Response of Diatoms from Gryazevoe Lake (Magadan Oblast) to Environmental Changes in the Northern Coast of the Sea of Okhotsk in the Late Pleistocene—Holocene

M. V. Cherepanova^{a, *}, P. S. Minyuk^{b, **}, D. K. Pozhidaeva^b, and S. S. Burnatny^b

^a Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch, Russian Academy of Sciences, Vladivostok, 690022 Russia

^b Shilo North-East Interdisciplinary Scientific Research Institute, Far East Branch, Russian Academy of Sciences, Magadan, 685000 Russia

> *e-mail: cherepanova@biosoil.ru **e-mail: minyuk@neisri.ru

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Abstract—The study of diatoms from the sediments of core Gz-1 (Gryazevoe Lake, Magadan oblast) has made it possible to identify the response of diatom communities to environmental changes in the Late Pleistocene and Holocene and to establish the main stages of the transformation of the lake ecosystem. Three diatom zones and four subzones, reflecting the evolution trend of the lake diatom flora during the transition period from the last glacial maximum to the Holocene, are distinguished based on the changes in the concentration of diatom valves in sediments, the ratio of representatives of ecological groups and dominants. This trend is similar to the changes in the lacustrine diatom communities of the Arctic regions noted in the last millennium in terms of the change in taxonomic composition and dominants. The data of diatom studies, lithological and petrophysical characteristics of sediments indicate that the most significant changes in the natural environment occurred at the Pleistocene—Holocene boundary from 12.6 to 11.1 ka.

Keywords: diatoms, climate changes, paleolimnology, Pleistocene, Holocene, Magadan oblast

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INTRODUCTION

Satellite imagery has been used to decipher over 27 thousand water bodies of various genesis and sizes with an area greater than 0.1 ha in Magadan oblast. The total area of water coverage is 1553 km², including the coverage by natural water bodies of 1103 km²; the total volume of lake water is 2.86 km³ (Izmailova, 2018). There are about 10 150 lakes >1 ha, including those >20 ha, which number 795. More than 17 thousand water bodies have areas ranging from 0.1 to 1 ha (The Lakes of Russia Information System. http://limno.ru//developments/catalogs/lakes_rus/).

Lacustrine sediments serve as important archives of data on past environmental changes, including sediment genesis, paleoclimate, vegetation, and bioproductivity. Their study involves a complex of biological, geophysical, geochemical, mineralogical, and other research (*Tracking* ..., 2001). Diatom analysis aimed at studying valves of diatoms having a silica frustule, which is well preserved in sediments, is one of the key methods for investigating continuous records of waterbody development and global environmental changes. Since diatoms, which are located at the base of trophic

pyramids, determine the existence and functioning of aquatic ecosystems, information about changes in fossil diatom communities can be used to reconstruct the state of these ecosystems at specific time intervals.

The variety of genetic types of lakes in the Sea of Okhotsk area and their relatively high trophic level create favorable conditions for existence of aquatic biota and consequently a significant level of species richness of aquatic organisms (Kharitonov, 2010). Numerous studies have focused on the taxonomic diversity of contemporary algal flora in the region and their ecological characteristics (Vasilieva and Pshennikova, 1996; Kuz'min, 1987; Kuz'min et al., 1990; Mikhailov, 1984a, 1984b, 1985; Potapova, 1991, 1992; Kharitonov, 1981, 1985, 2001, 2005, 2006, 2010, 2011, 2014; Kharitonov and Silin, 2007; Cherepanova, 2004; Potapova, 1996, etc.). Data on fossil diatom algae from the lakes of northeastern Russia are limited. Only the diatom paleoflora of Grand Lake located in Magadan oblast (60°43′47.87″ N, 151°53′05.84″ E) was characterized in detail. Based on the analysis of changes in species diversity, ecological structure of diatom paleocommunities, and diatom valve concentrations in 1g of dry sediment, three diatom complexes

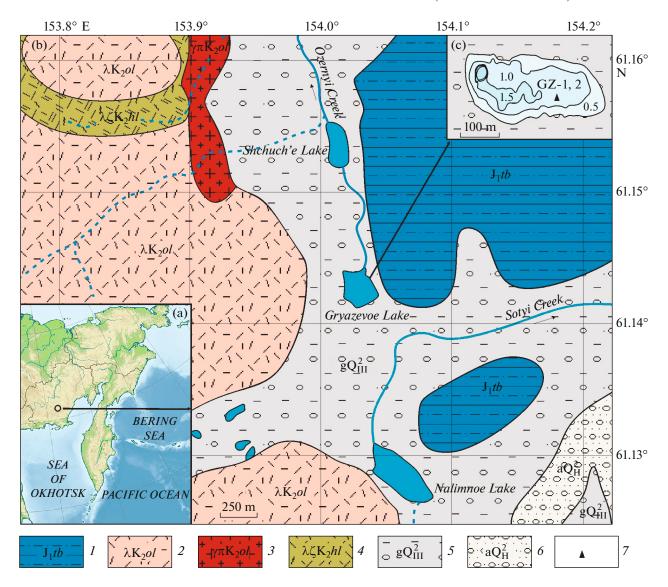


Fig. 1. (a) Location of Gryazevoe Lake, (b) geological chart of the lake vicinity, and (c) bathymetric map of the lake with core location: (1) sedimentary rocks of the Early Jurassic Taborninskaya formation, (2) Upper Cretaceous rocks of the Ola complex, (3) Late Cretaceous granites, (4) Upper Cretaceous rocks of the Kholchan Complex, (5) glacial deposits of the Zyryanian glaciation, (6) Holocene alluvial deposits, and (7) location of core.

were identified in the sediments of this lake formed in the different climatic epochs of the Late Pleistocene and Holocene (Cherepanova et al., 2013).

