In the Transbaikalia area, the regressive water-fill phase of the hydrological cycle is characterized by a decrease in precipitation in the area (Obiazov, 2012), which contributed to a decline in lake levels (to 25–100% of the original level) and, in turn, a rise in the total water salinity and pH. Salinity varied from fresh and oligohaline (0.7–2.6 g l^{-1}) in 1999 to hyperhaline (58.1–81.4 g l^{-1}) in 2014, and pH increased from 8.5–9.0 in 1999 to 9.3–10.3 in 2014. The decrease in the heat capacity of the lakes caused by the increase in salinity resulted in rapid, strong heating of the water in the summer months (water temperature rose from 17.8–23.4°C in 1999 to 24.2–28.8°C in 2014). The cascade of hydrodynamic and hydrochemical processes caused by the climate change inevitably have effects on the biota of endorheic saline lakes. These changes have also been observed in other European lakes (Shadrin, 2012; Dokulil, 2013; Shadrin et al., 2016).

Soda lakes are simple in biodiversity, but due to their highly stochastic environmental dynamics unexpected shifts in species composition do occur (Schagerl, 2016). Species in ephemeral lakes are adapted to large variability of water chemistry (salinity, pH, temperature) and cyclical droughts of varying

Table 2 Species composition and distribution of phyto- and zooplankton in localities sampled

Taxon	Locality		
	HLL	ILL	LLL
PHYTOPLANKTON			
Cyanobacteria			
Anabaenopsis sp.			2
Anagnostidinema amphibium (C. Agardh ex Gomont) Strunecký, Bohunická, J.R. Johansen & J. Komárek			6
Aphanizomenon flosaquae Ralfs ex Bornet & Flahault			2, 8
Cuspidothrix issatschenkoi (Usachev) P. Rajaniemi, Komárek, R. Willame, P. Hrouzek, K. Kastovská, L. Hoffmann & K. Sivonen			6
Dolichospermum flosaquae (Brébisson ex Bornet & Flahault) P. Wacklin, L. Hoffmann & J. Komárek			6
Gloeocapsa sp.	1	1, 3	1, 3
Merismopedia minima G. Beck in G. Beck & Zahlbruckner		3	3
Microcystis aeruginosa (Kützing) Kützing	2, 4		
Oscillatoria sp.	6	1	1
Planktolyngbya contorta (Lemmermann) Anagnostidis & Komárek			1
Pleurocapsa minor Hansgirg			7
Spirulina major Kützing ex Gomont			1
Chrysophyta			
Chrysococcus sp.	6, 9		
Mallomonas sp.	1, 3		
Bacillariophyta			
Planothidium lanceolatum (Brébisson ex Kützing) Lange-Bertalot	4		
Amphora ovalis (Kützing) Kützing	1, 2, 4	1, 2, 4	
Cocconeis placentula Ehrenberg		1, 3, 4, 7, 8	1, 3, 4, 7, 8
Cyclotella sp.	9	3	3
Cymbella sp.	2		
Diatoma vulgaris Bory		1–4, 5, 6, 8	1, 3, 8
Diatoma vulgaris f. *productum* (Grunow) A. Kurz		4–7	7
Epithemia sorex Kützing	4		
Gomphonema olivaceum (Hornemann) Brébisson	2		
Hippodonta capitata (Ehrenberg) Lange-Bertalot, Metzeltin & Witkowski	1, 4		
Lindavia comta (Kützing) Nakov, Gullory, Julius, Theriot & Alverson		3, 4	3
Navicula sp.	3, 4	4, 6, 8	7, 8
N. sp.[1]	1		
Nitzschia acicularis (Kützing) W. Smith			8
Nitzschia sp.	1, 2		
Rhoicosphenia abbreviate (C. Agardh) Lange-Bertalot	1		
Rhopalodia gibba (Ehrenberg) O. Müller	1		
Ulnaria ulna (Nitzsch) Compère	1	1, 3, 4, 8, 9	1, 3, 8, 9
Cryptophyta			
Cryptomonas marssonii Skuja	6, 9	3	

