Spatial distribution of environmental indicators in surface sediments of Lake Bolshoe Toko, Yakutia, Russia

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Abstract

Rapidly changing climate in the northern hemisphere and associated socio-economic impacts require reliable understanding of lake systems as important freshwater resources and sensitive sentinels of environmental change. To better understand time-series data in lake sediment cores it is necessary to gain information on within-lake spatial variabilities of environmental indicator data. Therefore, we retrieved a set of 38 samples from the sediment surface along spatial habitat gradients in the boreal, deep, and yet pristine Lake Bolshoe Toko in southern Yakutia, Russia. Our methods comprise laboratory analyses of the sediments for multiple proxy parameters including diatom and chironomid taxonomy, oxygen isotopes from diatom silica, grain size distributions, elemental compositions (XRF), organic carbon content, and mineralogy (XRD). We analysed the lake water for cations, anions and isotopes. Our results show that the diatom assemblages are strongly influenced by water depth and dominated by planktonic species, i.e. *Pliocaenicus bolshetokoensis*.

Species richness and diversity is higher in the northern part of the lake basin, associated with the availability of benthic, i.e. periphytic, niches in shallower waters. $\delta^{18}O_{diatom}$ values are higher in the deeper south-western part of the lake probably related to water temperature differences. The highest amount of the chironomid taxa underrepresented in the training set used for palaeoclimate inference was found close to the Utuk river and at southern littoral and profundal sites. Abiotic sediment components are not symmetrically distributed in the lake basin but vary along restricted areas of differential environmental forcing. Grain size and organic matter is mainly controlled by both, river input and water depth. Mineral (XRD) data distributions are influenced by the methamorphic lithology of the Stanovoy mountain range, while elements (XRF) are intermingled due to catchment and diagenetic differences. We conclude that the lake represents a valuable archive for multiproxy environmental reconstruction based on diatoms (including oxygen isotopes), chironomids and sediment-geochemical parameters. Our analyses suggest multiple coring locations preferably at intermediate depth in the northern basin and the deep part in the central basin, to account for representative bioindicator distributions and higher temporal resolution, respectively.

1   Introduction

Over the past few decades, the atmosphere in boreal and high elevation regions has warmed faster than anywhere else on Earth (Pepin et al., 2015;Huang et al., 2017). Dramatic socio-economic and ecological consequences are expected (AMAP, 2017) as well as substantial feedbacks from thawing permafrost and the associated release of greenhouse gas into the global climate system (Schuur et al., 2015). Boreal Russia is identified as a global hot-spot where surface air temperature increases have led to substantial ground warming over the past decade (Biskaborn et al., 2019). Accurate estimates of the amplitude of environmental impacts are compounded by an imprecise understanding of ecological indicators of past environmental conditions (Miller et al., 2010). Lake ecosystems, whose development is archived in their sediments, act as sensitive sentinels of environmental changes (Adrian et al., 2009) while even small changes in climate can profoundly deteriorate ecosystem services (Saulnier-Talbot et al., 2014). Assessments of the impact of climate change to lake systems rely on careful interpretation of suitable proxy data. Proxy information on present and past ecological conditions is provided by various biological and physicochemical properties of the sediment components (Meyer et al., 2015;Solovieva et al., 2015;Nazarova et al., 2017a). However, the spatial within-lake distributions of preserved remnants of ecosystem inhabitants and associated sediment-geochemical properties, depend on habitat differences between the

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83 epilimnion and the hypolimnion (Raposeiro et al., 2018), and are therefore expected
84 to be non-uniform. Accordingly, precise palaeolimnological reconstruction of past
85 environmental variability requires a detailed, quantitative understanding of the
86 modern (21st century) within-lake heterogeneity.

87   Here, we employ a multi-proxy approach to attain a holistic view of a lake's
88 depositional history in boreal Russia. Variables include diatom and chironomid
89 taxonomy, stable oxygen isotopes in diatom silica, grain size distributions, elemental
90 compositions, organic carbon content, and mineralogy. Abiotic sediment properties
91 may represent signals resulting from either the external input of material and lake-
92 internal conditions during deposition, or post-sedimentary diagenetic processes near
93 the sediment surface (Biskaborn et al., 2013b;Bouchard et al., 2016). Hence, our
94 integrated approach enables the identification and distinction between internal lake
95 processes and external forcing (Cohen, 2003).