The aim of this study was to determine the response of diatom algae in Gryazevoe Lake (Tal'skaya Lake group, Magadan oblast) to changes in the natural environment during the Late Pleistocene and Holocene.

OBJECT OF STUDY

Gryazevoe Lake (an informal name) is situated in a small depression near the town of Talaya (61°08′21.18″ N, 152°19′57.22″ E) (Fig. 1). It is 270 m long and 180 m wide and has a water surface area of

 $0.03~{\rm km^2}$, maximum depth of 2.7 m, and altitude 713 m a. s .l.

The lake is weakly flowing. A small shallow creek flows into it in the south, and the Ozernyi creek flows out in the north into the Talaya River (the left tributary of the Buyunda River).

The lake basin is found within the North Okhotsk segment of the Okhotsk—Chukotka volcanic belt. To the east of the lake, there are outcrops of the rocks from the Early Jurassic Taborninskaya Formation represented by aleurolites, argillites, and sandstones (*Geological* ..., 1974). West and southwest of the lake, at the volcanic hills with altitude of 1132 and 1389 m a.s.l., there are Late Cretaceous granites and volcanic



Fig. 2. General view of the (a) lake and (b-d) glacial deposits. The dashed line marks the boundary of glacial deposits.

rocks of the Ola and Kholchan complexes, composed primarily of lava breccias of rhyodacites and dacites.

The lake lies in a small intermontane valley filled with Zyryan glaciation deposits, represented by boulder-block material with pebbles, cobble, and gravel (Fig. 1b). Glaciers moved through the valleys from the south and southwest, where mountain masses with absolute heights above 1000 m are located.

The lower slopes of the volcanic hills surrounding the lake are covered with larch forests, while dwarf cedar and dwarf birch grow higher up the slopes. The lake is surrounded by diverse grassy vegetation, and the northern coast is marshy (Figs. 2a, 2b).

The region has a sharply continental, subpolar climate. According to the observations from 1969 to 2021, the average monthly temperature in January was -3.3° C, with a minimum temperature of -53.9° C. The maximum temperature in June and July was $+33.4^{\circ}$ C, and the average annual temperature was -9.9° C. The average annual precipitation was 439.7 mm, and the average atmospheric pressure was 927.3 mm Hg (http://pogoda-service.ru/).

The water in Gryazevoe Lake is classified as ultrafresh. The total dissolved solids is 49.80 mg/L, with pH = 6.80. Its composition corresponds to bicarbonate, calcium water (Alekin, 1953). Dominant cations include Ca^{2+} , 9.46 mg/L; Na^+ , 2.50 mg/L; Mg^{2+} , 0.88 mg/L; K^+ , 0.27 mg/L; and NH^{4+} , 0.04 mg/L.

The impurities are Mn^{2+} , 0.01 mg/L; Fe^{3+} , 0.02 mg/L; Cu^{2+} , 0.03 mg/L; Co^{2+} , 0.01 mg/L; and Zn^{2+} , 0.04 mg/L. The sum of the anions is 36.58 mg/L, including HCO^{3-} , 33.90 mg/L; SO^{4-} , 0.35 mg/L; NO^{2-} , 2.00 mg/L; NO^{3-} , 0.08 mg/L; and Cl^{-} , 0.25 mg/L (Minyuk et al., 2022).

Mineralization may be affected by groundwater. The total content of the cations and the anions in the water of the Talaya River is 62 mg/L, while it ranges from 450 to 980 mg/L in thermal wells (Bragin et al., 2021). The lake mud was used for balneological procedures at the Talaya resort (Glotov and Glotova, 2007).

MATERIALS AND METHODS

Sediment cores of Gryazevoe Lake were collected with a Livingstone corer (Wright et al., 1984). Two cores, Gz-1 and Gz-2, were drilled to depths of 579 and 476 cm, respectively, in the eastern part of the lake. This work presents the materials of studying the sediments from core Gz-1. Diatoms from the sediment of Gz-2 were not examined. Water samples (eight samples) with a volume of 2 L were collected during the summer at a depth of 10–30 cm below the water surface. The chemical analysis of the samples was performed at the Northeastern Center for Collective Use of the Shilo Northeast Interdisciplinary Scientific Research Institute, Far East Branch, Russian Academy of Sciences, using methods such as titrime-

try, photocolorimetry, and atomic-absorption spectroscopy with a UV mini-1240 spectrophotometer (Shimadzu) and an Agilent 4100 MP-AES atomic emission spectrometer, as well as ausing a weight method. Anions, cations, water hardness, and alkalinity, and pH values, as well as the trace elements Cd²⁺, Cr³⁺, Mo²⁺, Co²⁺, Ni²⁺, Pb²⁺, Cu²⁺, Ba²⁺, Sr²⁺, Mn²⁺, and Zn²⁺, were quantified. The detection limit for the elements was 0.005 mg/L.

After the Gz-1 core was described and photographed, it was divided into 1-cm-long segments for various analyses.

Radiocarbon dating of organic microparticles from the core was performed at the Ångström Laboratory, Uppsala University (Sweden). The calibrated age was determined using the Calib 8.20 program (http://calib.org/calib/calib.html).

