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Long-term dynamics of dominant diatom species abundance of spring phytoplankton in three basins of the pelagic zone of Lake Baikal in 1964-1984 and 2007-2016

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ABSTRACT. Analysis of long-term observations of dominant diatom species of spring phytoplankton of Lake Baikal *Synedra acus* subsp. *radians, Aulacoseira baicalensis*, *Aulacoseira islandica*, *Stephanodiscus meyeri* and *Nitzschia graciliformis* was demonstrated. It is shown, how the abundance of these species varied in Southern, Central and Northern Baikal in 2007-2016 compared to other observation periods in 1964-1968 and 1969-1984. It is found out that, species ratio changed in 2007-2016. The abundance of *S. acus* subsp. *radians* increased in Southern and Central Baikal, while for other species - *A. baicalensis*, *A. islandica*, *N. graciliformis* and *S. meyeri*, it significantly decreased. In Northern Baikal, the ratio of species in 2007-2016 was comparable to 1969-1984. Despite the change in the ratio of species over the past decade, the contribution of these five dominant species to the total abundance of spring phytoplankton of Lake Baikal has comparable values in all studied periods.

Keywords: Lake Baikal, phytoplankton, diatom algae, abundance, *Synedra acus* subsp. *radians, Aulacoseira baicalensis*, *Aulacoseira islandica*, *Stephanodiscus meyeri*, *Nitzschia graciliformis*

The article is dedicated to the memory of G.I. Popovskaya

1. Introduction

Lake Baikal in East Siberia is the oldest (25 My), deepest (1637 m) inland water body with a huge water volume (23 thousand km^3). It comprises 20 % of world stock of surface fresh waters of the planet (Atlas of Lake Baikal, 1993).

The phytoplankton of Lake Baikal play an important role in generation of primary production, on which the formation of the whole water body trophic structure depends. Main contribution into the biomass in spring belongs to diatom algae (Popovskaya, 2000). Their fraction is in average 70-90 % of total phytoplankton biomass.

Dominant diatom plankton species of Lake Baikal pelagic zone in spring, during highly productive years are *Aulacoseira baicalensis* (K. Meyer) Simonsen*, Synedra acus* subsp. *radians* (Kützing) Skabitchevsky, *Aulacoseira islandica* (O. Müller) Simonsen (=*Aulacoseira skvortzowii* Edlund, Stoermer et Taylor), *Stephanodiscus meyeri* Genkal et Popovskaya and *Nitzschia graciliformis* Lange-Bertalot et Simonsen emend. Genkal et Popovskaya.

Nowadays *Synedra acus* subsp. *radians* is considered as a unit of species *Ulnaria acus* (Kützing) Aboal /*Fragilaria radians* (Kützing) Williams et Round (Zakharova et al., 2023), but we will use the former name in this paper.

These species are characterized by their intensive development during under-ice period, immediately after lake opening as ice break, and by abrupt interannual oscillation of abundance and biomass (Antipova and Kozhov, 1953; Votintsev et al., 1975).

It is known that Lake Baikal has a well-expressed bed of three main lake basins — southern, central and northern separated from each other by two underwater boarder — the Akademicheskiy Ridge and Selenginskiy bridge (Atlas of Lake Baikal, 1993). It is stated that phytoplankton distribution among the lake basins is spatially heterogenous (Popovskaya, 1977; 1987; 1991). It is shown that the phytoplankton in Southern and Central Baikal by its abundance is 5 times, and by its biomass 6 times richer compared to Northern Baikal (Popovskaya, 2000).

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Permanent annual observations of Southern Baikal phytoplankton have been performed by the Institute of Biology since 1945 at a station near Bol'shye Koty 2.2 km away from the shore (Antipova and Kozhov, 1953; Antipova, 1963; Kozhov, 1963; Kozhova and Izmest'eva, 1998; Izmest'eva et al., 2001; Mokry, 2011; Hampton et al., 2008; 2014; Rusanovskaya et al., 2020). The authors did not reveal any considerable variations in phytoplankton in spring (Izmest'eva et al., 2001; Mokry, 2011). The analysis of perennial observation series (1951-2010) showed a negative linear trend for the abundance of *A. baicalensis* and absence of a directional trend for *A. islandica* (Izmest'eva and Shimaraeva, 2012).

The assessment of quantitative characteristics of spring phytoplankton for the whole pelagic zone of Lake Baikal has been performed by the Limnological Institute since 1964 (Popovskaya, 1967; 1977; 1987; 2000; Votintsev et al., 1975; Bondarenko, 1997; Popovskaya et al., 2006; 2007; 2008; 2015; Pomazkina et al., 2010; Bondarenko et al., 2019).

