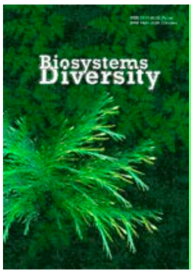

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Long-term dynamics of flora of karst lakes: Changes and current state

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Long-term observations of the rates and pattern of changes in flora and vegetation contribute to understanding of one of the most important contemporary global problems, the eutrophication of water bodies. In this study, using classical floristic methods, we attempt to determine (for a period of almost 80 years) the nature and possible causes of changes in the floristic composition of the lakes of karst origin, Velikoe and Parovoe (Pustinskaya lake-river system, the right bank of Nizhny Novgorod oblast). The paper shows that over a long period of observations a significant transformation of the vegetation cover has occurred in the lakes. The process was accompanied by the disappearance of a number of native species and appearance of others, including adventitious ones (for example, *Elodea canadensis* Michx., *Zizania latifolia* (Griseb.) Stapf, *Bidens frondosa* L. and *Epilobium adenocaulon* Hausskn.). The weak saturation of the flora with adventive species indicates that the reservoirs are subject to moderate anthropogenic transformation. This is also indicated by the presence of characteristic indicator species, for example, *Najas minor* All., *Glyceria fluitans* (L.) R. Br., *Hydrocharis morsus-ranae* L. and *Stratiotes aloides* L. in the plant communities. In addition, the studied water bodies are subject to a further increase in the degree of eutrophication. This can be judged by scattered records of *Potamogeton trichoides* Cham. et Schlecht., the disappearance of a number of species (such as *Elatine alsinastrum* L. and *Callitriche hermaphroditica* L.), as well as the presence of a significant number of macrophyte indicators of the eutrophic state of water bodies. We suggest that a gradual increase in the trophicity of the studied water bodies is due to a combination of anthropogenic impact (water withdrawal for economic needs, recreational load), natural and climatic features of the region (alternation of high and low water periods) and the natural succession processes associated with the current fundamental changes in the conditions of the runoff formation in the Volga River basin. As a result of studies conducted by authors in 2014–2015, it has been shown that in general the taxonomic and ecological structures of the flora of both lakes are quite diverse and traditional for the territory and the European part of Russia. Meanwhile, the flora of these two reservoirs insignificantly differs in taxonomic composition, which is due to their individual morphometric characteristics, the physical and chemical properties of the aquatic environment, and the nature of the anthropogenic load. At the same time, the equilibrium balance of coastal and aquatic plants in the flora of Lake Parovoe (in contrast to Lake Velikoe) indicates a degree of successional stability of its floristic complex.

Keywords: eutrophication; vascular plants; adventive species; rare plants; structure of flora; floristic richness

Introduction

Aquatic and shoreline-aquatic plants and their communities are an important component of the littoral zone of different types of aquatic-swamp ecosystem (Carpenter & Lodge, 1986; Chambers et al., 2008; Lacoul et al., 2011; Dhanam & Elayaraj, 2015; Sharma & Singh, 2017). They are an indicator of eutrophication processes – one of the main current global problems (Yang et al., 2008; Sender, 2012; Seo et al., 2014; Teneva et al., 2014). By changing the natural environments, aquatic plants can also indicate the extent of anthropogenic impact (Lehmann & Lachavanne, 1999; Clayton & Edwards, 2006; Lacoul et al., 2011; Pirini et al., 2011; Pereira et al., 2012; Evangelista et al., 2014; Sharma & Singh, 2017). It should be mentioned that a rising level of eutrophication causes a significantly manifested decrease in the water quality and is often followed by a decrease in the species diversity in water reservoirs (Egertson et al., 2004). Therefore, multi-year monitoring of the dynamics of flora and vegetation of different types of aquatic-swamp objects is especially relevant in this context. The results of such studies allow one not only to determine the tempi and the pattern of changes that occur in different types of plant communities, and to determine their cause-effect relationship, but also to objectively determine of the response of the biota to the conditions developing in a particular ecosystem.

In this context, we are especially interested in Lakes Velikoe and Parovoe of the Pustyn lake-river system in the basin of the Seryozha, Teshchia, and Piana rivers on the territory of the forest-steppe right bank of Nizhny Novgorod oblast (Arzamassky District, near the Staraia Pustyn village) (Bakka & Kiselyeva, 2008). As we have mentioned above (Belyakov et al., 2017), this area is characterized by especially well developed karst forms of relief, connected with the washing-out of outcrops of gypsum and limestone-dolomite rocks by the ground and above-ground waters. According to the botanical-geographical zoning, the studied lake-river complex is at the junction of the European broad-leaved and Eurasian taiga (coniferous) regions. According to the botanical-geographical zoning by Averkiev (1954), the Pustyn lakes are located at the junction of the Vyksa-Seryozha sub-district of the fir-pine forest zone and the Arzamassky-Vadsky sub-district of the forest-steppe zone.

The region is located in the zone of moderate continental climate with cold and long winters and quite hot, relatively short summers (Bakka & Kiselyeva, 2008). An interesting fact is that on the territory where today the objects of our study are located, was a large pre-glacial grand-Pustyn lake (over 10 km wide) the age of which was determined by contemporary scientists (Melnikova, 2014) as Dniprovsky. As Melnikova (2014) suggests, the reason for the formation of such a water body could have been the ponding of the natural flow of the Seryozha and Oka rivers, and also melted glacial water. During the epoch of degradation of the glaciation, the periglacial lake was drained off (Melnikova, 2014). The further development of the karst processes in the channel of the Seryozha contributed to the development of the large faults which exist today and which are filled by the Pustyn lakes among others. The essential role in the formation of their current condition (along with the processes of karst-formation) was played by the alluvial process, "which added additional features to the morphology of lake basins: enlarged and smoothened the relief of the karst basins to some extent" (Astashin et al., 2016, p. 53). The history of research on the flora and vegetation of the Pustyn Lakes began in the late 1920s. The first botanical surveys of Lake Velikoe were conducted in 1935 by Vorobyev (1943). Data on the flora of this water body are provided in a number of other studies (Smirnova & Nikitina, 1972; Lukina, 1982; Nikitina, 1982). The floristic study of Lake Parovoe was initiated in 1939 by A. D. Smirnova and were continued in 1965–1975 by E. V. Lukina and I. G. Nikitina (according to: Smirnova et al., 1975).

The objective of this study to evaluate the pattern and possible reasons for changes of the flora at the Velikoe and Parovoe Lakes during a period of almost 80-years, as well as its current condition.

Materials and methods

The baseline for this study was given by the material collected by the authors (Belyakov et al., 2015, 2017) in collaborative expeditions of the staff of the laboratory of the aquatic plants of the Institute for Biology of Inland Waters Russian Academy of Sciences and Botany Department of State University of Nizhny Novgorod, conducted in July–August of 2014 and 2015 at Lakes Velikoe and Parovoe.

Lake Velikoe is a large eutrophic water body with a water surface area of 58 ha and 5.5 m depth. The lake is of irregular oval shape, stretching from the east to the west (1600 m long, 780 m width). The deepest point – 3.42 m. Soil – silted sand which is succeeded by sapropel. The transparency of the water is up to 1.5 m, pH of water in the summer equals 8.0 ± 0.1. The southern bank of the lake is low, being formed by the floodplain of the Seryozha river. The northern bank slope is on the contrary steep. The shoreline is significantly indented. On the east side, the Seryozha river flows into the lake. In the north, a channel from Lake Sviato flows into Lake Velikoe. In the west, Lake Velikoe flows into Lake Glubokoe. Three islands are located on the lake: two of them are located at the mouth of the Seryozha. They were formed as a result of alluviation. The third island, Salilo, is located in the south-west part of the lake.