Table 2 continued

Taxon	Locality		
	HLL	ILL	LLL
Dinophyta			
Ceratium hirundinella (O.F. Müller) Dujardin	4		2, 6
Charophyta			
Closterium sp.	4		
Desmidium sp.			4
Elakatothrix genevensis (Reverdin) Hindák	4	2–4	2–4
Staurastrum sp.	4	3, 4	3, 4
Staurastrum sp.^{1}	4		4
Chlorophyta			
Actinastrum hantzschii Lagerheim			3
Actinastrum hantzschii var. *subtile* Woloszynska			3
Ankistrodesmus fusiformis Corda		6	6
Ankyra ancora (G.M. Smith) Fott	1, 4	1, 2, 4, 5, 7	1, 2, 4, 5, 7
Chlamydomonas sp.		1, 3, 6	1–3, 6
Chlorotetraedron incus (Teiling) Komárek & Kovácik			1, 4
Closteriopsis acicularis (Chodat) J.H. Belcher & Swale			1
Coelastrum microporum Nägeli in A. Braun		3	3
Coelastrum pseudomicroporum Korshikov	6		
Coenococcus planctonicus Korshikov			1
Desmodesmus bicaudatus (Dedusenko) P.M. Tsarenko	4		
Desmodesmus intermedius (Chodat) E. Hegewald	1, 4		
Lagerheimia wratislawiensis Schröder			7
Lemmermannia komarekii (Hindák) C. Bock & Krienitz in Bock et al.	1, 4		1, 3
Lemmermannia triangularis (Chodat) C.Bock & Krienitz in C. Bock et al.			4
Mucidosphaerium pulchellum (H.C. Wood) C. Bock, Proschold & Krienitz			3, 4
Monoraphidium arcuatum (Korshikov) Hindák	1, 3	1, 3, 4	1, 3
Monoraphidium contortum (Thuret) Komárková-Legnerová in Fott	4	1, 3, 4	3
Monoraphidium minutum (Nägeli) Komárková-Legnerová	4	3, 4	1, 3
Monoraphidium griffithii (Berkeley) Komárková-Legnerová	4	4	4
Monoraphidium komarkovae Nygaard			4
Oocystis borgei J.W. Snow	1, 2, 4, 9	3, 4, 7–9	1, 3, 4, 7
Oocystis marssonii Lemmermann			4
Oocystis submarina Lagerheim			1, 4
Oocystis rhomboidea Fott			1
Oocystis parva West & G.S. West			1
Oocystis sp.	3, 4	3, 4, 7, 9	
Pandorina morum (O.F. Müller) Bory in J.V. Lamouroux, Bory & Deslongschamps			1
Pediastrum duplex Meyen	1		4
Pseudopediastrum boryanum (Turpin) E. Hegewald in Buchheim et al.	4	4, 8	4, 8
Pseudoschroederia robusta (Korshikov) E. Hegewald & E. Schnepf	1, 2, 4		2
Scenedesmus quadricauda (Turpin) Brébisson in Brébisson & Godey	2, 4	2–4	3, 4
Scenedesmus obtusus Meyen			4
Schroederia setigera (Schröder) Lemmermann	1, 2	1, 2	