96   Diatoms (unicellular, siliceous microalgae) are major aquatic primary producers.
97 They appear ubiquitous and their opaline frustules ($SiO_2 \cdot nH_2O$) are well preserved in
98 the sedimentary record, allowing exact identification down to sub-species level by
99 high-resolution light microscope analysis (Battarbee et al., 2001). Diatoms are widely
100 applied bioindicators for past and present ecosystem changes in boreal environments
101 (Miller et al., 2010;Pestryakova et al., 2012;Hoff et al., 2015;Herzschuh et al.,
102 2013;Biskaborn et al., 2012;Biskaborn et al., 2016;Palagushkina et al., 2017;Douglas
103 and Smol, 2010). Widespread responses of planktonic diatoms to recent climate
104 change indicate that lakes in the northern hemisphere have already crossed important
105 ecological thresholds (Smol and Douglas, 2007;Rühland et al., 2008). The very rapid
106 cell life cycles of days to weeks (Round et al., 1990) enables changes in diatom
107 assemblages on very short time-scales in response to changes in environmental
108 circumstances, e.g. cooling or warming (Anderson, 1990). The link between climate
109 change and diatoms, however, cannot easily be addressed via simple temperature-
110 inference models and instead requires a more complete understanding of the
111 interactions between the aquatic ecosystem with lake habitat preferences,
112 hydrodynamics and catchment properties (Anderson, 2000;Palagushkina et al.,
113 2012;Biskaborn et al., 2016;Bracht-Flyr and Fritz, 2012;Hoff et al., 2015). It is thus
114 necessary to identify the relationship between diatom species occurrence, the
115 isotopic composition of their opaline valves, and internal physico-limnological factors
116 (Heinecke et al., 2017) within spatial heterogenic lake systems before drawing direct
117 inferences about external climatic driven factors from single core studies.

118   Chironomid larvae (Insecta: Diptera) make up to 90% of the aquatic secondary
119 production (Herren et al., 2017;Nazarova et al., 2004) and hence their preserved head
120 capsules well represent the aquatic heterotrophic bottom-dwelling ecosystem
121 component (Nazarova et al., 2008;Syrykh et al., 2017;Brooks et al., 2007).
122 Furthermore, literature reports a net mutualism of chironomids and benthic algae

between the primary consumer and primary producer trophic levels in benthic ecosystems (Specziar et al., 2018;Zinchenko et al., 2014). Factors influencing the spatial distribution of chironomids within single lakes are water temperature (Nazarova et al., 2011;Luoto and Ojala, 2018), sedimentological habitat characteristics (Heling et al., 2018) and/or water depth and nutrients (Yang et al., 2017), as well as hypolimnetic oxygen (Stief et al., 2005) and the availability of water plants (Raposeiro et al., 2018;Wang et al., 2012b).

As previous studies described, pollen distribution in lake sediments are less influenced by lake zonation than aquatic communities (Zhao et al., 2006). Accordingly, our study does not consider spatial pollen distributions.

Secondary factors influencing the spatial distribution of subfossil assemblages are selective transitions from living communities to accumulation of dead remains. Both biological remains and physico-chemical properties are influenced by sediment resuspension and redistribution processes described as sediment focusing (Hilton et al., 1986). These are primarily dependent on slope steepness (Hakanson, 1977) or, in shallow areas, wind-induced bottom shear stress (Bennion et al., 2010;Yang et al., 2009). Nevertheless, it already has been proven for other lake sites that within-lake bioindicator distributions are laterally non-uniform, contradicting the assumption that mixing processes cause homogenous microfossil assemblages before deposition (Anderson, 1990;Wolfe, 1996;Anderson et al., 1994;Earle et al., 1988;Kingston et al., 1983;Puusepp and Punning, 2011;Stewart and Lamoureux, 2012;Yang et al., 2009). However, many palaeolimnological studies employ single-site approaches using only one sediment core, and hence do not encompass the full spatial extent and natural variability of the entire lake sediment archive. Heggen et al. (2012) report that sediment cores from the deep centre of small and shallow lakes with high spatial proxy variability in the littoral zones contain representative bioindicator assemblages. The authors also conclude, that in larger and deeper lakes similar multi-site studies are necessary to make recommendations about the "ideal" coring positions for multi-proxy palaeolimnological studies.

In this respect, our broad research question is: how spatially reliable are palaeolimnological proxy data in a complex lake system? To answer this question, we set up our research hypothesis: Bioindicators and abiotic sediment properties will respond to different habitat conditions and lake zonation, including water depth, proximity to the main inflow in the South and old moraines in the North of lake Bolshoe Toko.

