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Long-term changes in phytoplankton and macrophyte communities in an eutrophic shallow reservoir and prospects for its restoration

by

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Abstract

Long-term changes in hydrochemistry and community structure of phytoplankton and macrophytes were analyzed in the Sestroretskiy Razliv reservoir (northwestern Russia). The average content of total phosphorus (TP) in May–October increased from 73 µg P l^{-1} in 1980 to 163 µg P l^{-1} in 2000. A significant increase in average chlorophyll *a* content from 16.6 µg l^{-1} in 1980 to 84.7 µg l^{-1} in 2000 and a shift in phytoplankton composition to the dominance of cyanobacteria over diatoms indicated a change in the trophic status of the reservoir from meso-eutrophic to hypertrophic. In 2016 and 2018, average TP was 96 and 101 µg P l^{-1}, respectively. The average content of chlorophyll *a* was 43.6 µg l^{-1} in 2016 and 66.6 µg l^{-1} in warmer 2018, indicating persistent eutrophic conditions. Diatoms dominated both in 2016 and 2018, especially in 2016 characterized by unfavorable weather conditions. Cyanobacteria were more abundant in 2018 with higher summer temperatures. The decline of the total area covered by aquatic vegetation from 157 ha in 1980 to 76 ha in 2016 likely resulted from an increase in phytoplankton biomass and water turbidity. Based on the results of our observations, in addition to further reduction in nutrient loading, biomanipulation by introducing predatory fish as a restoration measure was proposed to improve the ecological status of the reservoir.

Key words: phytoplankton, cyanobacteria, macrophytes, shallow lakes, alternative stable states, eutrophication

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Introduction

Cultural eutrophication is one of the most pervasive courses of water quality impairment in shallow lakes around the world. Extensive nutrient loading may lead to sudden losses of macrophytes in shallow lakes, producing a shift from a clear-water state with abundant macrophytes to a turbid-water state dominated by phytoplankton (Scheffer et al. 1993). This shift can occur over a wide range of total phosphorus concentration, indicating that factors other than nutrients are also responsible for maintaining shallow lake ecosystems in one of the two alternative stable states (Wetzel 2001). In macrophyte-dominated lakes, macrophytes support the clear-water state by suppressing phytoplankton through competition for nutrients and production of allelochemicals and by providing refuge for zooplankton from fish predation (Scheffer et al. 1993). In phytoplankton-rich lakes, zooplanktivorous fish often dominate and stabilize the turbid-water state while preying on the zooplankton, thus reducing the zooplankton pressure on phytoplankton (Gulati 1990).

To restore eutrophic shallow lakes, many restoration projects have been undertaken to induce a shift from the turbid phytoplankton-dominated state to the clear state dominated by macrophytes (Søndergaard et al. 2007; Gulati et al. 2008). Stoking with predatory (piscivorous) fish is one of the biomanipulation methods aimed at reducing the number of zooplanktivorous fish and improving the zooplankton abundance and phytoplankton grazing (Benndorf 1995; Skov & Nilsson 2007). However, restoration attempts are not always successful and largely depend on internal and external factors affecting the resilience of the turbid algae-dominated state of lake ecosystems (e.g. Søndergaard et al. 2007). It is yet unclear how changes in weather conditions may interact with trophic cascade mechanisms and whether this may contribute to switching between alternative stable states in shallow lakes (Scheffer & Van Nes 2007). There is some evidence that even a small increase in temperature may create a shift in turbid shallow lakes to a clear-water phase (Scheffer et al. 2001). Contrary to this view, Jeppesen et al. (2003) presented data showing that probability of a shift to the clear-water state in nutrient-rich lakes decreases with higher temperature. Studies of long-term effects of changing anthropogenic pressure on phytoplankton and macrophyte dynamics can provide useful information on the degree of environmental impairment and extrinsic and intrinsic factors stabilizing the alternative states of lake ecosystems.

The composition of phytoplankton communities changes in relation to increasing lake fertility (Hutchinson 1967). However, the response of phytoplankton to eutrophication is highly dependent on other ecological factors such as light availability. In clear-water lakes, the increased dominance of cyanobacteria along the eutrophication gradient is a well-known phenomenon (e.g. Trifonova 1990). Compared to clear-water lakes, a significantly weaker response of cyanobacteria to increased nutrient loading was observed in brown-water humic lakes (Ptacnik et al. 2008). Light availability is also an important predictor of abundance and distribution of aquatic plants. Low light conditions caused by organically colored waters and sediment resuspension promote the dominance of helophytes (i.e. emergent plants) and floating-leaved plants over submerged ones (Toivonen & Huttunen 1995; Nurminen 2003). Furthermore, due to the low availability of light in humic and turbid lakes, the distribution of submerged aquatic plants is restricted to shallow, littoral habitats (Stewart & Freedman 1989; Nurminen 2003). Although much information is available on the interactions of macrophytes and phytoplankton in clear-water lakes, relatively little is known on how limited availability of light may affect the interaction between macrophytes and phytoplankton along the eutrophication gradient.

Sestroretskiy Razliv is the largest water body located in the suburban area of Saint-Petersburg (northwestern Russia). It was established in 1723 to provide for the energy needs of Sestroretsk's tool manufacturing plant by building a dam on the Sestra River at 5 km from its discharge into the Gulf of Finland. At present, it is an important element of the urban landscape and is under constant anthropogenic pressure. The surrounding areas feature industrial and agricultural enterprises, landfills and highways, and intensive construction has been conducted on the shores of the reservoir since the 1990s. Furthermore, the reservoir is traditionally used as a recreational site. Regular monitoring of water quality parameters of the Sestroretskiy Razliv reservoir was initiated in 1966, when a new water supply plant was constructed and the reservoir has started to be used for drinking water supply. Since 2000, the reservoir is no longer used for water supply purposes. The first comprehensive ecological research on the reservoir was conducted by the Institute of Limnology RAS (St.-Petersburg) in 1980 (Stravinskaya et al. 1984b). The second research on the reservoir, which was carried out by the Institute of Limnology RAS in 2002, showed a drastic deterioration of water quality (Belyakov et al. 2002). Although the sewage treatment plants situated at the tributary of the reservoir, the Chernaya River, were reconstructed in 2012, high values of total phosphorus recorded in the reservoir water indicated that external and internal nutrient loads remained high during the 2010s (Kondratyev et al. 2016). The modern assessment of environmental conditions and biological structure of the Sestroretskiy Razliv reservoir was carried out in 2016 and 2018 by the Institute of Limnology RAS in collaboration with the State Research Institute on Lake and River Fisheries (St.-Petersburg).

The main objective of the present paper was to examine long-term changes in the structure of phytoplankton and macrophyte communities in the Sestroretskiy Razliv reservoir over the period from 1980 to 2018. We investigated whether long-term changes in phytoplankton biomass were related to phosphorus concentration. We were particularly interested how macrophyte and phytoplankton communities interacted under conditions of low light availability caused by relatively high concentration of humic compounds and intensive sediment resuspension, which are characteristic features of the Sestroretskiy Razliv reservoir. In addition, based on the analysis of current environmental conditions and biological structure, restoration measures were proposed for the reservoir.

