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RESEARCH PAPER

LONG-TERM STUDIES OF SURFACE-SEDIMENT DIATOM ASSEMBLAGES IN ASSESSING THE ECOLOGICAL STATE OF LAKE LADOGA, THE LARGEST EUROPEAN LAKE

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ABSTRACT. The study continues a series of observations started in the late 1950s, aimed at inferring changes in the Lake Ladoga ecosystem state recorded in the surface-sediment diatom assemblages. At the pre-anthropogenic stage (prior to the 1960s), the composition of the surface-sediment diatom assemblages indicated an oligotrophic state of Lake Ladoga. With the increased P load to the lake (late 1960s–1980s), the transition to a mesotrophic state was recorded via increased proportions of eutrophic species and decreased abundances of the taxa typical of the pre-anthropogenic stage. In the early 1990s, the composition of the surface-sediment diatom assemblages still indicated a mesotrophic state despite a decreased external P load. At the present de-eutrophication stage of Lake Ladoga (the 2000s), the abundances of eutrophic taxa steadily decrease while some taxa typical of the pre-anthropogenic period return to their dominating position in the surface-sediment diatom assemblages. However, despite the decreased P concentrations, the Lake Ladoga ecosystem has not returned to its pre-anthropogenic state as indicated by the present-day composition of the surface-sediment diatom assemblages. This suggests a delayed ecosystem response to the decreased anthropogenic pressure, and possibly some irreversible changes resulting from the eutrophication. At present, de-eutrophication processes and ecosystem recovery are superimposed upon the recent climatic changes that govern the onset and duration of the vegetative seasons for the phytoplankton communities in Lake Ladoga. The diatom-inferred changes in the ecological state of Lake Ladoga are in agreement with the results of long-term hydrochemical and hydrobiological studies.

KEY WORDS: Lake Ladoga, surface-sediment diatom assemblages, lake ecological state assessment, anthropogenic eutrophication, recovery, climate change

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INTRODUCTION

Being indispensable for all living things on Earth, freshwater is also one of the most limited resources. It only accounts 2,5% of all freely available water in the world, only 0,3% of which is readily accessible in lakes, reservoirs and rivers (Kalff 2001). Population growth and enhanced industrial and agricultural activities have played important role in water pollution and rapid deterioration of aquatic ecosystems starting from the mid-20th century. As a result, in the 21st century, water shortage and/or water quality become one of the major problems for humanity (Ansari and Gill 2014).

Cultural eutrophication, i.e. anthropogenic nutrient (P and N) loading to aquatic ecosystems, is acknowledged as the most widespread form of lake pollution on a global scale (Smol and Stoermer 2010). The lake's ecosystem response to nutrient enrichment results in various ecological problems, such as massive growth of algae or macrophytes, shifts in food web structure, loss of aquatic organisms and depletion of aquatic biodiversity. Furthermore, poor water quality caused by eutrophication restricts its use for drinking, irrigation, industry, transportation, recreation, fisheries, etc. Although major advances in the scientific understanding and management of eutrophication have been made since the late 1960s, eutrophication continues to be ranked as the most common water-quality problem in the world, and remains an active area of scientific research (Schindler 2006; Smol 2008).

In last decades, a series of measures were undertaken in different countries to reduce the nutrient load to the lakes and restore aquatic ecosystems. As a result, many lakes, especially in Europe and North America, have now entered an oligotrophication phase which, however, is a less well-understood and consequently less predictable process (Smol and Stoermer 2010). Basin morphometry, water chemistry, and the nature of the phosphorus sources are among the factors that govern the rate at which lake productivity will revert toward conditions that had existed before cultural eutrophication started (Wetzel 2001).

Besides, recent climate change may fundamentally alter the physical (e.g. stratification, duration of ice cover) and food-web structure of the lake, biogeochemical processes and land-water interactions. This would impact on the pathways and success of lake restoration efforts and may prevent re-establishment of communities typical of the pre-anthropogenic period (Battarbee et al. 2005).

Lake Ladoga in north-western Russia (Fig. 1a), is the largest lake in Europe and ranked among the top fifteen world's freshwater lakes in terms of surface area and water volume. Lake Ladoga represents the only source of potable water for St Petersburg, the second largest city in Russia, as well as for many smaller towns in the Leningrad Region and Republic of Karelia. It also serves as an important transportation route connecting the North-West Region with central and southern regions of the Russian Federation as well as with European countries. Lake Ladoga has rich and diverse biological resources and hosts ca. 400 animal and ca. 600 plant species. Furthermore, it is a unique natural aquatic system for recreation and fishery (Rumyantsev and Kondratyev 2013; Rumyantsev 2015).

Since Lake Ladoga drains a substantial area of north-western European Russia as well as eastern Finland, it also acts as a natural accumulation pool for different kinds of pollutants (Rumyantsev 2015). Nowadays, the state of the Lake Ladoga ecosystem is largely controlled by a complex interplay between natural and anthropogenic processes occurring both within the lake and in its catchment.

Although the lake's shores were inhabited by early humans already in the Early Holocene (e.g. Gerasimov and Subetto 2009), prior to the 1960s human impact on the lake can be considered negligible. Any environment disturbances caused by human activities were apparently leveled due to the Lake Ladoga great size and self-purification capacity. In the early 20th century the state of Lake Ladoga was assessed as clear-water oligotrophic (Balakhontsev 1909), and remained oligotrophic until the late 1960s. Therefore this state of the lake's ecosystem is hereinafter referred to as "pre-anthropogenic", and could be considered as its reference state (Bennion et al. 2011). During the 1960s-1980s, enhanced economic activity in the catchment area of Lake Ladoga resulted in increased nutrients concentration (primarily P) in the lake's tributaries and consequently in the lake itself. The main sources of P enrichment were untreated waters from the aluminium smelter at the lower course of the River Volkhov, waste-waters from pulp and paper industry, sewages from the cattle-farming and surface run-off of artificial fertilizers excessively used in agricultural areas. Lake Ladoga's trophic state shifted from oligotrophic to mesotrophic, as reflected by changes in a series of physico-chemical and hydrobiological parameters. In recent decades, gradual improvement of the ecological situation has taken place facilitated by the economic depression of the early 1990s and the subsequent decline in anthropogenic pressure on the lake ecosystem. However, eutrophication still remains one of the most essential issues for Lake Ladoga (Rumyantsev and Kondratyev 2013).

Diatoms (Bacillariophyta) are one of the most important groups of indicative organisms widely used in assessing ecological conditions of fresh waters. These unicellular algae make up a considerable part of planktonic and benthic microalgal communities in temperate lakes (Davydova 1985; Dixit et al. 1992; Smol and Stoermer 2010). After the diatom cell's death, its siliceous walls settle down, accumulate on the lake bottom and may remain well-preserved in the sediments for hundreds of thousands years. Species-specific morphology enables identification of those sedimentary diatoms to species level, while fairly well-established ecological preferences of many diatom taxa make them useful indicators of past and recent limnological conditions (Cohen 2003; Smol 2010). Diatom assemblages from the surface sediments (0-1 cm) represent an integrated temporal and spatial sample of a lake diatom flora incorporating taxa from different habitats and including both dominating and auxiliary species that have accumulated in the recent 1-5 to 10 years depending on sedimentation rate. Therefore surface-sediment diatom assemblages smoothen and average seasonal changes in diatom species composition and effects of short-term or locally restricted impacts, providing more comprehensive characteristics of the diatom flora of a lake compared to the live algal communities (Davydova 1985; Bennion 1995; Smol 2008). Studying surface-sediment diatom assemblages has proven to be a time- and cost-effective approach in assessing ecological status of lakes all over the world (e.g. Lotter 1989, Yang and Dickman 1993; Smol and Stoermer 2010).