The perennial observations revealed highly productive (with phytoplankton biomass in spring > 1 g/m^3 in the layer of 0-25 m), mean productive (0.5-1 g/m^3) and low productive (< 0.5 g/m^3) years (Popovskaya, 1977). It is shown that in 1970-1980, compared to 1950-60, the abundance of *S. acus* subsp. *radians*, *A. islandica* and *N. graciliformis* increased several times in South Baikal (Popovskaya et al., 1997; Popovskaya, 2000).

Thus, before either abundance values for several species averaged by all the basins (Popovskaya et al., 1997) or only for South Baikal (Popovskaya, 2000; Izmest'eva and Shimaraeva, 2012) were presented. Special analysis of quantitative characteristics (abundance and biomass) of dominant species in different lake basins (southern, central and northern ones) in perennial aspect has not been performed up to the present.

The aim of this study is the analysis of perennial dynamic of the abundance of spring phytoplankton dominant species in three basins of Lake Baikal pelagic zone in 1964-1984 and 2007-2016.

2. Materials and methods

The material for the present paper is based on data of 2007-2016 we obtained during spring surveys of phytoplankton in 2006-2017 and perennial permanent series by G.I. Popovskaya of 1964-1984.

The phytoplankton surveys were performed on research vessels (R/V) "Akademik V.A. Koptyug" and "G. Yu. Vereshchagin" immediately after the lake opening as ice break (late May – early June). This time interval, according to the scheme of biological seasons on Lake Baikal (Kozhov, 1962), is called "late spring period". The sampling was done according to the scheme developed before (Votintsev et al., 1975), but we reduced it someway (Popovskaya et al., 2015).

Quantitative samples were collected using a system of bathometers of carousel SBE-32 (Carousel Water ampler, Sea-Bird Electronics, Inc. США). We studied the upper 25-meter layer. For quantitative counting, we used a settling method (Kiselev, 1969; Abakumov et al., 1992). The algae cells were counted using Hensen method (Kiselev, 1969) on a ruled thin ground slide in a drop taken with a piston pipet with volume of 0.1 ml in two- or three-fold repeatability using light microscopes "MBI-6", "Pereval" and "Axiovert 200" ZEISS (Germany) with a photographic camera Pixera Penguin 600CL. Cells biomass was determined by a calculation method (Makarova and Pichkily, 1970; Belykh et al., 2011). The graphs show average values of a species abundance for each basin calculated by addition of the abundance at different station and division by stations number. The data were plotted using Microsoft Excel and Past 4.11.

3. Results

Cluster analysis of data on the abundance of dominant diatom species in 1964-1984 and 2007-2016 showed a distribution over three periods – 1964-1968, 1969-1984 and 2007-2016 (Fig. 1). We performed the analysis of abundance dynamics in diatom phytoplankton dominant species during 2007-2016 in Southern, Central and Northern Baikal pelagic zone compiled with past observation periods of 1964-1968 and 1969-1984.

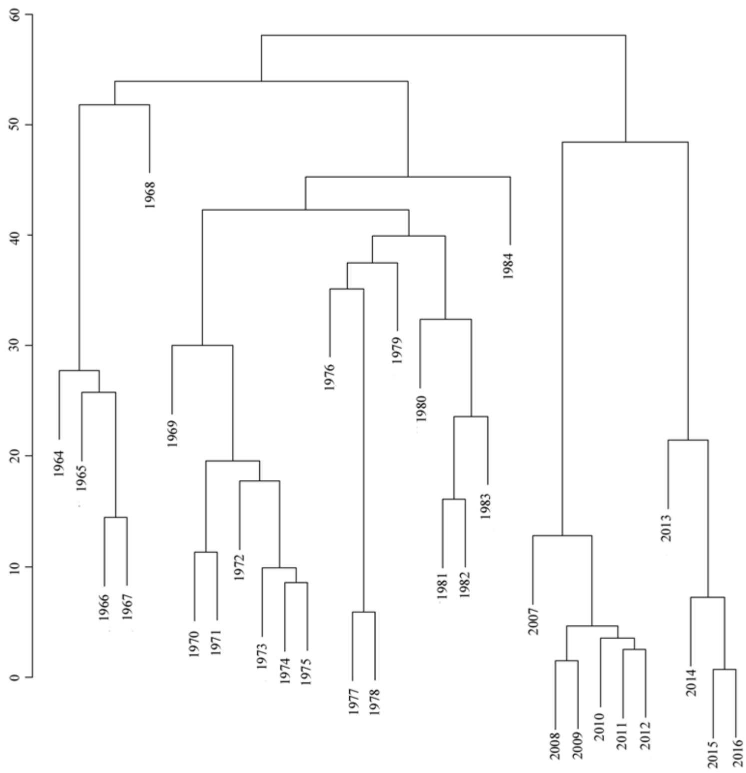

Fig.1. Cluster analysis of the abundance of dominant diatom species in 1964-1984 and 2007-2016.