Materials and methods

Characteristics of the water body

The Sestroretskiy Razliv reservoir (60°05′00″N, 30°00′00″E) is located in the southwestern part of the Karelian Isthmus in the Lakhta lowland. Sestroretskiy Razliv is the largest water body located within the suburban area of Saint-Petersburg. It has a surface area of 10.3 km^2 and water volume of 0.018 km^3. Sestroretskiy Razliv is a polymictic shallow reservoir with a mean depth of 2.2 m and a maximum depth of 4.6 m (Stravinskaya et al. 1984a). The shoreline length of the reservoir is about 20 km. The western shore is shallower than the eastern one (Stravinskaya et al. 1984a). The western shore encroaches on the urban area of Sestroretsk. The eastern shore is covered with deciduous and coniferous forests. The territories adjacent to the northern shore are extensive waterlogged lands and bogs. Contemporary bottom deposits in Sestroretskiy Razliv are represented by sand and silt (Sergeeva et al. 1984). Silt is the most common sediment in the reservoir, forming about two thirds of the topmost part of the bottom deposits. It occurs in the form of large patches in the southern, northern and western parts of the reservoir. Sand occurs in the central part and along the western and eastern shores, in the most hydrodynamically active areas of the reservoir. The content of organic matter in the upper layer of sediments varies from 2 to 71%, reaching the highest values (48–71%) in the fine silt fraction.

The two main tributaries to the reservoir are the Sestra River, with a length of 75 km and a catchment area of 399 km^2, and the Chernaya River, with a length 35 km and a catchment area of 126 km^2. The total catchment area of Sestroretskiy Razliv is 586 km^2 (Stravinskaya et al. 1984a).

The first investigation into the reservoir carried out in 1980 showed that the Chernaya River is the main source of contamination of the reservoir (Stravinskaja et al. 1984b). The inflow of the Sestra and Chernaya rivers contributes 96.1% to the water balance of Sestroretskiy Razliv (Veselova & Judin 1984). The reservoir has a rather high water exchange rate (10 yr^{-1}). As the outflow from the reservoir is only moderately regulated, the annual water level fluctuations tend to follow its natural course, but with a lower level in spring and a smaller amplitude. The annual water level fluctuations vary between 0.6 and 0.8 m with the highest water level recorded during wet years.

Sample collection and processing

Previous studies of the quality characteristics of water and phytoplankton in the reservoir were conducted in 1980 (Stravinskaja et al. 1984b; Trifonova & Senatskaya 1984) and 2002 (Belyakov et al. 2002). In 1980 and 2002, water quality parameters and phytoplankton were sampled in May, July, August and October at two locations in the central zone and one location near the inflow of the Chernaya River (Fig. 1). In 2016 and 2018, samples for the analysis of water quality and phytoplankton were collected in May, August and October at approximately the same locations as in 1980 and 2002.

Water samples for chemical analysis were collected using a Limnos sampler (2.0 l) and transported to the laboratory in plastic bottles. In the field, pH measurements were made using a Hanna portable pH meter. Water transparency was determined with a Secchi disc. The following chemical analyses were performed in the laboratory using standard methods (Semenov 1977). Inorganic phosphorus (IP) was determined as a sum of dissolved and particulate orthophosphates by a modified molybdenum method of Murthy and Riley (1962), using ascorbic acid as a reducer; total phosphorus (TP) – using the same procedure after oxidation with $K_2S_2O_8$ in acidic medium. Total nitrogen (TN) was determined by oxidation with $K_2S_2O_8$ in alkaline medium with

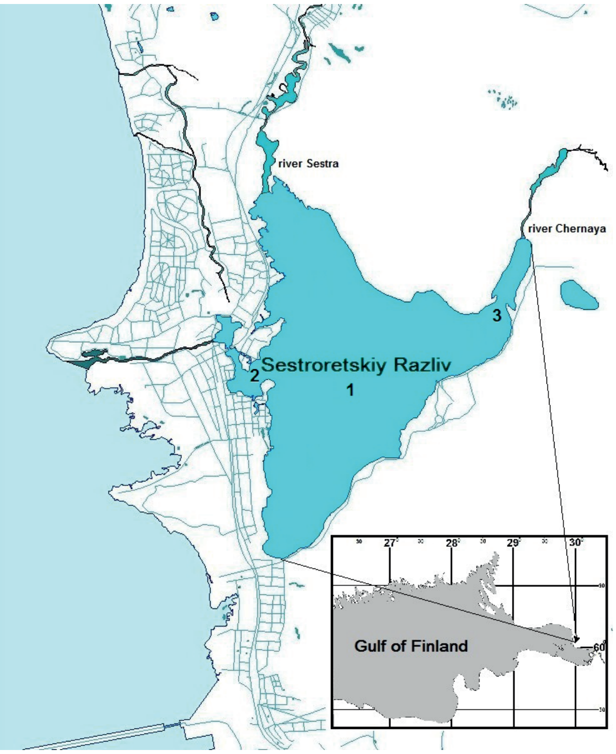

Figure 1

Map of the Sestroretskiy Razliv reservoir; 1, 2 and 3 are the sampling locations

subsequent reduction of NO_3^- on a Cd-reducer and determination of NO_2^- with a Griss reagent. Concentration of hydrocarbonates was determined using potentiometric titration with HCl, sulfates – using the turbidimetry method, chlorides – by mercurymetric titration, calcium and magnesium – using the titrimetric method with EDTA. The sum of sodium and potassium was calculated based on the balance of main cations and anions. The content of main ions (S ions) was assessed as a sum of HCO_3^-, SO_4^{2-}, Cl^-, Ca^{2+}, Mg^{2+} and $Na^+ + K^+$. Water color was determined using visual titration with a standard Pt-Co-reagent.

Phytoplankton samples for quantitative analysis were collected using a Ruttner water sampler (0.5 l) and preserved with Lugol's iodine solution in the field. In the laboratory, phytoplankton samples were concentrated by sedimentation up to 50 ml and counted in a Nazhott chamber of 0.05 ml (Guseva 1959) under light microscope AxioLab A1 (CarlZeiss). The biomass (mg l^{-1}) was estimated using geometric approximation as algal biovolume (Trifonova 1990). Phytoplankton identification was based on the modern taxonomic literature (Komárek & Anagnostidis 1999; 2005; Krammer & Lange-Bertalot 1991). Chlorophyll *a* concentration (μg l^{-1}) was measured in mixed acetone extract (UNESCO 1966) and calculated using equations of Jeffrey and Humphrey (1975).

The previous study of the aquatic vegetation in the reservoir was carried out in 1980 (Katanskaya 1984). In 2016 and 2018, aquatic macrophyte surveys were carried out in the full growing season (July and August). As in the previous study of 1980 (Katanskaya 1984), the taxonomic composition and distribution of macrophyte beds were examined from a boat, applying the phytolittoral mapping method (Katanskaya 1988; Kolada et al. 2012). In the field, the spatial distribution of macrophyte beds of dominant species was plotted on a bathymetric plan. The boundaries of macrophyte beds were determined by GPS coordinates from field studies during the seasonal maximum of vegetation. In order to assess temporal changes in the composition of macrophyte communities, the relative abundance of dominant species and functional vegetation groups (emergent, floating-leaved and submerged) were estimated. The area of macrophyte beds of dominant species was digitized with coordinate data using ArcView GIS 3.2, and then the percentage of these species in the total plant coverage was determined. Plants of each dominant species were collected by the quadrat sampling method to measure the aboveground biomass of macrophytes (Katanskaya 1988). Samples were collected from five randomly distributed plots (0.25 m^2 for helophytes and 1 m^2 for floating-leaved and submerged plants) by wading in a shallow area of the reservoir. A PVC quadrat frame was placed on the sediment surface and all plant shoots within the frame were removed manually by cutting the stems at the sediment. The collected plants were placed in labelled bags, transferred to the laboratory, air-dried and then weighted. Calculations of the total aboveground macrophyte biomass was based on the calculated areas of macrophyte beds and average biomass values of each dominant species.

In September 2015 and May 2016, the State Research Institute on Lake and River Fisheries carried out a survey on the fish community, the results of which were published earlier elsewhere (Pedchenko et al. 2017).