In Lake Ladoga, the surface-sediment diatom studies performed in the early 1960s, late 1970s, and early 1990s (Davydova 1968; Davydova et al. 1997; 1999) revealed that changes in the lake ecosystem resulted from human-induced eutrophication. In the early 2000s, slightly improved ecological conditions in the northern archipelago, one of the most polluted areas in Lake Ladoga, were inferred in response to reduced anthropogenic pressure (Ludikova 2017). The present study continues a series of observations of the environmental changes in Lake Ladoga recorded in the surface-sediment diatom assemblages. It aims to assess the current ecological status of the lake and compare it with the pre-anthropogenic (prior to 1960s) and eutrophication (late 1960s – early 1990s) periods. The study is also intended to demonstrate the value of surface-sediment diatom assemblages for tracking changes in water quality and lake ecological status.

MATERIALS AND METHODS

Study area and previous studies

Lake Ladoga (59°54´ to 61°47´N and 29°47´ to 32°58´E) is the second largest freshwater lake in Russia (water-surface area 17.765 km^2, average depth 48.3 m, maximum depth 230 m, water volume ~848 km^3). Its vast catchment area covering >258.600 km^2 extends through northwestern European Russia and the eastern part of Finland, including such large lakes as Onega, Ilmen and Saimaa. The rivers Svir, Volkhov and Vuoksa (Fig. 1b) draining these lakes are the main tributaries of Lake Ladoga that contribute 86% of the water inflow to the lake. Lake Ladoga drains to the Gulf of Finland via the River Neva. The period of water exchange in the lake is 11 years (Rumyantsev 2015).

Lake Ladoga is characterized with uneven bathymetry. The gently sloping shallow-water zone (to –20 m deep and up to 50 km-wide) extends along the southern shore. In the central basin, the depths gradually increase towards the north from –50 m to –100 m. In contrast to the smoother lake floor of the southern and central parts, the northern basin is characterized with contrasting topography formed by channels and ridge-like structures of various sizes, and greatest depths (>200 m) (Subetto et al. 1998). The very narrow littoral zone sharply transfers to steeply inclined slopes. The shoreline here is incised with a network of bays and coves with numerous islands forming the northern archipelago (Fig. 1b).

Thermal regime and related dynamics of the water masses are the main factors controlling the ecosystem processes in Lake Ladoga. Lake Ladoga is a dimictic lake and mixes from the surface to the bottom twice a year, in spring and autumn. From May until mid July, the thermal bar divides the lake water masses into a warmer shallow-water zone (>4°C) and a colder deep-water zone that includes the central and northern open-water parts of the lake. The nutrients arriving to the lake with the river inflow and spring runoff are concentrated in the shallow-water parts due to the lack of horizontal mixing, which favors spring phytoplankton development.

Planktonic diatom growth in Lake Ladoga can already start in early spring when the solar radiation is able to penetrate through the ice (Petrova 1968). However planktonic diatom blooms follow the ice-out that starts in the shallow-water parts of the lake, i.e. in the south and in the nearshore zone of the northern archipelago, in late April – early May. The low spring water temperatures and intense mixing favor the diatoms of the *Aulacoseira* genus, in particular, *A. islandica* that dominates in the spring phytoplankton (Petrova 1968). As the thermal bar collapses and thermal stratification is established, the summer biological season starts in Lake Ladoga, and *Aulacoseira* spp. are replaced by the planktonic diatom *Asterionella formosa*. In contrast to the spring biological season, when Ladoga phytoplankton is diatom-dominated, blue-green, green and cryptophytic algae are the main components of the planktonic communities in summer (Letanskaya and Protopopova 2012).

The pioneer surface-sediment diatom studies were performed in 1959-1960, and covered > 100 sampling sites all over the lake bottom (Davydova 1961, 1968). In 1978-1979, 19 sampling sites in the central and southern parts of Lake Ladoga were investigated. During the 1991-1994 field campaign, a total of 60 sited were sampled with the particular interest to the northern archipelago part (Davydova et al. 1997; 1999). All sampling campaigns took place during the open-water seasons. Up to 1 cm of the surface sediments were sampled using short gravity-type corers. The sampling sites of the different periods of surveys were quite dispersed and unevenly distributed, which induced distinguishing spatially representative sample sets for each period as summarized in (Davydova et al. 1999). Despite of the spatial heterogeneity of the sampling sites, short ordination gradients suggested fairly homogeneous composition of the diatom assemblages in the open-water part of the lake due to effective water mixing (Davydova et al. 1999, 2000).

Sampling and analytics

Surface sediments sampling was conducted in September 2001 at 9 regular monitoring sampling sites of the Institute of Limnology in the open-water part of Lake Ladoga, and in late October 2004 in the northern archipelago (7 sampling sites). In September 2016, 18 regular monitoring sampling sites (mainly in the open-water part) were sampled (Fig. 1b). Thus 9 sampling sites were visited during both 2001/2004 and 2016 sampling campaigns (Fig. 1b). The samples were collected with the Ekman-Berge sediment sampler. The retrieved sampler was fixed in vertical position, and the water above the sediment surface was allowed to drain. The uppermost ca. 0,2-0,5 cm of the sediments, depending on their composition (i.e. fine sands or silts) were carefully scraped from the sediment surface and used for diatom analysis.

The data from 2001 and 2004 were further treated as belonging to the same sampling period. The rationale for this merging was provided by the short time-span between the sampling campaigns and low sediment accumulation rates in Lake Ladoga (≤0,5 mm per year in average). The surface-sediment diatom assemblages of 2001 and 2004 are therefore believed to represent more or less the same state of Lake Ladoga ecosystem as compared to the previous and subsequent sampling periods (in early 1990s and 2016, respectively).

The laboratory treatment followed the standard procedure using 30% H_2O_2 to destroy organic matter (Davydova 1985). Diatom identification follows Krammer and Lange-Bertalot (1986-1991). Diatom data were expressed as % relative abundance. To estimate the contribution of individual diatom taxa to the diatom assemblages, they were classified as "dominating" (>10% of the diatom counts in a sample), "sub-dominating" (5-10%), "regular" (1-5%) and "rare" (<1%) species, according to Davydova (1985). Given the morphological variability of the planktonic diatom *Aulacoseira subarctica*, its "squat" form (i.e. short and wide, see Gibson et al. 2003) was counted separately from longer and narrower valves.