3.1. Southern Baikal.

In 2007-2016, spring phytoplankton were dominated only by 2 species of diatom algae – *S. acus* subsp. *radians* and *A. baicalensis*. *S. acus* subsp. *radians* occurred every year. Its average abundance varied from

5.2 to 670 thousand cells/l. The most productive were 2008, 2009, 2014, 2015 and 2016, when the average abundance for this basin was 230-670 thousand cells/l (Fig. 2A).

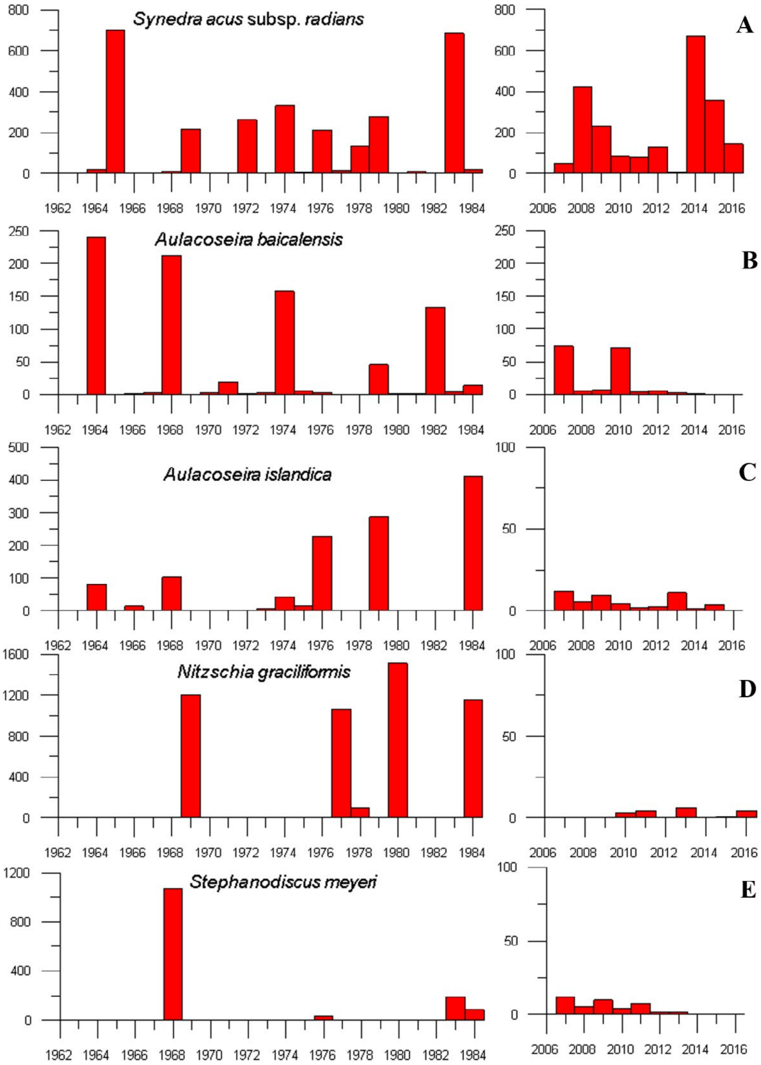

Fig. 2. Long-term dynamics of diatom species in the 0-25 m layer in Southern Baikal. On the y-axis - the abundance, thousand cells per liter. **A** – *S. acus* subsp. *radians*, **B** – *A. baicalensis*, **C** – *A. islandica*, **D** – *N. graciliformis*, **E** – *S. meyeri*.

During the past study periods of 1964-1968 and 1969-1984, *S. acus* subsp. *radians* in South Baikal had a rhythmic development with an increased abundance after 1-3 years (Fig. 2). Only once this species developed 2 years successively – in 1978 and 1979. In period 1964-1968, *S. acus* subsp. *radians* developed in mass in 1965, when average abundance reached up to 700 thousand cells/l (Fig. 2A). During other years of mass development (1969, 1972, 1974, 1976, 1978 and 1979), the abundance varied from 134 to 330 thousand cells/l. The maximum abundance of this species was in 1983 and was comparable to 1965 (Fig. 2A).

