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The role of atmospheric precipitation in the under-ice blooming of endemic dinoflagellate *Gymnodinium baicalense* var. *minor* Antipova in Lake Baikal

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ABSTRACT. The mass development of the phototrophic under-ice community is an interesting phenomenon known for the Arctic Ocean as well as for some rivers and freshwater lakes, including Lake Baikal. Species composition and productive characteristics of the under-ice phytoplankton in Lake Baikal are well studied. During the under-ice blooming, an endemic dinoflagellate *Gymnodinium baicalense* var. *minor* Antipova can have more than half of the annual primary phytoplankton production. However, there are still many questions to be answered regarding the factors limiting abundance and proliferation of the under-ice phytoplankton as well as mechanisms facilitating it to persist in Lake Baikal under conditions of the low salinity and low temperature. In present work, we studied the development dynamics of dinoflagellates and microalgae under the ice cover in Listvennichny Bay of Lake Baikal from February to April 2018. Simultaneously, the dynamics of the chemical composition and concentration of atmospheric precipitation were analysed. We observed the under-ice community with the domination of endemic dinoflagellate *Gymnodinium baicalense* var. *minor* in April. The biomass of this species considerably varied on different days from 0.04 to 10.0 x 10^3 mg/m^3. The results of this study indicated that nutrient supply from precipitation could be an important source of nutrition for organisms developing under the ice, in particular, *Gymnodinium baicalense* var. *minor*, and could be one of the factors causing the fluctuations in its biomass. We suggested that abrupt significant increases in abundance of *G. baicalense* var. *minor* could be a result of their active migration to the area with elevated concentration of nitrogen from atmospheric precipitation. Such an ability may help this species to prosper under the ice of Lake Baikal.

Keywords: dinoflagellates, phytoplankton, the under-ice blooming, Lake Baikal, atmospheric precipitation

1. Introduction

In Lake Baikal, during the ice-cover period that lasts from February until May (Shimaraev et al., 1994), dinoflagellates and diatom microalgae play an important role as the main food source for protozoa and multicellular organisms (Kozhova, 1957; Antipova, 1963; Votintsev et al., 1975; Popovskaya, 2000). In the high-crop years of phytoplankton, the number of the dinoflagellates in the lake photic zone (0-50 m) under the ice cover can reach $\times 10^6$ cells/L making them the dominant species of the under-ice community (Kozhova, 1957; Antipova, 1963; Popovskaya, 2000). During spring in such years, endemic dinoflagellates of the genus *Gymnodinium* can have up to 65% of the annual primary phytoplankton production (Votintsev et al., 1975).

Dinoflagellates are a group of primarily unicellular organisms belonging to the Alveolata superphylum combined by a set of unique characteristics, such as flagellar insertion, pigmentation, organelles, and features of the nucleus that distinguish them from other groups (Belyakova et al., 2006; Carty and Parrow, 2015). They are widespread in aquatic systems, occupying various ecological niches, and show a high diversity and physiological variability, including phototrophy, heterotrophy, mixotrophy, and fish parasitism (Anderson, 1989; Carty, 2014). Under certain conditions, marine dinoflagellates can reproduce rapidly to form water blooms or red tides that colour water and may lead to fish kills (Landsberg, 2002; Hallegraeff, 2003). The bloom of some dinoflagellates in summer freshwater phytoplankton can be responsible for serious problems in drinking water quality (Carty

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and Parrow, 2015). The dinoflagellate massive development can also occur under the ice cover both in marine (Spilling, 2007) and freshwater bodies (Phillips and Fawley, 2002; Carty and Parrow, 2015), including Lake Baikal (Votintsev et al., 1975; Obolkina et al., 2000; Annenkova et al., 2009; Bondarenko et al., 2012; Bashenkhaeva et al., 2015; 2017).

There are numerous studies on the species composition, abundance, duration of vegetation, and productive characteristics of the under-ice phytoplankton in Lake Baikal (e.g. Antipova and Kozhov, 1953; Kozhova, 1961; Antipova, 1963; Votintsev et al., 1975; Obolkina et al., 2000; Popovskaya, 2000; Bondarenko et al., 1996; 2012; 2013; Bashenkhaeva et al., 2015; 2017). However, there are still many questions to be answered regarding the factors limiting abundance and proliferation of the phytoplankton as well as mechanisms facilitating it to persist in Lake Baikal under the ice cover at the low salinity and low temperature. In the present work, we studied seasonal dynamics of the *Gymnodinium baicalense* var. *minor* abundance during its blooming under the ice cover in Listvennichny Bay of Lake Baikal in 2018, and discuss possible effects on this dynamics of some abiotic factors, such as nutrients intake from atmospheric precipitation.

