Dynamics of plankton biocenoses under water level fluctuations in steppe lakes

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Abstract. Barun-Torey and Zun-Torey lakes are located in the arid steppe zone of the Central (Inner) Asia, Eastern Siberia, Russia. The Torey lakes are characterized by unstable hydrological regime. The water level variation is explained by the periodic filling and drying of the lakes due to cyclical climatic changes in humidity and temperature. We conducted our studies during various water level phases of the climatic cycle: from high water level (1999, 2003) to drying out and the initial filling phase (2007, 2011, 2014, 2016, 2018, and 2020). The aim of this paper is to present long-term research results on changes in the plankton biocenoses of the Torey lakes during a climate cycle, the drying and initial filling of basins. Succession of plankton dominant species is in the direction of: diatoms+green algae and rotifers+crustaceans → green algae and crustaceans → green algae+cyanobacteria and crustaceans → no planktonic algae and invertebrates → cyanobacteria+diatoms+green algae and rotifers+cladocerans+copepods.

1. Introduction
Fluctuations in the common moisture content of the territory are reflected in fluctuations in the level of lakes, hydrological and hydrobiological processes. A lake is a kind of indicator of the demonstration of increasing and decreasing water content phases in the region [1]. The most important natural feature of the Barun-Torey and Zun-Torey lakes (arid steppe zone of the Central (Inner) Asia, Eastern Siberia, Russia) is the water level cyclical fluctuations associated with the variability of total moisture content of the territory, it is caused by secular and intrasecular climate fluctuations [2]. Climatic cycles cause periodic deep fluctuations of the water content of the Uldza and Imalka rivers and water level of steppe lakes, fluctuations in its turn determine the ecological state of the Torey lakes [3–6]. Understanding the processes occurring in wetland ecosystems during climatic cycles in aquatic communities and in ecosystems in general have key importance for providing the long-term preservation of the unique natural heritage of Torey lakes as objects of the Ramsar convention and have protected areas. We aim at aims to present long-term research results on changes in the plankton biocenoses of the Torey lakes during a climate cycle, the drying and initial filling of basins.

2. Materials and Methods
Barun-Torey and Zun-Torey lakes Torey lakes are large in area (550 and 285 km² respectively) and shallow (maximum depth is 4.3 and 6.7 m). They constitute of one hydrological system and are connected by an Utochi channel. The territory belongs to the Onon-Torey district of the dry
Mongolian-Manchurian steppe, which is the northeastern part of the Central Asian physical-geographical region (figure 1). Detailed description of the Torey lakes and environmental context are presented in the paper [6].

![Conceptual presentation of habitat and planktonic association diversity fluctuations in Torey lakes.](image)

**Figure 1.** Conceptual presentation of habitat and planktonic association diversity fluctuations in Torey lakes.

We conducted our studies in various water level phases of the climatic cycle: from high water level (1999, 2003) to drying out and the initial filling phase (2007, 2011, 2014, 2016, 2018, and 2020). Plankton samples were collected during the period when the water warms up to its maximum (July–August). The work was performed in the nearshore and deep waters. At the sampling location with depth more than one meter phytoplankton samples were collected from two to three depths (the surface layer, the Secchi depth, and the benthic layer) with Patalas bathometer; zooplankton was sampled by the total vertical tows with a Juday (a mesh size of 0.064 mm). In shallow waters (at a depth of less than one meter), we collected phytoplankton samples from the water surface; for zooplankton analysis we concentrated of water by filtering it through a plankton net of 94 µm mesh size.

3. Results and Discussion

At the stage of maximum filling, the water in the lakes is almost fresh (TDS=2.1 g L⁻¹) with an oxygen content up to 14 g L⁻¹. The transparency of the water is at least 0.5 m (figure, A, B) [6]. Plankton is represented by 31 algal taxa and 23 zooplankton species. The largest contributions to plankton diversity are made by green algae, diatoms, and rotifers. The majority of species composition is represented by plankton-benthic algal species and planktonic and eurybiontic zooplankton species
with a wide geographic distribution. The total abundance and biomass of algae average 95.9±21.8–944.5±390.7×10^3 cells L^{-1} and 60.5±35.9–1298.7±799.8 mg m^{-3}. Zooplankton abundance average 68.6±13–140.2±34.2×10^3 ind. m^{-3} and biomass 1.8±0.5–4.4±1.4 g m^{-3}. The dominate complex is formed predominantly by the haloxene species, common in fresh and brackish lakes: diatoms (Rhopalodia gibberula, Lindavia conto), green algae (Schroederia setigera, Oocystis borgei, O. submarina, Scenedesmus quadricauda), rotifers (Filinia longiseta), and crustaceans (Diaphanasoma mongolianum, Moina brachtiata, Arctodiaptomus bacillifer, A. niethammeri, Cyclops strenuus).