Maximal abundance of *A. baicalensis* during 2007-2016 occurred in 2007 and 2010 (74 and 71 thousand cells/l, respectively) (Fig. 2B). In 1964-1968, the concentration of this species in Southern Baikal was considerably higher. There were two peaks of development of *A. baicalensis* with interval of 3 years (1964 and 1968). During next period, a decrease in level of this species was recorded. *A. baicalensis* developed in mass only in 1974 and 1982. It is to notice that somewhat increased concentrations of *A. baicalensis* were in 1979, however, in that case it developed as a co-dominant with a mass development of *S. acus* subsp. *radians* and *A. islandica.*

The species *A. islandica*, *S. meyeri* and *N. graciliformis* did not develop in mass in the phytoplankton of Southern Baikal pelagic zone in 2007-2016 (Fig. 2C, 2D, 2E), while during previous periods, their abundance was considerably higher. For example, if the abundance of *A. islandica* varied during last years within 1.2-12 thousand cells/l, in 1964 – 1968, there were the years (1964, 1968) with abundance of 82 and 103 thousand cells/l, respectively. During next period, in 1976, 1979 and 1984, there were the highest values of abundance for this species during all the observation periods (227 – 410 thousand cells/l).

N. graciliformis in Southern Baikal reached a mass development in some years. A mass development of this species was firstly recorded in 1969, when its abundance exceeded 1 million cells/l (Fig. 2D). Then, during seven years (1970-1976), it occurred in very small amounts or was absent. It reappeared in mass (> 1 million cells/l) in 1977, 1980 and 1984.

S. meyeri is more characteristic for shallow-water lake sites and large gulfs and rarely develops in Southern Baikal pelagic zone in mass (Fig. 2E). During the entire study period it was only a year, 1968, when its average abundance in Southern Baikal exceeded 1 million cells/l. This species was occurred in 1976, 1983 and 1984 in small amounts (32-190 thousand cells/l) (Fig. 2E).

3.2. Central Baikal.

It was possible to observe the same two diatom species in mass in Central Baikal pelagic zone in 2007-2016, as in Southern Baikal. *S. acus* subsp. *radians* developed every year. Its average abundance varied within 38-843 thousand cells/l. A mass development of this species occurred in 2008, 2014, 2015 and 2016, and we noticed in 2014 maximal abundance values for all observation periods in Central Baikal. The analysis of perennial observation series showed that in Central Baikal, before 1976, *S. acus* subsp. *radians* did not developed in mass. Thus, its abundance varied at that time within 0.4-148 thousand cells/l (Fig. 3A). Its mass development was recorded since 1976, and high concentrations (247-505 thousand cells/l) were in 1976, 1977, 1979 and 1980. During other years, the abundance of this species varied from 0.38 to 76 thousand cells/l (Fig. 3A).

In 2007-2016, a high development level of *A. baicalensis* was recorded only in 2007, and its quantitative values in the central basin that year were somewhat higher than in the south (Fig. 3B). It occurred in noticeable amounts only in 2010, while in other years, was a very small abundance or absent. However, it is shown that during 1964-1968, *A. baicalensis* more intensively developed in Lake Baikal. Three development peaks were registered in 1964, 1967, 1968 with the abundance maximum in 1964 (165 thousand cells/l). During 1969-1984, *A. baicalensis* developed every 2-3 years with different intensity as well (Fig. 3B). Its abundance in 1971, 1975, 1979 and 1982 was 32, 28, 35 and 220 thousand cells/l, respectively.

The abundance of *A. islandica* in Central Baikal in a perennial aspect varied not considerably and did not exceed 50 thousand cells/l (Fig. 3C).

N. graciliformis was not representative of the periods of 2007-2016 and 1964-1968 (Fig. 3D). Its single outbreaks were observed in 1978 and 1980.

Development of *S. meyeri* in Central Baikal was more characteristic compared to South. During 1964-1968, a mass development of this species was observed only once, in 1968. Its abundance was 487 thousand cells/l. During 1969-1984, *S. meyeri* occurred practically every year, but in small amounts (up to thousand cells/l). Its maximal development during all observation periods was registered in 1983 (Fig. 3E). In 2007-2016, the abundance of *S. meyeri* did not exceed 30 thousand cells/l; there were no peaks of mass development for that period.

3.3. Northern Baikal.

In the pelagic zone of Northern Baikal, the abundance of diatoms was significantly lower compared to Southern and Central Baikal. *S. acus* subsp. *radians* occurred in Northern Baikal plankton in 2007-2016 every year. Minimal abundance values (2.2-3.1 thousand cells/l) were recorded in 2010 and 2013. Its maximal abundance (224 thousand cells/l) was recorded in 2014. During 1964-1968, the abundance of this species varied from 0.3 to 56 thousand cells/l. In 1976, there was the peak of mass development of *S. acus* subsp. *radians* with abundance of 418 thousand cells/l (Fig. 4A).