Lake Parovoe is an eutrophic water body with a water surface area equaling 41.3 ha and average depth of 2.1 m (the deepest point is 5.2 m). The lake stretches from the north-east to the south-west along the channel of the Seryozha and has irregular elongated shape with a signifycantly indented shoreline, dominated by low marshy banks, especially in the west part of the lake. Its average width is 163 m. The lakebed is sandy with silty areas (Smirnova et al., 1975) followed by sapropel. The reaction of pH of the water is alkalescent or neutral. The lake is connected with Lake Glubokoe by a narrow channel. In the west corner, a channel from the old stream bed of the Seryozha river flows into the lake.

The study of the vegetative cover of Lakes Velikoe and Porovoe was conducted according to the classic methodology (Shchennikov, 1964; Katanskaya, 1981). During the study of the lakes, we took into account all the species of vascular plants discovered in the waters and in the water edge (Papchenkov, 2001). In the inventorisation of the flora, we used the materials of our studies and herbarium funds of the State University of Nizhny Novgorod (NNSU) and the Institute for Biology of Inland Waters (IBIW), and also the available literature data. Species of plants were identified using identification guides (Lisitsyna et al., 2009; Maevskiy, 2014). The Latin names of the taxa followed Cherepanov (1995), at the same time often taking into account more recent analyses of a number of taxa (Christenhusz et al., 2011; Christenhusz & Chase, 2014; Byng et al., 2016). On the basis of the obtained annotated list of species, we conducted a taxonomic and ecological (Papchenkov, 2001) analysis of the flora of the lakes. The classification of life forms of the plants was made according to the system of Raunkiær (1937).

Results

According to our data, the current flora of Lake Velikoe is represented by 100 species of 2 orders, 32 families and 63 genera; the flora of Lake Parovoe contains 87 species of 2 orders, 37 families and 64 genera. It should be mentioned that in the past researchers (Smirnova et al., 1975; Lukina, 1982) did not include in the lists of the lake flora trees and shrubs which grow here on periodically drying-out shallow water areas and the shoreline. At the same time, several species, *Salix* and *Alnus*, are familiar to us from different areas of the Pustynskaia lake-river system since the 1960-s from herbarium collections. It seems that this is related to the fact that at that time, the researchers may have consciously excluded these taxa from the list of the lake flora, as also with some species of herbaceous plants of excessively moistened habitats. For more accurate comparison of our data with the existing materials (in the article further), we excluded the assessment of tree-shrub vegetation from our list (Table 1). Nevertheless, it should be mentioned that along the shores of Lake Velikoe, we found four species of willows (*Salix alba* L., *S. cinerea* L., *S. triandra* L., *S. viminalis* L.) and *Alnus glutinosa* (L.) Gaertn., whereas on Lake Parovoe – only three species – *Salix* (*S. alba*, *S. cinerea*, *S. triandra*), *Alnus glutinosa*, *Ribes nigrum* L., *Ulmus laevis* Pall. and *Tilia cordata* Mill.

Table 1
Number of taxa of different rank in the macrophyte flora of Lakes Velikoe and Paravoe over an 80-year period of observation (without taking into account tree-shrub components)

Indicator	Lake Velikoe			Lake Parovoe		
	1935	1980	2014–2015	1939	1955–1975	2014–2015
Number of phyla	2	2	2	2	2	2
Number of classes	2	3	3	2	2	3
Number of orders	17	20	19	18	18	19
Number of families	25	34	30	27	27	32
Number of genera	38	72	61	53	54	59
Number of species	50	116	89	72	72	76

Since the middle of the 1930s, two orders have still remained dominant – Poales and Alismatales. In the flora of Lake,Velikoe their share at different periods ranged 47.4–56.0% of the total number of species, whereas in the Lake Parovoe it ranged 42.5–51.4%. In the 1930s, two families chiefly dominated in Lake Velikoe – Potamogetonaceae Dumort. and Cyperaceae Juss. (7 and 6 species, respectively), whereas in Lake Parovoe 3 dominated – Poaceae Barnhart, Potamogetonaceae and Cyperaceae (11, 8 and 6 species, respectively) (Table 2, 3). Since 1980, Poaceae has been the first among the dominating families (along with Potamogetonaceae and Cyperaceae). in the flora of Lake Velikoe, These three taxa are the dominant ones in the flora of this lake now. At Lake Parovoe in 2014–2015, the Potamogetonaceae family, on contrary, had lost its position, therefore as a result only two main dominating families remained (Poaceae and Cyperaceae). This occurred due to decrease (gradually 5 species disappeared) in the taxonomical diversity of *Potamogeton*. Therefore, currently, the share of these three families equals 32.6% of all species which grow at Lake Velikoe and 26.4% at Lake Parovoe. The remaining taxa include 1 to 5–6 species each. In the flora of Lake Velikoe (since 1935), two genera are dominant – *Potamogeton* L. and *Carex* L., whereas only one genus dominates in the current flora of Lake Parovoe – *Carex* (Table 2, 3). It should be mentioned that in 1975 at this lake, the genus *Potamogeton* prevailed by the number of species.

In the geographic structure of the flora of LakesVelikoe and Parovoe in the zonal relation, boreal and plurizonal elements (Table 4) always predominated, of which their share fluctuated within 85.0–88.0%. The third place belongs to the group of boreal-nemoral species (around 8.0–11.0%). All other zonal elements (in total) throughout the study did not exceed 2.0–5.0% of the all flora. In terms of biogeographic region, throughout the study period, the permanent domination of Holarctic species in the flora of both lakes was established (38.0–40.5% at Lake Velikoe and 32.0–41.3% at Lake Parovoe). Along with this group, we should mention three other elements of the flora which do not occupy last position by the number of species – European-West Asian, European-Siberian and Eurasian (Table 4). In the current conditions, at Lake Velikoe, the European-West Asian species grouping has been substituted by the hemicosmopolites.

Table 2
Contribution of the dominant families and genera to the species diversity of the flora of Lake Velikoe over the 80-year period of observation (without taking into account tree-shrub components)

Period of study		The share of the plant species of the total flora of the lake, %		
		1935	1980	2014–2015
Families	Poaceae	8.0	13.8	13.5
	Cyperaceae	12.0	9.5	10.1
	Potamogetonaceae	14.0	6.9	9.0
	Araceae	8.0	3.4	6.7
	Ranunculaceae	6.0	5.2	4.5
	Asteraceae	0.0	3.4	5.6
Genus	*Potamogeton*	14.0	6.9	9.0
	Carex	6.0	6.0	6.7
	Ranunculus	4.0	4.3	3.4
	Juncus	2.0	4.3	1.0
	Lemna	4.0	1.7	4.5

Table 3
Contribution of the dominant families and genera to the species diversity of the flora of Lake Parovoe over the 80-year period of observation (without taking to account tree-shrub components)

Period of study		The share of the plant species of the total flora of the lake, %		
		1939	1955–1975	2014–015
Family	Poaceae	15.3	16.7	10.0
	Cyperaceae	8.3	6.9	10.0
	Potamogetonaceae	11.1	9.7	3.8
	Araceae	5.6	4.2	5.0
	Ranunculaceae	5.6	6.9	2.5
	Asteraceae	2.8	2.8	3.8
Genus	*Potamogeton*	11.1	9.7	3.8
	Carex	5.6	4.2	6.3
	Ranunculus	4.2	5.6	1.3
	Lysimachia	2.8	2.8	3.8
	Glyceria, Lemna	2.8	2.8	2.5

