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RESEARCH ARTICLE

Effects of water levels on species diversity of silica-scaled chrysophytes in large tributaries of Lake Baikal

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Abstract
Large tributaries of Lake Baikal considered as a "hotspot" for silica-scaled chrysophytes diversity. Here we presented the updated species composition of silica-scaled chrysophytes and ecological parameters of their habitat in the Barguzin and Selenga River tributaries and delta in a high water level period. The number of registered taxa was significantly lower compared to the low water conditions (23 versus 66 species) and included the following genera with a given number of species: *Chrysosphaerella* – 1; *Paraphysomonas* – 2; *Clathromonas* – 1; *Spiniferomonas* – 3; *Mallomonas* – 9; *Synura* – 7. *Mallomonas guttata* and *Synura borealis* were identified in Russian waters for the first time. Thus, the corrected total list of silica-scaled chrysophytes in the Baikal Region includes 79 taxa. Though, the high water level reduced the total number of silica-scaled chrysophyte taxa, it made the water ecosystem more dynamic by enriching it with the entirely new species for this region.

Keywords
Barguzin River, high water level, hydrochemistry, Lake Baikal, Selenga River, silica-scaled chrysophytes

Introduction

Lake Baikal is the most ancient and deepest (1637 m) lake in the world (Baikal. Atlas 1993). It has a tectonic origin and lies in a deep depression surrounded by mountain chains. Baikal ranks first with regards to the diversity of many groups of organisms (Mazepova et al. 1995; Timoshkin 2004).

Chrysophytes, whose cells are covered with scaled siliceous frustule, belong to the class of Chrysophyceae Pascher, families of Chromulinaceae Engler, Paraphysomonadaceae Preisig & Hibberd, Mallomonadaceae Diesing and Synuraceae Lemmermann; they include approximately 250 species and intraspecific taxa (Kristiansen and Škaloud 2017). They are very sensitive to changes in the habitat and considered to be the biological indicators (Siver 1995; Siver and Lott 2017; Wolfe and Siver 2013). The growth of populations of silica-scaled chrysophytes in some boreal and arctic lakes of North America and Canada during the last decades (Ginn et al. 2010; Mushet et al. 2017; Wolfe and Siver 2013) is thought to be related with global climate change and increasing CO2 concentrations (Paterson et al. 2008; Rühland et al. 2008; Schindler 2001). Diatoms in the Holocene and the Upper Pleistocene deposits of Lake Baikal show the same response to global warming (Bezrukova et al. 1991; Bradbury et al. 1994; Grachev et al. 1997; Khursevich et al. 2001). The valves of diatoms, as well as the stomatocysts of chrysophytes, are used as indicator of climate and trophic changes in Lake Baikal (Edlund et al. 1995; Khursevich et al. 2001; Likhoshway 1999; Stoermer et al. 1995) and other waters worldwide (Adam and Mahood 1981; Cronberg 1980; Smol 1985; Duff et al. 1995; Kristiansen 2005; Kristiansen and Škaloud 2017).

The effect of global warming was reported in the Baikal Region in early 1970s and caused deglaciation of degrading permafrost rock and an episodic increase of the Baikal tributaries run-off (Shimaraev et al. 2002; Sinyukovich et al. 2010; Sorokovikova et al. 2015). Since 1996, the catchment area of Lake Baikal and especially of the Selenga River has been characterized by a low water level, high water temperature in the summer, low stream velocities and changes in concentrations of chemical components (Sorokovikova et al. 2017). This period has been marked with high diversity of silica-scaled chrysophytes. Seventy-six species and intraspecific taxa have been identified in Lake Baikal (Bessudova et al. 2017), specifically in the mouth areas of its main tributaries: the Selenga and the Barguzin Rivers (Bessudova et al. 2018a), the Upper Angara River and the Kichera River, and in three mouths (Dushkachanskoye, Sredneye, and Dagarskoye) of the Angara-Kichera Delta (Bessudova et al. 2018b). According to the terminology of Němcová et al. (2012), the Baikal Region can be considered to be a “hotspot” of silica-scaled chrysophyte diversity. Lake Baikal ranks first in number of hydrobionts, but neither high diversity nor new species of silica-scaled chrysophytes have been found in the limnetic pelagic zone during the seasonal and interannual studies. The species composition of silica-scaled chrysophytes includes only 25 species and intraspecific taxa (Bessudova et al. 2017).

Changes in water level, temperature, stream velocity, nutrient concentration, and suspended matter content impact the abundance, biomass, and diversity of phytoplankton in the Selenga River and its tributaries (Popovskaya and Tashlykova 2008; Sorokovikova et al. 2009, 2017). Thus, the lowest values of phytoplankton abundance and species diversity were recorded during the flood in July 2013 (Sorokovikova et al. 2017). The aim of our study was to investigate the impact of the high water level in July 2018 on the flora of silica-scaled chrysophytes in the Selenga and Barguzin River with their tributaries. We also compared the species composition in the tributaries under high and low water conditions.

Description of the area

The studied waterbodies are located in Russia, specifically in the south of East Siberia in the Republic of Buryatia (50°70'–53°82' N and 106°25'–109°90' E). They include the Selenga River, the mouth of the Kharauz Creek of the Selenga Delta, Lake Zavernyaikha, the Dzhida, the Temnik and Chikoy tributaries of the Selenga River, and the upstream portion of the Barguzin River (upward of the Ulyun River) with its mouth (Fig. 1).

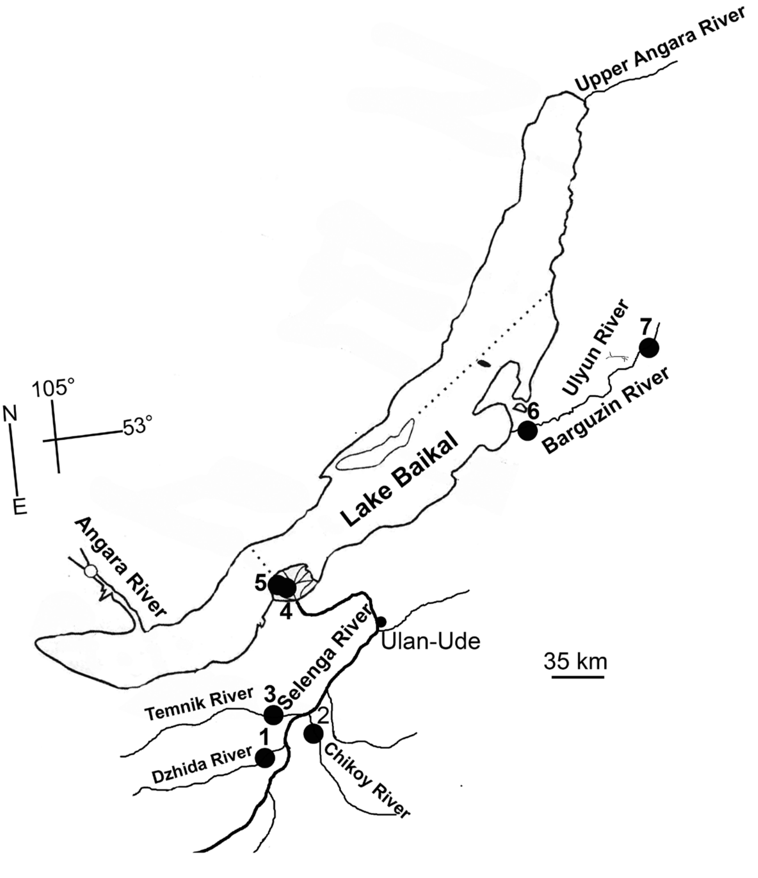

Figure 1. Map of the study area and location of sampling stations: 1 – Dzhida River; 2 – Chikoy River; 3 – Temnik River; 4 – Lake Zavernyaikha; 5 – Selenga River, mouth of the Kharauz Creek; 6 – Barguzin River upward of the Ulyun River; 7 – mouth of the Barguzin River.