A. baicalensis was a constant component of phytoplankton in 2007-2016. It occurred in small amounts and only in 2007 and 2012 it contributed considerably into the biomass. (It has to be noted that as this is a large-cell species, at its abundance of 63

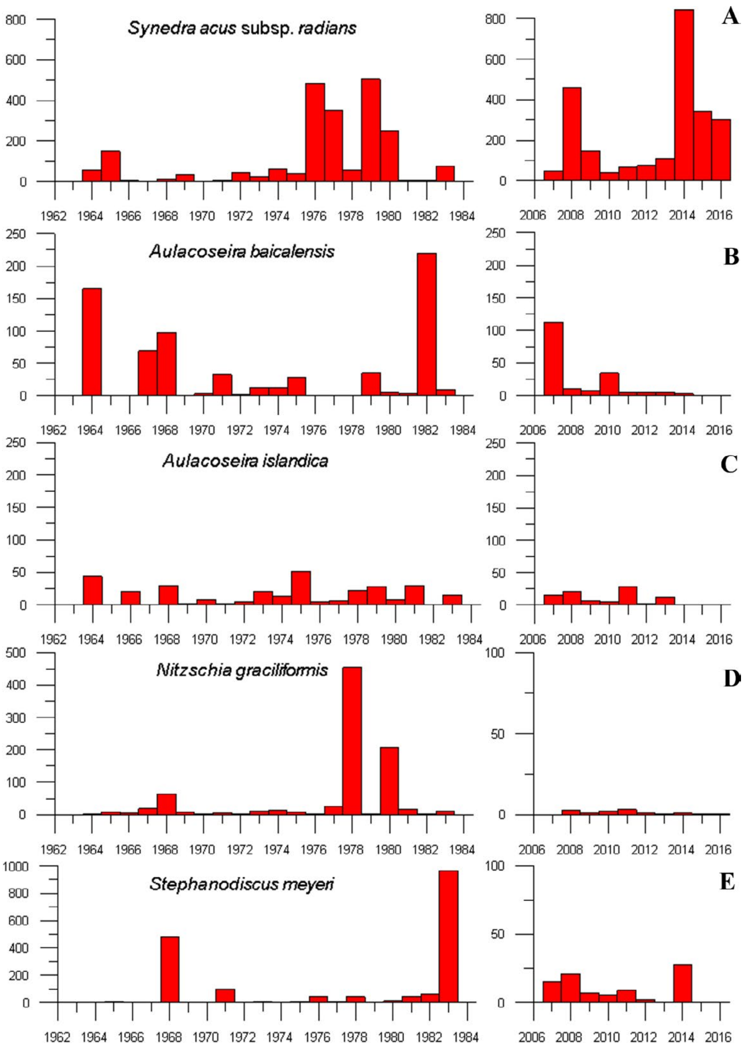

Fig. 3. Long-term dynamics of diatom species in the 0-25 m layer in Central Baikal.
On the y-axis - the abundance, thousand cells per liter. **A** – *S. acus* subsp. *radians*, **B** – *A. baicalensis*, **C** – *A. islandica*, **D** – *N. graciliformis*, **E** – *S. meyeri*.