The grain-size analysis was conducted at the Far Eastern Geological Institute, Far East Branch, Russian Academy of Sciences, using a SALD-2300 laser diffraction analyzer (Shimadzu, Japan).

The magnetic susceptibility (MS) of the sediments was measured with a multifunctional MFK 1FA magnetic susceptibility meter (AGICO Ltd.).

The relative content of organic material was quantified by the loss on ignition (LOI) method after heating the samples to 500°C (Heiri et al., 2001). Tephraparticle forms were examined in transparent slides under transmitted light by means of a Motic DM-BA-300 microscope.

A total of 46 samples were examined by the method of diatom analysis.

Technical processing of the samples was done according to the standard procedure (Proshkina-Lavrenko, 1974). To remove organic material and loosen the sediments, the samples were boiled in a solution of sodium tripolyphosphate with an added 1-5 mL of 30% hydrogen peroxide solution. The sediments were separated into fractions and had chemical reagents rinsed off by elutriation in distilled water. Permanent slides were prepared from the obtained material using El'yashev medium (with a refractive index of 1.67– 1.68) to ensure clear visibility of the valve structures. The permanent slides were prepared in an identical way: for all studied samples, the sediment aliquot was 1 g; after the chemical treatment, the sediment was diluted in 100 mL of distilled water, 0.06 mL of mixed suspension was applied onto an 18×18 -mm cover slip. This allowed us to calculate the valve concentration in 1 g of dry sediment (Avramenko et al., 2015).

An Axioplan 40 light microscope with immersion oil at 1000× magnification was used to study algae, to count the valves in the slides, and to take micrographs of diatoms. Well-preserved diatom valves were found in the sediments. In some intervals of the core (335, 365–427, 515, 561 cm), single diatoms were detected with 1–14 valves in ten horizontal rows of the slide.

Some intervals (291–321, 351, 441–455, 485, 531, and 575 cm) had no valves at all. Within the interval of 11— 271 cm, each slide was recorded to contain more than 300 valves. At depths of 255, 471, 501, and 545 cm, the number of valves in the samples hardly exceeded 100. The total number of diatom valves was used to clarify the contribution of individual taxa to fossil assemblages of diatoms. To interpret the diatom data, the following ecological groups were established (Passy. 2007: Rimet and Bouchez. 2012: Zelnik et al., 2018): (1) free-living and colonial planktonic; (2) tychoplanktonic, dwelling at the bottom part during a part of the life cycle and in plankton communities during the rest part of their life; (3) substrate-attached benthic with large valves, inhabiting waters with high nutrient content; (4) substrate-attached benthic with small valves, capable of inhabiting waters with low nutrient content; and (5) free-living benthic taxa. The distribution of representatives from these groups made it possible to reconstruct the conditions of the diatom habitat during the sedimentation.

Diatom diagrams illustrating the distribution of major taxa and ecological groups across the section were constructed using the TILIA and TILIA Graph programs (http://www.tiliait.com). The local diatom zones were identified based on the cluster analysis using the method of incremental sum of squares (CONISS) (Grimm, 1987).

We used the classification of diatoms according to AlgaeBase in this work (http://www.algaebase.org). The ecological—geographical characteristics of the taxa were taken from the monograph (Barinova et al., 2006) and other relevant sources cited here.

RESULTS

Lithology

Two layers are distinguished in the section of well Gz-1 (Fig. 1).

(1) Layer 1, depth of 0-230 cm. Silt, nonlaminated, organogenic, and olive-gray; in the unoxidized state, the color is gray or dark gray, with sporadic inclusions of organic matter, mainly branch fragments of plant (Fig. 3a). The sediments contain vivianite in the form of earthy blue structures, several mm in diameter. A white tephra layer is found at a depth of 196.5-198 cm (Fig. 3b). The lower contact is disrupted and not well-defined, perhaps because of bioturbations. The glass fragments are mainly transparent, sharp-edged, and platelike, with a longitudinally fibrous structure and gas bubbles (Fig. 3f). The tephra is related to the caldera-forming eruption of the Kurile Lake volcano in Kamchatka that occurred at 7.6 ka according to the radiocarbon analysis (Ponomareva et al., 2004). The grain-size spectra of the deposits in this layer are unimodal, with particle sizes ranging from 1 to 200 µm (Fig. 3d). The sediments are low magnetic, the values of magnetic sus-

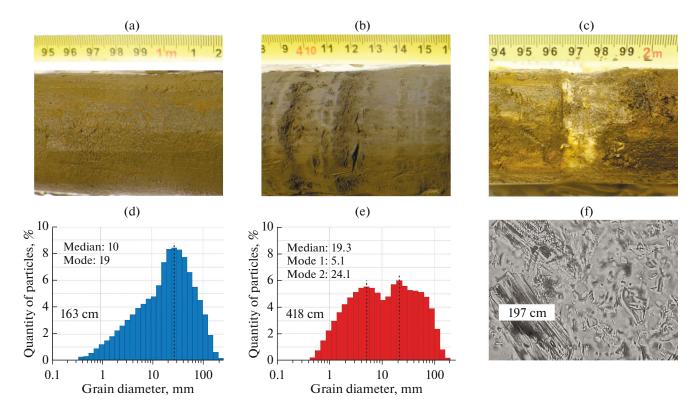


Fig. 3. Lithological characteristics of lacustrine sediments (well Gz-1): (a–c) photos of deposits in layers 1 and 2 and the tephra interbed, respectively; (d, e) typical grain-size spectra of sediments in layers 1 and 2; and (f) transmitted-light micrographs of tephra.

ceptibility are $(0.010-0.086) \times 10^{-6} \text{ m}^3/\text{kg}$ (the average is $0.037 \times 10^{-6} \text{ m}^3/\text{kg}$).