With the beginning of the dry period, the water level in the Torey lakes begins to decrease, and water salinity (up to 8–9.7 g L^{-1}) and pH (from 9 to 9.6) increase. The water transparency reduces to 0.3 m (figure, C) [6]. Reed thickets (Phragmites australis) and other near-water vegetation disappear, but hydrophytes, especially pondweed (Potamogeton pectinatus) flourish [4]. Water level decrease contributes to the complete freezing of lakes in winter, which leads to the mass death of fishes [4]. In 2004–2006, the shores of the Barun-Torey Lake for tens of kilometers were covered with a thick layer of Carassius auratus gibelio that had died in winter [7, 8]. During periods of intermediate water level, the species number of algae and invertebrates decreases (to 11 and 7 species respectively) due to the loss of freshwater and stenohaline species (chrysophytes: Malomonas sp., diatoms: Amphora ovalis, Hippodonta capitata, Rhoicosphenia abbreviata, Rhopalodia gibberula, green algae: Desmodesmus intermedius, Pediastrum duplex, Pseudoschroederia robusta, rotifers: Asplanchna sieboldi, Keratella quadrata, Kellicottia longispina, Filinia longiseta, crustaceans: D. mongolianum, Daphnia magna, Mixodiaptomus incrassatus, A. bacillifer, A. niethammeri, Cyclops vicinus). Salt-loving species appear (Diatoma vulgare, Monoraphidium contortum, Brachionus plicatilis, Metadiaptomus asiaticus). Phytoplankton abundance and biomass decrease (to 53.5±12.46 ×10^3 cells L^{-1} and 28.43±6.58 mg m^{-3}), and zooplankton density increases (to 92.2±15.3×10^3 ind. m^{-3} and 3.5±0.8 g m^{-3}). Green algae (S. setigera, Lemmermannia komareki) and crustaceans (M. brachiata, M. asiaticus) prevail. The trophic structure of plankton communities is simplified and reconstruct, leading to an increase in the impact of benthic algae and colonial and/or aggregated forms of algae (Spirulina, Coccones, Gymphonema, Navicula, Pinimularia), a loss of predatory invertebrates (Asplanchna, Cyclops), and a decrease in the effects of fine filter feeders. The increase in water turbidity in shallow lakes due to the wind mixing of bottom sediments affects the species composition of phytoplankton in terms of a change in the dominant taxa of diatoms (replacing the plankton species by benthic forms) and/or an increase of the share in monad green algae [9].

With a further decrease in the lake level, salinity (above 20 g L^{-1}) and pH (to 9.9) continues to increase, water temperature rose (from 20.4–23.4 °C to 21.4–26.4 °C). The significant lake areas at shallow depths promote wind mixing of the water mass and its saturation with oxygen (dissolved oxygen increases from 5.6 to 8.6 g L^{-1}). Water transparency decreases to 0.2 m (figure, D) [6]. Wide mud bars, sandy and pebble beaches are forming around the lakes. Underwater pond meadows gradually disappear, but filamentous algae begin to multiply in mass [3, 4]. In plankton biocenoses it is observed increases in the species number of algae due to increase benthic form (20 taxa) and in the total abundance (81.58±9.14×10^3 cells L^{-1}) and decreases in the total biomass (11.92±9.66 mg m^{-3}). In phytoplankton species composition green algae dominate. Green algae (Oocystis borgei, L. komareki) and cyanobacteria (Gloeocupsa sp., Coelomoros pusillum, Planktoylony nga contorta) are formed the basis of abundance. In zooplankton, the species richness further decreases (to 4 species), and the total abundance (530.5±227.2×10^3 ind. m^{-3}) and biomass (24.5±14.3 g m^{-3}) increase due to increase of some species (M. brachiata and M. asiaticus). Dominate species from cyanobacteria, green algae and crustaceans tend to persist and even increased their proportion at higher saline-alkaline levels; owing to these dominant species have certain tolerance to salinity and alkalinity to certain extent. An increasing density of some crustacean species is associated with a decrease in the available food supply and changes of water volume also [10]. For example, from 1999 to 2016, the number of crustaceans in the Zun-Torey Lake increased by more than a hundred times.

