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Article

Dynamics of spatial distribution of macrophyte vegetation in Lake Kenon, a cooling reservoir of a thermal power plant (Eastern Transbaikalia)

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Abstract. Long-term monitoring of the dynamics of spatial distribution of macrophyte vegetation in Lake Kenon (a cooling reservoir of the Chita Thermal Power Plant-1) shows evidence of variations (25–90%) in its overgrowth area for a ~50-year observation period (1965–2015). In all years of investigations, the main areas of charophyte algae made up 62–89% of the total overgrowth. In the 1970s, *Nitella flexilis* was the leader (33%) in terms of the occupied area. However, in the last years of observations, the role of *Chara tomentosa* was growing (up to 39%). Among vascular plants, the area of *Potamogeton crispus* thickets reduced (from 32% to less than 1%) in contrast to *Stuckenia pectinata* (8.6%). *Myriophyllum sibiricum* was a permanent component of a thermal zone since 1965. At high water levels (above 654 m a.s.l.), the area of overgrowth decreased, and at low levels (under 653.5 m a.s.l.) it increased. With low water levels, the lake ecosystem had a macrophyte type and at high ones a phytoplankton type of functioning. A combination of anthropogenic impacts, i.e. water level regulation, thermal pollution and herbivorous fish introduction were the driving factors responsible for spatial restructuring of the lake vegetation.

Keywords: anthropogenic impact, charophytes, aquatic plants, overgrowth, water level

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Научная статья

Динамика пространственного распределения макрофитной растительности оз. Кенон – водоема-охладителя теплоэлектростанции (Восточное Забайкалье)

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Аннотация. Материалы многолетних наблюдений за динамикой пространственного распределения макрофитной растительности оз. Кенон (водоема-охладителя Читинской ТЭЦ-1) показывают, что за ~50-летний период наблюдений (с 1965 г. по 2015 г.) площадь зарастания озера варьировала в пределах 25–90%. Основные площади во все годы исследований занимали харовые водоросли, на долю которых приходилось от 62 до 89% от площади зарослей. При этом в 1970-е гг. по площади лидировала *Nitella flexilis* (33%), в последние годы наблюдений возросла роль *Chara tomentosa* (до 39%). Среди сосудистых растений сократились заросли *Potamogeton crispus* (с 32% до менее 1%), при этом увеличилась площадь, занимаемая *Stuckenia pectinata* (8.6%). Постоянным компонентом термальной зоны с 1965 г. является *Myriophyllum sibiricum*. Показано, что при высоких уровнях воды, превышающих 654 м н.у.м., площадь зарастания снижается, а при низких, менее 653.5 м н.у.м. – возрастает. При низких уровнях воды экосистема озера функционирует по макрофитному типу, а при высоких – по фитопланктонному. Основные причины изменений в пространственной структуре растительности озера – совокупность антропогенных воздействий: регулирования уровня режима, теплового загрязнения и вселения растительноядных рыб.

Ключевые слова: антропогенное влияние, харовые водоросли, водные растения, зарастаемость, уровень воды

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Introduction

Global climate change and anthropogenic impacts significantly affect water bodies transforming their evolutionarily formed hydrodynamic, hydrochemical and hydrobiological parameters. The study of such transformations is among the currently central problems.

Lake Kenon, located within the city of Chita, is one of the important water bodies of Transbaikalia exposed to the influence of both natural and anthropogenic factors. The lake has been used as a cooling reservoir of the Chita Thermal Power Plant-1 since 1965. Over the CTPP-1 operation period, the habitat conditions of aquatic organisms in Lake Kenon have undergone significant changes as compared to the 1960-1970s (Sizikov and Shishkin, 1972) and 1980–1990s (Itgilova et al., 1998). The type of alimantation altered to the anthropogenic-riverine one, water exchange increased almost twice, and a thermal regime also changed. At the place of heated water discharge (northwestern section of the lake), the non-freezing (in winter) thermal zone was formed. Increased mineralization brought to the change in a water type (Itgilova et al., 1998; Usmanova, 2012). An alien plant species *Elodea canadensis* Mich appeared in the lake (Bazarova et al., 2012). The combination of variable abiotic and biotic parameters transformed the structural and functional organization of the ecosystem of Lake Kenon, including its macrophyte vegetation (Bazarova et al., 2019). Macrophytes in shallow lakes play an important environment-forming role and, according to the hypothesis of alternative stable state, they are the major link regulating the development of aquatic ecosystems (Scheffer, 2001, 2004).

The aim of this work is to analyze the long-term dynamics of spatial distribution of macrophyte vegetation in Lake Kenon based on the original and literature data.