Statistical analysis

Prior to statistical analysis, all water quality parameters (except pH), phytoplankton biomass and chlorophyll *a* were $\log_{10}$ transformed and relative biomass of diatoms and cyanobacteria were arcsine square root transformed to approximate a normal distribution (e.g. Sokal & Rohlf 1995). As there were no statistical differences in the limnological variables between the sampling locations (except S ions), the measured values from all three locations were combined. The significance of differences between four sampling years (1980, 2002, 2016 and 2018) in hydrochemical parameters and phytoplankton biomass, chlorophyll *a* and the relative biomass of diatoms and cyanobacteria was tested using one-way analysis of variance (ANOVA) with the Tukey–Kramer test of pairwise comparisons. Levene's and Shapiro–Wilk's tests were used to examine the assumptions of normality of distribution and homogeneity of variance for one-way ANOVA, respectively. Both tests did not show any serious violations in these assumptions after data transformation.

The relationships between the phytoplankton biomass and chlorophyll *a* and TP as well as between the relative biomass of cyanobacteria and the TN/TP ratio were assessed using Pearson's linear correlation.

Results

Water quality

The measured values of water quality parameters during the years when samples were collected from the Sestroretskiy Razliv reservoir are shown in Figure 2. The data from the whole study period shows that the reservoir has poorly mineralized water, with the content of main ions (S ions) fluctuating between 53 and 76 mg l^{-1} (Fig. 2a). Despite an increasing trend in average values of S ions from 57 mg l^{-1} in 1980 to 71 mg l^{-1} in 2018 in the May–October period (Table 1), no statistically significant differences were found between the sampling years ($F = 1.82$, $p = 0.171$). Consistently higher values of S ions (up to 98 mg l^{-1}) were recorded close to the Chernaya River delta ($F = 9.91$, $p < 0.001$), indicating that this tributary is the main source of contaminated water in the reservoir.

Bicarbonate alkalinity (HCO_3^-) varied during the study period from 12 to 35 mg l^{-1} (Fig. 2b). Although there were significant differences in average values of bicarbonate alkalinity between 2002 and 2018 ($F = 7.22$, $p < 0.01$; Table 1), they show no consistent trend during the study period.

The Secchi depth varied from 0.21 to 0.82 m (Fig. 2c). Significantly higher values of the Secchi depth were recorded in 1980 compared to 2002, 2016 and 2018 ($F = 8.14$, $p < 0.001$; Table 1).

The color of water ranged from 79 to 228 Pt-Co (Fig. 2d). The maximum values of water color were recorded in late summer (August) in 1980, 2002 and 2018. In 2016, the maximum value of water color was recorded in autumn (October). Comparing different sampling years, a statistically significant increase in the average water color was observed in 2016 ($F = 7.70$, $p < 0.001$; Table 1), indicating high loading of allochthonous organic matter from watersheds caused by heavy precipitation.

The pH values of water in the reservoir ranged from 6.1 to 9.5 (Fig. 2e). Higher pH values were recorded in the summer months, when the maximum values of phytoplankton biomass were observed. Significantly higher values of mean pH, fluctuating within a slightly alkaline range (7.8–8.6), were observed in 1980 and 2002 ($F = 14.48$, $p < 0.0001$; Table 1). In 2016 and 2018, mean pH fluctuated close to slightly acidic and neutral levels (6.8–7.0; Table 1), probably due to increased input of allochthonous organic matter caused by intense rainfall.

Considering May–October average values of the TP concentration, statistically significant differences were observed in 2002 compared to other sampling years ($F = 7.85$, $p < 0.001$; Table 1). The highest TP values, which reached 203–208 μg P l^{-1}, were recorded in summer of 2002 (Fig. 2f). The average TP value increased significantly (more than twice) from 73 μg P l^{-1} in 1980 to 163 μg P l^{-1} in 2002 (Table 1). Compared to 2002, the average TP value decreased significantly to 96 and 106 μg P l^{-1} in 2016 and 2018, respectively. There were no significant differences in the average TP values between 1980, 2016 and 2018 ($p = 0.236–0.992$), although TP values recorded in summer and autumn of 2016 and 2018 were higher than those in 1980 (Fig. 2f).

The May–October average values of the IP concentration were statistically significantly different between the sampling years ($F = 25.83$, $p < 0.0001$; Table 1). The minimum IP values, ranging from 4 to 17 μg P l^{-1}, were recorded in 1980 (Fig. 2g). There was a significant increase in mean IP from 10 μg P l^{-1} in 1980 to 31 μg P l^{-1} in 2002 (Table 1). The average IP values showed no significant differences between 2002, 2016 and 2018 ($p = 0.205–0.844$), although there was a weak upward trend, fluctuating between 31 and 51 μg P l^{-1} (Table 1).

During the whole study period, TN values fluctuated between 0.47 and 1.29 mg N l^{-1}, with maximum TN values recorded in 1980 (Fig. 2h). In 2002, 2016 and 2018, the average TN values were significantly lower compared to those in 1980 ($F = 19.10$, $p < 0.0001$; Table 1), probably as a result of reduced agricultural activity in the catchment. The molar ratio of nitrogen to phosphorus (TN/TP) ranged from 37 in 1980 to 10–15 in 2002, 2016 and 2018, suggesting a shift from phosphorus limitation in the phytoplankton growth in 1980 to nitrogen limitation in the 2000s and the 2010s.