As the water recedes, the bare areas of the bottom overgrow first with coastal, then with steppe vegetation. At the same time, distinct belts of different vegetation are often formed along the coast.
The width of each such belt corresponds to the width of the lake bottom that is exposed during one year [7]. Finally, the lake completely dries up. In the final stages, residual water usually disappears very quickly. Vast salt marshes are formed, on windy days clouds of dust and salt crystals stand above them. Gradually, these areas also overgrow [8]. In this period aquatic biota is absent. Algae are in the cyst stage and invertebrate in the resting eggs, which could “sleep” for many years without water (figure, E).

In the beginning of the wet period, at the northernmost point of Barun-Torey Lake, there are small water bodies (pools and/or puddles) on its bottom. These filling pools are freshwater (TDS=0.5–1.0 g L⁻¹), alkaline (pH = 8.2–9.0), well warmed up (26–30°C), and originating from differential thawing along cracks in the permafrost and arising from groundwater and precipitation (figure, F). Semiaquatic (P. australis) and aquatic plants (Charales, Lemna, Potamogeton) and filamentous algae grow in the pools. Meadow plants are well developed around the pools [6]. In the filling water bodies, the diversity and density of hydrobionts increase multiple. Algae flora contains 73 taxa (species number varies from 1 to 49) and zooplankton include 39 species (14–26). The most taxa are habitat-littoral, phytophilic, ubiquist, freshwater, and cosmopolitan species. Taxa of Bacillariophyta, Chlorophyta, Rotifera, and Cladocera prevail. Abundance and biomass varies widely and average 22.6–444.1 ×10³ cells L⁻¹ and 19.1–434.3 mg m⁻³ for phytoplankton, and 140.2±34.2–1267.7±646.4 ×10³ ind. m⁻³ and biomass 4.4±1.4–117.9±62 g m⁻³ for zooplankton. The dominant complex differs and consists of Coelomorron pusillum, Oscillatoria sp., Gloecapsa sp., P. contorta from cyanobacteria, Navicula sp. from diatoms, S. setigera, Tetraedron incus from greens, Brachionus angularis, Polyarthra vulgaris from rotifers, Daphnia magna, Ceriodaphnia pulchella, C. quadrangula, Chyodus sphaericus, Eucyclops serrulatus, Thermocyclops dybowskii.

During perennial wet periods, the Barun-Torey Lake is first filled with the waters of the Uldza River, then water flows through the Utochi channel to the Zun-Torey Lake. Fish, brought in by the rivers, appear in the lakes. P. australis is reborn and begins to occupy the coastline quickly [7]. If in the early 1980’s (the end of the dry period) stunted low growth has been preserved only at the mouths of the Uldza and Imalka rivers [8], but by 1999 the reed has almost completely encircled the Torey lakes with a dense wall [4]. The water fills the bottoms and sides of the lake basins overgrown with steppe vegetation, creating the most excellent conditions for various ecological groups of aquatic organisms and an increase in their abundance. When the lakes are filled, salinity increases (to 3.5–7.9 g L⁻¹) due to the dissolution of salts. At this time (according 1986), the dominant position in the planktooceneses passes to green algae (species of the genus Oocystis, S. setigera, Crucigenia tetrapedia) and crustaceans (M. brachiata, M. incrassatus, Daphnia) [11].

Thus, the dynamics of hydrobiocenoses on large steppe lakes in conditions of varying water content may be described. The continuous change in the water level ensures the periodic occurrence of suitable habitat conditions for organisms with completely different ecological requirements in one lake. Therefore, the total diversity of aquatic organisms on pulsating steppe lakes is quite high. At the same time, it is important to note that, depending on size, basin sides’ steepness, presence or absence of flowing rivers or underground springs and other circumstances, each lake has its own individual rate of change of it’s water level. Thus, the shallow-water Barun-Torey Lake dries up faster than the deeper-water Zun-Torey Lake. In this regard, there are some differences in the degree of development of hydrobiocenoses in the lakes.

4. Conclusion
The continuous changes of the water level ensure the periodic occurrence in one reservoir of suitable habitat conditions for aquatic organisms with completely different ecological requirements. At the different stages of the climatic cycle, in the Torey lakes the succession of plankton dominant species is in the direction of: diatoms+green algae and rotifers+crustaceans → green algae and crustaceans → green algae+cyanobacteria and crustaceans → no hydrobionts → cyanobacteria+diatoms+green algae and rotifers+cladocerans+copepods.
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