An analysis of spatio-temporal within-lake bioindicator distribution requires a suitable and large lake system with an anthropogenically untouched ecosystem and sufficient variability in water depth, catchment setting, and sedimentological regime. These demands are met by Lake Bolshoe Toko, the deepest lake in Yakutia, Russia (Zhirkov et al., 2016) (Fig. 1). Our study aims to gain a better local understanding of

163 proxy data for future palaeoenvironmental analyses of long sediment cores from
164 Bolshoe Toko. Therefore, our objectives are to (1) detect the spatial variability of
165 abiotic (elements, minerals, grain size) and biotic (diatoms, chironomids, organic
166 carbon) components of the lake's surface sediments, (2) reveal the causal
167 relationship between the distribution of aquatic microfossils, lake basin features, and
168 sedimentary parameters, and (3) attribute proxy variability to specific environmental
169 factors.
170

2 Study site

172   Lake Bolshoe Toko (56°15'N, 130°30'E, 903 m.a.s.l) is an oligotrophic, freshwater
173 lake located in the Sakha Republic, Russia (Fig. 1). The lake surface area is 84.3
174 km^2, with a mean water depth of 29.5 m (maximum, 72.5 m) and secchi depth of 9.8
175 m (Zhirkov et al., 2016). The Utuk river runs through Lake Maloe Toko and brings
176 water from the southern igneous catchment. Lake Maloe Toko (called "small Toko",
177 size 2.7 x 0.9 km, 168 m depth, tectonic origin) is located between high mountains
178 south of Bolshoe Toko. The river inflow south of Bolshoe Toko forms deltaic
179 sediments. The bay in the southeast is called Zaliv Rybachiy ("Fishing bay"). It is
180 partly separated from the main basin and supplied with water by a small creek that
181 itself is connected to a small lake (Fig. 1). The bay is reported to have a somewhat
182 different fauna as compared to the Bolshoe Toko main basin, i.e. occurrence of fish
183 that are typical for small lakes and not found out of the basin (Semenov, 2018). The
184 "Banya lake" in the northeast is isolated from Bolshoe Toko and is not considered in
185 this study. The Mulam river is the lake's predominant outflow towards the North along
186 the south eastern border of Yakutia flowing into the Uchur, Aldan and finally into the
187 Lena rivers.
188   There are no permanent settlements in the study area. During the time of field work
189 there was a temporary mining settlement (built in 2011) located 17 km northwest from
190 Bolshoe Toko in the upper course of the Elga river. This settlement was accessible
191 by off-road vehicles we used to reach the lake, partly along temporary winter roads
192 (frozen rivers and lakes) in March 2013. The exploitation of the El'ginsky coal
193 deposits, planned for a productivity of 15-20 million tons year^{-1} (Konstantinov, 2000),
194 will strongly affect the lake and its catchment. The territory of the watershed will
195 increasingly be damaged and contaminated by off road vehicles and rain fall will
196 produce muddy water which potentially can cause lake pollution (Sobakina and
197 Solomonov, 2013).
198   The lake basin is adjoined to the northern slope of the eastern Stanovoy mountain
199 range in a depression of tectonic and glacial origin between two northwest-trending
200 right-lateral strike-slip faults (Imaeva et al., 2009). A southward thrust fault runs along
201 the southern border of the lake separating the Precambrian igneous rocks in the south

from sandstones and mudstones of the Mesozoic Tokinski Plateau in the north. The Stanovoy mountain range in the southern catchment of the lake consists mainly of highly mafic granulites and other high-pressure metamorphic rock types (Rundqvist and Mitrofanov, 1993). At its north-eastern margins the lake is bordered by moraines of three different glacial sub-periods (Kornilov, 1962) (Fig. 1).