Table 4
The share of different zonal and regional elements in the macrophyte flora of Lakes Velikoe and Parovoe over the 80-year period of observation (without taking to account tree-shrub components)

	The share of the plant species of the total flora of the lake, %					
	Lake Velikoe			LakeParovoe		
Period of study	1935	1980	2014–2015	1939	1955–1975	2014–2015
Zonal element of flora						
arctoboreal	0.0	0.0	1.1	0.0	0.0	0.0
hypo-Arctic-boreal	2.0	1.7	1.1	2.8	2.8	2.5
boreal	34.0	45.7	37.1	41.7	43.1	37.5
boreal-nemoral	10.0	9.5	11.4	8.3	8.3	11.3
nemoral	0.0	0.0	1.1	0.0	0.0	0.0
forest-steppe	0.0	0.9	1.1	1.4	1.4	0.0
plurizonal	54.0	42.2	48.0	45.8	44.4	48.8
Regional element of the flora						
Holarctic	38.0	40.5	39.3	34.7	32.0	41.3
European-West-Asiatic	12.0	16.4	9.0	19.4	18.1	11.3
European-Siberian	14.0	8.6	12.4	12.5	15.3	11.3
Eurasian	14.0	19.0	19.1	18.1	18.1	18.8
European	4.0	2.6	6.7	1.4	1.4	2.5
Eurasian-North-American	2.0	1.7	3.4	2.8	2.8	2.5
European-North-American	4.0	4.3	5.6	2.8	4.2	3.8
hemi-cosmopolite	12.0	6.9	11.2	8.3	8.3	8.8

In the ecological-cenotic aspect, the flora of the lakes is also specific and distributed non-uniformly (Table 5). Currently, traditionally, the highest number at Lakes Velikoe and Parovoe belongs to the group hygrophytes (30.3 and 30.0%, respectively), which is related to the moistd ecotopes. The other two dominant groups in the flora of Lake Velikoe lake are the hydrophytes and hygrohelophytes (25.8 and 22.5% respectively), and on the Parovoe lake – hygrohelophytes, and also hygromeso- and mesophytes (23.8 and 18.8%, respectively).

Table 5
Spectrum of ecological types (according to Papchenkov, 2011) of macrophytes of LakesVelikoe and Parovoe over the 80-year period of observation (without taking to account tree-shrub components)

		The share of the plant species of the total flora of the lake, %					
		Lake Velikoe			Lake Parovoe		
Period of study		1935	1980	2014–2015	1939	1955–1975	2014–2015
Ecolo-gical group	hydrophyte	44.0	24.1	25.8	30.6	31.9	16.3
	hygrophyte	10.0	32.8	30.3	26.4	25.0	30.0
	hygrohelophyte	30.0	22.4	22.5	20.8	20.8	23.8
	helophyte	14.0	8.6	13.5	12.5	13.9	11.3
	hygromeso- and mesophyte	2.0	12.1	14.6	9.7	8.3	18.8

The main areas of overgrowth of the studied water bodies are covered by hydrophytes, of which the dominant are the community *Potamogeton lucens* L., *Nuphar lutea* (L.) Snith, *Ceratophyllum demersum* L., *Stratiotes aloides* L. and *Trapa natans* L. Among the hygrohelophytes, the dominant were *Agrostis stolonifera* L., *Glyceria fluitans* (L.) R. Br., *Carex acuta* L., *Comarum palustre* L. and *Calla palustris* L. The least numerous by the species richness over the 80-year period of monitoring traditionally has been the helophites group. During different periods, the number of this group of species significantly ranged from 7 to 12 (8.6 to 14.0%) at Lake Velikoe and, from 9 to 10 (11.3 to 13.9%) at Lake Parovoe. The dominant species of this ecological group include *Phragmites australis* (Cav.) Trin. ex Steud., *Glyceria maxima* (Hartm.) Holmb., *Equisetum fluviatile* L., *Scolochloa festucacea* (Wild.) Link, *Sparganium emersum* Rehm. and *Sagittaria sagittifolia* L. The hygromeso- and mesophytes group in the current flora of Lake Velikoe constitute around 15% of the total number of taxa (13 species), while at Lake Parovoe it makes up around 19% (15 species).

In the current study, we used the classic system of types of living forms according to Raunkiaer (1937), distinguishing only the main groups (without dividing them into subgroups), as we have done earlier (Belyakov et al., 2017). As a result, we determined that the dominant type of life form in the flora of Lakes Velikoe and Parovoe has traditionally been cryptophytes, and the least numerous has been chamaephytes. Also, we observed a tendency towards decrease in the share of cryptophytes in the total flora of water bodies (Table 6).

Table 6
Spectrum of life forms of macrophytes (%) at Lakes Velikoe and Parovoe over the 80-year period of observation according to Raunkiaer (1937) (without taking into account tree-shrub components)

Type of living form	Lake Velikoe			Lake Parovoe		
	1935	1980	2014–2015	1939	1955–1975	2014–2015
Therophyte	10.0	17.2	14.6	5.6	8.3	16.3
Hemicryptophyte	12.0	34.5	31.5	33.3	33.3	32.5
Cryptophytes	74.0	45.7	57.3	58.3	55.6	47.5
Chamaephyte	4.0	2.6	3.4	2.8	2.8	3.8

Discussion

The data provided in the article indicate that the taxonomic and ecological structure of the flora of Lakes Velikoe and Parovoe is rather diverse, and in general, is traditional for this territory and the European part of Russia. At the same time, Lake Parovoe differs from Lake Velikoe in its by lower richness of flora. It seems that this is due to the fact that the shore line of Lake Velikoe (similarly to Lake Glubokoe, it is located lower in the current of the Seryozha river) has a significantly higher diversity of the biotopic structure and is affected by higher anthropogenic pressure. Therefore, the most antropogenically transformed area is the eastern shore of Lake Velikoe, where Staraia Pustyn village is located. Not accidently, on the shores of this water body, we observed growth of a number of weed plants. These include, for example, representatives of the following genera: *Epilobium* L. (*E. adenocaulon* Hausskn., *E. palustre* L. and *E. montanum* L.), *Chenopodium* L. (*Ch. album* L. and *Ch. rubrum* L.), *Bidens* L. (*B. cernua* L., *B. tripartita* L. and *B. frondosa* L.), *Polygonum* L. (*P. aviculare* L.) and *Rumex* L. (*R. maritimus* L.). Some of these species (for example, *Chenopodium album*, *Polygonum aviculare*, *Rumex maritimus*) we also observed on the shores of Lake Parovoe. We should mention that the presence of a significant share of grasses in the flora of the studied lakes could be also an indicator of increase in the anthropogenic load (Teteryuk, 2012; Belyakov et al., 2017). At the same time, individual peculiarities in the taxonomic composition of the flora of the studied water bodies could also be related to geomorphological peculiarities of the lake basins.