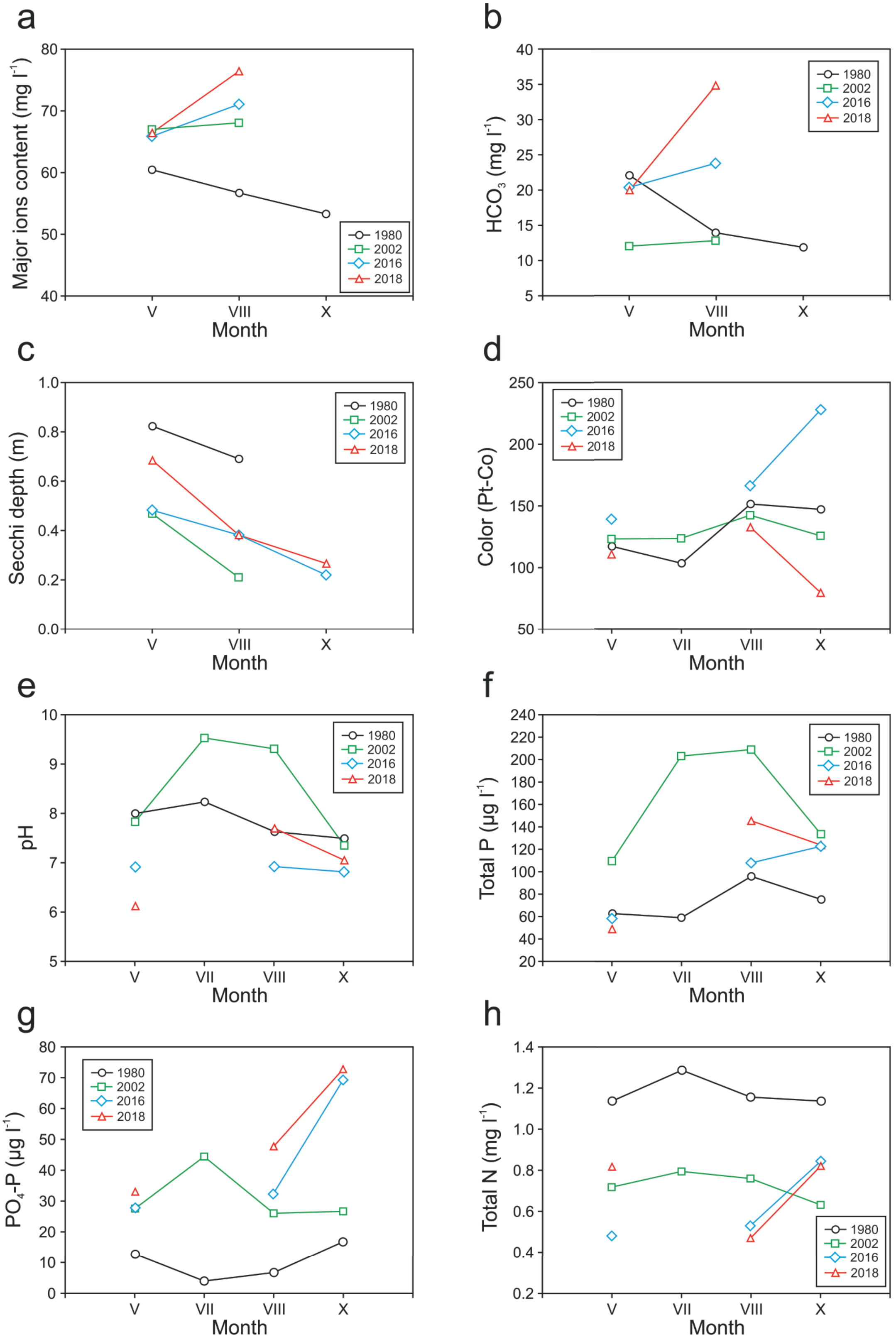

Figure 2

Changes in the water quality parameters during the sampling years (1980, 2002, 2016 and 2018) in the Sestroretskiy Razliv reservoir

Table 1

Means (and ranges) of the water quality parameters in the Sestroretskiy Razliv reservoir in different years (1980, 2002, 2016 and 2018). The comparison of the means among different years was carried out using ANOVA with the Tukey–Kramer test. The Tukey–Kramer test results are indicated by superscripts.

Parameter	1980	2002	2016	2018	*F*	*p*
Σ ions (mg l^{-1})	57 (37–84)	67 (64–71)	68 (47–98)	71 (55–85)	1.82	0.171
HCO_3^- (mg l^{-1})	16^{ab} (10–23)	12^{a} (9–15)	22^{ab} (14–32)	27^{b} (18–41)	7.22	< 0.01
Secchi depth (m)	0.76^{a} (1.00–0.60)	0.34^{b} (0.50–0.18)	0.36^{b} (0.50–0.15)	0.44^{b} (0.75–0.15)	8.14	< 0.001
Color (Pt-Co)	130^{a} (103–152)	128^{a} (112–144)	178^{b} (121–240)	107^{a} (77–140)	10.05	< 0.0001
pH	7.8^{a} (7.2–8.8)	8.6^{a} (7.3–9.8)	6.8^{b} (6.7–7.0)	7.0^{b} (6.1–8.1)	14.48	< 0.0001
TP (µg l^{-1})	73^{a} (32–158)	163^{b} (94–233)	96^{a} (49–150)	106^{a} (42–170)	7.85	< 0.001
PO_4-P (µg l^{-1})	10^{a} (4–38)	31^{b} (19–52)	43^{b} (13–77)	51^{b} (26–80)	25.83	< 0.0001
TN (mg l^{-1})	1.18^{a} (0.82–1.54)	0.72^{b} (0.45–0.86)	0.62^{b} (0.44–0.92)	0.70^{b} (0.39–0.95)	19.10	< 0.0001

Letters a and b indicate years with significantly different means.

Phytoplankton

In 1980, from May to October, phytoplankton biomass in the reservoir varied from 2.8 to 10.6 mg l^{-1}, with the maximum value recorded during the spring peak in May (Fig. 3a). The May–October average value of phytoplankton biomass was 6.8 mg l^{-1} (Table 2). The chlorophyll *a* concentration fluctuated from 9.9 to 23.7 µg l^{-1} (Fig. 3b). Diatoms *Aulacoseira islandica* (O.Müll.) Sim., A. *ambigua* (Grün.) Sim., *Asterionella formosa* Hass., *Fragilaria berolinensis* (Lemm.) Lange-Bert. were the dominant taxa, accounting on average for 55.8% of the total phytoplankton biomass (Table 2, Fig. 3c). The development of cyanobacteria was weak, representing on average 14.5% of the total phytoplankton biomass (Table 2, Fig. 3d).

In 2002, phytoplankton biomass varied from 19.3 to 86.9 mg l^{-1}, with the May–October average of 61 mg l^{-1} (Fig. 3a, Table 2). The chlorophyll *a* concentration changed from 22.2 to 153.7 µg l^{-1} (Fig. 3b). In spring (May), the diatom *A. ambigua* and the cyanobacterium *Planktothrix agardhii* (Gom.) Anagn. et Kom. dominated in the phytoplankton community. In addition to these two dominant species, *Aulacoseira granulata* (Ehr.) Sim., *A. islandica*, *A. formosa*, *Microcystis aeruginosa* Kütz., *M. wesenbergii* Kom. and *Aphanizomenon flos-aquae* (L.) Ralfs. were observed in significant numbers. In July and August, cyanobacteria dominated, developing a seasonal maximum of phytoplankton. *Dolichospermum lemmermannii* (Richter) Wacklin, Hoffmann & Komarek, D. *spiroides* (Klebhan) Wacklin, Hoffmann & Komarek, *Aphanizomenon flos-aquae*, *Microcystis aeruginosa*, *Planktothrix agardhii* dominated, accounting for 89–91% of the total phytoplankton biomass (Fig. 3d). The abundance of *P. agardhii* increased and accounted for about 50% of the total biomass. Diatoms constituted only 3–4% of the total biomass (Fig. 3c). The most numerous taxa were *Aulacoseira ambigua*, *A. granulata*, and *Stephanodiscus hantzshii* Grun. In October, cyanobacteria continued to dominate, accounting for 93% of the total phytoplankton biomass, of which *P. agardhii* constituted 70%.

In 2016, the phytoplankton biomass varied from 6.7 to 31.3 mg l^{-1}, with the May–October average of 17.6 mg l^{-1} (Fig. 3a, Table 2). The concentration of chlorophyll *a* fluctuated from 18.7 to 57.8 µg l^{-1}, with the average of 43.6 µg l^{-1} (Fig. 3b, Table 2). In the open water period from May to October, including the summer peak of phytoplankton biomass in August, diatoms (mainly *Aulacoseira muzzanensis* (F. Meister) Sim.) dominated, accounting for 64–88% of the total phytoplankton biomass (Fig. 3c). Cyanobacteria (mainly species of the genus *Microcystis*) were recorded only in small numbers, corresponding to 1–4% of the total biomass (Fig. 3d).

In 2018, phytoplankton biomass varied from 8.4 to 47.1 mg l^{-1} with the May–October average of 23.1 mg l^{-1} (Fig. 3a, Table 2). The chlorophyll *a* concentration fluctuated from 30.6 to 136.4 µg l^{-1}, with the average of 66.6 µg l^{-1} (Fig. 3b, Table 2). Cyanobacteria (mainly *Aphanizomenon flos-aquae*, *Microcystis aeruginosa* and *M. wesenbergii*) slightly dominated in relation to diatoms and other algal groups during the summer maximum of phytoplankton biomass, reaching 53% of