Table 2 continued

Taxon	Locality		
	HLL	ILL	LLL
Sphaerocystis planctonica (Korshikov) Bourrelly in Fott			4
Tetraëdron minimum (A. Braun) Hansgirg	3, 4	4, 8	3, 8
Tetraëdron triangulare Korshikov			4
Tetradesmus obliquus (Turpin) M.J. Wynne			4
Tetrastrum staurogeniiforme (Schröder) Lemmermann	4		
Euglenophyta			
Euglena sp.	2, 4	2, 4, 6, 7	4, 6, 7
Phacus limnophilus (Lemmermann) E.W. Linton & A. Karnkowska-Ishikawa in Linton et al.	4		
Phacus sp.	3		
ZOOPLANKTON			
Rotifera			
Asplanchna sieboldi (Leydig, 1854)	1	4	4
Asplanchna silvestris Daday, 1902	4		
Brachionus angularis Gosse, 1851	1	4	
Brachionus budapestipensis Daday, 1885	4		
Brachionus calyciflorus amphyceros Ehrenberg, 1838	4		
Brachionus diversicornis (Daday, 1883)	4		
Brachionus diversicornis homoceros (Wierzejski, 1891)	7		
Brachionus plicatilis Müller, 1786	2	1, 2, 6, 9	1, 6
Euchlanis dilatata Ehrenberg, 1832	6, 7		7
Filinia longiseta (Ehrenberg, 1834)	1–6, 8, 9	1, 4, 5	4, 5
Hexarthra mira (Hudson, 1871)	1–8	2–5, 7, 8	1–5, 7, 8
Kellicottia longispina (Kellicott, 1879)	1, 6		
Keratella cochlearis (Gosse, 1851)	4, 7		
Keratella quadrata (Müller, 1786)	1, 6, 7		
Lecane luna (Müller, 1776)			2
Polyarthra dolichoptera Idelson, 1925			7
Polyarthra sp.	4, 5		
Synchaeta sp.	4		7
Trichocerca sp.	1		
Cladocera			
Alona quadrangularis (O.F. Müller, 1776)	4		
Bosmina longirostris (O.F. Müller, 1785)	4, 6, 7		
Chydorus sphaericus (O.F. Müller, 1776)	6		7
Chydorus sp.	1		
Ceriodaphnia quadrangula (O.F. Müller, 1785)	7		
Coronatella rectangula (G.O. Sars, 1862)	6		
Daphnia sinensis Gu, Xu, Li, Dumont et Han, 2013	1, 2, 4	2, 4	2, 4
Daphnia galeata Sars, 1864		4	
Daphnia magna Straus, 1826	1–3, 5, 6	1–5	2, 3, 5, 8
Diaphanasoma mongolianum Ueno, 1938	1, 2, 4, 5	2, 4, 5	4, 7
Diaphanasoma sp.		3	
Eubosmina longispina Leydig, 1860		2	

Table 2 continued

Taxon	Locality		
	HLL	ILL	LLL
Macrothrix hirsuticornis Norman et Brady, 1867	2		4
Moina brachiata (Jurine, 1820)	1, 2, 5, 8, 9	1–6, 8	1, 3–5, 8
Pleuroxus trigonellus (O.F. Müller, 1776)			7
Copepoda			
Arctodiaptomus bacillifer (Koelbel, 1885)	1, 6	2, 5	2, 5
Arctodiaptomus niethammeri (Mann, 1940)	1–4, 8	2–4, 8	2–4, 8
Hemidiaptomus ignatovi Sars, 1903	3, 5		
Metadiaptomus asiaticus (Uljanin, 1875)	9	1, 6	1
Mixodiaptomus incrassatus (Sars, 1903)	1, 2, 5, 7, 8	7	7
Cyclops strenuus Fischer, 1851	2–4, 6–8	2–4, 7	3–5, 7
Cyclops vicinus Uljanin, 1875	1, 4		
Eucyclops arcanus Alekseev, 1990	3		
Eucyclops serrulatus (Fischer, 1851)	2, 3, 6, 8	2	2
Eucyclops speratus (Lilljeborg, 1901)	4	4	
Macrocyclops albidus (Jurine, 1820)	6		
Megacyclops viridis (Jurine, 1820)	4, 6		
Mesocyclops leuckarti (Claus, 1857)	4, 5	5	
Microcyclops sp.	6		
Paracyclops affinis (Sars, 1863)	4, 6		
Thermocyclops dybowskii (Lande, 1890)		3	8
Anostraca		1	9