As we know, according to the system of botanical-geographic zoning, the studied water bodies are located at the border of the European broad-leaved and Eurasian taiga (coniferous) zones, and according to climatic zoning, within the eastern part of the Atlantic-continental European moderate climate zone, the largest climatic zone in the Russian plain (Terentev & Kolkutin, 2004). The latter fully reflects the geographic structure, zonal location and specificity of the flora of Lakes Velikoe and Parovoe, which is typical for the middle belt of the European part of Russia. The analysis of the geographic structure of the flora demonstrates the azonality typical for aquatic plants (Zarubina & Sokolova, 2016). This is also indicated by the fact that the studied flora has the species with a broad range distribution (Holarctic and Eurasian) dominating. This is a distinctive feature of the flora of water bodies (Teteryuk, 2012). The large share of boreal species in the floras of both lakes could be also considered a characteristic of the flora of the taiga zone.

In relation to moisture, the flora of the water bodies is divided into two blocks (Katanskaya, 1981; Belavskaya, 1994; Papchenkov, 2001): the first includes species of humid (swampy) shore habitats (ecological groups: hygrophytes, hygromesophytes and mesophytes), the second – species of open water areas and shoreline shallow water areas (ecological groups: hygrophytes, helophytes and hygrohelophites). In the current flora of Lake Parovoe the share of two blocks has an approximately equal ratio (49% and 51%, respectively), whereas in the flora of Lake Velikoe, the ratio is not equal. The share of the second block equals 62% of the total flora of the lake, whereas the share of the first – only 45%. We should mention that the balance between the shoreline and aquatic plants indicates certain successional stability of the flora complex of Lake Parovoe, which could not be stated regarding Lake Velikoe.

In the historical context, we should note that during the study of the flora at Lake Velikoe in 1935, the ecological group hygrophytes was not one of the dominant groups. This, in our opinion, is related to the fact that during the study of this lake, P. M. Vorobiev (according to Lukina, 1982) took into account only the species growing no further than the shoreline, therefore his list does include all species of humid habitats. This could also explain why between 1939 and 1975, in the flora of Lake Parovoe, hydrophytes were dominant, whereas hygrophytes took the second place.

The dominant type of life form in the flora of Lakes Velikoe and Parovoe has traditionally been cryptophytes, whereas in the total flora of the moderate-cold zone, hemicryptophytes are considered the most broadly distributed (Zhmylev et al., 2017). It seems that significant increase in the share of cryptophytes (compared to hemicryptophytes) also characterizes the intrazonal specificity of the aquatic flora. The relatively small contribution of therophytes to the lakes` flora indicates a low level of anthropogenic and natural disturbance (Zhmylev et al., 2017). Summarizing the existing literature data on the flora of Lakes Velikoe and Parovoe, we can state that the number of species in both water bodies during the almost eighty-year period of monitoring did undergo not identical changes. From 1935 to 1980, at Lake Velikoe, there was observed a significant (twofold) increase in the number of species, whereas at Lake Parovoe, the number of species in 1939–1975 remained the same. Currently, the number of species (without taking into account tree-shrub plants) at Lake Velikoe has decreased to 89, whereas at Lake Parovoe some increase in species diversity (80 species) was observed.

Native plants. No significant changes were observed in the pattern of the distribution of *Phragmites australis* and *Scolochloa festucacea* over the long period of studies on the territory of Lakes Velikoe and Parovoe lakes. Both species are rather common here, making formations on small plots. Along with these plants, *Glyceria maxima* and *G. fluitans* are not widely distributed currently, and we did not find *G. notata* Chevall. in the composition of the flora of the Pustyn lake-river system. We should mention that during the long period of observation, the phytocenotic positions of *G. maxima* at Lake Parovoe slightly weakened. In 1939, this species was recorded often and dominated in the formations on large areas (Smirnova et al., 1975). This species was recorded for the first time at Lake Velikoe only in 1980, when it was uncommon (Lukina, 1982). *G. fluitans* (unlike *G. maxima*) was found at Lake Velikoe in 1935. The species were not widely distributed (Lukina, 1982) and, further, its phytocenotic activity was not affected by significant changes. We found *G. fluitans* at Lake Parovoe for the first time, in 2014–2015. We should also mention that the occurrence and phytocenotic activity (area of overgrowth) of *Schoenoplectus lacustris* (L.) Palla has not significantly changed in recent years. Still common in the lakes is *Nuphar lutea* with injections of *Nymphaea candida* C. Presl. Both species grow at depths of 2.5 m. Throughout the period of study, the pattern of distribution and occurrence of *N. lutea* at Lakes Velikoe and Parovoe has not significantly changed, whereas for *N. candida*, there was recorded some decrease in its abundance. The same remained the position of *Potamogeton lucens*. This species is broadly distributed not only in the water area of Lakes Velikoe and Parovoe but also other water bodies of the Pustyn lake-river system, and dominates in the formations over comparatively large areas.

Along with *Nuphar lutea* and *Potamogeton lucens*, *Trapa natans* has become broadly distributed, the distribution peculiarities of which indicate relict pattern of its range (Vizer & Kipriyanova, 2010). Currently, this plant is broadly distributed at depths of 20–40 to 210 cm and is often included in various plant groups of practically all water bodies of the lake-river system, often forming pure stands of large size (density of the projective cover is up to 75–95%). According to our observations, per 1 m^2, one can find 3 to 13–18 (rarely 22) rosettes of different vitality, floating on the water surface. It seems that high number of this species nowadays is caused by the favourable level regime formed over the recent years. On the territory of the Volga basin, the species is occasionnally found in a few of the water bodies (Lisitsyna et al., 2009). This plant was recorded in the studied lakes by P. M. Vorobiev in 1939 (Smirnova et al., 1975). Between 1930 and the 1990s, this species was not numerous at Lakes Velikoe and Parovoe. It occurred rarely as singular specimens at Lake Velikoe, and was not broadly distributed at Lake Parovoe (Smirnova et al., 1975). In 1939 P. M. Vorobiev (1939 – according to Lukina, 1982), during the survey of Lake Velikoe found 8 specimens of *Trapa* L., 1753 in four locations at the lake, and in 1980 it remained here only in the Botanic Bay (the number of plants over the years ranged 3–5 to 8–10). There is a hypothesis that this plant could have initially appeared in Lake Parovoe, and then dispersed to the lakes up and down the flow of the Seryozha, mainly through transportation of its seeds by humans.

Among the broadly distributed species, we should also mention *Stratiotes aloides* L. which is common everywhere in the water bodies and is dominant here among the formations on large areas. Its distribution at Lake Velikoe is not uniform. Therefore, as single specimens, we observed this plant along the right shore, although around the Salilo island, and respectively, along the left shore of the lake, this species is becoming abundant. Here it is a dominant, and also codominant in associations with *Nuphar lutea*. On Lake Parovoe, patches of this plant can be observed all along the shore line.

In the period of our observations (2014 to 2015) in the composition of the flora of Lake Velikoe, we found 46 species of vascular plants, whereas in the composition of the flora of Lake Parovoe 31 species were found. At the same time, we recorded 21 and 9 species for the first time at these water bodies respectively. Let us examine examples of some species which have disappeared from the lakes and species which were recorded in these water bodies for the first time.

At Lake Velikoe, *Elatine alsinastrum* L. and *E. hydropiper* L. rarely occurred (Lukina, 1982) until the 1980s. At Lake Parovoe, during the period of the study between 1955–1975, only one of these species was found – *E. alsinastrum* (Smirnova et al., 1975). Along with the representatives of the *Elatine* L. genus, the lakes` flora lost the representatives of the *Callitriche* L. genus – *C. hermaphroditica* L. and *C. cophocarpa* Sendtn., which were recorded at Lake Velikoe until 1980 (Lukina, 1982). *C. hermaphroditica* also grew at Lake Parovoe in 1955–1975 (Smirnova et al., 1975). Most likely, *E. alsinastrum* and *C. hermaphroditica* could have reached Lake Parovoe from Lake Velikoe located upstream of the Seriezha river (Smirnova et al., 1975). During our fieldwork, these species were not found (nor was *Limosella aquatica* L. which was recorded once in 1980 at Lake Velikoe), though biotopes typical for its growth (Lisitsyna et al., 2009; Maevskiy, 2014) are broadly distributed in the territory of Lake Velikoe.