2. Methods

Species composition, total abundance, and biomass of dinoflagellates and microalgae from under the ice were studied using samples from the surface water of ice holes collected at a depth of 600 m in Listvennichny Bay of Lake Baikal from February to April 2018. Geographical coordinates of the sampling site are 51°51’49’’N, 104°50’093’’E. Samples were fixed with the Utermohl’s solution in 0.5-1.0 L plastic bottles and concentrated by sedimentation for 10 days (Kiselev, 1956). The species composition and cell number were estimated in triplicate for each sample using the Fuchs-Rosenthal counting chamber with a grid of 3.2 μl and an area of 16 mm^2, and an Olympus CX 21 light microscope (Tokyo, Japan) at ×20, and ×40 magnification. The species were identified using monographs “Diatomovye vodorosli…” (1988; 1992) and the keys by Matvienko and Litvinenko (1977), Popovskaya et al. (2011). The biomass was estimated by the cell true volume method according to Belykh et al. (2011). The cell volume of each species was determined according to their average size measured under the microscope. The average cell volume of *Gymnodinium baicalense* var. *minor* was calculated by the formula according to Belykh et al. (2011) given for *Gymnodinium baicalense* Antipova and was 23900 μm^3. The growth rate of *Gymnodinium baicalense* var. *minor* was calculated by the formula $\mu = (\ln N1 - \ln N0) / t$, where N0 and N1 are the numbers of cells at time moments t0 and t1, and t is the time difference between the samples.

The chemical composition and concentration of atmospheric precipitation (each case) were analysed from January to April 2018. The chemical analysis was carried out according to conventional freshwater chemistry methods (Rukovodstvo..., 2009; Khodzher et al., 2017; Wetzel and Likens, 1991) at the accredited Laboratory of the Hydrochemistry and Atmosphere Chemistry of Limnological Institute SB RAS using the equipment of the collective instrumental centre ‘Ultramicroanalysis’. The nutrient content in the filtered water was measured using the following colorimetric methods: indophenol blue method for NH_4^+, Griss’s method for NO_2^-, Deniges’s method for PO_4^{3-}, and the ammonium molybdate method for Si (Khodzher et al., 2017). Nitrate NO_3^- in the filtrates was quantified using ionic chromatography on an ICS-3000 ionic system (Dionex, USA).

Data on the air temperature dynamics in the fieldwork area were provided by the local weather station ‘Istok Angara’.

3. Results

In 2018, the ice cover in Listvennichny Bay of Lake Baikal formed on 23 January; it lasted until 27 April and was fully broken on 7 May. The maximum ice thickness in the fieldwork area was ca. 80 cm at the end of March. The water temperature under the ice was approximately 0 °C. The air temperature varied from −25.0 to +20.0 °C between February and April, starting to gradually increase in the early March and reaching positive values by the end of this month (Fig.1).

The nutrient concentrations measured in snow and rain precipitation varied considerably (Table 1). There was a significant difference between the average concentration of the ions in atmospheric precipitation and the lake water (Fig. 2, Table 1). Specifically, the

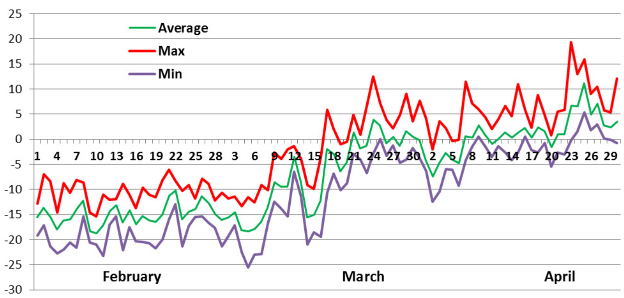

Fig.1. Daily fluctuations in the air temperature in Listvennichny Bay, Lake Baikal, 2018