RESULTS AND DISCUSSION

In 2001/2004, planktonic diatoms dominated in 15 out of 16 surface-sediment diatom samples. Generally, their proportion was lower in the northern archipelago part (58-79%) compared to the other sites (75-94%). The most numerous and widespread planktonic species was *Aulacoseira islandica* (10,5–60%) that prevailed at 15 sampling sites (Fig. 2), often co-dominated by planktonic *Aulacoseira subarctica* (4,5–28%). The latter was generally less common in the archipelago sites. Its "squat" form often contributes to ca. ½ of *A. subarctica* totals. *Cyclostephanos dubius* and *Stephanodiscus minutulus*, typical of highly eutrophic waters were found among the regular and subdominating species at 15 sampling sites. *C. dubius* mainly occurred in diatom assemblages in the archipelago part, while *S. minutulus* was observed at the majority of the sampling sites except for the Volkhov Bay in the south. At some sampling sites in the northern

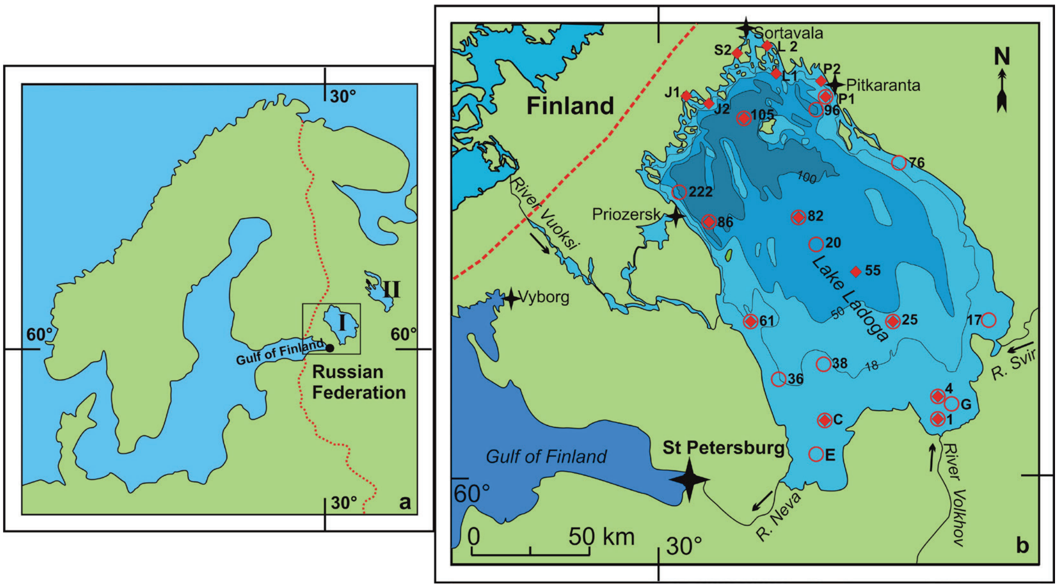

Fig. 1. Lake Ladoga location map (a) and Lake Ladoga bathymetry and location of sampling sites (b). I – Lake Ladoga, II – Lake Onega, diamonds – the sites sampled in 2001/2004, circles – the sites sampled in 2016; diamonds in circles – the sites visited during both sampling periods. 18-m contour shows the outer boundary of the littoral zone.

part of Lake Ladoga, including the archipelago, hypereutrophic *Stephanodiscus hantzschii* was also regular. Other *Stephanodiscus* taxa, mesotrophic or meso-eutrophic *Stephanodiscus medius* and *S neoastraea* reach the abundances of regular or sub-dominating species at 10 and 12 sampling sites, respectively, being less numerous in the archipelago part. Meso-eutrophic *Asterionella formosa* was observed at all sampling sites. Its higher proportions (3-8,5%) were typical of the northern part of Lake Ladoga. Higher abundances of eutrophic *Diatoma tenuis* (up to 10%) were also constrained to this area. Surface-sediment diatom assemblages of many sampling sites also included *Cyclotella radiosa* and *C. schumannii* among the regular and rare species, more common for the open-water part of the lake. Benthic taxa were more abundant in the northern archipelago part (21-59%) as well as at some shallower sites in the western and north-western parts of the lake and in the Volkhov Bay.

In the samples collected in 2016, planktonic diatoms dominated the diatom assemblages of 16 out of 18 sampling sites. Similar to the previous sampling period, *A. islandica* remained the most numerous and widespread taxon, and dominated at 16 sites (16-61%). *A. subarctica* was also observed in all sampling sites (Fig. 3). At 15 sites, it co-dominated and even overdominated *A. islandica*. The contribution of the short and wide morphotype of *A. subarctica* to *A. subarctica* totals is mainly <1/2. The comparison to the 2001/2004 dataset showed that out of the 9 sites sampled during 2001/2004 and 2016, in 4 sites, in the southern and western parts of the lake (Petrokrepost and Volkhov bays, and near the River Vuoksi mouth) the proportions of *A. subarctica* total and *A. subarctica* "squat" decreased.

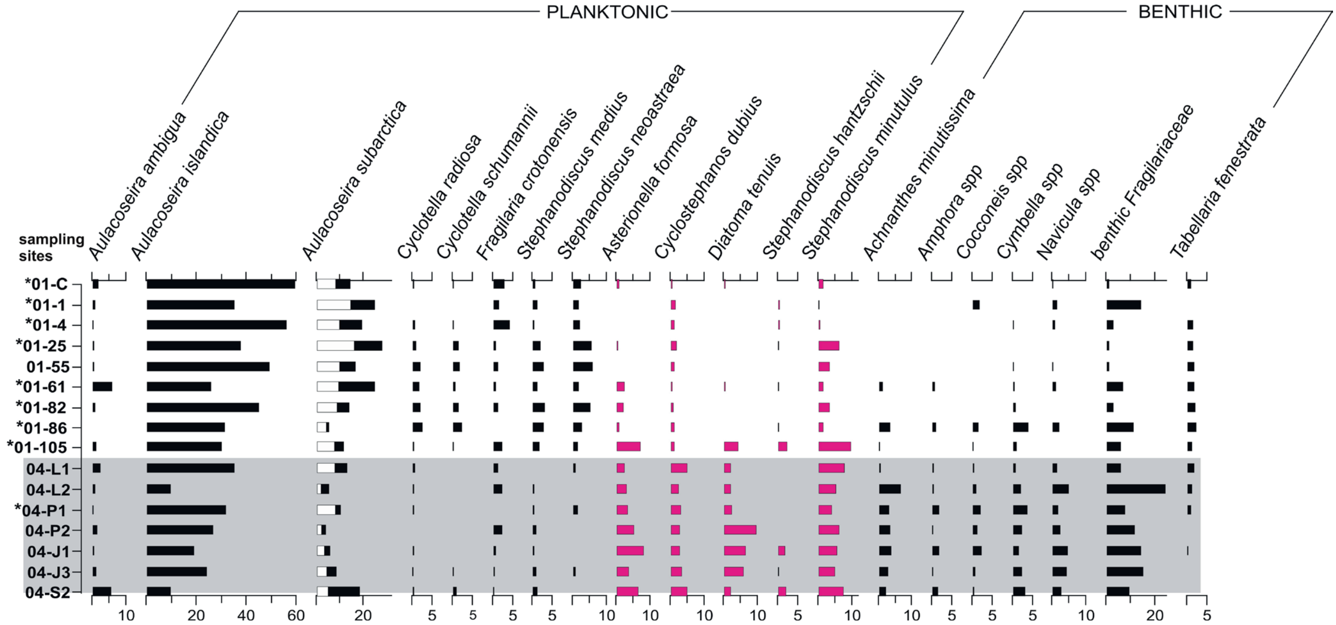

Fig. 2. Relative abundances (%) of the main diatom taxa in the surface-sediment diatom assemblages of 2001 and 2004 (y-axis – sampling sites: year-number). * – the sites sampled during both 2001/2004 and 2016 field campaigns. Shadowed area – the sites in the northern archipelago part. White bars in *Aulacoseira subarctica* – proportions of the "squat" morphotype previously identified as *A. distans* var. *alpigena* (see explanations in the text). Pink bars – species indicative for anthropogenic eutrophication of Lake Ladoga.