During the study of Lakes Velikoe and Parovoe, we also have not recorded *Utricularia vulgaris* L. and *U. minor* L. At the same time, the former species is quite common in the anabranches and other lakes of the Pustyn system. Large populations of this plant grow in Lake Narbus among the thickets of *Statiotes aloides* and actively blossom in favourable years. *U. minor* occurs throughout the territory of the middle zone of European Russia (Maevskiy, 2014). In 1939, it was recorded at Lake Parovoe (Smirnova et al., 1975); the species has not been found since the 1950s. Its disappearance here, in our opinion, was not accidental, for this plant is an indicator of waters poor in nutrients (Dubyna et al., 1993).

At both studied lakes, earlier and during the period of our study, there were recorded three species of *Potamogeton* – *Potamogeton compressus* L., *P. lucens* L. and *P. perfoliatus* L. At the same time, *P. berchtoldii* Fieber and *P. friesii* Rupr. disappeared from the flora of the two lakes. During the study, we recorded *P. natans* L. at Lake Velikoe, but it was absent from Lake Parovoe (it was found there frequently, Smirnova et al., 1975). Recently, at Lake Velikoe, we also recorded *Potamogeton obtusifolius* Mert. et Koch. This plant is broadly distributed mostly in the forest zone of the northern hemisphere (Gubanov et al., 2002), it rarely occurs throughout the territory of the Volga basin (Lisitsyna et al., 2009). Perhaps, in the earlier lists of the flora of Lakes Velikoe and Parovoe, it could have been mentioned under *P. compressus*. Possibly, the appearance and consolidation of this species Lake Velikoe could be related to increase in the trophic status of the water body. We should mention that recently, *P. pusillus* L. and *P. pectinatus* L. have, most likely, disappeared from the flora of the Pustyn lake-river complex.

Earlier, at both water bodies *Ranunculus circinatus* Sibth., a Eurasian species broadly distributed in the moderate zone (Gubanov et al., 2013) was recorded. According to Lukina (1982) at Lake Velikoe and Smirnova et al. (1975) at Lake Parovoe, the number of this species was gradually decreasing. In 1935 at Lake Velikoe, it occurred quite often and could form groups of its own on small plots. By 1980, the species had already lost its broad distribution at Lake Velikoe, as also at Lake Parovoe, where it grew during 1955 to 1975. Currently, this plant seems to have disappeared from the flora of the Pustyn lake-river complex. This could be caused by change in the level regime of the water bodies or the expulsion of this plant by more aggressive species. Apart from the above-mentioned species, on the territory of the Pustyn lake-river system, 4 other representatives of this genus grew: *R. flammula* L., *R. lingua* L., *R. repens* L., *R. sceleratus* L. The latter was not found during the period of our study. However, its presence on the shore of Lake Velikoe was recorded in 1980 (Lukina, 1982). *R. flammula* is a European species which is common in all regions of Central Russia (Gubanov et al., 2013). From 1939 to 1975, this species grew along the shores Lake Parovoe. Recently, we found only single specimens of it along the right shore of Lakes Velikoe and Glubokoe (which have drying out sandy areas), and also in the channel from Lake Velikoe to Lake Sviato (near the road bridge). Perhaps, the disappearance of this species from the flora of Lake Parovoe is caused by gradual silting up and overgrowing of its habitats with creeping plants, such as, for example, representatives of *Carex* L. genus. *R. lingua* is a common species in Europe, remaining currently only along the shore of Salilo island (situated along the eastern shore of Lake Velikoe as single shoots. It is possible that this species will soon also disappear from the floristic composition of the Pustyn lake-river system due to formation of dense sods. *R. sceleratus* is a broadly distributed circumboreal species (Gubanov et al., 2013); it was recorded in the territory of the Pustyn lake-river complex only once, on the shore of the Lake Velikoe in 1980.

During our study, we proved that *Leersia oryzoides* (L.) Sw. grows at Lake Velikoe of the Pustyn lake-river system. It is mostly a European-Asia Minor species, common in the northern part of European Russia, and known in all the non black soil oblasts (Gubanov et al., 2002). This species was recorded on sandbanks of this lake in the 1990s. We have not found this species in the other water bodies and anabranches of the system. Also, we have not found *Beckmannia eruciformis* (L.) Host, which in the 1980s was recorded at Lake Velikoe as a common plant, which is dominant in the formations on quite large plots (Lukina, 1982).

We should mention that currently, on the shores of the lakes and anabranches of the Pustyn system, we found three species of bentgrass (*A. capillaris* L., *A. gigantea* Roth., *A. stolonifera* L.) and two species of foxtail grass (*Alopecurus aequalis* Sobol., *A. geniculatus* L.) (Belyakov et al., 2017). Of these groups, we did not find *Agrostis canina* L., *A. gigantea* Roth. and *Alopecurus geniculatus* L. during the survey of the flora of Lakes Velikoe and Parovoe. These species occur quite rarely in the region and have not dispersed broadly (Smirnova et al., 1975; Lukina, 1982). Their ecological niches could be occupied by *Agrostis stolonifera* and *Alopecurus aequalis*, abundant species in Central Russia (Maevskiy, 2014). We should emphasize that in the early lists, the flora includes species of the *Poa* genus, whereas in the floristic list we obtained, its niche is occupied by species of bentgrass.

At the current stage of development of the flora of the Pustyn lakes we found four species of cattail: *Typha angustifolia* L., *T. austro-orientalis* Mavrodiev, *T. incana* Kapit. et Dyukina, *T. latifolia* L. We should mention that *T. incana* was described relatively recently (Kapitonova & Dyukina, 2008) and, most likely is a native plant in the area. *Typha incana* grows on different humid and waterlogged, often drying-out habitats (usually, secondary), is able to form large thickets (with common cattail, and some other species) (Kapitonova & Dyukina, 2008; Lisitsyna et al., 2009). Another interesting species of the Pustyn system of lakes is *T. austro-orientalis*, which we also found in the anabranch between Lakes Velikoe and Sviato (near the road bridge). This species grows in shallow water areas of large rivers, lakes, reservoirs, oxbow lakes in Astrakhan, Volgograd, Kaluga, Nizhny Novgorod, Orenburg, Samara, Saratov oblasts, the Republics of Kalmykia and Udmurtia (south) (general range: Kazakhstan, Uzbekistan); has a tendency towards northerly distribution (Mavrodiev & Sukhorukov, 2006; Mavrodiev & Kapitonova, 2015). In herbarium collections, *T. incana* and *T. austro-orientalis* were earlier identified as *T. latifolia*. During our study at Lake Velikoe we found not only *T. latifolia* (rare specimens of which had been recorded there earlier). In its sparse thickets, there were separate shoots of *T. incana*. Behind Salilo island, there was a small population of *Typha angustifolia*, a common species in the Caucasus and Western Europe (Mavrodiev & Kapitonova, 2015). We found thickets of this species at Lake Narbus of the Pustyn system. Except *T. latifolia*, we found no other species of cattail at Lake Parovoe.