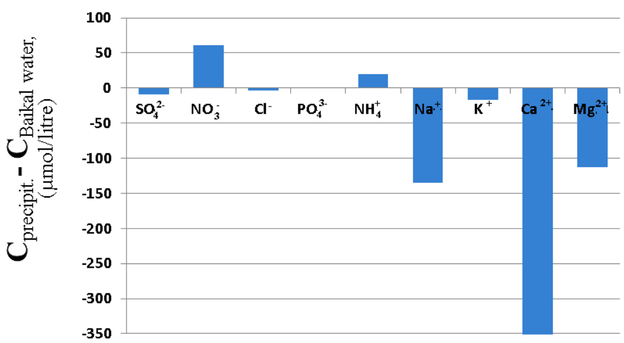

Fig.2. The difference of average ion concentrations in precipitation from February to May 2018 and in the Lake Baikal water according to Grachev (2002)

Table 1. Chemical composition of atmospheric precipitation during January-April 2018 and of the Lake Baikal water (Grachev, 2002).

Precipitation period		Precip.-amount, mm	Concentration, µmol/l										Deposition, µmol/м²		
			SO_4^{2-}	NO_3^-	Cl^-	PO_4^{3-}	NH_4^+	Na^+	K^+	Ca^{2+}	Mg^{2+}	H^+	NO_3^-	NH_4^+	PO_4^{3-}
12.01.18	13.01.18	2.4	30.0	74.3	4.8	0.3	11.7	5.7	3.1	43.2	8.6	7.9	178.3	28.1	0.6
19.01.18	20.01.18	0.9	67.6	80.4	11.6	0.1	5.7	6.5	7.4	128.5	25.5	0.2	72.4	5.1	0.1
27.01.18	28.01.18	1.2	58.3	71.3	11.9	0.0	2.6	10.0	2.8	96.8	16.0	1.0	85.6	3.1	0.0
07.02.18	08.02.18	2.1	43.2	76.4	9.3	0.0	8.9	5.7	2.3	61.4	10.7	4.9	160.4	18.7	0.0
08.02.18	09.02.18	2.7	20.3	44.9	8.2	0.1	6.7	7.8	3.1	29.9	5.3	5.2	121.2	18.0	0.2
12.02.18	13.02.18	2.8	19.4	37.4	9.7	0.0	2.6	5.2	3.1	30.4	5.8	3.8	104.7	7.3	0.1
20.02.18	21.02.18	1.2	53.4	91.5	13.8	0.1	4.8	9.6	5.6	71.3	16.4	4.0	109.8	5.8	0.1
25.02.18	26.02.18	4.2	21.2	47.1	2.9	0.0	11.1	3.5	1.5	25.7	5.3	11.2	197.8	46.6	0.2
03.03.18	04.03.18	3.1	22.1	44.9	6.5	0.1	12.2	6.5	3.1	26.9	4.9	8.5	139.2	37.8	0.2
11.03.18	12.03.18	2.4	42.7	73.2	6.3	0.1	25.5	7.8	3.8	45.7	9.0	12.3	175.7	61.2	0.2
24.03.18	25.03.18	1.4	45.3	55.0	5.0	0.2	37.2	7.0	5.6	38.4	8.6	4.4	77.0	52.1	0.3
08.04.18	**09.04.18**	1.9	**145.7**	**206.8**	**17.6**	**0.6**	**98.3**	**27.0**	**21.5**	**136.5**	**31.2**	17.0	**392.9**	**186.8**	**1.1**
18.04.18	19.04.18	2.7	14.6	9.1	5.4	0.3	17.0	4.8	1.3	10.7	1.6	4.9	24.5	45.9	0.8
26.04.18	27.04.18	2.6	38.1	36.8	3.4	1.4	51.2	3.9	18.2	22.5	6.2	7.4	95.7	133.1	3.7
Average in precipitation		**Sum 31.6**	**44.4**	**67.8**	**8.3**	**0.2**	**21.1**	**7.9**	**5.9**	**54.9**	**11.1**	**6.6**	**Total deposition**		
													1935	**650**	**7.6**
Baikal water (average)			***54***	***6.4***	***11***	***0.21***	***~ 1***	***143***	***23***	***407***	***123***	0.02			
Ratio $C_{precip.}/C_{lake\ water}$			***0.82***	***10.6***	***0.75***	***0.95***	***21.1***	***0.06***	***0.26***	***0.13***	***0.09***	***330***			

concentration of phosphate (PO_4^{3-}) was nearly the same in precipitation as in the lake water (Table 1); however, the concentrations of nitrate (NO_3^-) and ammonium (NH_4^+) were 10-20 times higher in precipitation (Table 1).