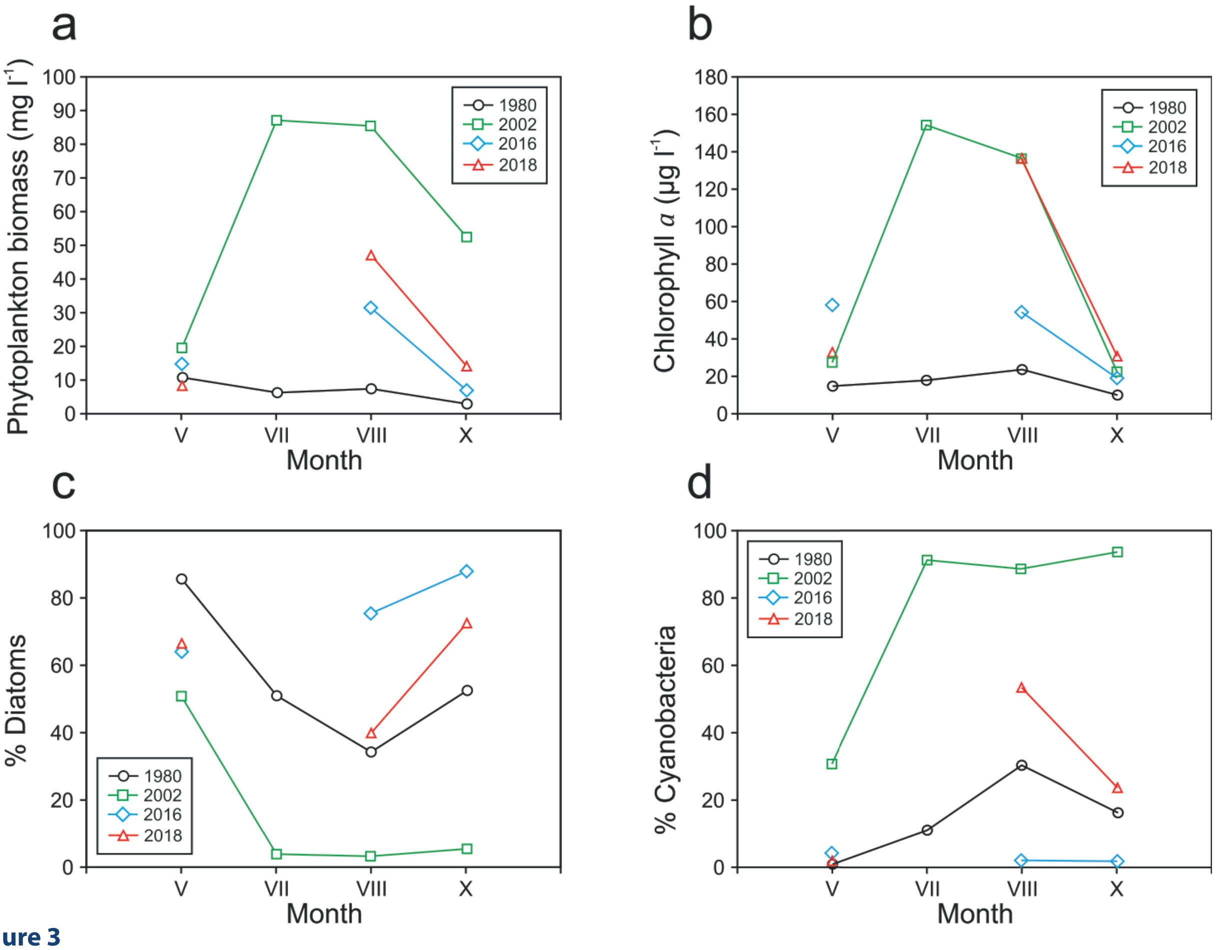

Figure 3

Changes in the total phytoplankton biomass, chlorophyll *a*, and relative biomass of diatoms and cyanobacteria during the sampling years (1980, 2002, 2016 and 2018) in the Sestroretskiy Razliv reservoir

the total biomass (Fig. 3d). On the other hand, diatoms (mainly taxa of the genus *Aulacoseira*) dominated in spring and autumn, reaching 67–73% of the total biomass (Fig. 3c).

The measurements made during the whole study period showed statistically significant differences in the May–October average values from different sampling years for the phytoplankton biomass

Table 2

Means (and ranges) of phytoplankton biomass (B), chlorophyll *a* (Chl *a*) and relative biomass of diatoms (% Diatom) and cyanobacteria (% Cyanobacteria) in the Sestroretskiy Razliv reservoir in different years (1980, 2002, 2016 and 2018). The comparison of the means among different years was calculated using ANOVA with the Tukey–Kramer test. The Tukey–Kramer test results are indicated by superscripts.

Parameter	1980	2002	2016	2018	*F*	*p*
B (mg l^{-1})	6.8^{a} (0.3–19.8)	61.0^{b} (15.8–99.6)	17.6^{c} (3.9–35.6)	23.1^{c} (7.0–49.8)	18.02	< 0.0001
Chl *a* (µg l^{-1})	16.6^{a} (0.7–27.2)	84.7^{b} (20.5–174.9)	43.6^{ab} (8.4–122.9)	66.6^{b} (27.4–157.6)	6.87	< 0.001
% Diatom	55.8^{a} (21.2–95.5)	15.7^{b} (2.1–58.6)	75.6^{a} (20.7–94.0)	59.7^{a} (32.5–88.6)	19.30	< 0.0001
% Cyanobacteria	14.5^{ac} (0–46.2)	75.9^{b} (26.9–96.4)	2.4^{c} (0.3–6.7)	26.2^{a} (1.2–62.1)	23.94	< 0.0001

Letters a and b and c indicate years with significantly different means.

(F = 18.02, $p < 0.0001$; Table 2) and chlorophyll *a* concentration ($F = 6.87$, $p < 0.001$; Table 2). A significant increase in the average values of phytoplankton biomass and chlorophyll *a* in 2002 suggested drastic changes in the trophic status of the reservoir from mesotrophic in 1980 to hypereutrophic in 2002. While a statistically significant decrease in the average values of phytoplankton biomass was recorded in 2016 and 2018, a relatively high level of phytoplankton biomass (average values of 17.6–23.1 mg l^{-1}) indicates that the reservoir still remains highly eutrophic (OECD 1982).

The linear correlation analysis showed that the correlation between TP and phytoplankton biomass ($r = 0.749$, $p < 0.01$) and chlorophyll *a* ($r = 0.608$, $p < 0.05$) were significant (Fig. 4a, 4b), which indicates that the long-term phytoplankton dynamics in the reservoir was controlled by phosphorus concentration. The significant negative correlation between the relative biomass of cyanobacteria and the TN/TP ratio ($r = -0.584$, $p < 0.05$; Fig. 5) suggests that the shift from phosphorus to nitrogen limitation was conducive to the cyanobacterial growth.

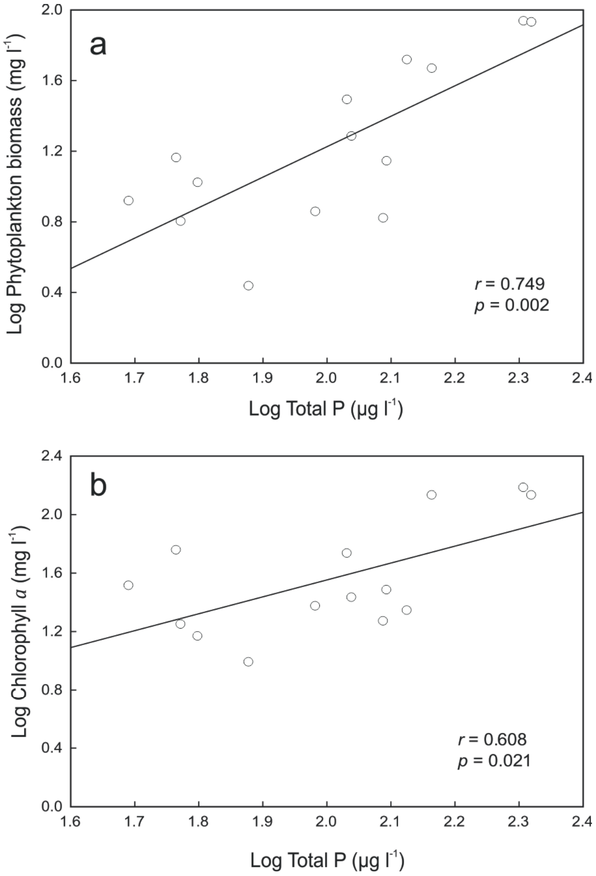

Figure 4

Relationships between phytoplankton biomass (a) and chlorophyll *a* (b) and total phosphorus (TP)