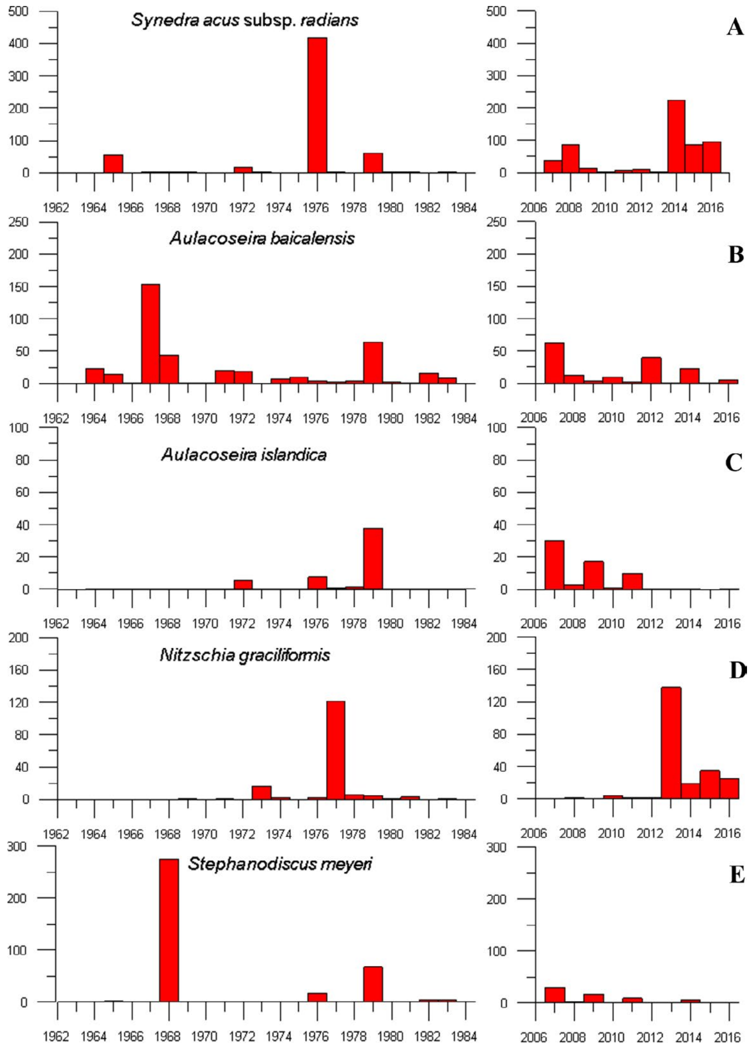

Fig. 4. Long-term dynamics of diatom species in the 0-25 m layer in Northern Baikal. On the y-axis - the abundance, thousand cells per liter. **A** – *S. acus* subsp. *radians*, **B** – *A. baicalensis*, **C** – *A. islandica*, **D** – *N. graciliformis*, **E** – *S. meyeri*.

thousand cells/l it gives biomass of 630 mg/m³, it corresponds to a year of average productivity). During earlier study period (1964-1968), it was possible to observe higher values of abundance of this species compared to 1969-1984 and 2007 -2016 (Fig. 4B). The maximum abundance of this species was in 1967 (153 thousand cells/l).

A. islandica was not characteristic for Northern Baikal (Fig. 4C). The abundance of this species did not exceed 38 thousand cells/l for all observation periods. During 2007-2016, three small peaks have been noted (2007, 2009 and 2011) (Fig. 4C).

N. graciliformis, in contrast, gave high abundance values in 2013-2016 with a maximum in 2013 (138 thousand cells/l). During two previous study periods, the comparable values were registered only in 1977 (Fig. 4D).

S. meyeri develops in Northern Baikal very rarely. Its maximal abundance was registered in 1968, it was 275 thousand cells/l (Fig. 4E). In 2007-2016, the concentrations of this species were not high (0.6-30 thousand cells/l).

4. Discussion

The present study is aimed to show the species structure in different lake basins in 2007-2016 compared to 1964-1968 and 1969-1984. It is shown that the absolutely dominant species was *S. acus* subsp. *radians* in Southern Baikal in 2007-2016. Its ratio was 88 % from total abundance of five dominant species, while in 1964-1968, this value was 30 %, and in 1969-1984 – 24 % (Fig. 5).

The increase of synedra's role both in Southern Baikal pelagic zone and in the whole lake water area was mentioned before as well (Antipova, 1974; Kalyuzhnaya and Antipova, 1974; Popovskaya et al., 2015; Bondarenko and Logacheva, 2016). In 2014, development of *S. acus* subsp. *radians* was maximal. In Southern Baikal, at some stations, its abundance reached 1742 thousand cells/l. Maximal value for this species recorded before (Antipova, 1974) was 1080 thousand cells/l for Southern Baikal. While comparing averaged data by basins we revealed that the peaks of the same intensity in development of *S. acus* subsp. *radians* were observed in Southern Baikal in 1965 and 1983 (Fig. 2A). The fraction of *A. baicalensis* in 2007-2016 was ca. 7 %. The role of other species - *A. islandica* and *S. meyeri* – was inconsiderable. There were no *Nitzschia graciliformis* among dominant species (Fig. 5). Among three observation periods in South Baikal pelagic zone, maximal abundance values of *A. baicalensis* and *S. meyeri* were recorded in 1964-1968. More *N. graciliformis* and *A. islandica* occurred in 1969-1984 (Fig. 5).

In Central Baikal, highly productive years did not always coincide with those in Southern Baikal (Fig. 2, Fig. 3). However, the species ratio in southern basin in 2007-2016 was similar to that in central basin of the lake (Fig. 5).

Species ratio in 1964-1968 and 1969-1984 differed. Thus, a considerable contribution into total