The catchment area of the Selenga River (the main tributary of Lake Baikal) is primarily located in Mongolia, but its run-off is mainly formed in Russia. It increases three times in size from the Russian-Mongolian border to the mouth. The high altitude of the watershed and its significant slope formed the mountainous character of studied tributaries. The most full-flowing river is the Chikoy River (the right tributary of the Selenga River); its annual average run-off is 267 m3/s. The Dzhida and Temnik Rivers fall from the left bank; their run-off is significantly lower – 67.6 and 29.9 m3/s, respectively (Sinyukovich 2005). The Selenga River forms a large delta that includes many creeks, lakes, and former riverbeds (Baikal. Atlas 1993). The Kharauz Creek is one of the largest in the delta. Lake Zavernyaikha is located in the Selenga Delta and is cut off the Kharauz Creek by a sand bar. During the floods and high water conditions, the lake is connected to the creek and thus has a good turnover. In winter and low water conditions, the lake is isolated from the creek (Popovskaya et al. 2011).

The Barguzin River is a tributary of Lake Baikal. Its run-off is the third largest by volume (after the Selenga and Upper Angara Rivers). At the upper reaches, this river is an impetuous mountain torrent that flows through a narrow gorge. When it enters into the Barguzin depression, the river flows on a broad valley and becomes a plain. Low parts of the flood plain have plenty of shallow eutrophic lakes and wetlands that are connected by a system of channels that provide the river with organic matter and other substances (Drucker et al. 1997).

Specimens were deposited in the following collection: MCTP, Coleção de Aracnídeos, Porto Alegre (curator: Renato Augusto Teixeira) and the Smithsonian Museum of Natural History (SMNH), Arachnida and Myriapoda collection, Washington DC (curator: Hannah Wood). We attempted DNA extraction and amplification of DNA barcodes from legs of borrowed specimens preserved in ethanol, however this yielded no viable DNA.

Material and methods

We obtained the samples from the Selenga tributaries (Dzhida, Temnik and Chikoy), the Kharauz Creek and Lake Zavernyaikha in the Selenga delta and the Barguzin River (mouth and upward of the Ulyun River) in July 2018. Fourteen samples were used for analysis of the silica-scaled chrysophytes (Fig. 1).

We used portable pH meter (IT-1101; Russia) to measure pH, water temperature, and dissolved oxygen concentrations at the sampling sites (Manual for chemical analysis of inland surface waters, 2009). We filtered the samples for chemical analyses through 0.45 μm membrane filters (Advantec, Japan) and measured the conductivity at 25°C with a conductometer DS-12 (Horiba, Japan). We also used colourimetric and dichromate oxidisability (COD – chemical oxygen demand) methods to determine the nutrient concentrations and total organic matter content, respectively (Manual for chemical analysis of inland surface waters 2009); Wetzel and Likens 2003).

We took the algal samples from the surface layer of water (0 m) with a 1 L water sampler and fixed with Lugol's solution (1% f.c.). We also took 10–15 mL samples by means of Whatman membrane filters (pore size 1 µm, Whatman, USA). We identify the scaled chrysophytes using scanning and transmission electron microscopy. The samples for SEM analysis were filtered, dried at room temperature, coated with gold and examined using a Quanta 200 (FEI Company, USA) scanning electron microscope. The samples for TEM analysis were taken with water sampler, settled by the sedimentation method (Kuzmin 1975), centrifuged (MiniSpin, Eppendorf, Germany) and washed in deionized water. The washed samples were processed with 30% H2O2 at 75°C for 2 h, than the procedure was repeated and the samples were put on 3-mm-diameter formvar coated grids, dried at room temperature and analyzed by means of a LEO 906E transmission electron microscope (Carl Zeiss, Germany). The scales identified by means of electron microscopy classified the certain species according to their fine structure described and represented by microphotographs (Siver 1988; Hällfors and Hällfors 1988; Siver 1995; Němcová et al. 2012; Škaloud et al. 2012; Scoble and Cavalier-Smith 2014; Siver 2015). We also used the Freshwater Algal Database of Škaloud et al. (2013). Data on river flow rates were retrieved from Hydrometeorological Research Center of Russian Federation (Hydrometcenter of Russia).

Results

Physical and chemical characteristics of the studied waterbodies

In July 2018, a continuous low water period in the catchment area of Lake Baikal ended when the Selenga and Barguzin Rivers rose and flooded their flood plains. Water discharge of the Barguzin and the Selenga Rivers during the sampling was up to 358 m^3/s and 1700 m^3/s, respectively (Table 1). It was 1.5–2 fold higher than in 2016 (Fig. 2).

The water temperature in the Selenga and its tributaries was 18.5–20.9°C (Table 1); it varied from 10.2°C in the upper reaches of the Barguzin River (station 7) up to 20.9°C in its mouth (station 6). High pH values were recorded in Lake Zavernyaikha (station 4), the Kharauz Creek (station 5) and at the upper reaches of the Barguzin River (station 7); the lowest pH was recorded in the Chikoy River (station 2). The highest conductivity of 228 µS cm−1 was observed in the Dzhida River (station 1); the lowest conductivity of 58 µS cm−1 was registered in the Chikoy River (station 2; Table 1). The dissolved oxygen content varied over a wide range (Table 1).

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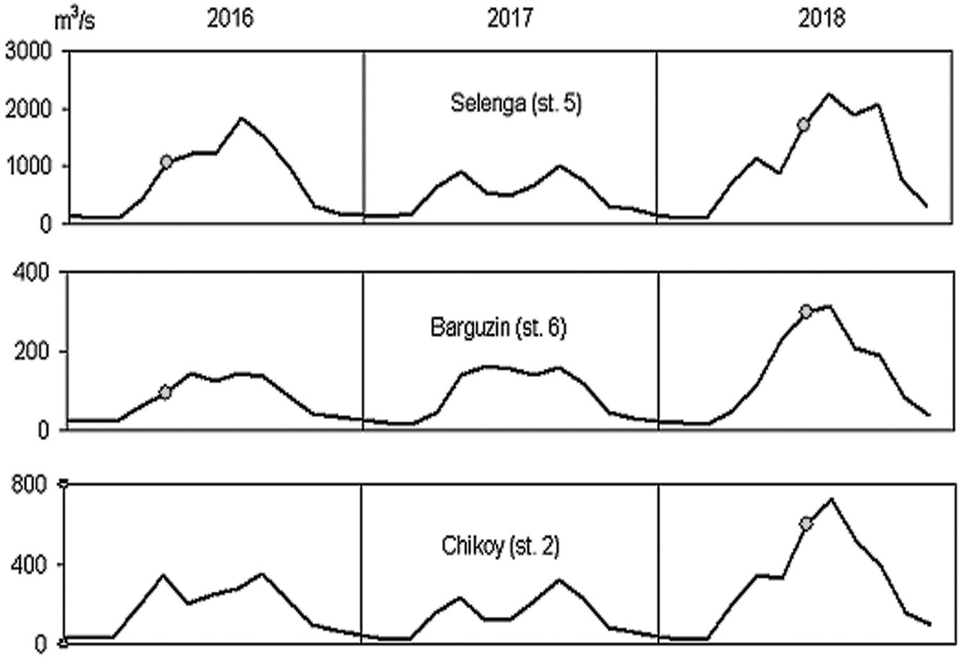

Figure 2. Changes of water discharge in the main tributaries. The ring indicates the water discharge during the sampling.

Table 1. Physical and chemical characteristics of water in investigated habitats.