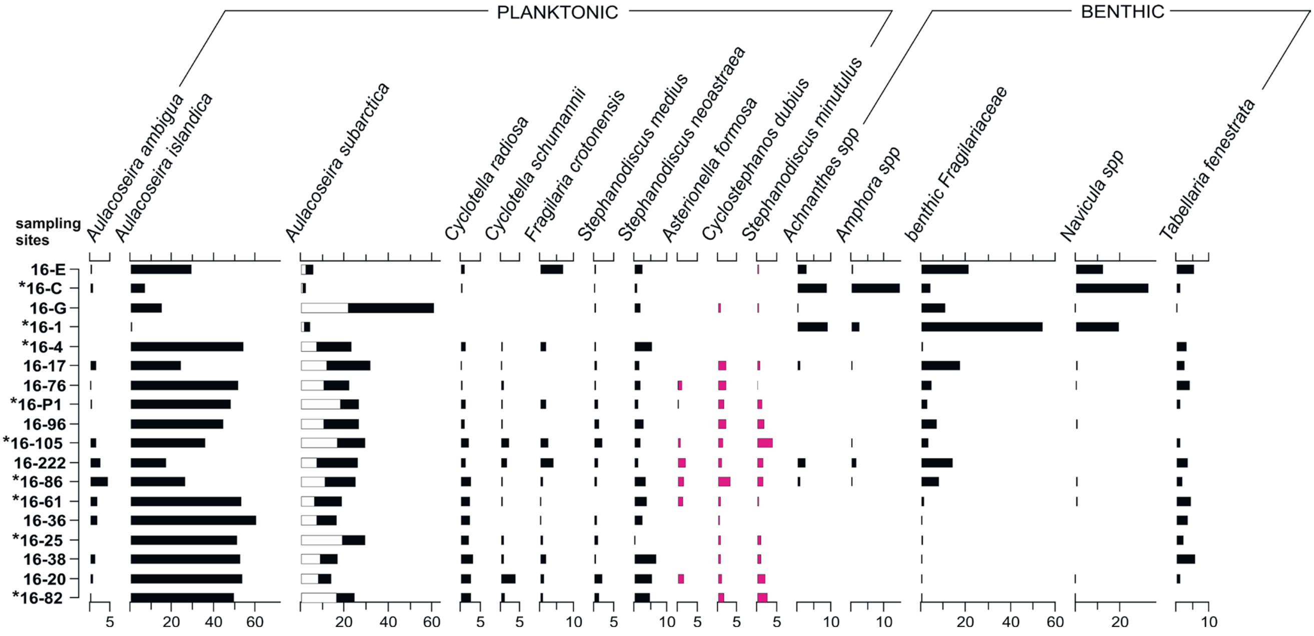

Fig. 3. Relative abundances (%) of the main diatom taxa in the surface-sediment diatom assemblages of 2016 (y-axis – sampling sites: year-number). * – the sites sampled during both 2001/2004 and 2016 field campaigns. White bars in *Aulacoseira subarctica* – proportions of the "squat" morphotype previously identified as *A. distans* var. *alpigena* (see explanations in the text). Pink bars – species indicative for anthropogenic eutrophication of Lake Ladoga.

The other 5 sites demonstrated increased abundances of both *A. subarctica* total and its "squat" form (Fig. 3). The proportions of eutrophic *C. dubius* and hypereutrophic *S. minutulus* slightly decreased compared to the 2001/2004 sampling period, and never exceeded 3,5-4%. Meso-eutrophic *A. formosa*, eutrophic *D. tenuis* and hypereutrophic *S. hantzschii* also decreased in abundance, and were only found among the rare species. Similarly to 2001/2004, other widespread planktonic taxa, included *S. medius* and *S. neoastraea* that were regular or, less commonly, subdominating species in all sampling sites, and *C. radiosa* and *C. schumannii* found at the majority of the sites among the regular and rare taxa. The highest proportions of benthic species were observed at the shallow-water sites in the southern part of the lake.

Comparing our findings with the results of the previous studies we can track the changes that occurred in the Lake Ladoga ecosystem starting from the late 1950s-early 1960s. Prior to this period, the lake was oligotrophic, and species typical of pure waters predominated among its algal population (Balakhontsev 1909). By the early 1960s human impact on its ecosystem remained negligible, as suggested by its hydrochemical and hydrobiological characteristics (Petrova 1968; Raspletina and Susareva 2002). Studies of the long-term diatom records (sediment cores) also indicate that pristine conditions existed in Lake Ladoga till recently. Dramatic eutrophication-related changes only occurred in the diatom assemblages in the topmost few centimeters of the sediments (Davydova et al. 1981; Davydova 1985), i.e. after the 1970s according to ^{210}Pb dates (Kukkonen and Simola 1997).

By the early 1960s, *Aulacoseira islandica* dominated in the diatom assemblages at all sampling sites (Fig. 4a), several times exceeding the abundances of other species (Davydova 1968). *A. islandica* was the most abundant species in the spring and autumn Lake Ladoga phytoplankton communities at this time (Petrova 1968). It has been dominating in Lake Ladoga sedimentary diatom assemblages starting from the Late Glacial when the Scandinavian Ice Sheet retreated from the Ladoga basin (Davydova 1985; Ludikova 2020). *Asterionella formosa* was another common species in the surface-sediment diatom assemblages during the sampling campaign of 1959-1960 (Fig. 4a). As fragile cell walls of *A. formosa* easily break and dissolve during the sedimentation, its abundances in the sedimentary diatom assemblages usually underestimate its contribution to the live communities (Davydova 1968). At the pre-anthropogenic stage *A. formosa* thrived in the late spring, and dominated in the summer phytoplankton of Lake Ladoga (Petrova 1968). At some sampling sites planktonic *Aulacoseira italica, A. (distans var.) alpigena*, some *Cyclotella* spp. and *Stephanodiscus* spp. were also abundant in the surface-sediment diatom samples (Davydova et al. 1997). Thus the predominance of taxa typical of large deepwater, oligotrophic lakes in the surface-sediment diatom assemblages in Lake Ladoga in the late 1950s (Davydova 1968) indicate that human impact on the lake ecosystem was negligible.

The oligotrophic state of Lake Ladoga inferred from the composition of the surface-diatom assemblages (Davydova et al. 1999) was also confirmed by hydrochemical and hydrobiological studies. By the early 1960s, the external P load to the lake was ca. 1,8 tons P year^{-1}. Mean annual inorganic phosphorus (IP) content was 3 μg l^{-1}, while mean total phosphorus (TP) concentration was 10 μg l^{-1} (Raspletina et al. 1967). Phosphorus deficiency and thermal regime of the large cold-water lake, in turn, limited the phytoplankton growth that was dominated by diatoms throughout the vegetative season (Petrova 1968).