At both lakes, as in the entire territory of the Pustyn system, three species of *Eleocharis* occur, of which the most abundant are two – *Eleocharis acicularis* (L.) Roem. et Schult. and *E. palustris* (L.) Roem. et Schult., and another species – (*E. mamillata* (H. Lindb.) H. Lindb.) – was mentioned only once (Belyakov et al., 2017). In 1980, at Lake Velikoe, *E. uniglumis* (Link) Schult. was recorded (Lukina, 1982). However, in our opinion, there is good possibility thatthis specimen was incorrectly identified. According to Lukina`s data (Lukina, 1982) on the dynamic of LakeVelikoe`s flora, throughout the study, this plant was found quite often, while it was less frequently recorded at Lake Parovoe (Smirnova et al., 1975). The condition of populations of *E. acicularis* at Lake Velikoe until now has remained stable – it is not widely distributed, whereas at Lake Parovoe, we discovered this species for the first time. It is interesting also to focus on the representatives of *Juncus* L. genus, which often occur on the shores of water bodies. In 1935, at Lake Velikoe, only one species of rush was recorded – *Juncus filiformis* L., whereas by the early 1980s, apart from this plant, 4 other representatives of the genus were found – *Juncus articulatus* L., *J. bufonius* L., *J. compressus* Jacq., *J. effusus* L. (Lukina, 1982). Currently, at Lake Velikoe, we have found only one species – *J. compressus*, whereas for the flora of Lake Parovoe, we recorded three species for the first time – *J. articulates*, *J. bufonius* and *J. effuses*. In general, in the territory of the Pustyn system, we found 7 species of *Juncus* (apart from the abovementioned, we found two more species – *J. ambiguus* Guss. and *J. atratus* Krock.). They all are typical for this territory (Lisitsyna et al., 2009; Maevskiy, 2014).

Adventive plants. As we know, the species diversity of macrophytes is closely related to the natural type and status of a lake (Mäemets et al., 2010). The saturation of the local flora of Lakes Velikoe and Parovoe with adventive species is extremely low. At Lake Velikoe, there are around four species of adventive plants, which is 4.2% of the total list of the flora, at Lake Parovoe – 3.7% (3 species). This fact can indicate that these lakes are affected by moderate anthropogenic transformation. The adventive component of the flora contains the following species – *Elodea canadensis* Michx., *Zizania latifolia* (Griseb.) Stapf, *Bidens frondosa* L. and *Epilobium adenocaulon* Hausskn. The high adaptive potential of these plants allows them to quickly disperse (Santamaria, 2002) and usually retain their positions in phytocenoses. Our data allow us to approximately assess the period when these plants appeared and the dynamic of their development in the flora of the studied water bodies.

Despite the fact that in the basin of the Volga, *Elodea canadensis* appeared only in the first decade of the XX century or in 1885 (Bazarova & Pronin, 2010), its introduction to the groups of aquatic plants of the Pustyn lake-river system (probably related to the activity of amateur aquarists) took place in the late 1950s (Smirnova et al., 1975). Due to active vegetative breeding, this plant quickly covered large areas and became dominant in some formations (Smirnova et al., 1975). Initially, *E. canadensis* was a North American plurizonal species typical for most moderate climate areas of the USA and Canada (Maltseva & Bobrov, 2017). It was brought to Europe in the XIX century, and then began active penetration of the continent (Maevskiy, 2014). Currently, at the studied water bodies, the species grows on the shoreline shallow water areas and is not broadly distributed. We should mention that during monitoring of the multi-year dynamic of development of American waterweed (*Elodea canadensis*), the researchers often recorded a certain periodicity – a decrease in the quantitative parameters follows a phase of rapid development, and then they stabilize (Bazarova & Pronin, 2010). Stabilization of phytocenotic activity of this plant is currently observed at Lake Parovoe, though from the mid-1950s to mid-1980s, this species was a dominant in the formations and was distributed in large areas (Smirnova et al., 1975). Monitoring of the flora and overgrowth of Lake Velikoe indicate that this species since the very beginning had no broad distribution here after the moment of its naturalization. Perhaps, this occurred due to the specific hydrological regime which formed here and the pattern of the littoral zone.

It seems that in the period from the1980s to 1990s, in the territory of the Pustyn lake-river system, there appeared also *Zizania latifolia*, a Far Eastern species (Maevskiy, 2014) introduced to the European part of Russia in 1934 for hunting purposes – increasing the food base and improvement of the habitat of semiaquatic animals (Lisitsyna et al., 2009; Maltseva & Bobrov, 2017). In the 1950s, this plant was introduced to many regions of the European part of Russia, including the basin of the Volga (Maltseva & Bobrov, 2017). The appearance of this species in the territory of the Pustyn lake-river complex could not have been accidental, but must have been deliberate due to the fact that in 1934, this territory belonged to the Pustyn State Biological (Hunting) Reserve of regional significance, the purpose of which was preservation of biodiversity of rare species of animals. In the places where it grows, *Z. latifolia* forms small areas of dense sod (usually no more than 3–5 m^2), blossoms and bears fruits. In our opinion, establishment of this species on new plots of the shorelines of the Pustyn system lakes occurs mostly due to vegetative reproduction – through breakaway of a part of the sod and its transportation via high water down the current of the Seriezha.

Relatively recently, *Bidens frondosa* L. was discovered in the flora of the Pustyn lakes. Similarly to the two other species which grow here (discovered for the first time: *B. cernua* L. – on the territory of the Pustyn lakes in 1981 in the anabranch of Lake Sviato and *B. tripartita* L. – in 1980 on the shore of Lake Velikoe), it is a herbaceous annual plant. The motherland of *B. frondosa* is North America (Lisitsyna et al., 2009). The plant appeared in Europe in 1762, although its active spread in the European continent began only in the second half of the XIX century (Maltseva & Bobrov, 2017). According to Lisitsyna & Artyemenko (1990), by the late 1980s – early 1990s, this species was recorded at Gorky Reservoir and adjacent territories. The plant spreads mainly along the shores of rivers, the main ways of its spread are hydrochory and epizoochory (Maltseva & Bobrov, 2017). Currently, *B. frondosa* occurs quite rarely on drying out areas of the shore line. Apart from Lake Velikoe, the species has been recorded at Lakes Dolgoe and Narbus, and also in different anabranches of the lake-river system. Further, hybridization of these species one with another is possible, as in the case of disappearance of *B. tripartita* from the phytocenses (Lisitsyna et al., 2009). We should mention that from the 1930s to 1970s (inclusive), representatives of the *Bidens* genus were not recorded along the shores of the Pustyn lake-river system.

Over the period of our study, we discovered another new adventive species – *Epilobium adenocaulon* Hausskn. This plant is a North American species distributed in all regions of the Central belt of European Russia (Maevskiy, 2014). Currently, single specimens of the plant have been recorded at the Velikoe, Sviato and Dolgoe lakes. On the shores of the water bodies in the territory of the reserve, three species of *Epilobium* appeared. In the 1970s, at Lakes Velikoe and Sviato, the first records appeared of *E. montanum* L., and in 1980 – at Lake Velikoe – *E. palustre* L., is the most common species now. *E. montanum* is not widely spread and we found it only once on the shore of Lake Parovoe.