Site	T, °C	pH	O_2, mg/L	Si, mg/L	$P_{total.}$ µ/L	COD, mg/L	Conductivity, µs cm^{-1}	Water content, date, water discharge, m^3/s	Refs
Dzhida R.	19.0	8.0	7.8	4.18	125	17.5	228	high water July 2018. 267	this study
Chikoy R.	18.5	7.39	8.5	4.88	115	13.0	58	high water July 2018 684	this study
Temnik R.	19.1	7.61	9.8	3.28	16	6.5	92	high water July 2018 46.0	this study
L. Zaver nyaikha	20.9	8.15	8.9	3.79	63	14.7	148	high water July 2018 1700	this study
	11	8.01	11	2.4	62	-	166	low water May 2016 1050	(Bessudova et al. 2018b)

Site	T, °C	pH	$O_{2,}$ mg/L	Si, mg/L	$P_{total.}$ µ/L	COD, mg/L	Conductivity, µs cm^{-1}	Water content, date, water discharge, m^3/s	Refs
Selenga R. Kharauz Cr.	20.5	8.15	8.1	4.63	123	17.4	143	high water July 2018 1700	this study
	12	7.99	9.9	3.2	76	-	143	low water July 2016 1050	(Bessudova et al. 2018a)
Barguzin R. mouth	20.9	7.87	5.6	3.1	89	23.0	174	high water July 2018 358	this study
	10	7.83	-	3.3	96	-	151	low water May 2016 138	(Bessudova et al. 2018a)
Barguzin R. upwards Ulyun R.	10.2	8.27	10.2	2.28	20	16.4	171	high water July 2018 166	this study

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The crossflow of water from the Kharauz Creek (station 5) to Lake Zavernyaikha (station 4) caused by the high water level of the Selenga River levelled the oxygen content, water temperature, pH, and conductivity at these stations.

The upper reaches of the Barguzin River (station 7) showed an increased oxygen concentration due to its better solubility in cold water and aeration due to the higher stream speed. The lowest oxygen concentration was registered in the river mouth (station 6). The concentration of silicon was high at all stations (Table 1).

The inundation of the flood plains enriched the rivers with a large amount of organic matter from the catchment area and increased its water concentration. The highest concentrations were recorded in the mouth of the Barguzin River (station 6), Dzhida River (station 1), and Kharauz Creek (station 5). The total phosphorous values at all stations (except 3 and 7) were typical for polluted eutrophic waters.

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Silica-scaled chrysophytes

Twenty-three species and intraspecific taxa, namely *Chrysosphaerella* – 1, *Paraphysomonas* – 2, *Clathromonas* – 1, *Spiniferomonas* – 3, *Mallomonas* – 9, and *Synura* – 7 species, were identified during the microscopic analysis of the samples taken in July 2018 (Table 2; Figs. 3, 4).

Only seven species were identified in the Selenga tributaries Chikoy (station 1) and Dzhida (station 2), six species were recorded in the Temnik River (station 3). No chrysophytes were found in Lake Zavernyaikha (station 4) and the upper reaches of the Barguzin River upward of the Ulyun River (station 7; Table 2).

During the high water period, the chrysophyte flora was mainly represented by widespread and cosmopolitan species typical in the temperate and subarctic regions of Eurasia and North America. A total of 16 species were identified: *Spiniferomonas cornuta*, *S. serrata*, *S. trioralis*, *Mallomonas acaroides*, *M. akrokomos*, *M. alpina*, *M. crassisquama*, *M. heterospina*, *M. guttata*, *M. striata*, *M. tonsurata*, *Synura echinulata*, *S. glabra*, *S. petersenii*, *S. spinosa*, and *S. uvella*.

Although the species composition varied in all waterbodies, two widespread species *M. tonsurata* and *S. petersenii* occurred everywhere. A single scale attributed to the genus *Clathromonas* was found in the mouth of the Barguzin River (station 6), but it was impossible to identify it to a species (Fig. 4e). It may belong to the species *Clathromonas poteriophora* (Moestrup & Kristiansen) Scoble & Cavalier-Smith, which was previously observed in the area (Bessudova et al. 2018a). Notably, four (*Chrysosphaerella baicalensis*, *Mallomonas guttata*, *S. serrata* and *Synura borealis*) of these 23 species were not previously identified either in the Selenga River (villages of Kabansk and Murzino) and the creeks of its delta or in the mouth of the Barguzin River. Two species were already described in the Baikal Region: *C. baicalensis* in Lake Baikal (Bessudova et al. 2017) and *S. serrata* in the Upper Angara River and in the mouths of the Dushkachan and Dagar Creeks of the Angara-Kichera Delta (Bessudova et al. 2018b). Two (*M. guttata* and *S. borealis*) of these four species were discovered for the first time in the Baikal Region as well as Russia.

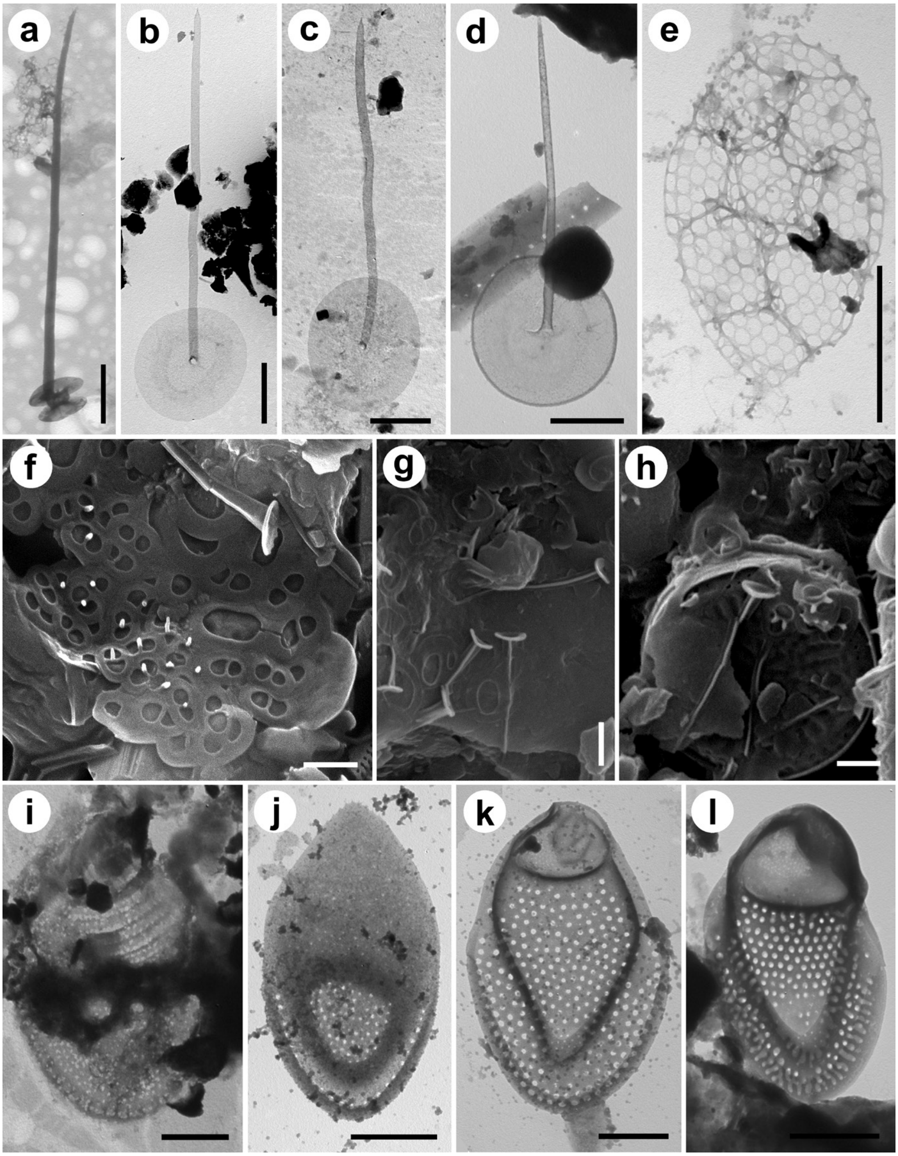

Figure 3. Scales and spines of silica-scaled chrysophytes of the genera Chrysosphaerella, Paraphysomonas, Spiniferomonas and Mallomonas; a – *Chrysosphaerella baicalensis* (Temnik River, station 3), b, c – *Paraphysomonas acuminata acuminata* (Chikoy River, station 2), d – *Paraphysomonas vulgaris* (Temnik River, station 3), e – *Clathromonas* sp. (mouth of the Barguzin River, station 6), f – *Spiniferomonas serrata* (mouth of the Kharauz Creek, station 5), g – *Spiniferomonas trioralis* (Chikoy River, station 2), h – *Spiniferomonas cornuta* (mouth of the Barguzin River, station 6), i *Mallomonas trummensis* (mouth of the Barguzin River, station 6), j – *Mallomonas akrokomos* (Dzhida River, station 1), k – *Mallomonas alpina* (Temnik River, station 3), l – *Mallomonas tonsurata* (Temnik River, station 3). Micrographs were obtained with scanning electron microscopy (f–h) or transmission electron microscopy (a–e, i–l). Scale bars are: 0.5 µm (e), 1 µm (a–d, f–l).