Materials and methods

Lake characteristics and its history

Lake Kenon is situated within the city of Chita. Its catchment area is 227 km². The area of the lake is 16.2 km², its length – 5.7 km, the average width and depth – 2.8 km and 4.4 m, respectively. By the 1970s, the lake was completely overgrown. In 1970–1973, herbivorous fish larvae were introduced to combat vegetation. The first batch of 20000 grass carp larvae *Ctenopharyngodon idella* (Valenciennes, 1844) and 10000 bighead carp larvae *Aristichthys nobilis* (Richardson, 1845) was delivered on June 26, 1970 from the Chikutsky fish hatchery of the Krasnodar Territory. The second batch of 50000 *C. idella* and 50000 *A. nobilis* larvae arrived on June 15, 1971. A total of 10000 *C. idella* larvae were imported in June 1972 and 100000 *A. nobilis* larvae in June 1973 (Gorlachev and Gorlacheva, 2017).

From the beginning of the Chita HPP-1 operation, waters of Lake Kenon are used to cool turbines, remove ash from the lake, and heat the facilities of the regional center. Water pumping from the Ingoda River (since 1975) provided a 1m rise in the lake level thus meeting the CHPP-1 technological needs (Itgilova et al., 1998; Vladimirova, 1979; Zolotareva, 1998).

First scientific data on the biota of Lake Kenon was obtained during the Amur Ichthyological Expedition in the summer of 1946 (Borutsky, 1952). In 1964–1967, the lake was surveyed by the fisheries expedition of the Chita Pedagogical Institute. The effect of heated water discharges on the lake regime was studied in 1969–1972 (Sizikov and Shishkin, 1972). From 1985 to 1994, the Laboratory of Aquatic Ecosystems of the Chita Institute of Hydrometeorology and Microbiology of the Siberian Branch of the Russian

Academy of Sciences monitored the ecosystem dynamics via studying individual groups of organisms (Itigilova et al., 1998) and lake vegetation. In 2010–2012, the comprehensive research of the lake were conducted within the grant of the Russian Foundation for Basic Research (11-04-98064_p_sibir_a) and later under State Assignments (No. 79.1.1; No. 0386-2014-0001).

Materials and working methods

Hydrobotanical works (2010–2015) at Lake Kenon were carried out according to the generally accepted method (Katanskaya, 1981). The study of lake vegetation was based on the route survey. Distribution of plants in the littoral was specified with the use of a HDS 5 Gen 2 echo sounder (Lowrance, USA) (accuracy of depth determination ± 1 cm and coordinates – ± 2 m). Four ecological profiles were laid in the central part of the lake, which connected opposite coasts. The echo sounder screen displayed overgrown and non-overgrown sites of the bottom, tiers, and transition boundaries of submerged plant communities. To verify images, hydrobotanical works in the model sections were implemented (Bazarova and Kuklin, 2023). We identified the species composition, defined water depth, measured water transparency by a Secchi disk, recorded soil types and coordinates. A total of 109 stations were examined. We employed a grappling hook with a metal mesh to lift plants from the reservoir. The coordinates of hydrobotanical and echo sounder surveys were added to the Google Earth Pro GIS program to determine the areas inhabited by communities. Taxonomy of vascular plants was given in accordance with the database “Catalogue of life”¹, and charophyte algae – from “Algaebase”².

Materials on the inter-annual dynamics of the average annual water level of Lake Kenon, the amount of precipitation, and water volumes pumped from the Ingoda River were provided by PJSC “TGC-14”. Water level was given according to the Baltic elevation system.

Results and discussion

Abiotic parameters

We compared the long-term data on the average annual water level in Lake Kenon and precipitation amount before (1938–1974) and after (1975–2018) its regulation by water pumping from the Ingoda River. Inter-annual dynamics of the average annual level and precipitation before 1975 were generally similar (Fig. 1). The unregulated period was characterized by the 4–7 year cycles of water level, depending on precipitation amounts (Obyazov, 2010).

In 1975–2003, the lake level was maintained above 654.5 m a.s.l. due to large volumes of pumped water (12520 ± 4940.108 thous. m³). Since the 2000s, less volumes of pumped water (8384 ± 2294.491 thous. m³) and small precipitation amounts were responsible for a drop in water level below 653.5 m a.s.l. and further reduction in the water surface area of the lake by 9.2% (archival data of PJSC “TGC-14”).

Water level fluctuations were accompanied by variations in depth, water transparency, concentrations of biogenic elements and main macrocomponents (Table 1). With smaller depths, water transparency became better and plant growth deeper. In 2015, the increase in depth, transparency and littoral area of the lake was recorded. The concentration of nitrites (NO₂⁻) was lower in 2010–2015 than in 1986. Nitrates (NO₃⁻) and ammonium (NH₄⁻) reached their maximum in 2011 and 2012, respectively. The concentration of total phosphorus (P_{total}) varied from 0.01 to 0.09 mg/l (Butenko and Tsybekmitova, 2017). The hydrochemical composition of waters qualitatively changed. For instance, mineralization showed a 1.5 increase (from 420 to 641 mg/l); the hydrocarbonate-sodium-magnesium water type was replaced by the sulfate-hydrocarbonate-chloride sodium-calcium-magnesium one (Table 1) (Usmanova, 2012).