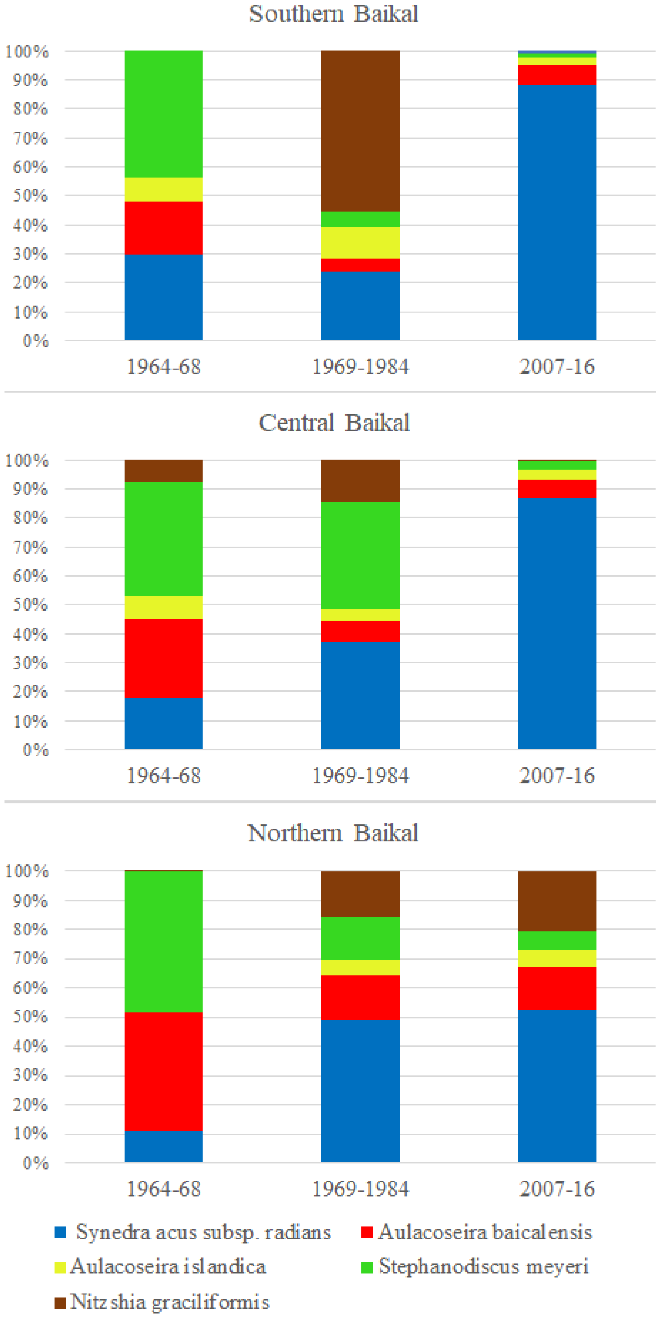

Fig.5. The ratio of the dominant species of diatom plankton in the pelagic zone of Southern, Central and Northern Baikal in different periods.

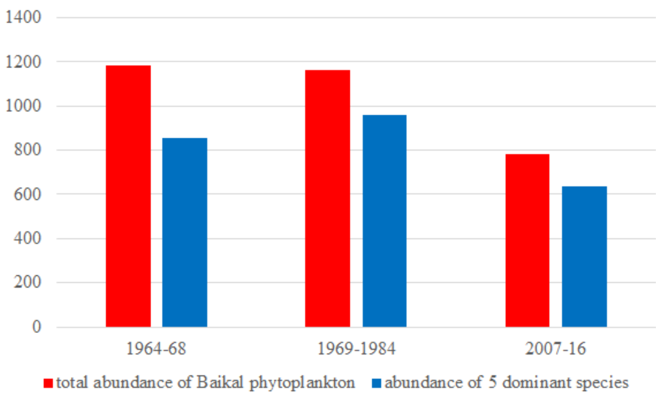

Fig. 6. Total phytoplankton abundance and the abundance of five dominant species in 1964-1968, 1969-1984 and 2007-2016. On the y-axis – the average abundance, thousand cells per liter.

abundance in 1964-1968 were done by *S. acus* subsp. *radians*, *A. baicalensis*, *A. islandica*, *S. meyeri* and *N. graciliformis.* In 1969-1984, the abundance of *S. acus* subsp. *radians* increased and one of *A. baicalensis* decreased.

In Northern Baikal, compared to southern and central basins, species ratio in 2007-2016 was similar to the period of 1969-1984, while in 1964-1968, main contribution into total abundance were done by *A. baicalensis* and *S. meyeri.* The increase of the ratio of *S. acus* subsp. *radians* and *N. graciliformis* recorded during 1969-1984 (Fig. 5).

Thus, we can state that, abundance of the studied taxa (except *S. acus* subsp. *radians*) reduced in Southern and Central Baikal in 2007-2016. However, in Northern Baikal, the abundance of *N. graciliformis* and *S. acus* subsp. *radians* increased in 1969-1984 and 2007-2016 compared to 1964-1968 (Fig. 5).

In general, the total abundance of phytoplankton in Lake Baikal in 1964-1968 was comparable with ones 1969-1984 (Fig. 6). Despite the fact that the total abundance of phytoplankton in 2007-2016 was lower, the total contribution of the five dominant diatom species to the total abundance of phytoplankton in the spring of 2007-2016 was comparable to the periods 1964-1968 and 1969-1984. and amounted to 81%, 72% and 83% respectively (Fig. 6).