In 2018, the dinoflagellate *Gymnodinium baicalense* var. *minor* and some microalgae represented the under-ice community in Lake Baikal. Cryptomonads *Rhodomonas pusilla* (Bachmann) Javornicky and *Cryptomonas* spp. Ehrenberg, as well as green alga *Koliella longiseta* (Vischer) Hindak, prevailed in the community from February until April. During this period, there was a gradual increase in the number of these species and the diatom *Fragilaria radians* (Kützing) Williams & Round in the 0-m water layer under the ice cover (Fig. 3, Fig. 4). The following microalgae were the minor or irregular components of the under-ice community at this depth: *Nitzschia graciliformis* Lange-Bertalot & Simonsen emend Genkal et Popovskaya, *Lindavia minuta* (Skvortzow) Nakov et al., *Monoraphidium* sp. Komarkova-Legnerova, *Dinobryon cylindricum* Imhof, *Chrysococcus* sp. Klebs, *Synechococcus* sp. Nägeli.

From the late February until March, single specimens of dinoflagellates were observed. A significant increase in *G. baicalense* var. *minor* was in early April (Fig. 3, Fig. 4). The biomass of *G. baicalense* var. *minor* in the lake water from the ice-hole generally tended to increase but varied on different days from 0.04 to 10.0 x 10^3 mg/m^3.

During the entire study period, other

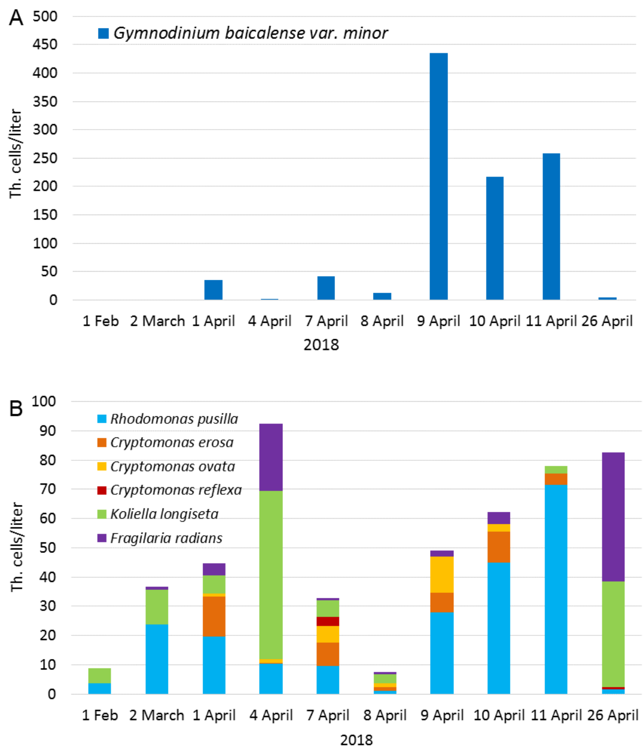

Fig.3. Seasonal changes in abundance of *Gymnodinium baicalense* var. *minor* (A) and dominant microalgae (B) in the 0-m water layer, Listvennichny Bay, Lake Baikal, 2018

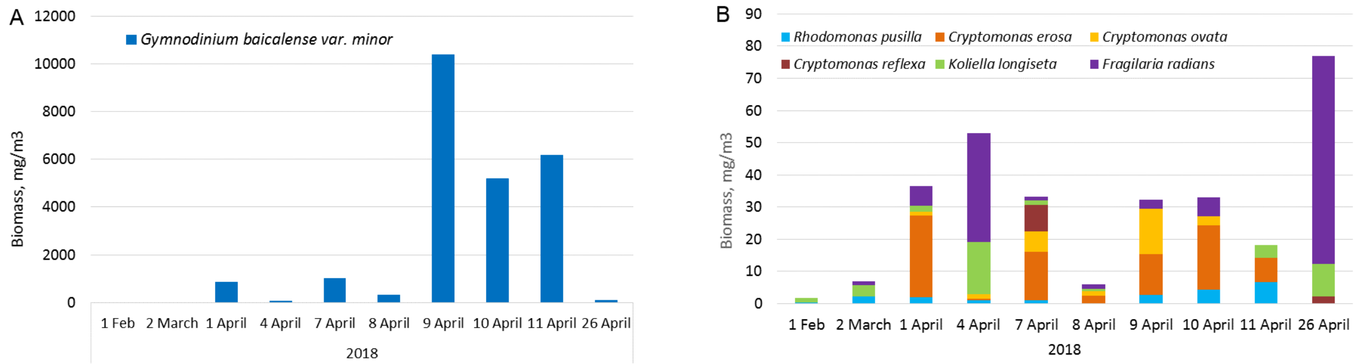

Fig.4. Seasonal changes in biomass of *Gymnodinium baicalense* var. *minor* (A) and dominant microalgae (B) in the 0-m water layer of Listvennichny Bay, Lake Baikal, 2018