(2) Layer 2, depth of 230-579 cm. The upper part (depth of 230-280 cm) consists of gray silt with unclear layering. The lower part (depth of 280-579 cm) is composed of plastic, bluish-gray, laminated silt (Fig. 3b). The lamination is represented by thin layers of sandy silt and organics with abundant blue vivianite inclusions. At the base of the layer, there lie gray sands. The layer sediments are poorly sorted compared to Layer 1. As a rule, the grain-size distribution is bimodal, with particle diameters ranging from micron fractions (clays) to $200~\mu m$ (sands) (Fig. 3e). The modes are located in the ranges of 1-10 and $10-100~\mu m$. The magnetic susceptibility of the upper part

of the layer varies from 0.0267 to 0.503×10^{-6} m³/kg (the average is 0.234×10^{-6} m³/kg). The lower part of the layer is more magnetic. The values of magnetic susceptibility range from 0.005 to 1.94×10^{-6} m³/kg (the average is 0.57×10^{-6} m³/kg).

Age Model

Four radiocarbon dates (Table 1) and the age of tephra (Ponomareva et al., 2004) were used to construct the age model (Fig. 4) in the Bacon software (Blaauw, Christen, 2011). The youngest date (1.927 years BP) was discarded during the calculations (Fig. 4). The calculated average sedimentation rate is 2 mm/yr.

Table 1. Radiocarbon ages of organic remains from core Gz-1

Laboratory no.	Depth, cm	δ ¹³ C‰V-PDB	¹⁴ C years BP	Cal. years BP
Ua-71985	146	-14.8	1927 ± 37	1838 ± 101
Ua-71986	211	-34.3	9334 ± 46	10387 ± 3
Ua-71987	346-347	-27.9	12556 ± 42	14632 ± 79
Ua-71988	407	_	12772 ± 57	15261 ± 208
Tephra	196.5-198		7618 ± 14	8401 ± 21

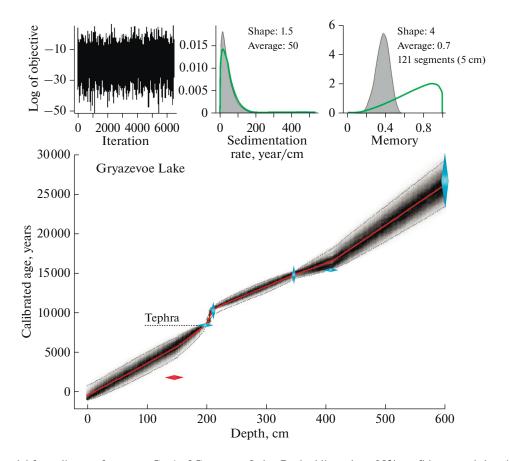


Fig. 4. Age model for sediments from core Gz-1 of Gryazevoe Lake. Dashed lines show 95% confidence; red rhomb represents discarded data.

Diatom Analysis

The sediments of Gryazevoe Lake are found to have diverse diatom flora represented by 189 species and intraspecies taxa (Fig. 5).

By analyzing the ecological structure of the fossil diatom assemblages, we distinguished three zones (DzGz) in the lacustrine sediments, where diatom complexes were formed under different habitat conditions. The main criteria for distinguishing the complexes were the change in diatom valve concentration and participation in taxa paleoassemblages that differ in habitat (plankton, benthos) with various tolerances to water-column dynamics and nutrient content in water (Figs. 6, 7).

DzGz 1 zone. The sediments (575–280 cm) have the lowest concentrations of valves. Only a few layers within this interval contain a required number of diatoms for statistical analysis (slightly over 100 valves). Dominant species change in the diatom paleoassemblages identified at different depths. For instance, the planktonic indicator of oligotrophic waters with low nutrient content, *Lindavia michiganiana* (Kireta, 2018; Stoermer, 1993), dominates at a depth of 545 cm (74.2%) and is a subdominant at depths of 501 (13.1%) and 471 cm (17.7%). The benthic *Ellerbeckia arenaria*

f. teres (Rimet and Bouchez, 2012), being also considered an inhabitant of oligotrophic water bodies (Krammer and Lange-Bertalot, 1991), dominates at a depth of 501 (85.2%) and 471 cm (66.0%) and is a subdominant at a depth of 545 cm (25.8%). K. Krammer and H. Lange-Bertalot (Krammer and Lange-Bertalot, 1991) include this taxon into a group of aerophilic diatoms, capable of living on sporadically moistened, intermittently drying surfaces. The benthic Iconella hibernica, found at the very bottom of the water bodies (Krammer and Lange-Bertalot, 1988), appears in a dominant group at a depth of 471 cm (11.6%). The complex is characterized by low species richness. The other detected taxa are represented by rare valves.