The studies performed in 1978-1979 demonstrated significant changes in the composition of the surface-sediment diatom assemblages (Fig. 4b) as mesotrophic *A. italica*, meso-eutrophic *A. formosa* and eutrophic *Diatoma tenuis* became co-dominants of *A. islandica* (Davydova 1968). The growth of *D. tenuis* was previously constrained to the southern part of the lake where it developed in the summer phytoplankton (Petrova 1968). Mass development of the eutrophic co-dominant indicates a shift of the trophic status of Lake Ladoga from oligotrophic to mesotrophic as a result of increased P loading to the lake started in the mid 1960s (Davydova et al. 1997; 1999). Drastically increased proportions of *A. formosa, D. tenuis* and *A. italica* were similarly observed in sediments of the most polluted areas of the neighboring Lake Onega, the second largest lake in the European Russia, where the highest anthropogenic pressure was also recorded in the 1970-1980s (Davydova et al. 1993).

Hydrochemical studies in Lake Ladoga also recorded 4-5 times increase in the mean annual IP concentrations by 1976-1979 as a result of increased influx of phosphates with industrial waste waters and agricultural runoff. External P load rapidly increased and reached 6-7 tons P year^{-1}, nearing the estimated critical values for Lake Ladoga (Raspletina and Susareva 2002). In 1976-1980, mean TP concentration reached 26 μg l^{-1} (Raspletina 1982). Increasing P concentrations, in turn, stimulated phytoplankton development. At the early eutrophication stage, it resulted in the increased abundances of common phytoplankton species such as *A. islandica* in spring and *A. formosa* in summer. As eutrophication proceeded, the proportion of eutrophic diatom species in the phytoplankton communities, phytoplankton biomass and primary productivity increased as well (Petrova 1982).

By the early 1990s, *A. islandica*, *A. formosa* and *D. tenuis* remained the most abundant taxa in the surface-sediment diatom assemblages, while the proportion of *A. italica* decreased (Fig. 4c). At some sampling sites, mainly located in the northern archipelago part of Lake Ladoga, the proportion of *A. islandica* significantly decreased due to increased abundances of the taxa indicative of anthropogenic eutrophication. Apart from the above-mentioned *A. formosa* and *D. tenuis*, they included *Cyclostephanos dubius* and *Stephanodiscus hantzschii* characteristic of highly eutrophic waters (Davydova et al. 1994). This indicated higher trophic status of the archipelago part, and therefore higher anthropogenic pressure resulting from the industrial and municipal waste water discharge from the nearby plants and coastal settlements. The environmental situation was exacerbated by the remoteness of some of the most polluted sites and slow water exchange between the archipelago and the open-water part of Lake Ladoga (Davydova et al. 1994; 1999). Thus, the surface-sediment diatom assemblages of the early 1990s recorded the mesotrophic state of Lake Ladoga, with a more eutrophied archipelago part.

Due to various water protection activities (e.g. introduction of sewage treatment facilities, closing of some pulp and paper mills) of the 1980s and subsequent economic decline of the early 1990s, external P load to the lake decreased to 2,4-3,9 tons P year^{-1} in 1996-2003. However, hydrochemical observations demonstrated that despite the decreasing external P load, mean TP concentrations remained high by the early 1990s (ca. 20 μg l^{-1}) still indicating the mesotrophic state of the lake (Raspletina and Susareva 2002). Furthermore, the phytoplankton composition and biomass studies also showed that Lake Ladoga remained mesotrophic in the early 1990s, with the most eutrophied

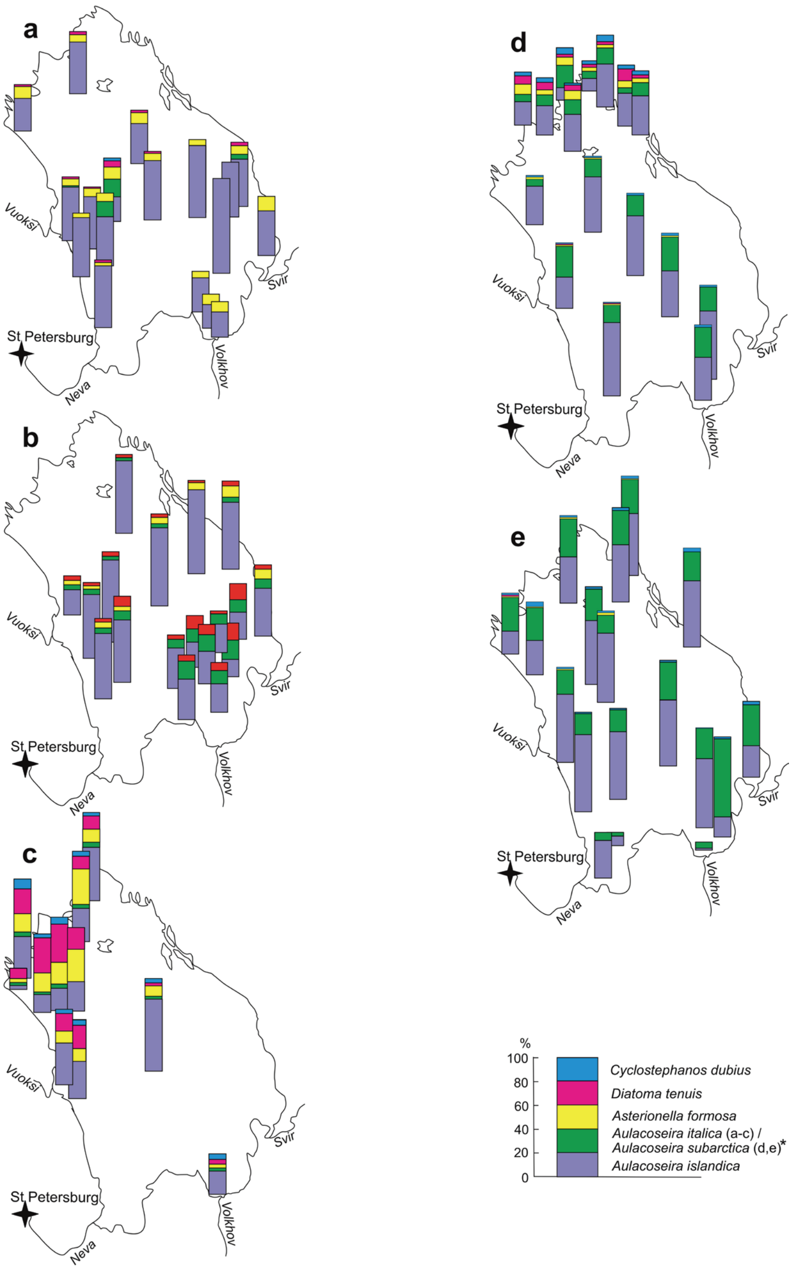

Fig. 4. Proportions of the main diatom species in the surface-sediment diatom assemblages in 1959-1960 (a), 1978-1979 (b), 1994 (c), 2001 and 2004 (d), and 2016 (e). (a-c according to Davydova et al. (1999), d and e – this study; * – see explanations in the text)

areas in the archipelago part and the mouths of the large rivers (Holopainen and Letanskaya 1999).

By the early 2000s, however, the predominance of *A. islandica* typical of the pre-anthropogenic stage, re-established in the surface-sediment diatom assemblages both in the open-water part of Lake Ladoga and in most archipelago sites, as demonstrated by the current study. *A. subarctica* appeared as a co-dominant of *A. islandica* at most of the sampling sites (Fig. 4d). The decline in *A. formosa* and *D. tenuis* that dominated in the surface-sediment diatom assemblages during the eutrophication stage, as well as highly eutrophic *C. dubius*, *S. hantzschii* and *S. minutulus*, indicates an improvement of the ecological state of Lake Ladoga as a result of decreasing anthropogenic pressure, started in the early 1990s. However, the eutrophic species still remained more abundant in the archipelago part, suggesting that the self-purification process in this part of the lake was delayed due to the slow water exchange with the open-water part of Lake Ladoga.