dinoflagellates known for Lake Baikal, such as *Gymnodinium baicalense* Antipova, *Gyrodinium helveticum* (Penard) Takano & Horiguchi, *Apocalathium baicalense* (Kiselev & Zvetkov) Craveiro, Daugbjerg, Moestrup & Calado, *Apocalathium* sp., were present as single cells or cysts.

A sharp increase in *G. baicalense* var. *minor* after the night precipitation with high nutrient concentration was observed on 9 April (Fig. 3, Fig. 4; Table 1). The massive development of *G. baicalense* var. *minor* manifested in the form of dense yellow masses having several centimetres in diameter on the walls of the ice-holes and cracks as well as in the lower layer of the ice cover (Fig. 5, Fig. 6). A decline in the development of *G. baicalense* var. *minor* was at the end of April (Fig. 3, Fig. 4).

4. Discussion

Development of Gymnodinium baicalense var. minor under the ice cover in 2018

In 2018, we observed the under-ice community with the domination of endemic dinoflagellate *Gymnodinium baicalense* var. *minor* in Listvennichny Bay of Lake Baikal. The development pattern of this species was quite typical according to other reports (Antipova, 1955; Kozhova, 1959; Votintsev et al., 1975; Obolkina et al., 2000; Bondarenko et al., 2012). Specifically, the abundance of its cells in the surface water of the lake was low in February but significantly raised in April. In previous years, the development of this species was characterized by substantial outbreaks of its biomass with the subsequent decline (Antipova, 1955; Kozhova, 1959; Votintsev et al., 1975; Annenkova et al., 2009). In 2018, there were also significant and sharp increases in abundance of *G. baicalense* var. *minor* that caused temporary yellow colouring of the lake water and the ice cover. The biomass of *G. baicalense* var. *minor* in the lake water was irregular and considerably varied on different days. However, this variability was in a range documented for this species in other studies (Kozhova, 1960; Votintsev et al., 1975). For example, Votintsev et al. (1975) reported that the biomass of *G. baicalense* var. *minor* ranged between 0.65 and 40.0 g/m^3 in the surface waters of the lake. The biomass of the microalgae in 2018 also varied, but it was significantly lower than the biomass of *G. baicalense* var. *minor*.

Atmospheric recipitation as an important source of nutrients for the development of the under-ice community in Lake Baikal

The phenomenon of the mass development of the phototrophic under-ice community in Lake Baikal has received a great attention in scientific literature (e.g.

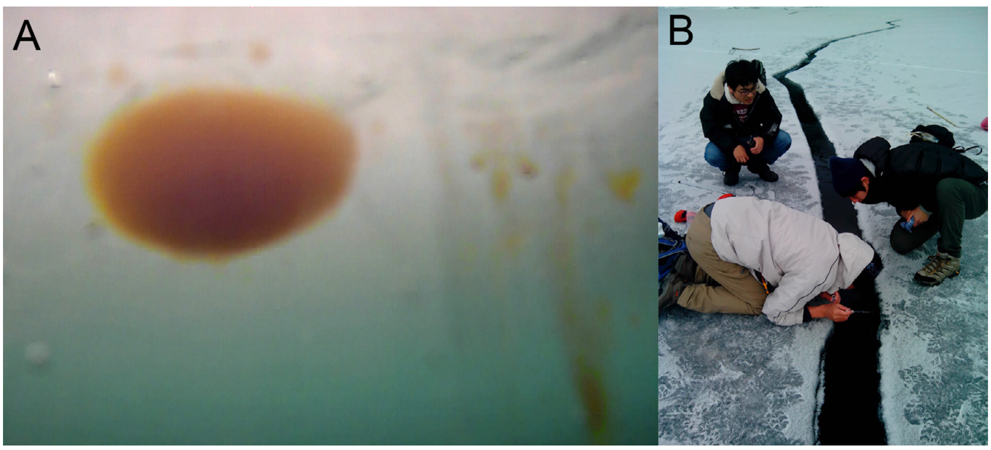

Fig.5. The concentration of *Gymnodinium baicalense* var. *minor* on the walls of the ice hole in the Lake Baikal ice cover, and its mass release to the water column from the ice interstitial (A); an ice crack where the concentration of dinoflagellates was typically observed (B)