The reasons for the increase in the role of *Synedra* and the decrease in *Aulacoseira* in recent years are not clear. It is known that Lake Baikal phytoplankton are characterized by abrupt interannual oscillations of dominant species abundance and biomass (Antipova and Kozhov, 1953; Votintsev et al., 1975, Popovskaya, 2000). In addition to abrupt interannual fluctuations, temporary rearrangement of community species sometimes occurs in the pelagic zone of Lake Baikal. At that time, the large-celled species *Aulacoseira* and *S. acus* subsp. *radians* are replaced by small-celled *N. graciliformis*. The reason of mass outbreak of *N. graciliformis* is not clear. There is an opinion that one of the causes of the increased abundance of the *N. graciliformis* population during the 1960s and 1970s are most likely to be linked to the economic development, that took place in the areas around Lake Baikal (Bondarenko, 1999). This species has a higher growth rate than the endemic diatoms to Lake Baikal and it population is highly limited by P (Bondarenko and Guselnikova, 1988; 1994). According to perennial observations, *N. graciliformis* developed in small amounts since 1950s (Antipova, 1963) and only 4 years (1969, 1977, 1980 and 1984) it developed in mass reaching in some sites abundance 1-7 million cells/l (Popovskaya et al., 1997).

When comparing the three periods, it can be seen that in 1969-1984 in the south, the contribution of *Nitzschia* to the total abundance of the five dominant species was 55%. In 1964-1974 and 2007-2016 this species was not among the dominant species at all (Fig. 5).

Absolute dominance of *S. acus* subsp. *radians* in 2007-2016 may be due to biocenotic relations between the species and the climate. It is known that the phytoplankton is very sensitive to environmental condition changes (Grachev, 2002; Berthon et al., 2014).

In recent years, information on climate change was proved to have led to an increase in air and water temperatures all over the world (Houghton et al., 2001), including Baikal region (Shimaraev et al., 2002; Smith et al., 2005; Walter et al., 2006; Izmest'eva et al., 2016). Lake Baikal now freezes later and opens from the ice earlier (Sizova et al., 2013; Shimaraev and Domysheva, 2013), the vegetation period of algae reduced and they sink faster out of the water column (Bondarenko et al., 2019). The shortening of the ice cover period is caused by warmer winter conditions around Lake Baikal between 1896 and 2010, with air temperatures increasing by 1.9 ºC in winter and 1.5 ºC in spring over the last 100 years (Shimaraev and Domysheva, 2013).

Southern Baikal has demonstrated the tendencies of the increase in water temperature in the upper 50-meter layer over the last 70 years, water transparency and chlorophyll-*a* concentration in the open water season over the past 40 years (Rusanovskaya et al., 2020). Analysis of the dynamics of the dominant species of phytoplankton has shown the increase in abundance of non-endemic small-cell species of diatom algae *S. acus* subsp. *radians* with simultaneous tendency of decrease in the abundance of endemic large-cell species of under-ice developing diatom algae. These authors concluded that the observed trends can be explained by global climatic change (Rusanovskaya et al., 2020).

Probably *S. acus* subsp. *radians* is more competitive with other dominant spring phytoplankton species as it adapts to a larger temperature range. Abundant amounts of this species were observed in the past as well. Lake Baikal paleorecord manifest three temporal intervals with mass development of *S. acus* subsp. *radians* – in the Pleistocene (439-417 and 127-125 ky BP) and in the Holocene (3.8-2.65 ky BP). In the Pleistocene this species was a companion one, but in the Holocene it represented a diatom zone (Kuzmin et al., 2009). The authors noticed that thin sediment layers enriched by valves of *Synedra acus* subsp. *radians* formed *ca.* 3.8 ky BP were occurred practically in all Baikalian sediment cores, and is an important lithological marker, which reflects an episode of a considerable regional warming, at least, in summer (Karabanov et al., 2000; Kuzmin et al., 2009).

Other paleolimnological studies confirm that Lake Baikal diatom community is sensitive to climate (Khursevich et al., 2001; Bradbury et al., 1994; Mackay et al., 1998). These studies have shown fluctuations in abundance of *Aulacoseira* spp., *S. acus* and other diatom species in connection with climatic shifts.

5. Conclusions

Thus, the comparison of three observation periods showed that in 2007-2016 the contribution of each dominant species to the total abundance of diatom plankton changed. The contribution of *S. acus* subsp. *radians* considerably increased. The abundance of *A.*

baicalensis, *A. islandica* and *S. meyeri* decreased, and *Nitzschia* stopped completely being among dominant unit in southern and central basins. The revealed changes probably reflect climate change on the planet and biocenotic relationship between species, but they do not reveal any changes in the water body productivity. As Lake Baikal is a World Heritage Site, it is necessary to perform regular monitoring of the whole lake pelagic zone during different seasons.

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Conflict of interest

The authors declare no conflict of interest.

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