¹ Catalogue of life. Web page. URL: <https://www.catalogueoflife.org/> (accessed: 29.11.2024).

² Algaebase. Web page. URL: <https://www.algaebase.org/> (accessed: 29.11.2024).

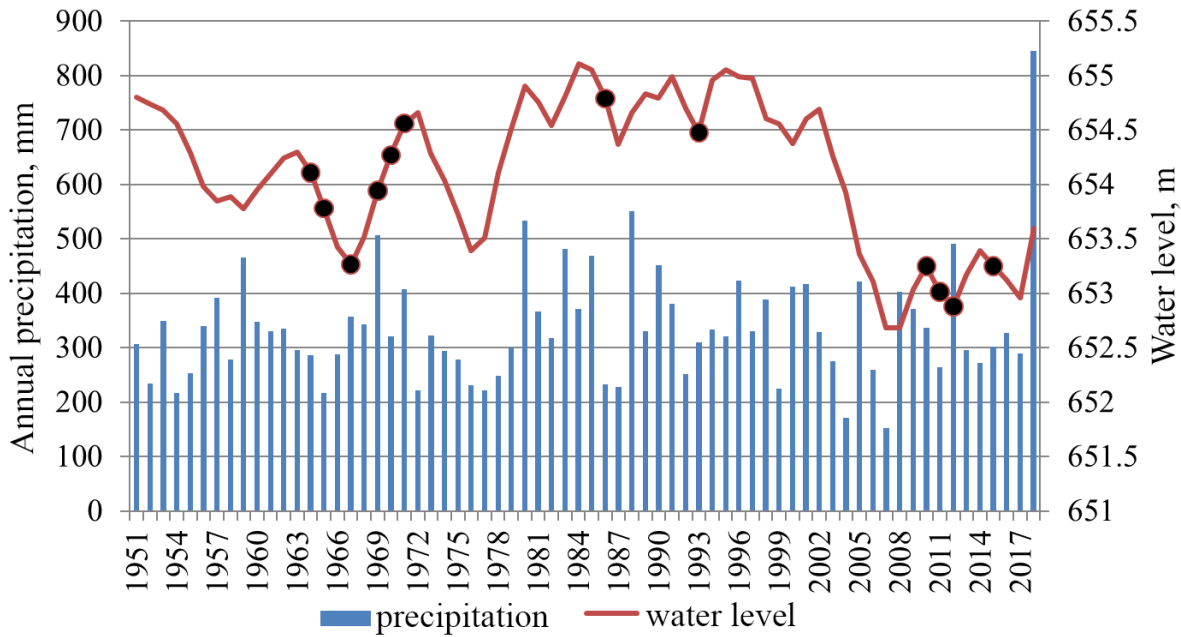


Fig. 1. Long-term dynamics of water level in Lake Kenon and precipitation amounts; dots indicate the years of vegetation observations.

Table 1. Abiotic parameters of Lake Kenon in different years. H is maximum depth; H_{veget} – maximum depth of plant growth; Tr – water transparency; TDS – water mineralization; “–” – no data; the hydrochemical composition of waters is given according to: Butenko and Tsybekmitova, 2017; Ivanov and Trofimova, 1982; Itgilova et al., 1998; Sizikov and Shishkin, 1972; Usmanova, 2012; Zamana and Usmanova, 2017.

Year	Physico-chemical parameters and cationic composition of waters								
	H, m	Tr, m	H_{veget} , m	TDS, mg/l	pH	Ca^{2+} , mg/l	Mg^{2+} , mg/l	Na^+ , mg/l	K^+ , mg/l
1971	7.0	2.0	5.5	585.40	-	24.00	43.80	62.10	10.10
1986	7.0	3.1	2.0	641.00	8.25	68.00	38.30	61.90	-
2010	5.1	3.0	4	520.10	8.40	55.40	36.80	52.10	2.38
2011	4.7	3.7	4	563.68	8.98	43.20	41.98	69.18	2.23
2012	4.7	3.8	4	575.20	8.27	54.25	40.55	53.10	1.94
2015	5.2	4.5	5	510.20	8.61	58.50	30.10	52.30	1.60
Year	Anionic and biogenic composition								
	Cl^- , mg/l	F^- , mg/l	SO_4^{2-} , mg/l	CO_3^{2-} , mg/l	HCO_3^- , mg/l	NO_3^- , mg/l	NO_2^- , mg/l	NH_4^+ , mg/l	P_{total} , mg/l
1971	11.40	-	73.90	-	360.00	0.07	0.01	0.18	-
1986	20.30	-	250.30	6.80	202.20	0.03	0.03	0.13	0.10
2010	58.70	2.63	201.90	0.53	126.30	0.01	0.00	0.08	0.09
2011	66.19	2.17	189.64	1.38	147.72	1.48	0.01	0.11	0.04
2012	67.80	190	225.00	0.00	131.50	0.00	0.00	0.43	0.01
2015	76.70	1.62	185.10	3.60	100.70	0.00	0.00	0.00	0.01