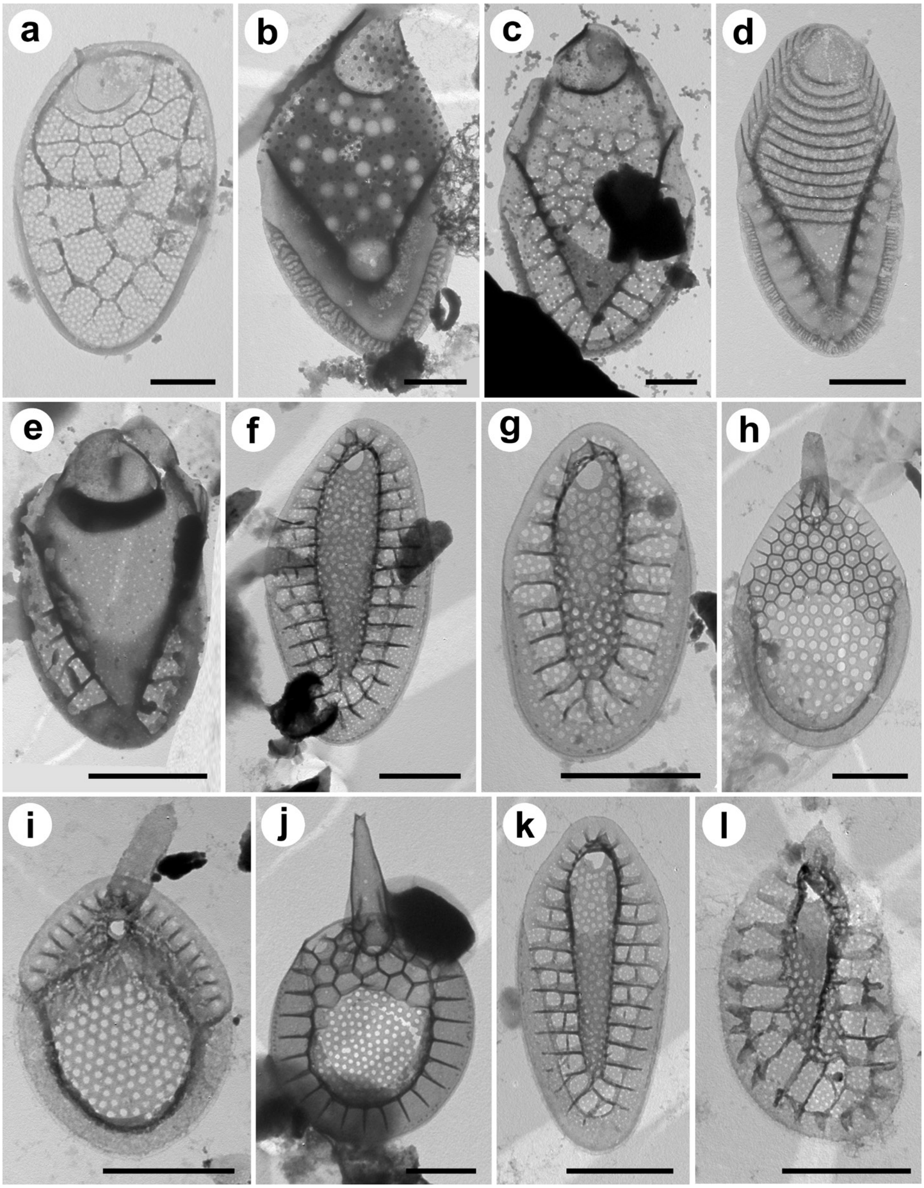

Figure 4. Scales and spines of silica-scaled chrysophytes of the genera Mallomonas and Synura; a – *Mallomonas heterospina* (Chikoy River, station 2), b – *Mallomonas guttata* (mouth of the Barguzin River, station 6), c – *Mallomonas crassisquama* (Temnik River, station 3), d – *Mallomonas striata* (mouth of the Kharauz Creek, station 5), e – *Mallomonas acaroides* (mouth of the Barguzin River, station 6), f – *Synura borealis* (mouth of the Barguzin River, station 6), g – *Synura heteropora* (Chikoy River, station 2), h – *Synura spinosa* (Dzhida River, station 1), I – *Synura echinulata* (mouth of the Barguzin River, station 6), j – *Synura uvella* (mouth of the Barguzin River, station 6), k – *Synura petersenii* (Temnik River, station 3), l – *Synura glabra* (mouth of the Barguzin River, station 6). Micrographs were obtained with transmission electron microscopy; scale bars are 1 μm.

Table 2. List of species and intraspecific taxa of the silica-scaled chrysophytes identified by electron microscopy in the Selenga tributaries and Barguzin River area in July 2018. See Fig. 1 for the location of the stations. A plus (+) indicates the presences of the species at the station. The asterisk (*) indicates the species observed in the Baikal Region for the first time.

Species	**Station**						
	1	**2**	**3**	**4**	**5**	**6**	**7**
Chrysosphaerella cf. *baicalensis* Popovskaya			+				
Paraphysomonas acuminata acuminata Scoble & Cavalier-Smith	+	+					
P. vulgaris Scoble & Cavalier-Smith			+				
Clathromonas sp.						+	
Spiniferomonas cornuta Balonov					+		
S. serrata Nicholls					+		
S. trioralis Takahashi		+					
Mallomonas acaroides Perty						+	
M. akrokomos Ruttner	+					+	
M. alpina Pascher & Ruttner	+		+			+	
M. crassisquama (Asmund) Fott			+				
M. guttata Wujek*						+	
M. heterospina Lund		+					
M. striata Asmund		+			+	+	
M. tonsurata Teiling	+	+	+		+	+	
M. trummensis Cronberg						+	
Synura echinulata Korshikov						+	
S. borealis Škaloud & Škaloudová *	+					+	
S. glabra Korshikov						+	
S. heteropora Skaloud, Skaloudová & Procházková in Skaloud et al.		+					
S. petersenii Korshikov	+	+	+		+	+	
S. spinosa Korshikov	+					+	
S. uvella Ehrenberg						+	
Total	7	7	6	0	5	14	0

Discussion

Biogeographical structure of silica-scaled chrysophytes of the studied area

The flooding on the Selenga and Barguzin Rivers decreased the species diversity of silica-scaled chrysophytes (23 species) versus 66 species observed before this study-during the low water period (Bessudova et al. 2018a). Although the chrysophyte species diversity decreased almost threefold, their biogeographical distribution changed proportionally (Table 3).

Table 3. Changes in geographical distribution of silica-scaled chrysophytes according to J. Kristiansen (2000, 2008) towards water level.

geographical distribution	low water (Bessudova et al. 2018a)	high water (present study)
cosmopolitan	27%	35%
widely distributed	33%	30%
scattered	11%	4%
endemic	0%	4%
arcto-boreal	26%	22%
unknown, the species were identified only to the genus level	3%	4%

Three species identified during this study rarely occur in Russian waters. One of them, *C. baicalensis*, is endemic to Lake Baikal, and two are arctoboreal species: *Paraphysomonas acuminata acuminata* and *Paraphysomonas vulgaris*.

C. baicalensis, previously described by Popovskaya (1981), occurs in Lake Baikal and occasionally forms colonies in the ice (March-April) and open water (May-June; Bessudova et al. 2017; Popovskaya 1981; Vorobyova et al. 1992). This species was identified in the Temnik River (station 3).