The concentration of valves increases gradually in **DzGz 2 zone** sediments (280–230 cm). Like DzGz 1, this zone is characterized by distinct dominance of different taxa along the core. At a depth of 271 cm, the tychoplanktonic taxon *Staurosira venter* (83.1%) dominates with a subdominant from the same ecological group, *Pseudostaurosira brevistriata* (15.0%). At 255 cm, *I. hibernica* (63.2%) dominates with subdominant *S. venter* (12.8%). The diatom species richness sharply increases from a depth of 238 cm, where *S. venter*

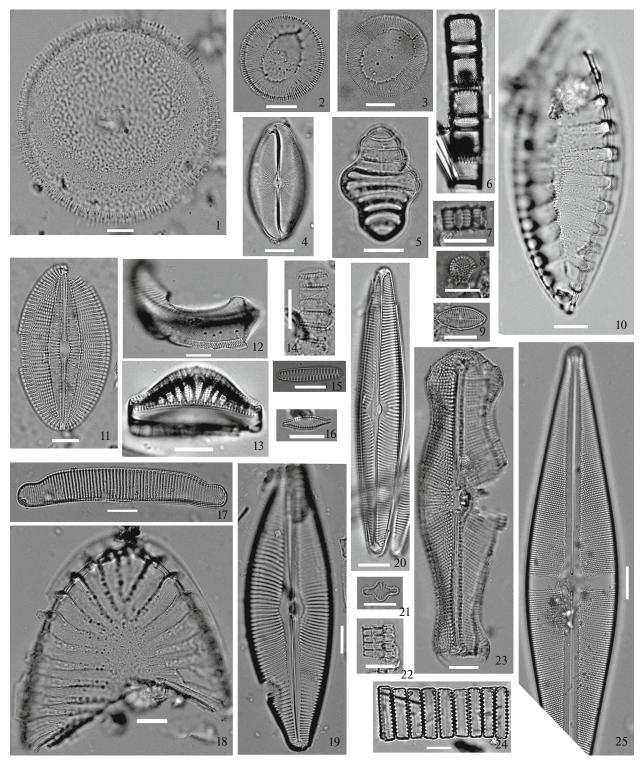


Fig. 5. Fossil diatoms of Gryazevoe Lake: (1, 12) Ellerbeckia arenaria f. teres (Brun) R.M. Crawford: (1) valve face; (12) girdle band; (2, 3) Lindavia michiganiana (Skvortsov) T. Nakov, Guillory, M.L. Julious, E.C. Theriot, and A.J. Alverson; (4) Eucocconeis flexella (Kützing) Meister; (5) Tetracyclus glans (Ehrenberg) F.W. Mills; (6) Aulacoseira valida (Grunow) Krammer, chain; (7, 8) Aulacoseira humilis (A. Cleve) Genkal and Trifonova: (7) chain; (8) valve face; (9) Skabitshewskia oestripii (A. Cleve) Kulikovskiy and Lange-Bertalot; (10) Iconella linearis (W. Smith) Ruck and Nakov; (11) Diploneis finnica (Ehrenberg) Cleve; (13) Epithermia smithii Carruthers; (14) Staurosua venter (Ehrenberg) Cleve and J.D. Möller: chain; (15, 24) Staurosirella lapponica (Grunow) D.M. Williams and Round; (15) valve face; (24) chain; (16) Pseudostaurosira brevistriata (Grunow) D.M. Williams and Round; (17) Eunotia monodon Ehrenberg; (18) Iconella hibernica (Ehrenberg) Ruck and Nakov; (19) Cymbopleura inequalis (Ehrenberg) Krammer; (20) Navicula vulpina Kützing; (21, 22) Staurosira construens Ehrenberg: (21) valve face; (22) chain; (23) Didymosphenia geminata (Lyngbye) Mart. Schmidt; and (25) Stauroneis phoenicentron (Nitzsch) Ehrenberg. Scale bar is 10 µm.

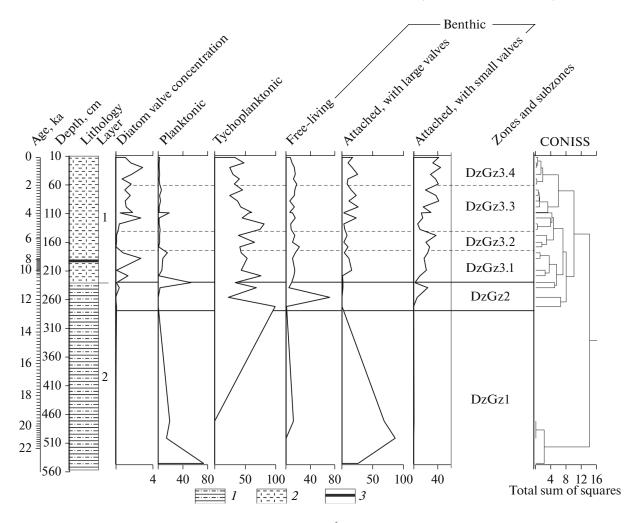


Fig. 6. Concentration of diatom valves per 1 g of dry sediment (\times 10⁶) and distribution of representatives of ecological groups (%) in core Gz-1: (1) thinly laminated silt, (2) massive organogenic silt, and (3) tephra.

(45.6%) is dominant and the benthic *Skabitschewskia oestrupii* (16.4%) is subdominant. The composition of the dominant group changes upward the interval. At a depth of 230 cm, the dominant species are the small, centric planktonic *Aulacoseira humilis* (42.5%) with a valve diameter <10 µm, an inhabitant of oligotrophic waters (Genkal and Kulikovskiy, 2014), and *S. venter* (25.1%). We also note a high abundance of heavily silicified *Aulacoseira valida* (9.7%).