Kozhov, 1955; Kozhova, 1961; Obolkina et al., 2000; Jewson et al., 2009; Evstafiev et al., 2010; Bondarenko et al., 2013, etc.). It is rather peculiar and occurs due to exceptional purity and transparency of the Baikal ice, as ca. 65-80 % of solar radiation penetrates through it enabling microalgae and dinoflagellates to develop (Shimaraev et al., 1994; Jewson et al., 2009). Since the transparency of the ice greatly reduces when it becomes covered with snow, it was considered that the under-ice extensive development of phytoplankton, which usually starts in February, most likely depended on releasing of the lake ice cover from snow by winds that normally were especially strong in that month (Kozhov, 1955; Kozhova, 1961). However, no strong relations between the under-ice phytoplankton and the thickness of the snow cover, as well as the wind activity, have been determined (Kozhova, 1961; Bashenkhaeva et al., 2015). Although the example of the under-ice community in marine ecosystems (Różańska et al., 2009) and recently in Lake Baikal showed that diatom microalgae tended to develop under the ice partially covered with snow (Jewson et al., 2009; Bashenkhaeva et al., 2015), whereas dinoflagellates dominated the under-ice community under the maximum snow cover (Bashenkhaeva et al., 2015). Therefore, even though an increase in solar radiation availability can affect the beginning of the under-ice development of the species capable of phototrophy, it is unlikely the key factor determining their enormous abundance and biomass. No direct relation was found between nutrients and the under-ice phytoplankton in the lake (Votintsev, 1975; Kozhova, 1961). Nonetheless, in addition to the solar radiation, a suitable environment within and under the ice as well as the availability of nutrients should be crucial for microalgae and dinoflagellates to persist and develop in such extreme conditions. For example, Obolkina et al. (2000) revealed that development of cryophilic community in Lake Baikal was associated with occurrence of the numerous capillaries in the ice filled with water, whilst only cysts and resting stages were detected in the solid phase of newly formed ice cover (Obolkina et al., 2000; Bondarenko et al., 2012; 2013).

During the ice-cover period, which lasts for four-five months on Lake Baikal (Shimaraev et al., 1994), there is a limited influx of nutrients due to the absence of the wind-wave mixing of water masses (Kozhova, 1961). The results of our study suggest that nutrient supply from precipitation can be an important source of nutrition for organisms developing under the ice in Lake Baikal. In particular, in 2018, the concentrations of nitrates and ammonium were 10 and 20 times higher, respectively, than their average concentrations in the Lake Baikal water. (Fig. 2, Table 1). A significant rise in the air temperature to +5 +10° C in the late March (Fig. 1) caused melting of the upper layer of the ice, resulting in the seepage of the melt-water with nutrients accumulated from precipitation into capillaries of the ice cover. Usually, the development of the under-ice phytoplankton in Lake Baikal is maximum during March and April (Kozhova, 1960; Votintsev et al., 1975; Obolkina et al., 2000). Evidently, acquiring a structure permeated with capillaries and pores by the ice and its further saturation with water facilitates the effective penetration of nutrients from the melt precipitation, making them available for phytoplankton. Mineralisation of the organisms that massively developed in the capillaries of the ice was shown to provide an intake of nitrates and ammonium (Bondarenko et al., 2013). However, we propose that initial increase in abundance and biomass of the under-ice phototrophic community in Lake Baikal, like in April 2018, is likely enhanced by nutrients from atmospheric precipitation.