We should mention that in 2014–2015, apart from *Lemna minor* L. and *L. trisulca* L. broadly distributed at the Pustyn lakes, we found two more species at Lake Velikoe – *L. gibba* L. (earlier this could have simply been "missed") and *L. turionifera* Landolt. At the same time, *L. turionifera* was described by Landolt (1975) relatively recently for the southern part of Poland. The original range of this plant is within the moderate climate regions of North America and Asia (Landoldt, 1986; Dzhus, 2011). The ability of forming specialized structures – turions which contribute to maintaining the diasporas in the autumn-winter period – makes the plant the most resistant among the species of the section to harsh climates (Dzhus, 2011). The status of the species in Europe is still discussed, though for the continent on the whole, it is considered native (Dzhus, 2011; Kravchenko et al., 2016). In some countries, *L. turionifera* is classified more as alien – "it is presumed that the species is not Holarctic, but American-Siberian, dispersing recently from the Siberia to the west by migrating Anseriformes" (Kravchenko et al., 2016, p. 80).

Apart from low adventive component, the moderate anthropogenic load on the lakes is indicated by presence of such species as *Najas minor* All., *Elodea canadensis* Michx., *Glyceria fluitans* (L.) R. Br., *Iris pseudacorus* L., *Hydrocharis morsus-ranae* L. and *Stratiotes aloides* L. (Dubyna et al., 1993). Singular specimens of *Potamogeton trichoides* Cham. et Schlecht. indicate slow eutrophication of the water bodies. It was no accident that *Elatine alsinastrum, Callitriche hermaphroditica*, as we mentioned above, disappeared over time from the flora of the Velikoe and Parovoe lakes. These plants are indicators of non-polluted aqutic ecosystems (Dubyna et al., 1993). We should mention that the disapperance of certain species of plants from the flora of the lakes, for example *Ranunculus circinatus* Sibth., could be caused by the high extent of accumulation of precipitations in the areas where the plant grows. The prolonged development of the processes of anthropogenic eutrophication of the water bodies is also seen in the presence of *Lemna gibba* and *Spirodela polyrrhiza*, and thickets of *Ceratophyllum demersum* and *Lysimachia thyrsiflora*. In both studied water bodies, many species of plants (for example, *Nuphar lutea*, *Nymphaea candida*, a number of *Potamogeton* species (*P. compressus*, *P. lucens*, *P. perfoliatus* and others), *Alisma plantago-aquatica*, *Sagittaria sagittifolia*, *Schoenoplectus lacustris*, and also species of the *Sparganium* and *Typha* genera) are indicators of eutrophic water bodies.

Current condition of rare and protected species of the flora. In general, the number of rare and protected species in the territory of Nizhny Novgorod oblast (The Red Book…, 2005) in the Pustyn lake-river system has decreased. From the list of the flora of Lakes Velikoe and Parovoe. *Najas major*, *Ceratophyllum platyacanthum*, *Iris sibirica* and *Jacobaea paludosa* subsp. *lanata* (Holub) B. Nord. et Greuter (*Senecio tataricus* Less.) have disappeared, from the flora of Lake Parovoe *Najas minor*, *Potamogeton praelongus* and *P. trichoides* have disappeared.

Ceratophyllum platyacanthum Cham. et Schlecht. (*C. pentacanthum* Haynald, *C. demersum* L. subsp. *platyacanthum* (Cham.) Nym.) was collected for the first time in the territory of the Pustyn lake-river system by A. D. Smirnova in August 1939. Studying the specimens, Smirnova & Nikitina (1972, p. 354) mention that the collected plants "have fruits with three-four spikes and two rounded projections, but have no clearly seen wings, therefore correspond to the name *C. penthacanthum*, rather than *C. platyacanthum*". A well known specimen of *C. platyacanthum*, collected by E. V. Lukina and E. L. Khazova is dated 13 July 1981 [Staraia Pustyn village of Arzamassky district of Gorky oblast, south shore of Lake Velikoe (MW, № 2516)]. This species is very rare in the territory of the Volga basin, occurs in Moscow, Nizhny Novgorod, Samara, Saratov, Vologda and Astrakhan oblasts (Lisitsyna et al., 2009). We should mention that currently, the nearest place where the plant is reliably known to grow is in the territory of Republic of Mordovia (Temnikovsky District, Mordovia State Reserve named after P. G. Smidovich) 106 km south-east of the Pustyn lakes at Lake Taratinskoe (MW, GMU, HMNR; Vargot et al., 2012). Plants with fruits were found in 2011.

We made some interesting observations of representatives of *Najas* L. genus. At Lake Velikoe there still remains a place where *Najas minor* All. – a Eurasian (Gubanov et al., 2002), a relic species, grows. The northern border of its range crosses the territory of Nizhny Novgorod oblast (Birykova et al., 2017). Here, *N. minor* was recorded from 1963, but from 1999 there was a gap in the data on places where it grows. Only in the summer of 2014, was *N. minor* found in the anabranch between Lake Velikoe (Shyrokoe) and Lake Sviato, and also in Lake Dolgoe lake (Birykova et al., 2017). In 2015, it was found on a sand spit formed by aggradation of sand in the place where the Seryozha flows into Lake Velikoe, where it was earlier found by E. V. Lukina in 1966 (NNSU). At Lake Parovoe, the *N. minor* population seemed to have disappeared. However, this species was collected on a single occasion by A. I. Shyrokov in August 1963. Along with brittle naiad, the Pustyn system of lakes also has *Najas major* All. – a relic species with a mostly European range (Gubanov et al., 2002). It was recorded for the first time at Lake Parovoe in 1939 as *N. marina* L. (Belyakov et al., 2015). On a single occasion, E. V. Lukina (Lukina, 1970 – in: Smirnova et al., 1975) mentioned spiny naiad also for Lake Velikoe. Currently, it seems that some populations of this species remain only at Lake Dolgoe (Belyakov et al., 2015). Both species of *Najas* have a pulsating dynamic of growth by years, which is demonstrated by the results of our studies (Birykova et al., 2017).

In 1939 at Lake Parovoe and in 1980 at Lake Velikoe, *Iris sibirica* L. (Smirnova et al., 1975; Lukina, 1982) was observed, which has not been found recently. Lisitsyna et al. (2009) do not mention this species for the flora of the water bodies of the Volga basin. Perhaps, the plant disappeared from the flora of the lakes due to the locals who were replanting it in their private plots.

As we mentioned before, a population of *Potamogeton praelongus* Wulf. still remains at Lake Velikoe; we also found single plants of *Potamogeton trichoides* Cham. et Schltdl. The first species is common in the moderate climate zone of the northern hemisphere (Gubanov et al., 2002; Maevskiy, 2014). It has been recorded many times both at Lake Velikoe and Lake. S. P. Urbanavichute (The Red Book…, 2005, p. 78) mentions that the abundance of this plant in the water bodies of Nizhny Novgorod oblast is not constant and often changes – increases or decreases in the number of specimens. In 1939 at Lake Parovoe, this species formed small communities, and by 1965–1975 it was recorded only as single specimens (Smirnova et al., 1975). A decrease in the number of specimens of this species was also mentioned in 1980 at Lake Velikoe (Lukina, 1982). Currently, this plant persists as single shoots along the eastern shore in thickets of *Nuphar lutea* (L.) Sm. (Belyakov et al., 2017). The species prefers water bodies with still or slowly flowing cold clean and highly mineralized water (Lisitsyna et al., 2009), and is often found at considerable depths (Gubanov et al., 2002). Therefore, the decrease in the number of this species at Lake Velikoe and its disappearance from Lake Parovoe can be related to decrease in the water level regime and rise in water temperature. *Potamogeton trichoides* Cham. et Schltdl. is mostly European (Maevskiy, 2014) not stable in competition (Lisitsyna et al., 2009), the species was recorded in 1939 at Lake Parovoe (Smirnova et al., 1975), and in 1980 at Lake Velikoe (Lukina, 1982). In 2014, we recorded this plant also for Lake Dolgoe. However, the species was not found during a detailed survey of this water body in 2015. Also, this plant is a vegetative short-lived perennial plant, the peculiarities of its biology require detailed study.