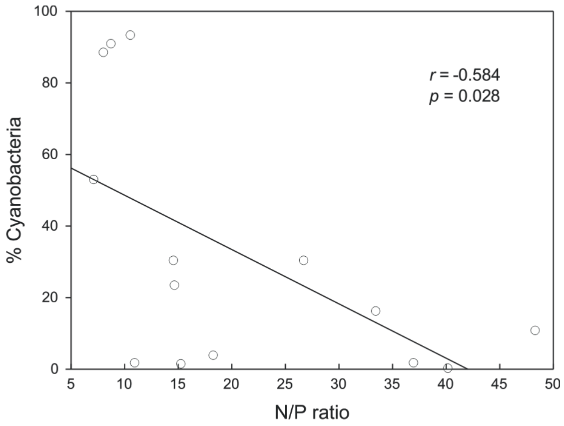

Figure 5

Relationship between relative biomass of cyanobacteria and the N/P ratio

Macrophytes

A comparison of the spatial macrophyte distribution in the Sestroretskiy Razliv reservoir between 1980 and 2016 revealed that the largest beds of emergent plants (helophytes) were still located along the western shore and in the northern part of the reservoir near the inflow of the Sestra River (Fig. 6). The outer edge of helophyte beds composed of reeds (*Phragmites australis* (Cav.) Trin. ex Steud.) and bulrush (*Scirpus lacustris* L.) was located at a distance of 700–900 m from the western shore. Open areas within helophyte beds were occupied by communities of floating-leaved plants. A narrow strip of reeds, with a width of 5–7 m, spanned over the eastern shore of the reservoir. The northern shore connected with a marsh was practically devoid of aquatic vegetation. In a bay, near the delta of the Chernaya River, dense and large beds of floating-leaved plants *Nuphar lutea* (L.) Smith. and *Potamogeton natans* L. were found.

A comparison of the total area covered by aquatic vegetation between 1980 and 2016 showed that it decreased twice, from 157.3 ha to 75.9 ha, respectively (Table 3). The calculations of the reservoir area covered by macrophytes showed its decrease from 14.8% in 1980 to 6.8% in 2016 (Table 3). Considering the functional vegetation groups, the area covered by helophytes and floating-leaved plants decreased by a factor of two. Submerged macrophytes showed the highest reduction in the coverage area by a factor of four. At the same time, the relative contribution of helophytes and floating-leaved plants to the total aquatic vegetation cover remained practically unchanged (Table 3), whereas the relative contribution of submerged plants decreased twice, from 1.6% to 0.8%.

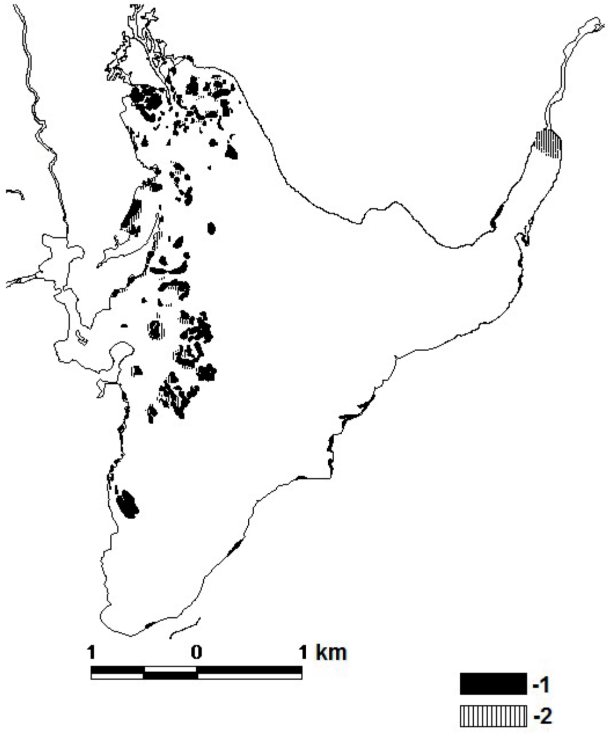

Figure 6

Map of the spatial distribution of aquatic vegetation, including emergent helophytes (1) and floating-leaved plants (2) in the Sestroretskiy Razliv reservoir in 2016

The total aboveground plant biomass in the reservoir is approximately 684 tons (Table 4). Helophytes, floating-leaved and submerged plants produce 95.7, 4.2 and 0.03% of the total plant biomass, respectively. The comparison of 2016 with 1980 showed that the total plant biomass decreased by a factor of 0.7. The relative contribution of helophytes to the total plant biomass slightly increased from 94% to 96%, while the relative contribution of floating-leaved and submerged plants decreased from 6% to 4% and from 0.06% to 0.03%, respectively (Table 4).

The survey of macrophyte communities in 2016 showed that the relative abundance of helophytes and floating-leaved plants in the reservoir remained fairly constant compared to 1980. On the other hand, there were changes in relative abundance of individual macrophyte species (Table 3). In the functional group of floating-leaved plants, the dominance shifted from *Persicaria amphibia* (L.) S.F.Gray to *Nuphar lutea*. Also the relative abundance of *Nymphaea candida* J.Presl. and *Nuphar pumila* (Timm) DC. significantly decreased. In the group of helophytes, an increase in the relative abundance and spatial distribution of *Typha latifolia* L., *Sparganium erectum* L., *S. emersum* Rehm. and *Butomus umbellatus* L. was observed. A significant decrease in the relative abundance of *Equisetum fluviatile* L. was caused by the spatial expansion of *Carex* spp., replacing horsetail beds by sedge beds. The latter occur in the delta of the Sestra River in the northwestern part of the reservoir, where islands overgrown with low sedge species such as *Carex acuta* L. and *C. rostrata* Stokes were formed. The current distribution of the islands overgrown with sedges suggests that their formation was caused by siltation processes and sediment transported by the Sestra River.

Compared to 1980 and 2016, the significant reduction in the area covered by submerged plants was accompanied by their reduced distribution in the reservoir. In 2016, the distribution of submerged vegetation moved into a shallower zone of the reservoir, compared to 1980. In 1980, submerged plants (mainly *Potamogeton perfoliatus* L.) occurred to a maximum depth of 1–1.2 m, while in 2016, submerged plants were not found at depths greater than 0.5–0.6 m. In 2016, *P. perfoliatus*, which dominated in submerged vegetation patches, occurred in the form of rare small beds distributed along the western shore and in the deltas of the Sestra and Chernaya rivers. The distribution of other submerged species such as *Potamogeton compressus* L., *Elodea canadensis* Michx. and *Ceratophyllum demersum* L. was also restricted to the tributary deltas.

The macrophyte survey conducted in 2018 showed a slight increase in the area covered by mixed beds of low-growing emergent plants (such as *Sagittaria sagittifolia* L., *Butomus umbellatus, Sparganium erectum*, *S. emersum*, and *Equisetum fluviatile*) along the western shore and floating-leaved plants in the bay near the delta of the Chernaya River. As regards the main helophyte beds composed of reeds and bulrush, there were no considerable changes in their cover between 2016 and 2018. The area covered by sparse submerged vegetation did not change significantly either. Due to the increase in the area covered by meadow helophytes (2.1 ha) and floating-leaved plants (1.6 ha), the total area covered by aquatic vegetation increased to 79.7 ha, which constitutes 7.2% of the total water surface.