Atmospheric precipitation is an important source of nutrients for freshwater ecosystems (Russell et al., 1998; Zhai et al., 2009; Chen et al., 2018), especially when the water masses are limited by poor mobility and mixing; thus, they are sensitive to atmospheric nutrient inputs (Zheng et al., 2019). The fluctuations in abundance of microalgae and dinoflagellates in Lake Baikal, which were especially significant in April 2018 (Fig. 3, Fig 4), could be due to fluctuations in the nutrient concentration released with precipitation into the lake water and the flooded ice. A further short-term decrease in the air temperature at the beginning

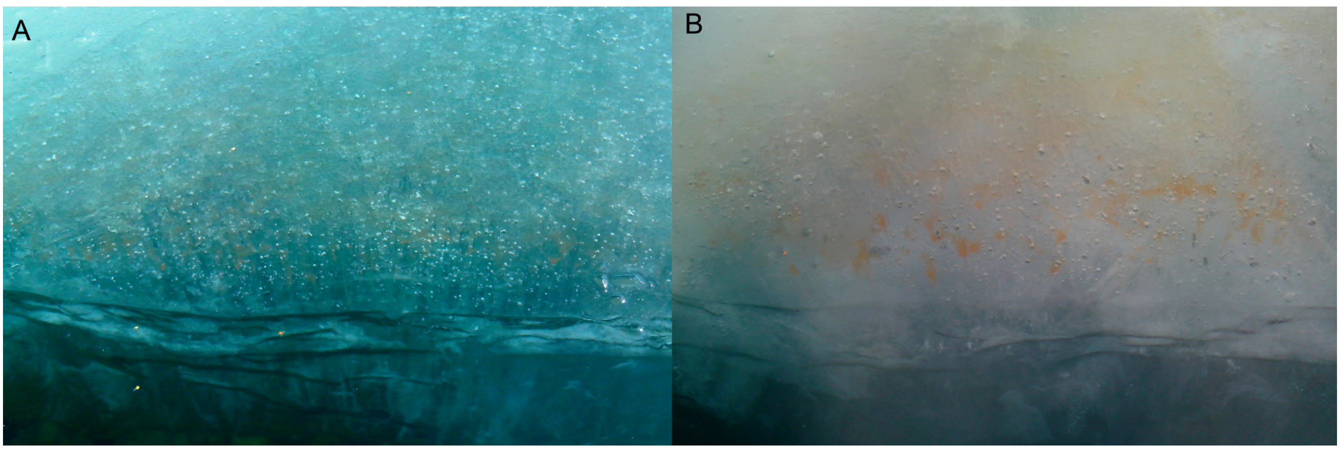

Fig.6. The flooded ice floe on 8 April before the rain precipitation (A) and the same ice floe after the rain precipitation at night on 9 April with concentration of dinoflagellates, mostly *Gymnodinium baicalense* var. *minor* (yellow spots), in the water above the ice (B)

of April stopped the ice melting and, consequently, the influx of nutrients. This might result in a decline of some microalgae and dinoflagellates in the lake water. Accordingly, the further sharp increase in the number of *G. baicalense* var. *minor* on 9 April (Fig. 3 - Fig. 6) could be related to the rain precipitation at night on 9 April that had exceptionally high nutrient concentrations, in particular, nitrogen (Table 1). Dinoflagellates are capable of assimilating nitrogen both in the form of nitrates and ammonium (Dagenais-Bellefeuille and Morse, 2013). They also can temporarily accumulate inorganic and organic nitrogen available in the environment (Maguer et al., 2007; Kopp et al., 2013).

High concentrations of certain nutrients can be toxic for dinoflagellates (Chang and McClean, 1997). For instance, $NH4^+$ concentrations higher than 25 μmol/l inhibit the growth of *Alexandrium minutum* Halim (Chang and McClean, 1997). However, in Lake Baikal, high concentrations of nutrients from precipitation could be substantially diluted with the lake water, which has an extraordinary low salinity (Grachev, 2002). Thus, the rain precipitation at night on 9 April was relatively small, ca. 1.9 mm (Table 1), but it had a high NH_4^+ concentration of 98 μmol/l (Table 1), whereas the water layer above the flooded ice cover, where we observed the massive yellow accumulations of *G. baicalense* var. *minor* (Fig. 5, Fig. 6), was ca. 100 mm. The total concentration of the NH_4^+ after mixing of precipitation with the lake water should be deluded up to 50 times (100 mm/2 mm). Therefore, the concentration of NH_4^+ increased but not significantly, and, instead of average 1 μmol/l (Grachev, 2002), it could reach 3 μmol/l in the lake water, which should favour the development of dinoflagellates and microalgae but not inhibit it. During the next few days after the rain precipitation, the abundance of *G. baicalense* var. *minor* and microalgae decreased (Fig. 3, Fig. 4, Fig. 6). This might be because of a decrease in the concentration of nutrients due to its dilution with the lake water and/or its active assimilation by dinoflagellates and algobacterial community (Bondarenko et al., 2013; Bashenkhaeva et al., 2017). For example, previous studies revealed that the lowest concentration of ammonium and nitrates were in the areas with the highest abundance of the organisms in the ice cover, which indicated active assimilation processes (Bondarenko et al., 2013). Grazing may be another factor affecting the abundance of microalgae and dinoflagellates under the ice, and it requires special research.