DzGz 3 zone (230–11 cm). The concentration of valves increases in the sediments characterized by this complex and reaches its maximum, but it does not remain constant in the interval. This complex features high species diversity of diatoms and the constant presence of taxa with small valves (<20 μm) in the dominant group: *S. venter, Staurosirella pinnata, Staurosirella lapponica, Staurosira construens*, and *P. brevistriata*, collectively united into *Fragilaria* sensu lato group (Smol et al., 2005), as well as the diversity and relative abundance of representatives from the family *Cymbellaceae* Greville, assigned to the genera *Cym*-

bella, Cymbopleura, Encyonema, and Encyonopsis—a total of 15 taxa. The changes in valve concentrations in the sediments, the proportions of representatives from the different ecological groups, and the composition of the dominant group enabled us to identify four subzones (DzGz 3.1–DzGz 3.4) within the interval.

DzGz 3.1 subzone (230–174 cm). The concentration of valves in the sediments increases by almost a factor of 10. A markedly pronounced dominance of *S. venter* (up to 44.9%) characterizes the formation of monodominant fossil diatom assemblages. At a depth of 208 cm (ca 10 ka), the valve concentration decreases, and the abundance of *S. venter* decreases to 28.2%. The dominant group is now complemented by *Cymbella aspera* (12.3%), which inhabits moss-covered moistened edges of small brooks (Jüttner et al., 2010), and *Stauroneis phoenicenteron* (8.5%) encountered on muddy grounds (Mann and Stickle, 1995). There is an increasing diversity and abundance of marshy taxa in the genus *Eunotia* (*E. minor*, *E. monodon*, *E. glacialis*, *E. incisa*, and others).

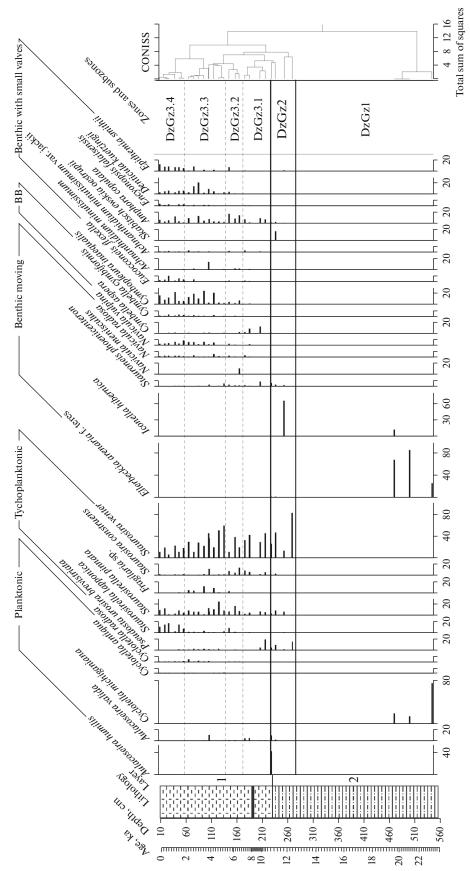


Fig. 7. Percentage content of individual diatom taxa in sediments of core Gz-1: BB is benthic diatoms with large (>100 μm) valves.

DzGz 3.2 subzone (174–140 cm). The diatom valve concentration is recorded to decrease in the sediments of this subzone. The most abundant taxa are the tychoplanktonic species *S. venter* (up to 35.9%), *S. construens* (up to 12.3%), and *S. pinnata* (up to 15.9%). The group of dominant also includes *Amphora copulata*, an inhabitant of epilithon (Baker et al., 2022) that adheres to rocks (Round, 1991).

DzGz 3.3 subzone (40–68 cm). The concentration of valves in the sediments sharply increases. The fossil diatom assemblages show a gradual decrease upward the core in the abundance of S. venter (from 58.4 to 11.1%) and S. pinnata (from 24.7 to 8.4%) and an increase in the number of the larger (over 100 µm) benthic Cymbopleura inaequalis (up to 24.6%) that prefers slowly flowing calcareous waters (Krammer and Lange-Bertalot, 1986) and inhabits mountainous regions (Barinova and Niyatbekov, 2019; Catalan et al., 2009). Species from different habitats are encountered at different depths with high abundances: benthic Achnanthidium minutissimum (up to 14.0%), A. copulata (up to 12.6%), Navicula vulpina (up to 6.2%), N. radiosa (up to 6.0%), planktonic A. valida (up to 10.6%), tychoplanktonic *Fragilaria* sp. (up to 11.1%), and epiphytic *Epithemia smithii* (8.9%). Benthic Denticula kützingii appears and gradually increases in abundance (from 4.0 to 20.0%) from a depth of 117 cm. It prefers weakly alkaline waters with high conductivity (Zgrundo et al., 2017).

DzGz 3.4 subzone (68–11 cm). The concentration of valves remains high. The markedly pronounced dominance of S. venter terminates, and its abundance ranges from 5.9 to 22.6%. The diatom assemblages become polydominant. Among the most abundant taxa are C. inaequalis (up to 22.6%), Staurosirella lapponica (up to 16.5%), S. pinnata (up to 12.8%), Cymbopleura incerta var. spitsbergensis (up to 12.2%), A. copulata (up to 11.9%), N. vulpina (up to 8.5%), and Eucocconeis flexella (up to 9.8%), which dwell in various habitats, such as plankton and benthos, and have various tolerance to environmental parameters. The abundance of benthic Epithemia smithii increases (up to 12.20%). K. Krammer and H. Lange-Bertalot (Krammer and Lange-Bertalot, 1988) reported that this taxon is widely distributed in Northern Europe, often as an epiphyte in mesotrophic and eutrophic ponds, lakes, and rivers.