1–9 Lake codes, according to Table 1, *HLL* high lake level, *ILL* intermediate lake level, *LLL* low lake level

duration (Hammer & Appleton, 1991; McCulloch et al., 2008; Horváth et al., 2019). To our data, among species composition including 81 taxa of phytoplankton and 51 taxa of zooplankton, the majority of algae are represented by plankton–benthic forms (70%) with a wide geographic distribution (88%). Most of them are indifferent to salinity (89%), and alkaliphilic in relation to pH (62%). According to ecological and geographical analyses, zooplankton includes widespread (53%) and eurybiont species (41%). The most frequently occurring species are *Oocystis borgei* J.W. Snow, *O. submarina* Lagerheim, *Lemmermannia komarekii* (Hindák) C. Bock & Krienitz in Bock et al., *Ankyra ancora* (G.M. Smith) Fott, *Pseudoschroederia robusta* (Korshikov) E. Hegewald & E. Schnepf, *Schroederia setigera* (Schröder) Lemmermann, *Cyclotella* sp., *Cocconeis placentula* Ehrenberg, *Merismopedia minima* G. Beck in G. Beck & Zahlbruckner, *Aphanizomenon flosaquae* Ralfs ex Bornet & Flahault, *Anagnostidinema amphibium* (C. Agardh ex Gomont), *Cryptomonas marssonii* Skuja, *Euglena* sp. from phytoplankton, and *Hexarthra mira* (Hudson, 1871), *Filinia longiseta* (Ehrenberg, 1834), *Daphnia magna* Straus, 1826, *M. brachiata*, *Diaphanasoma mongolianum* Ueno, 1938, *Arctodiaptomus niethammeri* (Mann, 1940), *A. bacillifer* (Koelbel, 1885), and *Cyclops strenuus* Fischer, 1851 from zooplankton. The species composition and the ratio of divisions/groups in the phyto- and zooplankton in the soda lakes of the Uldza-Torey Basin are common in the other soda lakes (Hammer et al., 1983; Williams, 1991; Leland & Berkas, 1998; Zhao & He, 1999; Kazanci et al., 2004; Zhao et al., 2005;