Analysis of the main ecological factors which caused the change in the flora diversity of the studied water bodies. The observed changes in the composition of the aquatic and shoreline-aquatic plant flora, in our opinion, could be caused by the complex of the following factors: 1) anthropogenic impact on the studied ecosystems and 2) natural successional processes related to radical changes in the conditions of formation of the water flow in the basin of the Volga (Belyakov et al., 2017). Since 1962, in the territory of Lake Velikoe , for practical measures, a water intake facility was built, the active work of which led to decrease in the water level regime and flowage of not only Lake Velikoe, but all lakes located downstream of the Seryozha (including Lake Parovoe) (Lukina, 1982). It seems that this could be the reason for increase in the pH level from 6.6 to 7.2 (Lukina, 1982). In the summer of 2015, in some plant groups (in the period of water bloom), the pH of the surface water layer reached 8.0–8.4. All this contributed to increase in trophicity of the water bodies. We should mention that use of the water resources by humans leads not only to increase in the range of annual and interannual fluctuations of water level, but to change in the timing of minimum and maximum levels (including change in the tempi of increase and decrease in the water level) (Wantzen et al., 2008; Zohary & Ostrovsky, 2011). Besides, there are data that frequent fluctuations in the water regime can decrease the functioning of the ecosystem, causing decrease in the water transparency (Coops et al., 2003; Beklioglu et al., 2007; Xu et al., 2011). The latter, as we know, has a negative effect on growth and development of aquatic plants and their communities (Riis & Hawes, 2002; Zhang et al., 2015). To be able to survive in such conditions, plants have to have structures which allow them to form a reserve of nutrients (for example, large root systems or tubers) which in turn would allow them to restore the vegetative parts (especially during the spring season).

However, some researchers (Bornette et al., 1994; Higgins & Cain, 2002; Riis & Hawes, 2002; Lenssen & de Kroon, 2005; Peintinger et al., 2007; Wang et al., 2016) suggest that moderate changes which occur during the functioning of biosystems are in some cases useful for retaining species diversity. The effect of such changes can positively affect the colonizing ability of species (Higgins & Cain, 2002). Indeed, some researchers (Belote et al., 2012; Franklin et al., 2016) agree that active impact on an ecosystem will ultimately have a negative effect on plant communities. For example, significant fluctuations in the water level decrease growth and development, and therefore the colonizing ability of *Phragmites australis* (Vretare et al., 2001), whereas a stable level regime contributes to the growth of this plant (Deegan et al., 2007). A similar feature was also observed for other macrophytes, for example *Myriophyllum spicatum* (Zhang et al., 2013).

Currently, the water intake at Lake Velikoe does not function at great intensity and the water regime of the studied lakes mostly depends on natural-climatic factors which determine the volumes of the incoming (from the Seryozha, the water intake area and accumulation of precipitation, etc) and lost (natural flow, wind speed and the evaporation intensity) water (Zohary & Ostrovsky, 2011). Regarding this aspect, we made some interesting observations on the dynamic of *Oenanthe aquatica* (L.) Poir., the abundance of which at the water bodies of the Pustyn system changes from year to year. In August during the dry year 2014, we found separate plants of this species, and found massive development of the specimens of generative origin along the shores. In early July of the wet year 2015, we observed massive blossoming of *Oe. aquatica* which formed large plant groups. Therefore, the abundance of this species varies from year to year and depends on the water level regime. The indicators of changes in the water level regime here can also be species which are able to form different ecomorphs (morphological flexibility) and redistribute biomass (Yu & Yu, 2009; Cao et al., 2012; Zhang et al., 2013), for example, such plants as *Sparganium emersum*, *Sagittaria sagittifolia*, *Persicaria amphibia*, *Glyceria fluitans* and others. At the same time, plants which are not able to survive frequent and long periods of fluctuations in the water level due to absence of characteristic morphological and physiological adaptations disappear from the flora of water bodies (Zhang et al., 2013; Luo et al., 2016).

Conclusion

Over a long period of monitoring, 46 species have disappeared from the flora of Lake Velikoe and 31 from that of Lake Parovoe. The number of species found for the first time in these water bodies is 21 and 9 species respectively. Species which have disappeared from both studied lakes include representatives of the *Elatine* L., *Callitriche* L genera, some *Potamogeton* species (*P. pusillus* and *P. pectinatus*), *Utricularia minor* and a number of other plants. Also, we found several species which belong to the adventive component of the flora – *Elodea canadensis* Michx., *Zizania latifolia* (Griseb.) Stapf., *Bidens frondosa* L. and *Epilobium adenocaulon* Hausskn. We found an increase in the number of Poaceae species and weeds which belong to the *Epilobium*, *Chenopodium*, *Bidens*, *Polygonum* and *Rumex* genera. No significant changes were found in the pattern of distribution of *Phragmites australis*, *Scolochloa festucacea*, *Nuphar lutea* and *Potamogeton lucens*, the relic of the tertiary flora – *Trapa natans* turns out to be widely distributed (especially in recent years). The number of rare and protected species in both water bodies decreased, such species as *Ceratophyllum platyacanthum*, *Iris sibirica* and *Jacobaea paludosa* subsp. *lanata* (Holub) B. Nord. et Greuter (*Senecio tataricus* Less.) and others have disappeared.

We found that the balanced ratio between the shoreline and aquatic plants in the current flora of Lake Parovoe indicates a certain successional stability of its floristic complex, which could not be said regarding the flora composition of Lake Velikoe. The lower seral stability of Lake Velikoe over the last few years is indicated by the decrease in the taxonomic diversity of its flora. The saturation of the flora of Velikoe and Parovoe lakes with adventive species is also extremely low, which could indicate that both water bodies are affected by moderate anthropogenic transformation. The anthropogenic load is also manifested in large share of grasses in the flora of the lakes. Besides, a clear domination of a number of macrophytes in the lakes` flora was recorded, which are indicators of eutrophic condition of the water bodies.

The current flora of Lake Velikoe is represented by 100 species of 2 orders, 32 families and 63 genera, whereas the flora of Lake Parovoe includes 87 species of 2 orders, 37 families and 64 genera. The specificity of each studied lake indicates a non-uniform distribution of species (into different groups), which depends, first of all, on morphometric characteristics (including the width of the shallow water area of the lake), physical-chemical properties of the water environment, and also the pattern of anthropogenic load on the water objects. The thesis about specificity of the flora of Velikoe and Parovoe lakes is substantiated by particular peculiarrities in the structure of taxonomic groups over different periods of study.

Thus, over a long period of monitoring, the vegetative cover of the lakes has significantly transformed due to disappearance of a number of native species and appearance of adventive plants. Also, the studied water bodies are affected by further increase in the extent of eutrophication. The increase in the parameters of trophicity of the water bodies during a long period resulted from a combination of anthropogenic impact (active water intake which causes decrease in the level regime of the water bodies), natural-climatic peculiarities of the region (alternation of wet and dry periods) and natural successional processes related to the current radical changes in the conditions of formation of the flow in the Volga basin.

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