Fish community

Fish surveys conducted in 2015 and 2016 showed that the fish community in the reservoir was represented by eight taxa belonging to three families: Esocidae (pike), Cyprinidae (bream, bleak, gudgeon, and roach), and Percidae (perch, pikeperch, and ruffe; Pedchenko et al. 2017). The core of the fish community

Table 3

Contribution of different species of helophytes, floating-leaved and submerged plants to the total plant coverage and the area of the Sestroretskiy Razliv reservoir in 1980 and 2016

Ecological groups and species	Area, ha		% of plant cover		% of reservoir area	
	1980*	2016	1980*	2016	1980*	2016
Helophytes						
Phragmites australis	53.4	26.1	33.9	34.4	5.03	2.30
Scirpus lacustris	42.5	16.2	27.0	21.3	4.00	1.50
Carex spp.	0.3	9.5	0.2	12.5	0.03	0.90
Equisetum fluviatile	24.6	4.7	15.6	6.2	2.32	0.40
Typha latifolia	(+)	1.2	(+)	1.6	(+)	0.10
Sparganium erectum + *S. emersum* + *Butomus umbellatus*	5.6	3.6	3.6	4.7	0.53	0.30
Total:	126.4	61.3	80.4	80.8	11.91	5.50
Floating-leaved plants						
Nuphar lutea	3.0	6.7	1.9	8.8	0.29	0.62
N. pumila	0.1	(+)	0.1	(+)	0.01	(+)
Potamogeton natans	3.4	3.2	2.2	4.2	0.32	0.30
Persicaria amphibia	6.3	2.4	4.0	3.2	0.60	0.22
Sparganium gramineum	0.1	0.7	0.1	0.9	0.01	0.07
Nymphaea candida	3.6	0.1	2.3	0.1	0.34	0.01
Mixed beds	11.9	0.9	7.6	1.2	1.13	0.08
Total:	28.4	14.0	18.1	18.4	2.70	1.30
Submerged plants						
P. perfoliatus	2.5	0.6	1.6	0.8	0.20	0.10
Total:	157.3	75.9	100.0	100.0	14.81	6.80

* data of Katanskaya (1984); (+) – found sporadically

consisted of six taxa (roach, ruffe, bream, perch, pikeperch, and bleak). Roach was the most abundant species in the seine surveys, reaching up to 69% of the total fish abundance. The percid fish (ruffe, perch, and pikeperch) varied in relative abundance from 19% to 28%. Pike was the rarest taxon, its relative abundance in the seine surveys was no more than 0.2%. Cyprinids (roach and bream) reached the highest abundance in the deepest open part of the reservoir. On the other hand, percids (ruffe and perch) were more abundant in reed and bulrush stands. In general, the seine surveys showed that planktivorous species dominated in relation to piscivores in the fish community of the Sestroretskiy Razliv reservoir. The average value of fish standing crop in the reservoir was 98 kg ha^{-1} (Pedchenko et al. 2017).

Table 4

Contribution of ecological groups of aquatic plants to the total aboveground biomass in the Sestroretskiy Razliv reservoir in 1980 and 2016

Ecological group	Aboveground biomass			
	1980*		2016	
	10^3 kg	%	10^3 kg	%
Helophytes	872.6	93.95	654.9	95.72
Floating-leaved plants	55.6	5.99	29.0	4.24
Submerged plants	0.6	0.06	0.2	0.03
Total	928.8	100	684.2	100

* data of Katanskaya (1984)

Discussion

Nutrient and phytoplankton dynamics

In the study period from 1980 to 2018, the simultaneous data on nutrient dynamics and phytoplankton development allowed us to track the long-term changes in the trophic status of the Sestroretskiy Razliv reservoir. According to the phytoplankton biomass level corresponding to the May–October average of 6.8 mg l^{-1} (Table 2), the reservoir was meso-eutrophic in 1980 (Trifonova & Senatskaya 1984). During the 20 years from the beginning of the 1980s, the annual phosphorus loading doubled (from 2.2 to 4.5 g m^{-2}; Belyakov et al. 2002). Measurements of TP concentration showed an increase in the average TP from 73 μg P l^{-1} in 1980 to 163 μg P l^{-1} in 2002 (Table 2), with a value above 100 μg P l^{-1} considered to be hypertrophic

(OECD 1982). Due to the higher phosphorus input, an increase in phytoplankton biomass by a factor of 8 to 9, corresponding to the average value of 61 mg l^{-1}, was recorded in 2002 (Trifonova & Pavlova 2005). In the course of seasonal succession, diatoms were almost completely replaced by cyanobacteria, mainly *Planktothrix agardhii*, which is an indicator of organic pollution (Trifonova 1990). The high abundance and dominance of *P. agardhii* is a prominent feature of urban water bodies receiving domestic and industrial waste discharges. Similar changes in the phytoplankton community composition under the impact of eutrophication were recorded in many lakes located in urbanized landscapes (e.g. Edmondson & Lehman 1981; Chorus & Wesseler 1988). The blooming caused by *P. agardhii* results in a rapid deterioration of water ecosystems, which necessitates restoration efforts (Ahlgren 1978; Edmondson & Lehman 1981; Pawlik-Skowrońska et al. 2008). The increasing abundance of nitrogen-fixing cyanobacteria (such as *Anabaena* and *Aphanizomenon*) indicated that the reservoir ecosystem changed from being P-limited to N-limited (e.g. Wetzel 2001). In general, the significant increase in the average chlorophyll a concentration from 16.6 μg l^{-1} in 1980 to 84.7 μg l^{-1} in 2002 (Table 2) and the shift in phytoplankton composition from diatoms to cyanobacteria indicated a change in the trophic status of the reservoir from meso-eutrophic to hypertrophic (OECD 1982).

Compared with 2002, a 40–35% reduction in TP concentration in 2016 and 2018 was followed by a significant decline in phytoplankton biomass (Tables 1, 2). Despite the decrease in phytoplankton biomass in 2016 and 2018, the Sestroretskiy Razliv reservoir remains a hypertrophic system, as indicated by the average chlorophyll *a* values fluctuating between 43.6 and 66.6 μg l^{-1} (OECD 1982). The phytoplankton biomass values in summer are the most indicative for the lake trophic status (Trifonova 1990). In 2016, diatoms dominated during the summer peak of phytoplankton biomass (Fig. 3c). The dominant species was *Aulacoseira muzzanensis* (F. Meister) Krammer, which is characteristic for shallow eutrophic reservoirs and adapted to conditions of mixing and high turbidity (Trifonova 1990). Cyanobacteria (mainly species of the genus *Microcystis*) were recorded only in small numbers. It appears that the poor development of cyanobacteria and the dominance of diatoms in 2016 resulted from unfavorable weather conditions such as low water temperature and continuous mixing. In addition, the increased water color observed in 2016 (Fig. 2b, Table 1) indicated heavy precipitation events that led to intensive loading of allochthonous organic matter from watersheds. It appears that a change in light quality toward red light with increasing humic content in water of the reservoir could reduce the competitive advantage of cyanobacteria with respect to light use and thus reduce their abundance (Ptacnik et al. 2008). During the warmer summer of 2018, cyanobacteria (mainly *Aphanizomenon flos-aquae*, *Microcystis aeruginosa* and *M. wesenbergii*) became dominant in the phytoplankton of the reservoir (Fig. 2d). The increased abundance of cyanobacteria in response to a low water level and high temperature was confirmed by observations conducted in the hot summer of 2010, when cyanobacteria [mainly *Aphanizomenon flos-aquae*, species of the genus *Anabaena*, *Limnothrix planctonica* (Woloszynska) Meffert, and *M. aeruginosa*] also dominated in the phytoplankton of the reservoir (Chernova et al. 2014). In general, inter-annual fluctuations in the phytoplankton biomass and species composition in 2016 and 2018 indicate that eutrophication processes including cyanobacterial blooms become more pronounced in years with low water levels (Trifonova 1990).