At present, the composition of the dominating species remains similar to the early 2000s, however, in a number of sites sampled in 2016 the abundance of *A. subarctica* is higher than in 2001/2004 (Fig. 4d and 4e). Further decrease in *A. formosa* and *D. tenuis* and the other species indicative of anthropogenic eutrophication (*C. dubius, S. hantzschii, S. minutulus*) reveals the continuous lowering of the lake trophic state. The diatom-inferred de-eutrophication of Lake Ladoga is supported by the hydrochemical studies. They demonstrate that TP concentrations in 2009-2018 were around 11-13 µg l^{-1} while IP content in 2013-2018 did not exceed 3 µg l^{-1} (Petrova 2019), both nearing their pre-anthropogenic levels. Since 2006 the amounts of P from external sources ranges from 2,5 to 3 tons P $year^{-1}$ (Rumyantsev and Kondratyev 2013).

However, comparison of the composition of the dominating species in the present-day diatom assemblages with those of the pre-anthropogenic stage reveals some important discrepancies. In particular, in the late 1950s – early 1960s, *Aulacoseira islandica* was the only dominating species in the surface-sediment diatom assemblages (Fig. 4a), while in most of the samples collected in the 2000s it is co-dominated by *A. subarctica* (Fig. 4d, 4e). *A. islandica* is the most abundant taxon in the sedimentary diatom assemblages of Lake Ladoga throughout the Holocene (Davydova 1985; Ludikova 2020). Besides Lake Ladoga, high abundances of *A. islandica* were also reported both in naturally productive small lakes (Räsänen et al. 2006) and in large turbulent freshwater basins, e.g. Lake Onega, Baikal, Laurentian Great Lakes, large Swedish lakes, etc. (Willén 1990 and references therein). There it similarly co-occurs with its congener, *Aulacoseira subarctica* (Stoermer et al. 1985; Barbiero and Tuchman 2001; Popovskaya et al. 2002; Willén 2002; Ludikova et al. 2020) as their massive growth is favored by seasonal mixing.

The lack of mentioning of *A. subarctica* in the earlier Lake Ladoga datasets (Davydova 1968, Davydova et al. 1997, 1999) is explained by the fact that various morphotypes of *A. subarctica* were previously misidentified as three different taxa, namely *Aulacoseira italica, A. italica* ssp. *subarctica* and *A. (distans* var.) *alpigena* (Genkal 1996). Of these, "*A. italica*" and "*A. italica* ssp. *subarctica*" have more or less elongated valves, while the valves of "*A. alpigena*" are short ("squat") and characterized with low height to diameter ratio. Presently the "squat" form is considered as part of the continuum (Gibson et al. 2003), and the length/width ratio is thought to change with environmental conditions (Tuji and Houki 2004), although the role of particular factors in controlling the morphology of *A. subarctica* remains unclear.

Recent studies of the Holocene Lake Ladoga sediments confirmed this erroneous splitting of *A. subarctica*. They revealed only single finds of *A. alpigena* and no *A. italica* throughout the study period, while *A. subarctica*, in turn, was regularly observed in significant amounts starting from the second half of the Holocene (Kostrova et al. 2019; Ludikova 2018, 2020; Sapelko et al. 2019). Therefore *A. subarctica* significantly contributed to the microalgal communities in Lake Ladoga already in the oligotrophic period, and even long before any human impact on the lake's ecosystem became appreciable. Moreover, between ca. 4000-3500 and 1800 yrs BP, it co-dominated *A. islandica* similarly to present. Both "short and wide" and "longer and narrower" forms were concurrently found during this period, although the "squat" morphotype constantly prevailed (A. Ludikova, unpublished).

By the early 1960s, *Aulacoseira subarctica* "complex" (former *A. italica, A. italica* ssp. *subarctica* and *A. (distans* var.) *alpigena*) was regularly registered in the phytoplankton communities in the late spring biological season (Petrova 1968). All these taxa were also frequently observed in the surface-sediment diatom assemblages in the late 1950s (Davydova 1968). However, a different technique of estimating the species abundances applied in the 1960s complicates a comparison of *A. subarctica* contribution to the surface-sediment diatom assemblages of the pre-anthropogenic stage and at present.

According to Lund (1954), *Aulacoseira subarctica* commonly occurs in moderately oligotrophic to moderately eutrophic lakes in temperate and subarctic regions. In strongly eutrophic conditions, however, *Aulacoseira subarctica* can be replaced by *A. islandica* (Lund 1954, Canter and Haworth 1991; Gibson et al. 2003). *A. islandica*, in turn, is suggested to tolerate wider range of trophic conditions (van Dam et al. 1994). The studies of small lakes in NW Russia and Central Europe revealed its mass development at the early stage of cultural eutrophication (Trifonova 1990; Bennion et al., 1995). However, as eutrophication proceeds its abundances also decline (Stoermer et al., 1981; Trifonova, Genkal, 2001) to eventual displacement by planktonic pennate and / or small centric diatoms (Pienitz et al. 2006; Räsänen et al. 2006). This was also observed in Lake Ladoga, where relative decrease in *Aulacoseira* taxa and simultaneous increase in the pennate *Asterionella formosa, Diatoma tenuis*, and small-sized *Cyclostephanos dubius* and *Stephanodiscus hantzschi*i were recorded with increased trophic state.

Another specific feature of the present surface-sediment diatom assemblages is underrepresentation of planktonic *A. formosa* as compared to the earlier datasets (Davydova 1968; Davydova et al, 1997, 1999). Although the species is known as indicative of moderate nutrient enrichment, it can be also abundant in rather nutrient-poor lakes (Sivarajah and references therein). In large and deep stratified temperate lakes it is typically found in late-spring and summer epilimnetic phytoplankton (Petrova 1990; Willén 2002; Chekryzheva 2015). In Lake Ladoga, *A. formosa* was a common species in the surface-sediment diatom assemblages at the oligotrophic stage (Davydova 1968) alongside with *Aulacoseira* spp. However, the phytoplankton surveys demonstrated that during the vegetative season these taxa occupied different "temporal niches" (Petrova 1990). For instance, *Aulacoseira islandica* in Lake Ladoga already starts blooming under the ice, as was also recorded elsewhere (Stoermer et al. 1981; Bradbury et al. 2004; Nõges 2004), and continues after the ice-out, when there are no other successful competitors in the early spring phytoplankton. As the mixing proceeds and water temperature rises, it is supplemented by *A. subarctica* "complex" that massively develops in late spring, accompanied by *Asterionella formosa* (Petrova 1968, 1990). By the onset of the biological summer season, around mid July, *Aulacoseira* cells submerge to the hypolimnion, while the abundance of *A. formosa* increases. During the oligotrophic stage of Lake Ladoga *A. formosa* dominated in the summer diatom plankton as thermal stratification established (Petrova 1968).