The study area is situated within the East Siberian continental temperate climate zone exhibiting taiga vegetation (boreal forests) and fragments of steppes and a predominant westerly wind system (Shahgedanova, 2002). The meteorological station in Yakutsk has recorded historical climate data (Gavrilova, 1993). In the 19th Century the mean annual temperature (Jan-Dec) was circa -11° to -11.5°C and during the 20th Century these temperatures have increased to around -10.2°C, in parallel with an increase in precipitation from 205 to 250 mm per year (Konstantinov, 2000). The meteorological station "Toko" located approximately 10 km northeast of the lake, however, recorded an increase of air temperature of ca. 0.48 °C per decade from the 1970's to 2010 (calculated from NOAA data, only those years involved that have average air T data in 12 months). Measurements taken directly at the lake were lower, indicating the influence of cold melt water from the Stanovoy mountain range in summer and the high volume of ice during wintertime. Since the average air temperature in southern Yakutia increases with height (temperature inversion of ~2°C 100 m^{-1}), permafrost can be locally discontinuous where taliks (unfrozen zones) underneath topographically high and deep lakes penetrate the permafrost zone (Konstantinov, 1986). As observed in 1971 (Konstantinov, 2000) ice cover lasts at least partly until mid-July.
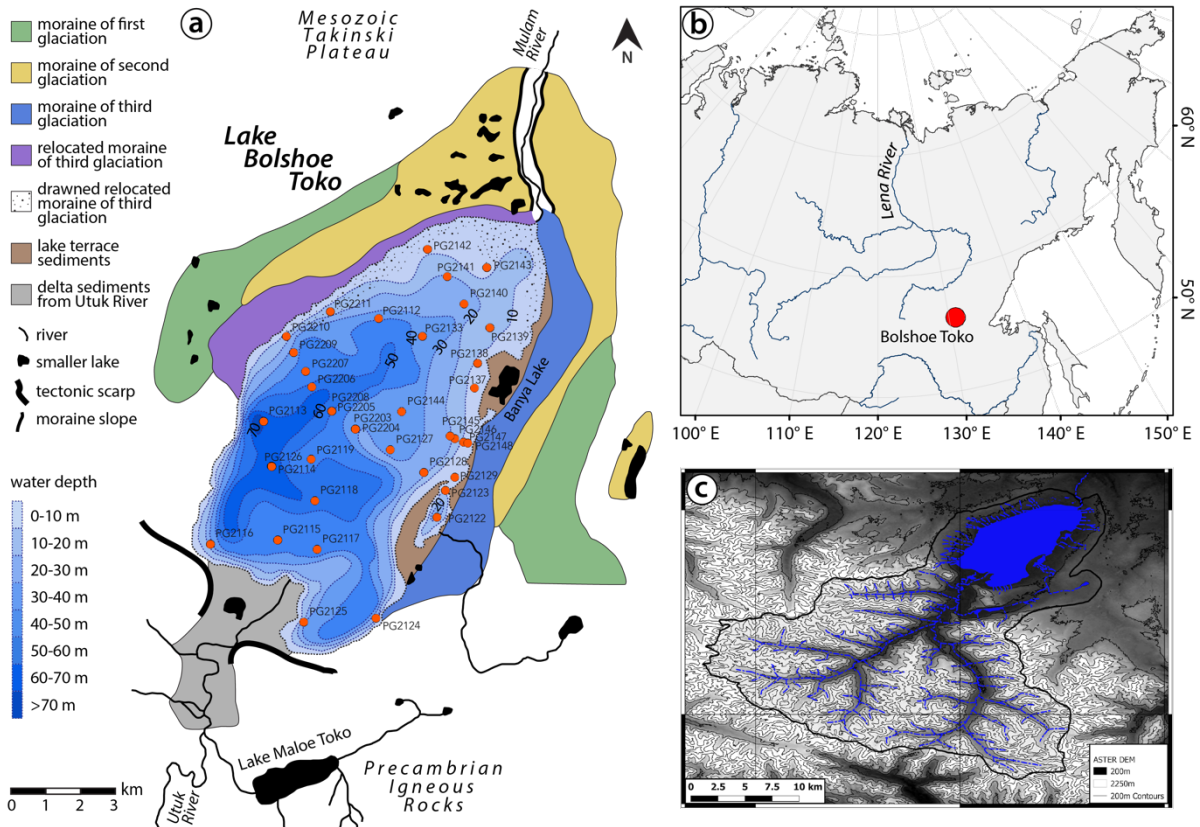
Fig. 1 Lake Bolshoe Toko study site. **a** Geological map, bathymetry and moraines. Map compiled using data from Konstantinov (2000) and Kornilov (1962). **b** Overview map of Siberia. World Borders data are derived from http://thematicmapping.org/downloads/world_borders.php and licensed under CC BY-SA 3.0. **c** Catchment area around Bolshoe Toko delineated from the ASTER GDEM V2 model between the latitudes N54° and N56° and longitudes E130° to E131° (1) (Meyer et al., 2011) and a corresponding multispectral Landsat 8 OLI TIRS satellite image using QGIS (QGIS-Team, 2016). Most of the river catchment is located in the igneous Precambrian Stanovoy mountain range supplying the southern part of the lake with water and sediment. The shallower northeastern part of the lake is influenced by the surrounding moraines and Mesozoic sand- and mudstones.