DISCUSSION

The obtained data enabled us to detect the response of fossil diatom assemblages to environmental changes and to establish the stages in the development of the lacustrine ecosystem in the late Pleistocene—Holocene.

The DzGz 1 complex (24.844–19.564 ka) was formed in the Late Pleistocene, during cold marine isotope stage (MIS) 2. Low concentrations of diatom

valves in the sediments or their complete absence indicate the presence of a permanent ice cover on the lake, which impeded the development of photosynthetic algae. Nevertheless, almost constant sedimentation rates upward the core suggest a continuous influx of fine detrital material to the water body, which has no organic remains and is characterized by high values of magnetic susceptibility. This material was likely to come during the summer when the narrow ice edge at the shore thawed. The presence of ice in the central part of the lake impeded wind-induced water mixing and oxygen enrichment, creating anoxic conditions in the bottom waters and upper sediment layers that are favorable for the formation of vivianite (Fe₃(PO₄)₂) 8H₂O) and iron sulfides (Minyuk et al., 2013; Suits and Wilkin, 1998; Wilkin and Barnes, 1997). The presence of thinly laminated sediments indicates the absence of bioturbations. It is known that similar conditions were typical of many lakes in Northeastern Russia at the cold climate stages (Minyuk and Borkhodoev, 2006; Melles et al., 2007, 2012; Minyuk and Subbotnikova, 2021).

The sporadic diatom layers revealed in this sediment interval might indicate possible short-term warming periods, which were recorded during the cold MIS 2. For instance, at a depth of 545 cm, diatom sediments could have formed ~23.4 ka during Greenland Interstadial GI 2.2 (Cohen and Gibbard, 2019; Rasmussen et al., 2014). During the warming periods, the thawed zone of the ice sheet expanded, which contributed to the development of benthic species or an inhabitant of shallow tundra zone lakes, such as *L. michiganiana* (Balhs et al., 2018). The pronounced dominance of one taxon could result from specific ecological conditions and a short period of their existence, followed by a rather sharp change.

It is likely that the lake basin began to form at MIS 2. The study of the deposits around Gryazevoe Lake showed that they were formed during the Zyryanian glaciation (MIS 4), whereas, according to the obtained radiocarbon dates, core Gz-1 was not found to contain sediments of this age.

The features of the DzGz 2 complex (12.689– 11.116 ka), which differs primarily in the variability of the dominant group composition, indicates its transitional nature due to the changing ecological conditions. The complex was formed at the Pleistocene-Holocene boundary that is marked by the end of the Younger Dryas—cold event at 11.7 ka, corresponding to Greenland Stadial GS-1 (Cohen and Gibbard, 2019; Walker et al., 2009). Tychoplanktonic species appeared and started to develop actively at the initial stage of sediment formation in this complex when the temperatures were still low. Algae were likely to distribute only in the uppermost heated layer of the water. We assume that they were brought into the lake by streams. There was no aquatic vegetation where diatoms could settle, and bottom-layer temperatures were

too low for diatom development. The limited choice of habitats did not contribute to high taxonomic diversity. The appearance of *Iconella* in the overlying sediments can be regarded as an indicator for the onset of stable warming of climate and the related subsequent development of the more complex and diverse diatom flora in the lacustrine ecosystem. Similar trends in the development of diatom flora have been recorded in the last millennium in Arctic Canada's lakes (Besonen et al., 2008). Species diversity remains low; planktonic and epiphytic taxa are absent, which is determined by the temperatures, which are still low, and by the continuous ice regime, which may correspond to a cooling event 11.4 ka (Rasmussen et al., 2014); however, in the shallow water zone of the lake, the water is heated well enough for benthic *I. hibernica* to develop. Circa 11.3 ka, diatom valve concentration and diversity increase, and representatives of the genus Aulacoseira appear, including large-valve species, that inhabit waters with increased turbulence that allows them to be in the water column (Round et al., 1990; Rüuhland et al., 2015). Thus, the warming trend continues, leading to more contrasting seasons, as indicated by the growing diversity of diatoms assigned to the different ecological

The character of the incoming detrital material also changes. Alcurites with poorly defined lamination are accumulated; they contain a greater amount of organic material compared to the lower layers. Magnetic susceptibility decreases due to dilution of sediment with organic matter.

The beginning of the period corresponding to DzGz 3.1 (11.116–7.103 ka) marked a sharp increase in diatom valve concentrations in the sediment. The steady growth of abundance of small representatives of Fragilaria sensu lato is likely related to a moderate increase in surface-water temperatures. A similar situation recorded in Holocene sediments of a small subarctic lake in Canada was characterized as a common response of diatom communities to warming (Podritske and Gajewski, 2007). At the same time, the environmental conditions remain inconstant. The identified subzones indicate their changes during the sediment formation in this zone. For example, the warming that began ~10.7 ka was followed by relative cooling (at 10.0 ka), which probably increased the icecovered period on the lake and shortened the vegetation period for planktonic and tychoplanktonic diatoms. This was accompanied by the formation of marshes in the area surrounding the lake. The marsh forms of diatoms were carried to the lake with the waters of small streams. The sediments accumulated during this time contain a significant amount of organic matter, leading to dilution of detrital material and low values of magnetic susceptibility.