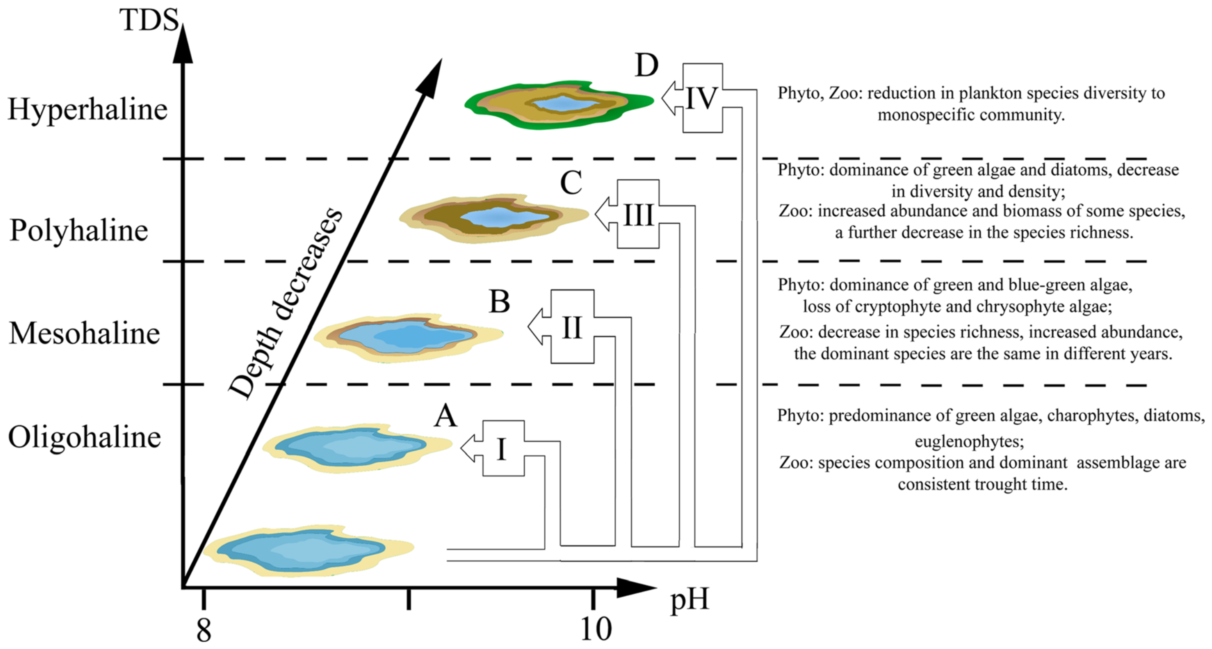

Fig. 3 Patterns of plankton community change (I–IV) in soda lakes (A–D groups) of the Uldz Gol-Torey Basin (Transbaikalia, Russia) during the period of drier climatic conditions

Phyto, Zoo: reduction in plankton species diversity to monospecific community.

Phyto: dominance of green algae and diatoms, decrease in diversity and density;
Zoo: increased abundance and biomass of some species, a further decrease in the species richness.

Phyto: dominance of green and blue-green algae, loss of cryptophyte and chrysophyte algae;
Zoo: decrease in species richness, increased abundance, the dominant species are the same in different years.

Phyto: predominance of green algae, charophytes, diatoms, euglenophytes;
Zoo: species composition and dominant assemblage are consistent trought time.

Litvinenko, 2008; Schagerl & Oduor, 2008; Tóth et al., 2014; Afonina & Tashlykova, 2018).

Soda lakes are among the world's most productive natural ecosystems, but the plankton flora and fauna consists of only a few specialized groups which can attain high biomass, seasonally or throughout the year. Fluctuations in water level also influence phyto- and zooplankton community structure (Comín et al., 1999). In Transbaikalia soda lakes with a change in water level and the consequent effect on salinity, the total abundance and biomass of aquatic species may both increase as noted in Mongolian and Siberian lakes (Litvinenko, 2008; Afonina & Tashlykova, 2018) or decrease as in Canadian and European lakes (Hammer, 1990; García & Niell, 1993). Changes in the water budget greatly affect endorheic systems which at times may be extreme, resulting in drastic plankton abundance and biomass crashes and big changes in community composition (Schagerl et al., 2015). During periods of low water level and increasing salinity abundance of organisms and the amplitude of these changes shows an increase, but not to extreme values (García et al., 1997).

Salinity and pH are the primary factors that determine the nature of biological communities (Williams, 1998; Ivanova & Kazantseva, 2006). Diversity and density shows opposing trends along the salinity gradient (Horváth et al., 2014). The effect of TDS manifests itself to a greater extent during the low water period, when lakes are shallow and well-heated through, which is also characteristic of the other saline lakes (Vignatti et al., 2012; Nédli et al., 2014). The inverse relationship between zooplankton species richness and salinity in saline lakes is well established (Hammer, 1986; Williams et al., 1990), and it is clearly seen for zooplankton in soda lakes of the Uldz Gol-Torey Basin. It should be noted a decrease in the species number of zooplankton in oligohaline lakes (lake group A) also may be due to reduce in the littoral microhabitats during intermediate and low lake water levels. In phytoplankton, on the contrary, there is an increase in the species richness of algae (mainly due to benthic forms from Bacillariophyta and Chlorophyta) in low water period. Due to wind mixing of benthic sediments, species composition of phytoplankton in shallow lakes is influenced by an increased content of suspended particles, which results in dominance of benthic forms over true plankton species among diatoms and increase in specific weight of monad forms of green algae (Afonina & Tashlykova, 2019). The effect of other factors is rather difficult to identify on account of the overwhelming action of TDS and pH

Table 3 Long-term changes in plankton communities in soda lakes of the Uldz Gol-Torey Basin (Transbaikalia, Russia) during the period of drier climatic conditions