3   Materials and methods

3.1   Field work

Field work was conducted during the German-Russian expedition "Yakutia 2013" between March 19th to April 14th 2013 by the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research (AWI) and the North Eastern Federal State University in Yakutsk (NEFU). Vertical holes were drilled in the lake ice cover using a Jiffy ice auger with a diameter of 250 mm. Lake basin bathymetry was measured using a portable Echo Sounder. Ice cores were retrieved by drilling multiple holes around a central part. Water samples for hydrochemical analyses were collected prior to sediment coring using a UWITEC water sampler. Water samples were analysed in situ using a WTW Multilab 340i for pH, conductivity, and oxygen values at the day of retrieval during field work. A sub-sample of the original water was passed through a 0.45 μm cellulose-acetate filter, stored and transported in 60-ml Nalgene polyethylene

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bottles for subsequent anion and cation analyses in AWI laboratories in autumn 2013. Cation samples were acidified during field work with HNO_3, suprapure (65%) to prevent microbial conversion processes and adsorptive accretion.

At 42 sites within the lake, short cores containing intact sediment surface material were retrieved using an UWITEC gravity corer. Water depth at sampling sites was measured using either a hand-held HONDEX PS-7 LCD digital sounder and/or the cord of the coring device when the lake ice cover disturbed the signal. The sediment was identified as clayish silt deposits with predominant dark (black) color and a weak smell of hydrogen sulphide, a sticky and viscous mud mixed with plant and other organic residues. The uppermost ca. 2 cm at some sites had a dark red colouring indicating the redox boundary between oxygenated and anoxic sediments. We identified the uppermost 0.5 cm of short cores as surface sediments and subsampled these layers onsite during fieldwork to avoid sediment mixture during transport. Sediment samples were transported in sterile "Whirl-Pak" bags and sediment cores were transported in plastic liners to the AWI laboratories in Potsdam, Germany, and stored at 4°C in a dark room for further analyses and as back-up. During this expedition also long core material was retrieved from multiple sites including the northern and central part of the lake and is planned for publication in a separate manuscript.

According to the amount the uppermost 0-0.5 cm layer in the short cores available the sample size n for different sediment properties measured in this study vary.

3.2 Laboratory analyses

3.2.1 Hydrochemistry

Water depth profiles were taken during the March 2013 expedition from the deepest part of the lake (PG2208, water depth 70m) and in the lagoon (PG2122, 18 m) as well as in August 2012 (sample site near the western shoreline, 37 m). The temperature was determined in the field and the samples analysed for isotopes ($\delta^{18}O$, δD, see Fig. 6). From the water samples anions were analysed using ion chromatography (Dionex DX 320) and cations were determined using inductively coupled plasma–optical emission spectrometry (ICP-OES, Perkin-Elmer Optima 8300DV Perkin-Elmer – Optical Emission Spectrometer. Alkalinity was measured by titration with 0.01 M HCl using an automatic titrator (Metrohm 794 Basic Titrino).

Stable hydrogen and oxygen isotope analyses were carried out with Finnigan MAT Delta-S mass spectrometers with two equilibration units using common equilibration techniques (Meyer et al., 2000), and given as $\delta^{18}O$ and δD in ‰ vs. VSMOW (Vienna Standard Mean Ocean Water) with respective analytical errors of better than ±0.1% and 0.8‰. The secondary parameter d-excess (d) is calculated as d= δD-8 $\delta^{18}O$ (Dansgaard, 1964;Merlivat and Jouzel, 1979).