Changes in the macrophyte community

The composition of macrophyte communities in the Sestroretskiy Razliv reservoir is typical for humic lakes, where the dominance of helophytic and floating-leaved plants over submerged ones is often observed (e.g. Toivonen & Huttunen 1995; Nurminen 2003). When comparing the aquatic vegetation of the reservoir in 1980 and 2016, it is clear that eutrophication had a profound effect on the composition and abundance of macrophytes. The field survey conducted in 1980 showed a very limited development (about 2% of the total area covered by vegetation) of submerged macrophytes, suggesting that the submerged vegetation has been affected by eutrophication since the early 1980s. The further decrease in the total cover of macrophytes, particularly the cover of submerged plants, observed in 2016, suggests that eutrophication of the reservoir has been accompanied by an increasing impact of phytoplankton dominance (Scheffer et al. 1993). The most likely mechanism behind the observed decline in the abundance and species richness of aquatic plants in the Sestroretskiy Razliv reservoir is the shading effect of dense phytoplankton populations on the growth of plants and propagule germination (e.g. Arthaud et al. 2012). Our findings that the decline of submerged macrophytes was more pronounced compared to emergent and floating-leaved plants are in accordance with many studies that report that submerged plants are particularly vulnerable to increasing eutrophication (e.g. Sand-Jensen 1997; Sand-Jensen et al. 2000; Egertson et al. 2004; Papastergiadou et al. 2010). Considering other functional vegetation groups, the effect of increasing eutrophication was also reflected in changes in the composition of emergent plants. In the reported period from 1980 to 2018, the group of helophytes increased in relative abundance and spatial expansion of *Typha latifolia*, *Sparganium erectum*, and *Butomus umbellatus*, which are resistant to eutrophication (e.g. Toivonen & Huttunen 1995).

Apart from the effect of eutrophication, water level fluctuations apparently had a considerable effect on the composition of macrophyte communities. The analysis of vegetation changes between 2016 and 2018 suggests that the spatial expansion of mixed beds of low-growing emergent plants, typically inhabiting the upper littoral zone and floating-leaved plants, was a likely response to the lowered water level in the summer of 2018. The positive effect of low water levels on the expansion of the area covered by helophytic and floating-leaved plants was previously documented for many lakes (e.g. Chow-Fraser 2005; Hudon et al. 2005; Rusanov 2008; Papastergiadou et al. 2010).

Restoration prospects

The ecological concept underlying the restoration practice implies that shallow lakes can be in two alternative stable states: the clear-water state with abundant submerged macrophytes and the turbid-water state with small abundance of submerged plants and extensive development of phytoplankton (Scheffer et al. 1993). One of the main conclusions drawn from practical applications is that reducing the external nutrient loading alone cannot lead to successful restoration of eutrophic lakes. High internal phosphorus loads from sediments and changes in the biological structure of eutrophic lakes delay the recovery to the clear-water state (Søndergaard et al. 2007). Among the important feedback mechanisms delaying the lake's recovery, small abundance of submerged vegetation and high abundance of planktivorous fish should be mentioned. Macrophytes play an important structuring role in shallow lakes, stabilizing the clear-water state via allelopathy, competition with phytoplankton for nutrients and refuge for zooplankton (Scheffer et al. 1993). On the other hand, the high biomass of planktivorous fish reduces the top-down control of zooplankton over phytoplankton, thus affecting the macrophyte-dominated state (Gulati 1990). In the Sestroretskiy Razliv reservoir, the average standing crop of fish (with the dominance of planktivorous species over piscivorous) was 98 kg ha^{-1}, which is close to the lowest value of fish production variability in eutrophic lakes (100–400 kg ha^{-1}; Gulati et al. 2008). According to the alternative stable state concept (Scheffer et al. 1993), the Sestroretskiy Razliv reservoir is a phytoplankton-dominated system. Negative effects associated with small abundance of macrophytes and dominance of planktivorous fish are the most likely structural mechanisms stabilizing the phytoplankton-dominated state in the reservoir. The dark color and high turbidity of water due to wave-induced sediment resuspension are the additional factors limiting the growth of submerged plants and preventing the regime from shifting from phytoplankton to macrophyte dominance. Our results suggest that despite the limited availability of light in the Sestroretskiy Razliv reservoir, submerged macrophytes were still negatively impacted by phytoplankton, especially during warm years when underwater light was stronger and summer cyanobacterial blooms occurred. Therefore, the reduction of nutrient loading as a restoration measure will reduce the phytoplankton biomass and thus remains the most effective method for restoring the submerged vegetation in the reservoir.

The comparison of data on the abundance and composition of macrophyte and phytoplankton communities in 2016 and 2018 showed that the phytoplankton-dominated state remained stable in the reservoir, despite considerable fluctuations in water turbidity and temperature. As far as the phytoplankton development is concerned, the comparison of 2016 with 2018 showed that a slight increase in phytoplankton biomass occurred in 2018 at a higher summer temperature (Fig. 3a,b, Table 2). In the colder year of 2016, the area covered by submerged plants did not change in response to lower phytoplankton biomass and remained similar to the area observed in 2018 with greater phytoplankton development. This indicates that in 2016, high water turbidity due to wave-induced sediment resuspension limited the growth of submerged vegetation despite the lower level of algae-induced turbidity. Based on data collected from Dutch shallow lakes, Scheffer et al. (2001) showed that a small increase in temperature could lead to a shift toward a clear-water phase due to increased zooplankton grazing activity. Therefore, our findings seem to contradict this view and suggest that other mechanisms, such as higher temperature-dependent algal growth, reduced feeding of zooplankton on cyanobacteria and higher predation pressure of fish on zooplankton were responsible for the observed increase in phytoplankton biomass at increasing temperature (Jeppesen et al. 2003).

Based on the above-mentioned characteristic features of the Sestroretskiy Razliv reservoir, the management approach to the restoration of the reservoir should include:

(a) Further reduction in nutrient loads from both the catchment area and the sediment to reduce nutrient concentrations in water of the reservoir. To reduce the internal nutrient input, harvesting and removal of helophyte vegetation at sites with high density of macrophytes should be implemented.

(b) Biomanipulation by introducing native predatory (piscivorous) species such as pike and pikeperch fry should be applied to minimize populations of planktivorous fish (Benndorf 1995; Skov & Nilsson 2007). This will produce the top-down trophic cascade effects on fish and lead to the re-establishment of submerged macrophytes.

Conclusion

The comparison of data from 1980 to 2002 showed an increase in the total phosphorus concentration and phytoplankton biomass indicating a change in the trophic status of the Sestroretskiy Razliv reservoir from meso-eutrophic to hypertrophic. The increase in phytoplankton biomass coincided with a shift in the community composition from diatoms to cyanobacteria with the dominance of *Planktothrix agardhii*. In 2016 and 2018, despite the lower rate of phytoplankton development, compared with 2002, the reservoir remained a hypertrophic system. Diatoms dominated in both 2016 and 2018, especially in 2016 with unfavorable weather conditions. Cyanobacteria were more abundant in 2018 at higher summer temperatures. A decrease in the total cover of macrophytes (mainly submerged plants) during the last 40 years, suggests that eutrophication of the reservoir is accompanied by the growing impact of phytoplankton dominance. The dark color and high turbidity of water due to wave-induced sediment resuspension are additional factors that limit the growth of submerged plants and stabilize the turbid, algae-dominated state. The fish community is characterized by high biomass of planktivorous species, reducing the top-down control of zooplankton on phytoplankton and the recovery potential of the reservoir ecosystem to the clear-water state. Further reduction of nutrient loads to improve the ecological state of the reservoir is required. The introduction of predatory fish can be proposed as a restoration measure for the Sestroretskiy Razliv reservoir to minimize planktivorous fish populations.

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