P. acuminata acuminata was found and described in one Austrian freshwater lake (Scoble and Cavalier-Smith 2014). We identified the species in the mouth of the guzin River, the creeks of the Selenga Delta (including Lake Zavernyaikha; Bessudova et al. 2018a), Lake Baikal (Bessudova et al. 2017) and in the mouth of the Srednyaya Creek of the Angara-Kichera Delta (Bessudova et al. 2018b). This species occurs in spring, summer and autumn, while most numerous in May. During this study, the species was found in the Dzhida (station 1) and the Chikoy (station 2) Rivers.

P. vulgaris was found and described in freshwaters of England (Scoble and Cavalier-Smith 2014). To date, this species has been identified in the mouth of the Barguzin River and the Selenga tributaries (Bessudova et al. 2018a). A spine morphologically similar to those of *P. vulgaris* was also found in Lake Toko, Japan (see Gusev et al. 2018, fig. 39). During this study, *P. vulgaris* was registered in the Temnik River (station 3). Two species, *Mallomonas trummensis* and *S. heteropora,* have a limited distribution in Russian waters. *M. trummensis* occurs in waters of the temperate and subarctic zones of Europe (Škaloud et al. 2013).

In Russia, the species was identified only in the mouth of the Barguzin River and the creeks of the Selenga Delta (Bessudova et al. 2018a). Here, we found it only at one station, namely the mouth of the Barguzin River (Station 6). *S. heteropora* occurs in waters of Europe (Škaloud et al. 2014), but in Russia it was previously observed only in Lake Baikal (Bessudova et al. 2017), the mouth of the Barguzin River and the creeks of the Selenga Delta (Bessudova et al. 2018a). During the present study, *S. heteropora* scales occurred only in the Chikoy River (station 2).

Ecology of silica-scaled chrysophytes

The studied area is interesting not only to study the effect of floods on species composition of silica-scaled chrysophytes, but also to evaluate the impact on species ecology. The water parameters in study area during the low and high water levels were in a sharp contrast with the optimum for high diversity of silica-scaled chrysophyte (Eloranta 1995; Kristiansen 2005; Siver 1995; Siver and Lott 2017).

The highest silica-scaled chrysophyte diversity has been recorded in waters with pH low or close to neutral (below 7), low mineralization, conductivity close to or slightly less than 40 µs cm^{-1}, low nutrient content (oligotrophic to mesotrophic), and moderate quantity of dissolved humic compounds (Eloranta 1995; Kristiansen 2005; Němcova et al. 2003; Siver 1995; Siver and Lott 2017). A recent study in Newfoundland Island corroborated high silica-scaled chrysophyte diversity (47 species) in waters with pH 3.9–6.7, high content of humic substances and low nutrient concentration (Siver and Lott 2017).

Numerous studies allowed Siver (2015) to divide the silica-scaled chrysophytes into four groups with congruent boundaries along a pH gradient: (1) species that inhabit waters with a low pH (below 6); (2) species that inhabit waters with modern levels of alkalinity (pH below 7 but above 5); (3) species that inhabit waters with a neutral pH (pH-indifferent species), (4) species that inhabit waters with a high pH (above 7). One species, *S. echinulata* despite their affiliation with the low pH group, was found in waters with high pH (7.87; station 6). *S. echinulata* was previously observed in the Selenga Delta and Lake Zavernyaikha at pH 8.01 and 8.03, respectively (Bessudova et al. 2018a). We also found two species characteristic to average waters: *M. heterospina* (station 2) observed at pH 7.39 and *S. spinosa* (stations 1 and 6) observed at pH 7.87 and 8.0, respectively. *M. heterospina* was previously identified in the Selenga River and in creeks of its delta at high pH values (7.85 and 7.98), but it was erroneously identified as *Mallomonas pugio* Bradley (Bessudova et al. 2018a). *S. spinosa* was also previously observed in the Selenga River and in delta creeks at pH 7.7 and 8.03 (Bessudova et al. 2018a). Only two species characteristic to alkaline waters, namely *M. alpina* and *M. tonsurata*, occurred in the study area at pH 7.39–8.15.

Němcová et al. (2003) demonstrated that the high diversity of silica-scaled chrysophytes was typical in waters with conductivity close to or below 40 µs cm^{-1}, whereas conductivity above 200 µs cm^{-1} reduced the species diversity.

The study area had high conductivity values during low and high water levels. The minimum conductivity values of 58 and 92 µs cm–1 were recorded only at two sites, stations 2 and 3, respectively (Table 1). However, this factor did not influence the diversity of silica-scaled chrysophytes; indeed, we observed the opposite situation where it were twice as many species at high conductivity value (174 µs cm^{-1}; station 6). The highest silica-scaled chrysophyte diversity, (35 species and intraspecific taxa) was registered during the previous study in the mouth of the Barguzin River at a conductivity of 151 µs cm^{-1} (Bessudova et al. 2018a).

Despite some evidences that silica-scaled chrysophytes prefer oligo- and mesotrophic conditions (Eloranta 1995; Němcová et al. 2003; Siver 1995; Siver and Lott, 2017), high species diversity and biomass were also recorded in eutrophic waters (Cronberg 1996; Kristiansen 1985, 2005; Kristiansen and Tong 1989; Siver 2015; Siver and Wujek, 1993), including the mouth of the Barguzin River in the Selenga Delta (Bessudova et al. 2018a). Notably, none of the species that would prefer oligo- and mesotrophic conditions according to Siver (2015) was found in the area studied. At the same time, *M. tonsurata* and *M. alpina*, both considered to prefer eutrophic waters, were found during our study in high and low water levels. Furthermore, these species also occurred in the plankton of the oligotrophic Lake Baikal (Bessudova et al. 2017).

Overall, the Baikal Region significantly expands the optimal conditions to develop and maintain high diversity of silica-scaled chrysophytes.

Impact of floods on silica-scaled chrysophyte diversity

Floods can either stimulate the development of phytoplankton, mainly cyanobacteria (Junk et al. 1989; McCullough et al. 2012; Silva et al. 2013) or inhibit it (Lederer 1998; Uehlinger et al. 2003; Uehlinger 2008; Paerl et al. 2011, 2014a). The most important factors that influence plankton communities during the floods are changes in nutrient concentrations (mainly PO43-), light availability (transparence of water), and stream velocity in the flooded ecosystems (Cottenie 2005; Paerl et al. 2014a, 2014b; Rojo et al. 2016; Van der Gucht et al. 2007).

In large rivers, the flow rates increase proportionally to the rise of water discharge (Fig. 5). Hence, the conditions for phytoplankton growth in 2018 were less favorable compared to 2016.

The flood pulse concept elaborated by Junk et al. (1989) stated that a seasonal flood is useful for river ecosystems and could affect their biotic composition, nutrient transport, and sediment distribution. However, violent floods can be destructive for aquatic organisms (Talbot et al. 2018).

The seasonal flood in the study area was one of the factors influenced the species composition of silica-scaled chrysophytes in the mouths of the Selenga and Barguzin Rivers. During the flood, we observed a significant depauperisation in the chrysophyte species composition compared to the previous data. Thus, recent studies demonstrated that the beginning of a flood was accompanied by species impoverishment in plankton communities, even if the silicon and nitrogen concentrations were sufficient for their development (Talbot et al. 2018). We suggested that the concentrations of chemical components, including oxygen, silicon, nitrogen, and phosphorous could not limit the development of silica-scaled chrysophytes in studied area. These concentrations were similar or sometimes higher than in low water period (Table 1). However, most species previously observed in the creeks of the Selenga Delta and the mouth of the Barguzin River were absent during the flood. Nevertheless, the number of registered species were proportionally distributed among the genera (Fig. 6).