Lake group/patterns	Parameters	Lake level		
		High	Intermediate	Low
A				
I Oligohaline → oligohaline				
Phytoplankton	Number of species	28	6–20	7–23
	N_{mean}, $\times 10^3$ cells l^{-1}	1036.8	28.6–422	32–476
	B_{mean}, mg m^{-3}	1996.7	5.2–300	2.5–324.6
	Dominant species*	*T. minimum* *E. genevensis*, *Cyclotella* sp.	*T. minimum* *E. genevensis* *O. borgei* *P. minor* *Cyclotella* sp. *A. flosaquae*	*L. komarekii* *O. borgei* *Euglena* sp. *P. minor* *A. flosaquae*
Zooplankton	Number of species	7–20	6–13	5–11
	N_{mean}, $\times 10^3$ ind. m^{-3}	56.9–227,4	43.8–318	27.4–490.2
	B_{mean}, g m^{-3}	3.1–5.4	2.1–5.9	1.9–10.4
	Dominant species*	*H. mira* *A. bacillifer* *A. niethammeri* *C. strenuus*	*H. mira* *A. bacillifer* *A. niethammeri* *C. strenuus*	*H. mira* *M. brachiata* *A. niethammeri* *C. strenuus*
B				
II Oligohaline → mesoohaline				
Phytoplankton	Number of species	6–11	3–18	1–20
	N_{mean}, $\times 10^3$ cells l^{-1}	23.8–121.5	15.5–700.3	8.7–1694.4
	B_{mean}, mg m^{-3}	31.9–40.8	3.2–150.1	0.07–191.5
	Dominant species*	*M. aeruginosa* *R. gibberula* *O. borgei* *Phacus* sp.	*L. komarekii* *M. aeruginosa* *A. ancora* *O. borgei*	*L. komarekii* *M. minima* *S. quadricauda* *Anabaenopsis* sp. *A. ancora*
Zooplankton	Number of species	8–12	7–11	5–7
	N_{mean}, $\times 10^3$ ind. m^{-3}	42.6–263.8	115.1–431.7	176.3–323.2
	B_{mean}, g m^{-3}	1.8–6.7	4.8–8.8	5.4–11.0
	Dominant species*	*H. mira* *D. mongolianum* *M. brachiata* *A. bacillifer* *A. niethammeri* *C. strenuus*	*H. mira* *F. longiseta* *D. mongolianum* *M. brachiata* *A. bacillifer* *A. niethammeri* *C. strenuus*	*H. mira* *F. longiseta* *A. bacillifer* *A. niethammeri* *C. strenuus*

Table 3 continued

Lake group/patterns	Parameters	Lake level		
		High	Intermediate	Low
C				
III Oligohaline → polyhaline				
Phytoplankton	Number of species	18	11	20
	N_{mean}, × 10^3 cells l^{-1}	96	53.5	38.3
	B_{mean}, mg m^{-3}	65.5	28.4	7.8
	Dominant species*	*S. setigera* *R. gibberula*	*S. setigera* *L. komarekii*	*O. borgei* *L. komarekii* *Gloecapsa* sp. *C. placentula*
Zooplankton	Number of species	16	6	4
	N_{mean}, × 10^3 ind. m^{-3}	51.3	92.2	378.8
	B_{mean}, g m^{-3}	1.6	4.4	17.5
	Dominant species*	*F. longiseta* *D. mongolianum* *A. bacillifer*	*M. brachiata* *M. asiaticus*	*M. brachiata* *M. asiaticus*
D				
IV Oligo-, mesohaline → hyperhaline				
Phytoplankton	number of species	4	3–6	1–7
	N_{mean}, × 10^3 cells L^{-1}	13–30.2	9.9–350.6	1.3–20,575.2
	B_{mean}, mg m^{-3}	7.2–14.9	15.3–280.1	21.4–952.4
	Dominant species*	*Oscillatoria* sp. *O. borgei* *C. marssonii*	*A. amphibium*	*A. flosaquae* *A. amphibium*
Zooplankton	Number of species	3–16	1–3	1
	N_{mean}, × 10^3 ind. m^{-3}	68.1–538.7	924.3–11,733.3	473.1–6136
	B_{mean}, g m^{-3}	3.5–9.5	8.2–55.3	8.9–27.7
	Dominant species*	*M. brachiata* *M. asiaticus*	*B. plicatilis*	*B. plicatilis* Anostraca