Low diatom concentrations in the sediments from the DzGz 3.2 subzone (7.103–5.329 ka) are likely associated with intensive dilution by mineral particles settling to the lake bottom, which is confirmed by relatively high values of magnetic susceptibility in the sediments of this zone and low organic content. The presence of *S. pinnata* in the dominant group may indicate the low temperatures. The inverse relationship between the abundance of *S. venter* and *S. pinnata*, which is associated with climate changes in Holocene sediments of Arctic lakes (Michelutti et al., 2003; Podritske and Gajewski, 2007), evidences the lower temperatures for the *S. pinnata* habitat. The absence of epiphytic diatoms and the presence of epilithon inhabitants may indicate the absence of aquatic macroscopic plants, on which some diatom species settle.

The trend towards an increase in the surface-water temperature remains during the formation of the DzGz 3.3 subzone (5.329–2.360 ka). The diatom valve concentration increases in the sediments sharply, nearly tripling at 4.4 ka. Since that time, benthic taxa with large valves have been constantly present in the dominant group. Their appearance can be considered a reaction to warming (Perren et al., 2003). With increasing temperatures, there is an evident shift from small littoral taxa (e.g., S. venter, S. pinnata) to larger epiphytic benthic species (Lotter, Bigler, 2000), in our case, e.g., C. inaequalis and Navicula vulpina. Similar sequences of diatom taxa shifts were recorded in glacial/postglacial lake ontogeny at lower latitudes (Round, 1981). These changes in fossil diatom communities were likely to record an event known as the "Holocene Turnover" (Paasche and Bakke, 2009) that occurred at the Middle-Late Holocene boundary. This event triggered the reorganization of ocean and atmospheric circulation and was observed in multiple regions worldwide (Mayewski et al., 2004; Railsback et al., 2018; Walker et al., 2018). The subsequent frequent, but short-time, changes in the dominant groups may indicate unstable ecological conditions against the background of a warming trend. In addition, if the temperature was likely to follow a rising trend, the water pH and trophicity changed quite chaotically. Such changes also could result from increased diversity of biotopes inhabited by diatoms and from enhanced convective water mixing and a lack of clear water stratification. Moreover, the inflow of streams, delivering not only nutrients and minerals but also diatoms, might have increased during that time.

The DzGz 3.4 subzone (from 2.360 ka) reflects the establishment of the modern diatom flora, which is diverse both taxonomically and ecologically. The high concentrations of diatom valves in the sediments may be due to the absence of competitive algal groups that thrive at surface-water temperatures being relatively low though sufficient for diatoms to extract silica from the water column to construct their frustules. High abundances of taxa inhabiting bicarbonate-rich mountain lakes, such as *C. inaequalis*, *Cymbopleura incerta var. spitsbergensis*, *N. vulpina*, and *Eucocconeis flexella* (Barinova and Niyatbekov, 2019), indicate the

establishment of the modern character of mineralization and type of water. Thus, starting at 1.95 ka, all conditions are provided for diatom algae to thrive in the lake. The water macroscopic plants that emerged during the formation of the previous subzone complex began to spread actively in the lake, offering new habitats for diatoms and increasing the trophicity of water, where mesotrophic diatom taxa began to thrive.

CONCLUSIONS

The study of diatom algae in the sediments of Gryazevoe Lake allowed us to reveal their response to habitat changes during the transitional period from the Last Glacial Maximum to the Holocene. The response manifested itself primarily in variations in diatom valve concentrations in the sediments, transformation of the ecological structure and the dominant group of diatom taphocoenoses.

Diatoms are almost entirely absent in the sediments formed in the Late Pleistocene during the cold MIS 2. The slight increase in diatom valve concentrations at the base of the section may be determined by a short-term period of warming corresponding to the interstadial GI 2.2 (~23.4 ka), while the dominance of one taxon is likely due to specific ecological conditions and their short existence.

Frequent changes in the dominant group of fossil communities at the Pleistocene—Holocene boundary indicate multiple shifts in ecological conditions. For example, low taxonomic diversity and dominance of benthic and tychoplanktonic diatoms were associated with the cooling at 11.4 ka, while the increase in species richness and the appearance of planktonic taxa from 11.3 ka marked the onset of a trend towards relatively stable warming.

A sharp increase in diatom valve concentration and abundance of small-valve species at 10.7 ka was related to a significant temperature increase, which was followed by cooling at 10.0 ka, highlighted by the decreasing overall diatom abundance, dominant coldwater taxa, and appearance of marshy species.

The observed trends to changes in the diatom flora of Gryazevoe Lake during the transition from the Glacial Maximum to the Holocene are similar in many respects to the shift in diatom communities in Arctic regions that were recorded for the Last Millenium.

A sudden spike in diatom valve concentration in the sediments at 4.4 ka and the permanent presence of large-valve benthic taxa in the dominant group marked a "warm" event at the Middle—Late Holocene boundary.

The formation of modern taxonomic diversity of diatom flora in the lake is considered to start at the boundary of 2.360 ka, while favorable conditions for diatom thriving were developed 1.95 ka, which led to the increase in the number of their valves in the sediments.

The observed diatom response, particularly to climate fluctuations during the Late Pleistocene—Holocene, enabled us to identify the key stages in the evolution of the lacustrine ecosystem from a shallow oligotrophic lake with permanent ice cover to a relatively deep mesotrophic lake with abundant diatom flora.

The data from the diatom studies, as well as lithological and petrophysical characteristics of the sediments, indicate that the most significant environmental changes occurred at the Pleistocene—Holocene boundary from 12.6 to 11.1 ka.

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CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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