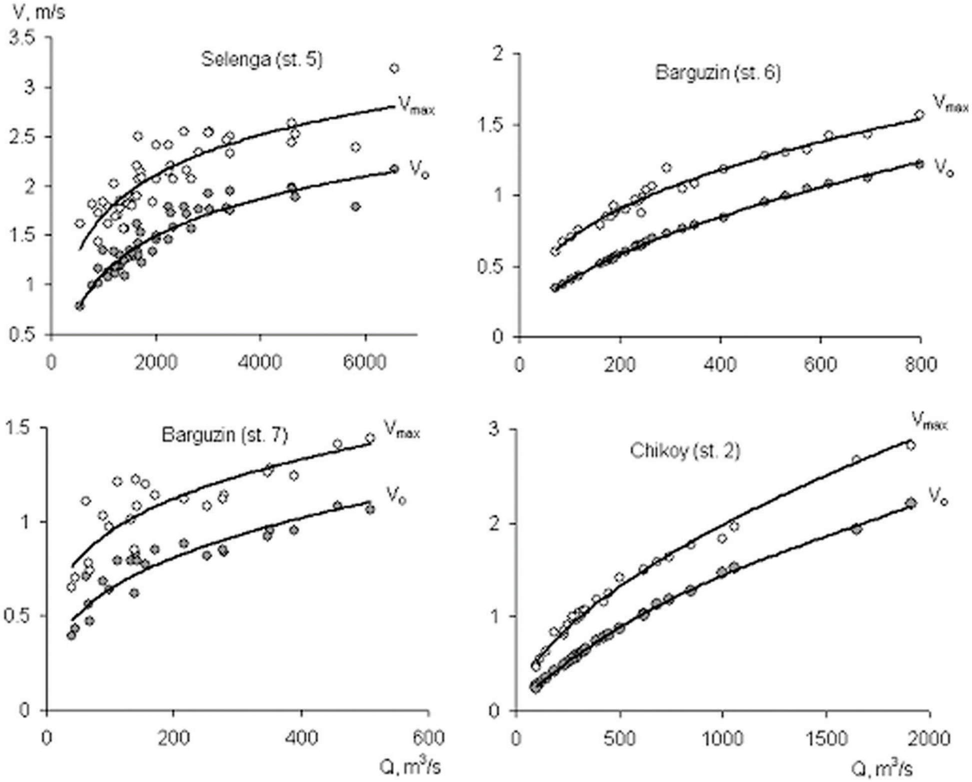

Figure 5. Dependence of maximal (Vmax) and average (Vo) flow rates on water discharge (Q).

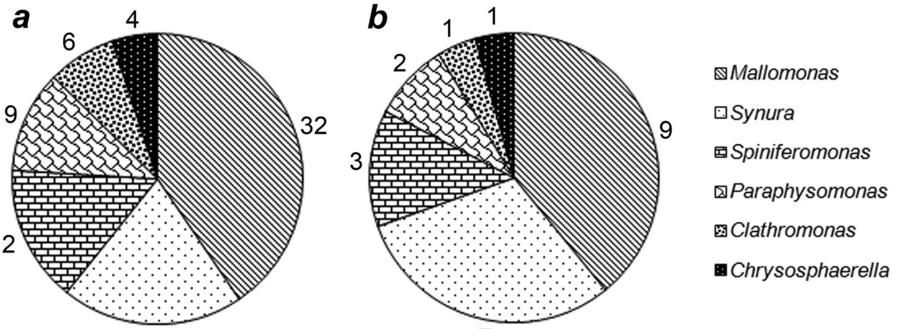

Figure 6. Changes in the distribution of silica-scaled chrysophyte species among genera towards water level: a – low water (Bessudova et al. 2018a); b – high water, this study.

In previous studies, 15 and 20 species of silica-scaled chrysophytes were identified in Lake Zavernyaikha and in the mouth of the Barguzin River, respectively, under the low water level. However, chrysophytes were absent from the mouth of the Kharauz Creek in

May, July and September 2016 (Bessudova et al. 2018a). The increased water content in the main tributaries of Lake Baikal favoured significant changes in chrysophyte diversity in these areas. Thus, only 14 species were identified in the mouth of the Barguzin River (station 6) and five species in the Kharauz Creek (station 5), while they were absent in Lake Zavernyaikha (station 4). The high water level connected the waterbodies (stations 4 and 5), which levelled the difference in hydrochemical conditions (oxygen content, water temperature, pH, and conductivity). This phenomenon limited the development of some chrysophytes but did not favour similarity in their species composition.

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The high diversity of silica-scaled chrysophytes in the mouths of the main tributaries of Lake Baikal, the Selenga, Upper Angara River and Barguzin Rivers in low water conditions could be caused by anterior floods. The inundation of the flood plains leads to integration of small creeks and lakes that enrich their flora due to dissemination of a broad spectrum of species (Fernandes et al. 2014; Junk et al. 1989). Water retreats control the bloom of phytoplankton, inter alia chrysophytes, in the warm and shallow waterbodies with high level of biological production, which favours the diversity of silica-scaled chrysophytes in the Baikal Region. Additionally, the climatic changes recorded worldwide during the previous decades, including the Baikal Region, may also underscore the quantitative and qualitative development of silica-scaled chrysophytes (Shimaraev et al. 2002; Sinyukovich et al. 2010; Sorokovikova et al. 2015). Global climate change influences the hydrology of waterbodies (Mushet et al. 2017) that will significantly impact the development of aquatic organisms. The interchange of floods and low water levels created various environmental conditions (Table 1) and stimulated dynamics of the ecosystem allow the formation of a "hotspot" for silica-scaled chrysophytes diversity.

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References

Adam DP, Mahood AD (1981) Chrysophyte cysts as potential environmental indicators. Geological Society of America Bulletin 92: 839–844. https://doi.org/10.1130/0016-7606(1981)92<839:CCAPEI>2.0.CO;2

Baikal. Atlas (1993) Cartographic Factory, Omsk. [in Russian]

Bessudova AYu, Domysheva VM, Firsova AD, Likhoshway YV (2017) Silica-scaled chrysophytes of Lake Baikal. Acta Biologica Sibirica 3: 47–56. https://doi.org/10.14258/abs.v4i3.4411

Bessudova AYu, Sorokovikova LM, Tomberg IV, Likhoshway YV (2018a). Silica-scaled chrysophytes in large tributaries of Lake Baikal. Cryptogamie, Algologie 39: 145–165. https://doi.org/10.7872/crya/v39.iss2.2018.145

Bessudova AYu, Firsova AD, Tomberg IV, Sorokovikova LM, Likhoshway EV (2018b) Biodiversity of silica-scaled chrysophytes in tributaries of northern limit of Lake Baikal. Acta Biologica Sibirica 4: 75–84. https://doi.org/10.14258/abs.v4i3.4411

Bezrukova EV, Bogdanov YuA, Williams DF, Granina LZ, Grachev MA, Ignatova NV, Karabanov EB, Kuptsov VM, Kurylev VM, Letunova PP, Likhoshway EV, Chernyaeva GP, Shimaraeva MK, Yakushin AO (1991) Deep changes in the ecosystem of North Baikal in the Holocene. Doklady Akademii Nauk SSSR 321(5): 1032–1036. [in Russian]

Bradbury P, Bezrukova EV, Chernyaeva GP, Colman SM, Khursevich GK, King JW, Likhoshway YeV (1994) A synthesis of post-glacial diatom records from Lake Baikal. Journal of Paleolimnology 10: 213–252.

Cronberg G (1980) Cyst development in different species of *Mallomonas* (Chrysophyseae) studied by scanning electron microscopy. Archiv fur Hydrobiologie 56: 421–434.

Cronberg G (1996) Scaled chrysophytes from the Okavango Delta, Botswana, Africa. Nova Hedwigia, Beiheft 114: 99–109.

Cottenie K (2005) Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8: 1175–1182. https://doi.org/10.1111/j.1461-0248.2005.00820.x

Drucker VV, Sorokovikova LM, Sinyukovich VN, Potemkina TG, Nikulina IG, Molozhavaya OA, Korovyakova IV (1997) Water quality in the Barguzin River under current conditions. Geography and Natural Resources 4: 72–78. [in Russian]

Duff KE, Zeeb BA, Smol JP (1995) Atlas of Chrysophycean stomatocysts. Kluwer Academic Publishers, Dordrecht.