Vegetation dynamics

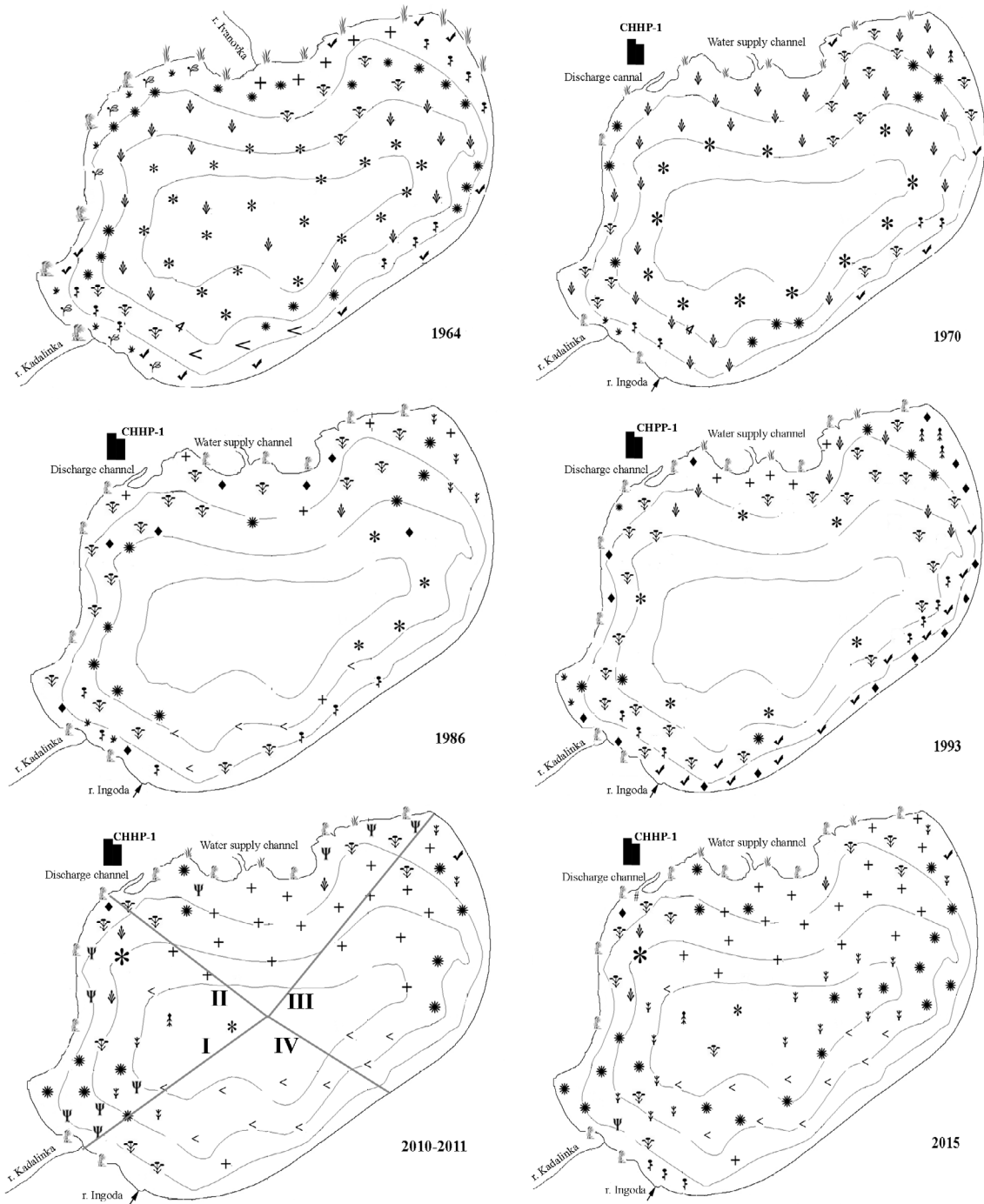
The results of long-term studies of Lake Kenon vegetation suggest that spatial distribution of plant communities changed quantitatively, whereas their composition qualitatively (Fig. 2). The data in Table 2 demonstrate alterations in the total overgrowth area of the lake and the ratio of the areas with the dominant aquatic species.