Taken these considerations, the variations in proportions of the main species in the surface-sediment diatom assemblages with progressing eutrophication can be explained as follows. As P concentration in Lake Ladoga steadily increased during the late 1960s – early 1980s, *Aulacoseira islandica* still remained abundant due to its early blooming (Fig. 4a, 4b). Proliferation of *Asterionella formosa* and *Diatoma tenuis* at the expense of *Aulacoseira* taxa is often recorded in eutrophying lakes (Stoermer et al. 1985; Willén 1987; Liukkonen et al. 1993; Hobæk et ak. 2012). However, in Lake Ladoga lower frequencies of *A. islandica* observed in the early 1990s dataset (Davydova et al. 1999) might not indicate its decreased contribution to the microalgal communities but rather results from a relative increase in *A. formosa* and *D. tenuis* (Fig. 4c), accompanied by *Cyclostephanos dubius*, the latter two taxa having been rather uncommon at the oligotrophic stage. Both *A. formosa* and *D. tenuis* used to start growing in Lake Ladoga by the end of the biological spring. However, as eutrophication proceeded, their bloom shifted to the late spring due to intense competition for nutrients with summer-blooming blue-greens (Petrova 1990). Since *A. formosa* and *D. tenuis* are known to outcompete *Aulacoseira* taxa under high TP conditions (Petrova 1990; Reavie at al. 2002) they should have largely displaced the late-spring *A. subarctica* "complex" as reflected by decreased contribution of *A. subarctica* pro parte (*A. italica* and *A. italica* spp *subarctica*) both to the phytoplankton communities (Petrova 1986, 1990) and surface-sediment diatom assemblages (Davydova, 1968; Fig. 4c). It is remarkable, though, that the long-term phytoplankton studies also revealed the opposite trend in abundances of the "squat" form of *A. subarctica*, previously misidentified as *A.* (*distans* var.) *alpigena* that drastically increased in the 1970s-1980s (Petrova 1986). Thus, in Lake Ladoga this morphotype might have benefited from increasing trophic level, although all forms of *A. subarctica* were previously shown to have essentially the same TP optimum (Gibson et al. 2003 and references therein). Besides, this might suggest the competitive advantages of the "squat" morphotype over "longer and narrower" ones, i.e. former *A. italica* and *A. italica* ssp *subarctica* under increased TP levels. Another possible explanation could be in slightly different timing of their blooms, suggesting that the "short" form might start growing earlier when the resources competition is less tense. All these tentative suggestions, however, demand further comprehensive phytoplankton studies to be confirmed.

At the present de-eutrophication stage, the return to the *Aulacoseira*-dominated diatom assemblages is recorded in Lake Ladoga, similar to the other lakes where biological recovery from eutrophication took place (Gibson et al. 2003; Bennion et al. 2012; Fielding et al. 2020). Increased abundances of *A. subarctica* in the surface-sediment diatom assemblages of the 2000s (Fig. 4d, 4e) could result from lowered TP concentrations in the Ladoga waters, which might favored its mass development in the late spring, similar to the oligotrophic stage. The hydrobiological surveys performed in 2005-2009 reported, apart from *Aulacoseira islandica*, high biomass of "*A. italica*", "*A. distans*", and "*A. subarctica*", i.e. the taxa belonging to *A. subarctica* "complex", in spring and autumn phytoplankton (Letanskaya and Protopopova 2012).

Almost complete lacking of eutrophic *Diatoma tenuis* in the recent diatom assemblages is in agreement with decreased TP content in Lake Ladoga, as it was also observed elsewhere in course of de-eutrophication (Willén 1987; Hobæk et al. 2012). One would also expect that *Asterionella formosa*, a common species in Lake Ladoga both in oligotrophic and eutrophication stages, could remain abundant after lowering of P concentrations. However, the present study has documented a decline in its proportions (Fig. 4d, 4e). It is therefore suggested that despite the steady trend towards oligotrophication, the present state of the Lake Ladoga ecosystem is not determined solely by nutrients content, but rather by a complex interplay of various environmental factors that are somewhat different from the pre-anthropogenic stage. Apart from oligotrophication, among the reasons for species replacements and displacements, changing contributions of different functional groups, shifting nutrient requirements, and grazing pressure are often reported (Dokulil and Teubner, 2005). In Lake Ladoga, decreased abundances of *A. formosa* apparently reflect restructuring of the seasonal phytoplankton communities related to eutrophication and subsequent de-eutrophication of Lake Ladoga. With decreasing TP, the late spring blooms of *A. formosa* might be somehow constrained by competition with typical spring *Aulacoseira* species (*A. islandica* and proliferating *A. subarctica*). In summer, in turn, *A. formosa* is mainly replaced by other groups of algae with higher competitive abilities for P, and therefore does not reach its pre-anthropogenic abundances. This corresponds to the total decline of diatoms in the summer phytoplankton assemblages as the contribution of blue-greens and cryptophytic algae increased during de-eutrophication of Lake Ladoga (Holopainen and Letanskaya 1999; Letanskaya and Protopopova 2012). This differentiates the present state of the lake's ecosystem from the pre-anthropogenic period when diatoms dominated in the phytoplankton throughout the vegetative season (Petrova 1968).

However, de-eutrophication process may be not the only factor to determine the present state of the Lake Ladoga ecosystem, as the pathways and success of lake restoration efforts may be also influenced by climate change (Battarbee et al. 2005). In particular, the rise of air temperatures during the last 30 years has affected the ice regime of lakes (Leppäranta 2015), and a great number of studies documented that ice-cover periods have shortened remarkably across the Northern Hemisphere, and the durations of the ice-free and stratified seasons changed accordingly (Gerten and Adrian 2002 and references therein). A growing body of evidences demonstrates the recent climate-driven changes of lake physical and biogeochemical processes, aquatic communities composition and food-web structures (Adrian et al. 2009 and references therein). In particular, the timing of the spring overturn and the onset of stratification strongly affect phytoplankton development. For instance, heavily silicified *Aulacoseira* taxa forming long filamentous colonies require more turbulence to remain suspended in the photic zone (Lund 1954; Wilson et al. 1993), and are therefore widely acknowledged to benefit from long-lasting spring circulation (Kilham et al. 1996; Weyhenmeyer et al. 2008). Often reported as an abundant spring diatom, *Asterionella formosa*, in turn, can also proliferates under prolonged summer stratification due to its ability to form star-shaped colonies to sustain in the epilimnion and utilize available nutrients near the thermocline (Ruhland et al., 2015; Sivarajah et al. 2016). Besides, the displacement of larger and heavier *Aulacoseira* taxa by small-celled *Cyclotella* sensu lato, e.g. *Cyclotella comensis, Discostella pseudostelligera, D. stelligera*, etc.) has been also reported lately as a Hemispheric phenomenon recorded in a number of temperate, subarctic, circumpolar and mountain lakes (Rühland et al. 2015 and references therein; Reavie et al. 2017). Their high light-harvesting and prolific reproduction abilities altogether with lower sinking velocities, make these taxa successful competitors during the prolonged stratification periods (Rühland et al. 2015). Generally, climate changes are reported to have both positive and negative impacts on lake ecosystems, they do not therefore necessary hinder restoration efforts (Carvalho et al. 2012).