Although no relevant studies have been carried out for *G. baicalense* var. *minor*, specifically, many dinoflagellates considered as phototrophic are capable of mixotrophic nutrition (Kirchner et al., 1996). Particularly, some dinoflagellates feed on nitrogen-fixing cyanobacteria *Synechococcus* spp. (Jeong et al., 2005). Therefore, the accelerated development of *G. baicalense* var. *minor*, in addition to its direct assimilation of NO_3^- and NH_4^+, could be due to its ability to consume bacteria. The total amount of bacteria in the under-ice microbial community of Lake Baikal can be several times higher than in the melt-water of the ice cover as well as in the photic zone (0-25-50 m) of the lake (Bondarenko et al., 2013; Bashenkhaeva et al., 2017). A potential mixotrophy could help *G. baicalense* var. *minor* to develop under the ice cover with a thick snow layer (Bondarenko, 1995; Bashenkhaeva et al., 2015; 2017).

The role of migrations for Gymnodinium baicalense var. *minor*

The abrupt changes in the abundance of *G. baicalense* var. *minor* in the surface water layer, in particular, its increase, were quite remarkable. For example, it increased from $13x10^3$ to $430x10^3$ cells/litre after the night on 9 April. If such an increase in abundance was only due to cell division, the generation rate of the species should be equal to 3.5 cell divisions per day. However, according to the estimation in Votintsev et al. (1975), the generation rate of this dinoflagellate in the lake does not exceed a range of 0.2 – 1.2 divisions per day. In this regard, a more likely cause of such an abrupt increase in the abundance of this species may be its ability to actively migrate. Some marine dinoflagellates are capable of migration to the ocean areas with limited light availability but having the concentration of nitrates higher than on the water surface where the species are normally concentrated (Harrison, 1976; Smayda, 1997). These migrations were rather associated with reaction to nutrients availability than with circadian rhythms depending on the availability of solar radiation (Harrison, 1976; Smayda, 1997). The fact that variations in NO_3^- concentrations affect the endogenous clock of *Lingulodinium polyedra* (Stein) Dodge, regulating its migrations, also supports this hypothesis (Roenneberg and Rehman, 1996). Furthermore, dinoflagellates are among the fastest phytoflagellate swimmers: the swimming speed of many species is 0.2 – 2 meters per hour, and for some species, it reaches up to 5 m per hour (Kamykowski, 1995). Our observations in 2018 may also indicate the active migration of *G. baicalense* var. *minor* towards the higher nutrient concentration (Fig. 6). This can be one of the reasons for the fluctuations of its abundance in the surface water. Potential capacity for such rapid movement along with effective nitrogen accumulation may help *G. baicalense* var. *minor* to compete with other protists and occupy its ecological niche in the under-ice conditions of Lake Baikal.

5. Conclusion

The under-ice bloom of phytoplankton is highly important for the ecosystem of Lake Baikal, as it can have most of the annual primary production. The present study showed that atmospheric precipitation could be an important source of nutrition for the under-ice organisms in Lake Baikal where the water masses are limited by mobility, which prevents the influx of nutrients from the underlying water layers. An appropriate structure of the loose ice cover permeated with pores and capillaries apparently facilitates the effective penetration of nutrients from the melted precipitation, making them available for phytoplankton. The chemical analysis revealed that atmospheric precipitation in 2018 had nearly the same concentration of phosphate as the Lake Baikal water on average but elevated concentrations of nitrate and ammonium. We suggested that nutrients from precipitation, in particular, nitrogen, could be one of the key factors enhancing the mass development of the under-ice community in Lake Baikal. The endemic dinoflagellate *G. baicalense* var. *minor* dominated microalgae in the surface waters and the ice cover in April 2018, but its abundance varied significantly on different days. We proposed that such development dynamics of *G. baicalense* var. *minor* could be partly owing to its capacity for an active migration towards the high nitrogen concentration initially released into water from atmospheric precipitation. Atmospheric precipitation as a source of nutrients should not be underestimated as a driving force for the under-ice community and its potential influence on primary production, especially during the ongoing ecological changes in Lake Baikal.

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