Before the CTPP-1 construction (1964), at a water level of 654.42 m a.s.l. (Fig. 1), the lake was completely overgrown (Fig. 2). In its central part, thickets of *Nitella flexilis* prevailed. Along the southern shore, at a depth of 3.0–5.0 m, *Chara aspera* and *C. globularis* with *Potamogeton crispus* developed. *C. tomentosa*, *Myriophyllum sibiricum* and *Stuckenia vaginata* (Magnin) Holub were noted at depths 3.0–4.5 m in shallow waters along the northern shore. *Chara arcuatofoia* Vilh. were present almost throughout the lake perimeter. *Potamogeton perfoliatus*, found along the southwestern and northeastern shores, did not occupy large areas. Discontinuous thickets of *Phragmites australis* (helophytes) covered western and northwestern coasts, while *Schoenoplectus tabernaemontani* – the northern shore. In the shallow zone, at depths of 0.3–0.7 m, a belt of rooted submerged plants (neustophytes) with leaves floating on the water surface was formed. It was represented by the communities of *Nymphoides peltata* and *Persicaria amphibia* with a projective cover of 80–95% (according to the diaries of B.I. Dulepova: Zolotareva, 1998).

At water levels of 653.58 ± 0.34 m a.s.l. (Fig. 1), heated water discharged to the lake from CTPP-1 had a positive effect on pondweeds development in 1965–1967. The area of pondweed thickets *Potamogeton crispus*, *P. pusillis*, *Stuckenia vaginata*, *S. filiformis* (Pers.) Börner increased. In the northwestern and central sectors of the lake, *P. crispus* occupied 3.0–3.5 m bottom depths (more than 300 ha, or 32% of the total overgrowth area). *S. vaginata* was growing in the northwestern and southwestern sectors at depths of 0.6–3.0 m, whereas *S. filiformis* along western, southern and northern coasts at depths of 0.3–1.0 m. In the southwestern sector, *S. filiformis* bloomed and formed seeds, while in the south only vegetative forms of 0.3 m high. Dense thickets of *P. pusillis* were growing in the southwestern section at depths of 0.4–0.6 m. *Myriophyllum sibiricum* phytocenoses inhabited small sites in the northern, northwestern and southwestern parts of the lake. In charophyte thickets, unevenly distributed *Ranunculus circinatus* was encountered as a codominant at depths of 0.4–0.8 m. Neustophytes formed small clusters only in the southwestern and northwestern sites. Vegetation in the southern and southeastern parts remained unchanged and was represented by charophyte algae. Among helophytes, *Schoenoplectus tabernaemontani* dominated (Vladimirova, 1968).

The following years (1969–1971) were characterized by water level rise to 654.5 ± 0.19 m a.s.l. (Fig. 1) due to large amounts of precipitation for previous years. The lake overgrowth reduced to 68%. In the central section of the lake, vegetation disappeared, however, the *Nitella flexilis* communities were preserved at depths of ~4 m covering the area of more than 350 hectares. Rather large bottom sites (above 350 ha) were occupied by *Potamogeton crispus* (Table 2, Fig. 2). The area of *Myriophyllum sibiricum* thickets increased; the communities of *Chara tomentosa*, *Potamogeton perfoliatus*, *Chara arcuatofoia*, *Stuckenia vaginata* developed. Among helophytes, the *Schoenoplectus tabernaemontani* communities dominated (Vladimirova, 1972).

The study periods (1986, 1993) were characterized by high water levels, i.e. 654.66 and 654.48 m a.s.l., respectively (Fig. 1). With the increase in water content and formed population of herbivorous fish, a gradual decline (up to 44% and 25% of the total water area) in macrophyte-induced overgrowth was observed. A significant reduction occurred in *Potamogeton crispus*, which in previous years was found as an accompanying algae in the charophyte communities in the eastern sector of the lake. It is explained by the fact that pondweeds as “soft vegetation” are preferred food of herbivorous fish (Gaevskaia, 1966). In the northwestern thermal zone of the lake, the communities of *Myriophyllum sibiricum* and *Ranunculus circinatus* developed en masse. In the central part, the bottom sites devoid of vegetation appeared, whereas the communities of *Nitella flexilis* disappeared. Among helophytes, *Phragmites australis* took the leading position. Along the northern and northwestern coasts, phytocenoses of *Persicaria amphibia*, *Nymphoides peltata*, and *Sagittaria natans* still existed. Moreover, they were encountered in the clearances of *P. australis* thickets. In the northeastern sector, small groups of *Stuckenia pectinata* emerged. In these years, high water levels were maintained due to large volumes of pumped water (archival data of PJSC “TGC-14”). After 2000, drastically reduced



*1 *2 ✓3 +4 <5 6 7 8 9 10 11 *12 13 14 ◆15 Ψ16

Fig. 2. Schematic maps of vegetation distribution within Lake Kenon in different years. 1 – *Nitella flexilis*, 2 – *Chara tomentosa*, 3 – *Ch. arcuatoifolia*, 4 – *Ch. aspera*, 5 – *Ch. globularis*, 6 – *Myriophyllum sibiricum*, 7 – *Potamogeton perfoliatus*, 8 – *Stuckenia pectinata*, 9 – *St. vaginata*, 10 – *Potamogeton crispus*, 11 – *Persicaria amphibia*, 12 – *Nymphoides peltata*, 13 – *Schoenoplectus tabernaemontani*, 14 – *Phragmites australis*, 15 – *Ranunculus circinatus*, 16 – *Elodea canadensis*. I, II, III and IV – environmental profiles.