In Lake Ladoga, mild winters during the recent ca. 30 years corresponded to less severe ice conditions and frequency of ice occurrence (Karetnikov et al. 2017; Naumenko and Karetnikov 2017). Consequently the spring ice-out and the onset of summer stratification shifted to earlier dates (Naumenko 2021). It could be also hypothesized that the spring mixing period extends accordingly, although it is not clear by far whether the water stability period has also prolonged (M. Naumenko, personal communication). However, the present study of the surface-sediment diatom assemblages has not revealed shifts in their composition in response to the climate-driven changes, similar to those described in many other Northern Hemispheric lakes (Rühland et al. 2015; Sivarajah et al. 2016). Unlike the recent reports (Hadly et al. 2013; Berthon et al. 2014; Sivarajah et al. 2016), the abundances of *A. formosa* steadily decrease in Lake Ladoga during the 2000s possibly reflecting its poorer competitive abilities for resources both in spring and in summer under present conditions. Since *A. formosa* benefits from short circulation periods after long winters (Horn et al. 2011), its recent decline might evidence for changes in the thermal regime of Lake Ladoga, which is consistent with changes in lake ice conditions (Karetnikov et al. 2017). An appearance and proliferation of small *Cyclotella* species is neither a feature of the present state of the Ladoga ecosystem, in contrast to the other observations (Rühland et al. 2015). On the contrary, larger-sized summer-growing species, such as *Cyclotella radiosa* and *C. schumannii*, together with *Stephanodiscus medius* and *S. neoastraea*, are among the regular components of the present surface-sediment diatom assemblages, similar to the oligotrophic stage.

In spring, in turn, earlier ice-out and prolonged circulation period might be inferred from the increasing abundances of a spring diatom *Aulacoseira subarctica* recorded in the 2000s. Given that *A. subarctica* can tolerate relatively low-light conditions and is favored by turbulence, its recent massive growth could be also tentatively assigned, apart from de-eutrophication, to longer mixing periods after short and mild winters, as it has been suggested by recent findings (Horn et al. 2011; Sochuliaková et al. 2018). It can be thereby hypothesized that the above-mentioned co-dominating position of *A. subarctica* in the late Holocene Lake Ladoga sediment records, long before the start of the human impact on the ecosystem, might also reflect climate-related changes in the lake's thermal regime and circulation.

The composition of the present-day surface-sediment diatom assemblages therefore indicates that the Lake Ladoga ecosystem has not completely returned to its pre-anthropogenic state. Although there is a great number of evidences that eutrophication can be managed by reduced P inputs (Schindler et al. 2016 and references therein), a number of studies also report that lake recovery is not simply a process reverse to the degradation (Bennion et al. 2015). Internal nutrients loading, changes in food-web structures and climate changes are among the most common reasons why lake ecosystems response does not adequately track the improvement in water quality, or why ecosystems recovery is delayed (Battarbee et al. 2005 and references therein; Dokulil and Teubner 2005 and references therein; Bennion et al. 2015). Even though the chemical variables may return to their pre-disturbance levels, many lake systems demonstrate complex biological responses, often developing the communities that bear little resemblance to pre-disturbance assemblages (Rühland et al. 2015 and references therein). Therefore achieving reference state of a lake not only depend on the reduction of anthropogenic pressure but also on whether the reference conditions remained a relevant target. For instance, the climate impact in future can potentially modify the lake ecosystem characteristics to a point where the desired reference state is no longer realistic (Battarbee et al. 2005, Bennion et al. 2011).

In Lake Ladoga, one might not only think of somewhat delayed ecosystem response to the decreased anthropogenic pressure, but also of some irreversible changes resulting from eutrophication. Besides, the processes of de-eutrophication and ecosystem recovery are apparently superimposed upon the recent climatic changes that govern the lake's thermal regime and consequently, onset and duration of blooms of phytoplankton taxa in Lake Ladoga. Results of the recent studies of main biological communities of Lake Ladoga (Kurashov et al. 2018) also revealed a series of specific features that clearly indicate a completely new stage in the ecosystem development.

Extending the surface-sediment diatom studies from the late 1950s to present demonstrated that changes in the diatom assemblages composition adequately track the hydrochemical and hydrobiological shifts in Lake Ladoga related to anthropogenic pressure and, lately, to climate changes. The use of surface-sediment diatom assemblages in environmental research has long been proven efficient, and the present study reaffirmed its relevance in monitoring the ecosystem changes in Lake Ladoga. This approach also has certain advantages over the surveying of benthic and planktonic communities. Large sizes of Lake Ladoga provide a large variety of shallow-water habitats in terms of bottom substrate characteristics, macrophyte abundances and composition, wave energy, etc. Therefore benthic communities in Lake Ladoga rather represent local conditions, and do not appropriately reflect the state of the whole basin. The composition of the planktonic diatom communities in Lake Ladoga, in turn, is highly dependent on biological seasons, while intra-seasonal species successions occur as well. Local factors, such as depth, intensity of seasonal circulation, inflow of river waters with different chemical composition (e.g. the River Volkhov), etc. also affect the composition of the planktonic diatoms. Besides, some inter-annual variations may also take place as a result of interplay of temperature, precipitation, lake level fluctuations, etc. Thus sporadic phytoplankton surveys would only catch "snapshots" of specific conditions that may not represent the whole picture. Regular intra- and inter-seasonal phytoplankton studies are therefore required, which recently become increasingly expensive. The studies of the surface-sediment diatom assemblages are well supplemented by phytoplankton surveys, however, they can be also performed alone if regular phytoplankton data are unavailable. Due to low sediment accumulation rate in Lake Ladoga (≤0,5 mm per year in average), repeated surface-sediment diatom sampling can be conducted every 10 years (see also Davydova et al. 2000). Therefore studying surface-sediment diatom assemblages is suggested as an independent time- and cost-effective approach in assessing the ecological state of Lake Ladoga.

CONCLUSIONS

Studies of the surface-sediment diatom assemblages enabled enabled the changes that have occurred in Lake Ladoga ecosystem, starting from the late 1950s as a result of human impact and recent climate changes.

At the pre-anthropogenic stage (until the early 1960s), the predominance of the cold-water oligotrophic taxa in the surface-sediment diatom assemblages indicated the oligotrophic state of Lake Ladoga. As the P load to the lake progressively increased (late 1960s–1980s), increased proportions of eutrophic species and decreased abundances of the taxa typical of the oligotrophic period recorded the transition to a mesotrophic state. In the early 1990s, the species indicative of eutrophication were still abundant in the surface-sediment diatom assemblages suggesting that the lake remained mesotrophic.

At the present de-eutrophication stage of Lake Ladoga (the 2000s), some taxa typical of the pre-anthropogenic period return to their dominating position in the diatom assemblages while the abundances of eutrophic taxa steadily decrease. Declining proportions of the diatom species that previously dominated in the summer Lake Ladoga phytoplankton reflect the restructuring of the live algal communities at a higher taxonomic level, as a consequence of de-eutrophication. Even though P concentrations decreased nearly to their pre-anthropogenic values, the present-day composition of the surface-sediment diatom assemblages indicates that the Ladoga ecosystem has not yet returned to its pre-anthropogenic state. This suggests a delayed ecosystem response to the decreased anthropogenic pressure, and possibly some irreversible changes resulting from eutrophication. The de-eutrophication process as well as recent climate changes are thought to determine the present state of the lake's ecosystem.

The diatom-inferred changes in the ecological state of Lake Ladoga are in agreement with the results of hydrochemical and hydrobiological studies throughout the study period. Therefore studying surface-sediment diatom assemblages can be applied as an independent time- and cost-effective approach in assessing the ecological state of Lake Ladoga. ■

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