Edlund MB, Stroemer EF, Pilskaln CH (1995) Siliceous microfossil succession in the recent history of two basins in Lake Baikal, Siberia. Journal of Paleolimnology 14: 165–184. https://doi.org/10.1007/BF00735480

Eloranta P (1995) Biogeography of chrysophytes in Finnish lakes. In: Sandgren CD, Smol JP, Kristiansen J (Eds.), Chrysophyte Algae: Ecology, Phylogeny and Development. Cambridge, Cambridge University Press, pp. 214–231. https://doi.org/10.1017/CBO9780511752292.011

Fernandes IM, Henriques-Silva R, Penha J, Zuanon J, Peres-Neto PR (2014) Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities. Ecography 37(5): 464–475. https://doi.org/10.1111/j.1600-0587.2013.00527.x

Ginn BK, Rate M, Cumming BF, Smol JP (2010) Ecological distribution of scaled-chrysophyte assemblages from the sediments of 54 lakes in Nova Scotia and southern New Brunswick, Canada. Journal of Paleolimnology 43: 293–308. https://doi.org/10.1007/s10933-009-9332-9

Grachev MA, Likhoshway YeV, Vorobieva SS, Khlystov OM, Bezrukova EV, Veinberg EV, Goldberg EL, Granina LZ, Kornakova EG, Lazo FI, Levina OV, Letunova PP, Otinov PV, Fedotov AP, Yaskevich SA, Bobrov VA, Sukhorukov FV, Rezchikov VI, Fedorin MA, Zolotarev KV, Kravchinsky VA (1997) Signals of the paleoclimates of Upper Pleistocene in the sediments of Lake Baikal. Russian Geology and Geophysics 38(5): 957–980. [in Russian]

Gusev ES, Guseva EE, Gabyshev VA (2018) Taxonomic composition of silica-scaled chrysophytes in rivers and lakes of Yakutia and Magadanskaya oblast (Russia). Nova Hedwigia, Beiheft 147: 105–117. https://doi.org/10.1127/nova-suppl/2018/009

Hällfors G, Hällfors S (1988) Records of chrysophytes with siliceous scales (Mallomonadaceae and Paraphysomonadaceae) from Finnish innland waters. Flagellates in freshwater ecosystems. Hydrobiologia 161: 1–29.

Junk WJ, Bayley PB, Sparks RE (1989) The flood pulse concept in river-floodplain systems. Canadian Journal of Fisheries and Aquatic Sciences 106: 110–127

Khursevich GK, Karabanov EB, Prokopenko AA, Williams DF, Kuz'min MI, Fedenya SA, Gvozdkov AN, Kerber EV (2001) Detailed diatom biostratigraphy of Baikal sediments during the Brunhes chron and climatic factors of species formation. Russian Geology and Geophysics 42(1-2): 108–129.

Kristiansen J (1985) Occurrence of scale-bearing Chrysophyceae in a eutrophic Danish lake. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 22: 2826–2829.

Kristiansen J (2000) Cosmopolitan chrysophytes. Systematics and geography of plants 70: 291–300. https://doi.org/10.2307/3668648

Kristiansen J (2008) Dispersal and biogeography of silica-scaled chrysophytes. Biodiversity and Conservation 17: 419–426. https://doi.org/10.1007/978-90-481-2801-3_14

Kristiansen J (2005) Golden Algae: A Biology of Chrysophytes. Koenigstein, Koeltz Scientific Books.

Kristiansen J, Škaloud P (2017) Chrysophyta. Handbook of the Protists, second edition. Cham, Springer International Publishing, pp. 1–38. https://doi.org/10.1007/978-3-319-32669-6_43-1
Kristiansen J, Tong D (1989) Studies on silica-scaled chrysophytes from Wuhan, Hangzhou and Beijing, P.R. China. Nova Hedwigia 49: 183–202.
Kristiansen J (2005) Golden Algae: A Biology of Chrysophytes. Koenigstein, Koeltz Scientific Books.
Kristiansen J, Škaloud P (2017) Chrysophyta. Handbook of the Protists, second edition. Cham, Springer International Publishing, 1–38. https://doi.org/10.1007/978-3-319-32669-6_43-1
Kristiansen J, Tong D (1989) Studies on silica-scaled chrysophytes from Wuhan, Hangzhou and Beijing, P.R. China. Nova Hedwigia 49: 183–202.
Kuzmin GV (1975) Phytoplankton. Species composition and abundance. In: Mordukhay-Boltovsy FD (Ed) Methods for studying biogenocenoses of inland waters, Nauka Press, Moscow, 73–87. [in Russian]
Lederer F (1998) Algal flora of the Červené blato peat bog (Třeboň Basin, Czech Republic). Preslia 70, 303–311.
Likhoshway YeV (1999) Fossil endemic centric diatoms from Lake Baikal, upper Pleistocene complexes. In: Mayama S, Idei M, Koizumi I (Eds), Proceedings of the XIV International Diatom Symposium. Koenigstein, Koeltz Scientific Books, 613–628. [in Russian]
Manual for chemical analysis of inland surface waters, Part 1 (2009) NOK, Rostov-on-Don. [in Russian]
Mazepova GF, Timoshkin OA, Melnik NG, Obolkina LA, Tanichev AI (Eds) (1995) Atlas and Key of Baikal Pelagic bionts (with brief profiles of their ecology). Nauka Press, Novosibirsk [in Russian]
McCullough GK, Page SJ, Hesslein RH, Stainton MP, Kling HJ, Salki AG, Barber DG (2012) Hydrological forcing of a recent trophic surge in Lake Winnipeg. Journal of Great Lakes Research 38: 95–105. https://doi.org/10.1016/j.jglr.2011.12.012
Mushet GR, Laird KR, Das B, Hesjedal B, Leavitt PR, Scott KA, Simpson GL, Wissel B, Wolfe, JD, Cumming BF (2017) Regional climate changes drive increased scaled-chrysophyte abundance in lakes downwind of Athabasca Oil Sands nitrogen emissions. Journal of Paleolimnology 58: 419–435. https://doi.org/10.1007/s10933-017-9987-6
Němcová Y, Neustupa J, Novakova S, Kalina T (2003) Silica-scaled chrysophytes of the Czech Republic. Acta Universitatis Carolinae. Geographica 47: 285–346.
Němcová Y, Kreidlová J, Kosová A, Neustupa J (2012) Lakes and pools of Aquitaine region (France) – a biodiversity hotspot of Synurales in Europe. Nova Hedwigia 95: 1–24. https://doi.org/10.1127/0029-5035/2012/0036
Paerl HW, Hall NS, Calandrino ES (2011) Controlling harmful cyanobacterial blooms in a world experiencing anthropogenic and climatic-induced change. Science of the Total Environment 409: 1739–1745. https://doi.org/10.1016/j.scitotenv.2011.02.001
Paerl HW, Hall NS, Peierls BL, Rossignol KL, Joyner AR (2014a) Hydrologic variability and its control of phytoplankton community structure and function in two shallow, coastal,

lagoonal ecosystems: the Neuse and New River Estuaries, North Carolina, USA. Estuaries Coasts 37: 31–45. https://doi.org/10.1007/s12237-013-9686-0

Paerl HW, Hall NS, Peierls BL, Rossignol KL (2014b) Evolving paradigms and challenges in estuarine and coastal eutrophication dynamics in a culturally and climatically stressed world. Estuaries Coasts 37: 243–258. https://doi.org/10.1007/s12237-014-9773-x

Paterson AM, Winter JG, Nicholls KH, Clarks BJ, Ramcharan CW, Yan ND, Somers KM (2008) Long-term changes in phytoplankton composition in seven Canadian Shield lakes in response to multiple anthropogenic stressors. Canadian Journal of Fisheries and Aquatic Sciences 65: 846–861. https://doi.org/10.1007/s00027-012-0280-5

Popovskaya GI (1981) A new species of the genus *Chrysosphaerella* in plankton of Lake Baikal. News on Systematics of Lower Plants. Nauka Press, Leningrad, 9–12. [in Russian]

Popovskaya GI, Sorokovikova LM, Tomberg IV, Bashenkhaeva NV, Tashlykova NA (2011) Peculiarities of water composition and phytoplankton development in Lake Zavernyaikha. Geography and Natural Resources 4: 68–74. https://doi.org/10.1134/S187537281104007X. [in Russian]