Table 2. Lake Kenon overgrowth and areas of main macrophyte species in different years; “–” – no data.

Indicator	Year													
	1971	1986	2010	2011	2012	2015	S, ha	Share, %	S, ha	Share, %	S, ha	Share, %		
S of the lake, ha	1620	1620	1491	1491	1486	1474								
S of thickets, ha	1103.24	714	480.1	747.67	951.03	1358.19								
Overgrowth level, %	68.10	44.07	32.19	50.15	64.00	92.00								
Species	S, ha	Share, %	S, ha	Share, %	S, ha	Share, %	S, ha	Share, %	S, ha	Share, %	S, ha	Share, %	S, ha	Share, %
<i>Chara tomentosa</i> L.	156.6	14.19	20	2.8	100	20.83	130	17.32	370.00	38.91	496	36.52		
<i>Chara aspera</i> var. <i>subinermis</i> Kützing	160.7	14.57	170	23.81	150	31.24	150	20.05	170.00	17.88	317.5	23.78		
<i>Chara globularis</i> Thuill.	0.02	0.001	260	32.41	100	20.83	130	17.30	210.00	22.08	312	22.97		
<i>Nitella flexilis</i> (L.) C. Agardh	363.3	32.94	70	9.8	50	10.41	50	6.62	50.00	5.26	50	3.68		
<i>Myriophyllum sibiricum</i> Kom.	60.7	5.5	80	11.20	27	5.62	80	10.41	30.00	3.15	4.65	0.34		
<i>Potamogeton crispus</i> L.	351.5	31.87	–	–	0.5	–	80	10.41	0.02	–	0.02	–		
<i>Stuckenia pectinata</i> (L.) Börner	–	–	–	–	0.5	–	17.26	2.30	65.00	6.83	117	8.61		
<i>Potamogeton perfoliatus</i> L.	0.1	–	–	–	2	–	20.39	2.39	21.00	2.21	46	3.38		
<i>Elodea canadensis</i> Michx.	0	–	0	–	35	7.29	75	10.00	20.00	2.1	0.001	–		
<i>Ranunculus circinatus</i> Sibth.	0.003	–	80	11.20	0.01	–	0.01	–	–	–	–	–		
<i>Persicaria amphibia</i> (L.) Gray	0.005	–	0	–	0	–	0	–	0	–	0	–		
<i>Nymphoides peltata</i> (S.G. Gmel.) Kuntze	0.07	–	10	–	0	–	0	–	0	–	0	–		
<i>Phragmites australis</i> (Cav.) Trin. ex Steud.	–	–	24	3.36	15	2.01	15	3.10	15	1.57	15	1.10		
<i>Schoenoplectus tabernaemontani</i> (C.C. Gmel.) Palla	10.24	0.93	–	–	–	–	–	–	–	–	–	–		
Others	–	–	–	–	0.1	1.77	0.01	–	0.01	0.01	0.02	0.72		

volumes of pumped water together with low precipitation amounts caused a drop in water level and 2–3 fold increase in the lake overgrowth. By 2010, the latter made up 32% at 653.25 m a.s.l. In the next two years, water levels were falling and overgrowth increased to 64%. With a level rise up to 653.25 m in 2015, the lake overgrowth reached 92%.

Hydrobotanical surveys (2010) demonstrate a significant role of *Elodea canadensis* among submerged plants. It developed along the western shore at depths of 0.7–1.5 m forming dense monodominant thickets (Fig. 2). In 2011, *E. canadensis* was also noted in the southwest and north of the lake. In July 2012, it was solely an accompanying species in other communities of the southwestern sector, located opposite the Kadalinka River mouth (Bazarova, 2012).

In 2010, as in previous years of the study, Charophyta spread throughout the southern and eastern sectors of the lake. Found at depths of 2.5–4.0 m, it accounted for 85% of the total overgrowth area. *Nitella flexilis* was encountered sporadically in the central part of the lake. Quite dense thickets of *N. flexilis* were growing at a depth of 4.0 m in the northwestern sites. In 2011, the proportion of Charophyta in the total overgrowth area declined to 62%, being comparable with the data for 1971 and 1986. In 2012, the increased overgrowth was accompanied by an expansion of Charophyta thickets, the share of which reached 84%. The main contribution was made by the *Chara tomentosa* communities (39% of the overgrowth area), which occupied the southwestern sector of the lake from the water's edge to a 2.5 m depth, covering the bottom with an almost continuous layer. In the north, *Chara globularis* was detected in shallow waters from the water's edge to a depth of 3 m. In 2015, *C. tomentosa* thickets conquered the eastern and southern parts of the lake.