N_{mean} mean abundance, B_{mean} mean biomass

* $\geq$ 20% of total abundance

on hydrobiocenoses (Reati et al., 1997; Leland & Berkas, 1998; Litvinenko et al., 2013, Afonina & Tashlykova, 2018, 2019).

The effects of fluctuation on the lake biota are more evident at the level of dominant organisms at every fluctuation stage and their functions than in overall biodiversity (Reati et al., 1997). In studied lakes in the Uldz Gol-Torey Basin as well as in soda pans of the Carpathian Basin (Padisák & Dokulil, 1994; Pálffy et al., 2014; Lengyel et al., 2015, 2016), the Lake District in southwestern Turkey (Kazanci et al., 2004) and some lakes of Kenya, Botswana and Bogoria (Nogrady, 1983; Harper et al., 2003; McCulloch et al., 2008; Krienitz et al., 2013) nano- and picoplankton (*Oocystis*, *Lemmermannia*, *Merismopedia*, *Pleurocapsa*) and rotifers (*Hexarthra*, *Filinia*, *Brachionus*) dominance are characteristic. Besides picoalgae, genera such as *Euglena*, *Phacus*, *Nitzschia*, *Aphanizomenon*, *Anabaenopsis*, *Oscillatoria*, *Anabaena* and crustaceans (*Moina*, *Metadiaptomus*, *Arctodiaptomus*, and anostracans) are also important components of the plankton community, sometimes occurring as massive blooms of algae and huge abundance of invertebrate. Because salinity constrains species composition and resulted in communities of low complexity, where few tolerant species ensure high biomass production in the absence of antagonistic interactions (Horváth et al., 2014).

The discrete separation of the nine studied lakes (Table 3; Fig. 3) into four patterns reflects community responses on the very special environment offered in each of the lakes. Some lakes (first and second patterns) have been reported to be more stable compared to other studied lakes, because of their higher depth (e.g. Lake Bain-Tsagan), steep shores (e.g. Lake Tsagan-Nor) and continuous groundwater input (e.g. Lake Balyktui) preventing there from drying up. The influence of basin morphometry on the plankton diversity and density stability has also been observed in African soda lakes (MacIntyre & Melack, 1982; Harper et al., 2003; Schagerl et al., 2015).

In conclusion, there is not a smooth, but a sharp transformation of planktocenoses during salinization of the lakes (Zagorodnyaya et al., 2008), wherein lake ecosystems can be in several alternative stable states, which differ in the species structure of biota and functioning (Shadrin, 2018). In different ecosystem states, different types of producers and consumers are leader in plankton community. Phyto- and zooplankton community in the shallow soda lakes responds to climatic forcing in different ways depending on some factors not considered by us in this paper. We identified the fluctuation patterns of phyto- and zooplankton during transitions from high to low water levels. Four patterns of change in plankton communities in the saline lakes of southeastern Transbaikalia were identified, corresponding to increasing TDS, pH and temperature, and decreasing depth. Climate aridisation leads both to minor changes in plankton community diversity structure (patterns I and II for A and B group lakes) or leads to a new species composition (reduction in species richness) and community structure of planktonic algae and invertebrates (a marked increase in the density of species with a preference for higher-salinity waters) in the saline lakes due to their variable tolerance of changing environmental factors (patterns III and IV for C and D group lakes).

Acknowledgements This study was supported by the Program for Basic Research of the Siberian Branch of the Russian Academy of Sciences, Project No. IX.137.1.1.

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