Popovskaya GI, Tashlykova NA (2008) Phytoplankton. Delta of the Selenga River as a natural biofilter and status indicator for Lake Baikal, issue 15. SB RAS Publishing House Novosibirsk, 167–181. [in Russian]

Rojo C, Mesquita-Joanes F, Monrós JS, Armengol J, Sasa M, Bonilla F, Rueda R, Benavent-Corai J, Piculo R, Seguraet MM (2016) Hydrology affects environmental and spatial structuring of microalgal metacommunities in tropical Pacific coast wetlands. PLoS One 11(2). https://doi.org/10.1371/journal.pone.0149505

Rühland KM, Paterson AM, Smol JP (2008) Hemispheric-scale patterns of climate-related shifts in planktonic diatoms from North American and European lakes. Global Change Biology 14: 2740–2754. https://doi.org/10.1111/j.1365-2486.2008.01670.x

Shimaraev MN, Kuimova LN, Sinyukovich VN, Tsekhanovskii VV (2002) Lake Baikal as evidence of the global climate change in the XX century. Doklady RAN 383: 397–400. [in Russian]

Schindler DW (2001) The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. Canadian Journal of Fisheries and Aquatic Sciences 58: 18–29. https://doi.org/10.1007/978-1-4615-1493-0_11

Scoble JM, Cavalier-Smith T (2014) Scale evolution in Paraphysomonadida (Chrysophyceae): Sequence phylogeny and revised taxonomy of *Paraphysomonas*, new genus *Clathromonas*, and 25 new species. European Journal of Protistology 50: 551–592. https://doi.org/10.1016/j.ejop.2014.08.001

Silva TSF, Melack JM, Novo EML (2013) Responses of aquatic macrophyte cover and productivity to flooding variability on the Amazon floodplain. Global Change Biology 19: 3379–3389. https://doi.org/10.1111/gcb.12308

Sinyukovich VN (2005) Characteristics of the downstream run-off of the Selenga River and the creeks of its delta. International Conference 'Basic factors and patterns of delta formation. Their role in wetland ecosystems of various landscapes'. Ulan-Ude, 114–116. [in Russian]

Sinyukovich VN, Sorokovikova LM, Tomberg IV, Tulokhonov AK (2010) Climate Changes and the Selenga River Chemical Flow. Doklady Earth Sciences 433 (2): 1127–1131. https://doi.org/10.1134/S1028334X10080295. [in Russian]

Siver PA (1988) The distribution and ecology of *Spiniferomonas* (Chrysophyceae) in Connecticut (USA). Nordic Journal of Botany 8: 205–212.

Siver PA (1995) The distribution of chrysophytes along environmental gradients: their use as biological indicators. Chrysophyte algae. Cambridge University Press, Cambridge, 232–268.

Siver PA (2015) Synurophyte Algae. In: Wehr, J. D., R. G. Sheath, J. P. Kociolek (eds.) Freshwater Algae of North America: Ecology and Classification 2nd edition. Academic Press, Boston, 607–651.

Siver PA, Lott AM (2017) The scaled chrysophyte flora in freshwater ponds and lakes from Newfoundland, Canada, and their relationship to environmental variables. Cryptogamie, Algologie 38(4): 325–347. https://doi.org/10.7872/crya/v38.iss4.2017.325

Siver PA, Wujek DE (1993) Scaled Chrysophyceae and Synurophyceae from Florida: IV. The flora of Lower Lake Myakka and Lake Tarpon. Florida scientist (USA) 56: 109–117.

Škaloud P, Kynčlová A, Benada O, Kofroňová O, Škaloudová M (2012) Toward a revision of the genus Synura, section Petersenianae (Synurophyceae, Heterokontophyta): morphological characterization of six pseudocryptic species. Phycologia 51: 303–329. https://doi.org/10.2216/11-20.1

Škaloud P, Škaloudová M, Pichrtová M, Němcová Y, Kreidlová J, Pusztai M (2013) www.chrysophytes.eu – a database on distribution and ecology of silica scaled chrysophytes in Europe. Nova Hedwigia, Beiheft 142: 141–146.

Škaloud P, Škaloudová M, Procházková A, Němcová Y (2014) Morphological delineation and distribution patterns of four newly described species within the *Synura petersenii* species complex (Chrysophyceae, Stramenopiles). European Journal of Phycology 49(2): 213–229. doi:10.1080/09670262.2014.905710

Smol JP (1985) The ratio of diatom frustules to chrysophycean statospores: a useful paleolimnological index. Hydrobiologia 123: 199–204.

Sorokovikova LM, Popovskaya GI, Tomberg IV, Bashenkhaeva NV (2009) Spatial and temporal variability of nutrient and organic matter concentrations and phytoplankton in the water of the Selenga River and channels of its delta. Water Resources Research 36: 465–474. [in Russian]

Sorokovikova LM, Sinyukovich VN, Tomberg IV, Marinaite II, Khodzher TV (2015) Assessment of water quality of Lake Baikal tributaries from chemical parameters. Geography and Natural Resources 1: 37–45. https://doi.org/10.1134/S1875372815010059

Sorokovikova LM, Sinyukovich VN, Tomberg IV, Popovskaya GI, Chernyshev MS, Ivanov VG, Khodzher TV (2017) The status of the aquatic ecosystem of the Selenga river delta under long-duration low-water conditions. Geography and Natural Resources 1: 81–89. https://doi.org/10.1134/S1875372817010085. [in Russian]

Stoermer EF, Edlund MB, Pilskaln CH, Schelske CL (1995) Siliceous microfossil distribution in the surficial sediments of Baikal. Journal of Paleolimnology 14: 69–82. https://doi.org/10.1007/BF00682594

Talbot CJ, Bennett KM, Cassell K, Hanes DM, Minor Hans EC, Paerl H, Raymond PA, Vargas R, Vidon PG, Wollheim W, Xenopoulos MA (2018) The impact of flooding on aquatic ecosystem services. Biogeochemistry 141(3): 439–461. https://doi.org/10.1007/s10533-018-0449-7

Timoshkin OA (2004) "Freshwater Australia" of Siberia. Science First Hand 1(2): 62–75

Tomberg IV, Sinyukovich VN, Sorokovikova LM, Shiretorova VG, Pavlov IA (2019) Ecological status of the Selenga River at the present time. Modern trends and development prospects of hydrometeorology in Russia: materials of II Russian scientific conference timed to coincide with 55 years of the Hydrology and Nature Management Department of Irkutsk State University. Irkutsk, 264–271. [in Russian]

Uehlinger U (2008) Resistance and resilience of ecosystem metabolism in a flood-prone river system. Freshwater Biology 45: 319–332. https://doi.org/10.1111/j.1365-2427.2000.00620.x

Uehlinger U, Kawecka B, Robinson CT (2003) Effects of experimental floods on periphyton and stream metabolism below a high dam in the Swiss Alps (River Spöl). Aquatic Sciences 65: 199–209. https://doi.org/10.1007/s00027-003-0664-7

Van der Gucht K, Cottenie K, Muylaert K, Vloemans N, Cousin S, Declerck S, Jeppesen E, Conde-Porcuna J-M, Schwenk K, Zwart G, Degans H, Vyverman W, De Meester L (2007) The power of species sorting: Local factors drive bacterial community composition over a wide range of spatial scales. Proceedings of the National Academy of Sciences U.S.A. 104: 20404–20409. https://doi.org/10.1073/pnas.0707200104

Vorobieva SS, Bondarenko NA, Karpov SA, Pomazkina GV, Tanichev AI (1992) To the study of the species composition of Chrysophyta in Lake Baikal. Algology 2(3): 68–72. [in Russian]

Wetzel RG, Linkens GE (1991) Limnological Analyses. Springer-Verlag, New York, 69–80.

Wolfe AP, Siver PA (2013) A hypothesis linking chrysophyte microfossils to lake carbon dynamics on ecological and evolutionary time scales. Global and Planetary Change 111: 189–198. https://doi.org/10.1016/j.gloplacha.2013.09.014