Along with Charophyta, the area of the *Stuckenia pectinata* communities also increased. If in 2012 *S. pectinata* was recorded only in the southwestern section at depths of 0.8–1.5 m (Table 2, Fig. 2) with a share of 2.3% of the overgrowth area, then in 2015 its contribution made up 8.61%. This species occupied the central part of the lake and formed dense thickets at depths of 3.5–4.5 m.

The most complex mosaic spatial structure of vegetation was preserved in the northwestern thermal zone of the lake. Here, the *Myriophyllum sibiricum* communities dominated in 2010–2012. Small groups of *Potamogeton crispus* were found in the littoral depressions, while the *Ranunculus circinatum* communities along the western shore. In 2015, the *Potamogeton octandrus* Poir communities were detected in Lake Kenon for the first time. This species is a representative of the Far Eastern flora, not previously reported for the study lake (Bazarova and Bobrov, 2018). In general, the years 2010–2015 were characterized by mass development of macrophytes, which had colonized a significant area of the lake bottom. The largest areas were occupied by charophytes; the *S. pectinata* communities turned out to be dominants for the first time for the whole period of long-term observations. Among helophytes, *Phragmites australis* still played the leading role. Neustophytes were represented by single *Saggitaria natans* found in the southwestern sector of the lake.

The presented materials on the dynamics of the spatial macrophyte structure of Lake Kenon are evidenced of 25–90% variations in overgrowth areas over a ~50-year period. At high water levels (654.5 m a.s.l. and higher), the area of lake overgrowth declines, while at low indicators (653.5 m a.s.l. and lower) it grows. The established pattern is basically consistent with the data for other reservoirs (Mikhailova, 2022; Papchenkov, 2013; Poddubny et al., 2022; etc.). Prolonged staying in the natural state is the specificity of the studied reservoir. Before 1975, water level fluctuations were recorded as 4–7 year cycles of low and high levels depending only on precipitation amounts. Water level varied smoothly. There were no abrupt changes in the overgrowth area. After regulation, the 23-year period of high water and the 11-year period of low water level took place (archival data of PJSC TGC-14). As a result, water level increased sharply. Its long-lasting maintenance above 654.5 m a.s.l. caused a reduction in macrophyte overgrowth to 25% of the lake area. In addition, the introduction of herbivorous fish also reduced the vegetation area. Smaller volumes of pumped water (since 2003) and small amounts of precipitation contributed to expansion of the overgrowth area.

Water level fluctuations affected the lake functioning. A high water level maintained for long resulted in the ecosystem restructuring to a microphyte type. The area of macrophyte overgrowth decreased. We observed “outbreaks” of phytoplankton; its number increased from 70 million cells/l in 1969–1972 (Shishkin et al., 1972) to 186 million cells/l in 1986 (Itgilova et al., 1998). Additional sources of nutrients, i.e. wastes produced by herbivorous fish (Karpiński, 1994) and waters coming from the Ingoda River

owing to a water intake installed below the Kadala sewage discharge site may be a factor. During this period, about 62 tons of nitrogen and 6 tons of phosphorus entered the lake (Itgilova et al., 1998). As a consequence, primary production of phytoplankton increased by 2.6 times: from 1505 to 3930 kcal/m² (Itgilova et al., 1998; Ogly, 2008) thereby providing larger proportion of blue-green algae. In 1988, *Anabaena spiroides* Klebahn and abundant saprophytic bacteria caused “hyperbloom” of the lake water. Filamentous algae developed en masse practically throughout the lake, entangling aquatic plants and forming free-floating dome-like clusters (Zolotareva, 1998). In 1997–1999, the filamentous algae *Cladophora fracta* (Vahl.) Kütz. and *Spirogira* sp. formed powerful floating mats, which created the extended in-depth 4.0 m wide fields in the northwestern thermal zone of the lake (Kuklin, 2017).

Despite the transformations occurred, charophytes remained the basis of Lake Kenon vegetation in all study periods. Before 1986, it was the species *Nitella flexilis*. However, recent studies are evidenced of the dominance of *Chara tomentosa* and *Chara aspera*. Though charophytes are indicators of high water quality (Krause, 1981; van Donk and van de Bund, 2002), they can grow under different environmental conditions (Kolada, 2014; Søndergaard et al., 2013), suggesting different requirements to habitats. It is known that *Nitella flexilis* is the most demanding to purity and transparency of water; it prefers low-mineralized waters (Kolada, 2021; Urbaniak and Gabka, 2014). *Chara tomentosa* and *Chara aspera* are less demanding; they inhabit waters with higher mineralization, up to brackish ones (Kipriyanova and Romanov, 2013). *Chara globularis* is universal in terms of adaptability to widely variable environmental conditions (Auderset Joe and Rey-Boissezon, 2015; Baastrup-Spohr et al., 2015). Hence, the presence of charophytes does not necessarily guarantee good ecological state of water bodies (Poikane et al., 2018).

Vascular plants to date have undergone significant changes. For example, *Potamogeton crispus* has given up its leading role in overgrowth. This species is characterized by an autumn-spring development cycle with a spring peak (Shaltout et al., 2016). Discharges of heated waters since the CTPP-1 operation increased water temperature, especially during the freeze-up period that contributed to the occurrence of longer growing season and mass development of *P. crispus*. In 1970–1973, herbivorous fish species *Ctenopharyngodon idella* and *Aristichthys nobilis* were introduced to combat the lake overgrowth. In the first year, the introduced *C. idella* was twice as many as *A. nobilis*. In the second year, the number of both species was equal, and in the third, the ratio of *C. idella* and *A. nobilis* larvae made up 1:10. The total number of *A. nobilis* larvae was twice as many as *C. idella* over three years. Thus, the introduction of *C. idella* reduced overgrowth areas in the first year already (Gorlachev and Gorlacheva, 2017). *Myriophyllum sibiricum* and *Ranunculus circinatus* served as the indicator species of meso- and eutrophic conditions (Makrofyty..., 1994). Currently, *P. crispus* is occasionally found in the northwestern thermal zone of the lake.

Stuckenia pectinata increased its contribution since 2012. By 2015, the species forming dense communities had occupied 8.6% of the overgrowth area. The appearance of *S. pectinata* among the dominants and its growing role may indicate the beginning of a new stage in the development of the lake ecosystem (Brodersen et al., 2001; Hilt et al., 2013). This phenomenon coincided with changes (observed since 2010) in the hydrochemical water composition (Table 1). By 2015, the most significant transformations had occurred in concentrations of Cl⁻ ions (more than sevenfold increase), HCO₃⁻ (threefold decrease), and Ca²⁺ (twofold increase). Higher concentrations of calcium ions were, apparently, associated with mass development of *Chara tomentosa* and *C. aspera* able to deposit calcite in their thallomes.

A significant drop in volumes of pumped water along with scarce precipitation brought to lower contents of biogenic elements and better water transparency (Table 1) that, in turn, contributed to the expansion of charophyte algae thickets and the restructuring of the dominants' composition. Among charophytes, less demanding to the environmental conditions *Chara tomentosa*, *C. aspera* and *C. globularis* prevailed in 2010–2015. Charophyte expansion during this period stabilized the ecosystem state and provided the recovery of other aquatic macrophytes (Hutorowicz and Dzedzic, 2008; Noordhuis et al., 2002; Steinman et al., 2002; van den Berg, 1994, 1998). With increasing macrophyte proportions in Lake Kenon (2010–2015), phytoplankton abundance (0.1–0.001 million cells/l) and a proportion of blue-green algae reduced. A trend of inter-annual decline in quantitative characteristics of phytoplankton was recorded. In 2010, its abundance was 200–400 thous. cells/l, and

biomass around 1.5–2.1 g/m³, but in 2011–2015 these indicators were under 100 thous. cells/l and 50 mg/m³, respectively. (Afonina et al., 2017). Primary production also dropped from 122 to 178 gC/m³ in the 1970s and 411–738 gC/m³ in 1985–1987 up to 90–225 gC/m³ in 2010–2011. Destruction prevailed over production amounting to about 410 gC/m³ (Bazarova et al., 2019). Clusters of *Cladophora fracta*, *Spirogira* sp. disappeared, except for some small quantities preserved in macrophyte thickets. *Chaetophora lobuta* Schrank, *Mougeotia* sp., *Tribonema* sp., *Ulothrix zonata* (Weber et Mohr) Kützing – indicator species of clean waters emerged (Kuklin, 2017).

By species and cenotic composition of macrophytes, formed in 2010–2015 vegetation cover significantly differs from the original one (before 1965). It is currently balanced and supports the ecosystem of Lake Kenon at the macrophyte stage distinguished by high water transparency and generally favorable aquatic indicators. The recommended water level of 653.5 m is optimal for the lake ecosystem. Increase in precipitation amounts along with pumping water volumes is expected to rise a water level and reduce the overgrowth area. It is worth noting that the lake is unlikely to return to its original state.

Conclusion

By the example of Lake Kenon, it is shown that human activity (level regulation, thermal effects, water pumping, and herbivorous fish introduction) is responsible for irreversible changes in macrophyte vegetation and the reservoir ecosystem as a whole. Perhaps the appearance of the Far Eastern flora *Potamogeton octandrus* in the lake was induced by increasing average annual temperatures recorded in Transbaikalia since the beginning of the 21st century.

Vegetation cover of the lake is currently balanced. In terms of the species and cenotic composition of macrophytes, it significantly differs from the original one, but is able to maintain rather favorable state of the ecosystem.

Water level regulation is demonstrated to influence the ecosystem state of a shallow lake and alter its functioning from a macrophyte to a microphyte (phytoplankton) type. An inverse relationship between the reservoir overgrowth and its water level has been traced. Maintenance of water level at 653.5 m is expected to provide the macrophyte type of the ecosystem functioning that is most preferable for the lake state.

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