3.2.2 X-ray fluorescence and X-ray diffractometry

To gain information on the variability of the elemental sediment composition, 20 freeze-dried and milled surface samples were semi-quantitatively analysed by X-ray fluorescence (XRF) using a novel single sample modification for the AVAATECH XRF core scanner at AWI Bremerhaven. A Rhodium X-ray tube was warmed up to 1.75mA and 3 mA with a detector count time of 10s and 15s for elemental analysis at 10kV (No filter) and 30kV (Pd-Thin filter) respectively. The average modelled chi square values (χ^2) of measured peak intensity curve fitting for the relevant elements were variable, but generally low (Zr = 0.92, Mn = 1.49, Fe = 2.32, Ti = 1.53, Br = 3.65, Sr = 4.79, Rb = 4.98, Si = 16.11). Values above 3 were ascribed to suspiciously high count rates from sample PG2133 which was subsequently excluded from XRF interpretation. The relatively low amount of total sample material available did not facilitate the removal of organic matter prior to sample measurement and may have contributed to the variable modelled chi square values.

As interpretation of raw device obtained element intensities (in counts per second, cps) is problematic due to non-linear matrix effects and variations in sample density, water content and grain-size (Tjallingii et al., 2007), cps values were transformed using a centred-log ratio transformation (CLR). Element ratios were calculated from raw cps values and transformed using an additive-log ratio transformation (ALR) (Weltje and Tjallingii, 2008).

The mineralogical composition of 32 freeze-dried and milled samples was analysed by standard X-ray diffractometry (XRD) using a Philips PW1820 goniometer at AWI Bremerhaven applying Cobalt-Potassium alpha (CoKα) radiation (40 kV, 40 mA) as outlined in Petschick et al. (1996). The intensity of diffracted radiation was calculated as counts of peak areas using XRD processing software MacDiff 4.0.7 (freeware developed by R. Petschick in 1999). Individual mineral content was expressed as percentages of bulk sediment XRD counts (Voigt, 2009). Mineral inspection focused on quartz, plagioclase and K-feldspar, hornblende, mica, and pyrite. Clay minerals involved kaolinite, smectite and chlorite. Accuracy of the semi-quantitative XRD method is estimated to be between 5 and 10% (Gingele et al., 2001).

3.2.3 Grain-size, carbon and nitrogen analyses

In order to gain high-resolution information on the spatial variability of particle sizes and related water energy in the lake, we analysed the grain-size distribution using laser technique. Organic material was removed from 32 surface sediment samples by hydrogen peroxide oxidation over four weeks on a platform shaker. Two homogenised subsamples were weighted and 93 subclasses between 0.375 and 2000 µm were measured using a Coulter LS 200 Laser Diffraction Particle Analyser. Grain-size

fractions coarser than 2 mm were sieved out, weighted and added to the volume percentage data afterwards to indicate the proportion of gravel.

To assess the accumulation of organic matter in the lake, we analysed total carbon (TC) and total nitrogen (TN) of 35 freeze-dried and milled samples. For TC and TN we quantified bulk samples by heating the material in small tin capsules using a Vario EL III CNS analyser. Total organic carbon (TOC) was measured using a Vario MAX C in per cent by weight (wt%). The measurement accuracy was 0.1 wt% for TOC and TN, and 0.05 wt% for TC. TOC and TN were compared to calculate the TOC/TN_{atomic} ratio by multiplying with the ratio of atomic weights of nitrogen and carbon following Meyers and Teranes (2002).

To gain additional bioproductivity information we analysed the stable carbon isotope composition $\delta^{13}C$ of the total organic carbon fraction in 15 samples using a Finnigan Delta-S mass spectrometer. Dried, milled and carbonate-free (HCl treated) samples were combusted in tin capsules to CO_2. Results are expressed as $\delta^{13}C$ values relative to the PDB standard in parts per thousand (‰) with an error of ±0.15%.

Radiocarbon dating of two bulk sediment surface sample from short cores, each ranging from 0-0.5 cm depth below the sediment surface, was performed in the Poznan Radiocarbon Laboratory on the soluble (SOL) fraction using an Accelerator Mass Spectrometer.

3.2.4 Diatoms

23 samples were prepared for diatom analysis following the standard procedure (Battarbee et al. (2001). To calculate the diatom valve concentration (DVC) 5×10^6 microspheres were added to each sample following organic removal with hydrogen peroxide. Diatom slides were prepared on a hot plate using Naphrax mounting medium. For the identification of diatoms to the lowest possible taxonomic level we used several diatom flora including Lange-Bertalot et al. (2011), Lange-Bertalot and Metzeltin (1996), Krammer and Lange-Bertalot (1986-1991) and Lange-Bertalot and Genkal (1999). For rare taxa (i.e. *Pliocaenicus*) literature research was applied in scientific papers, including Cremer and Van de Vijver (2006) and Genkal et al. (2018). A minimum of 300 (and up to 400) diatom valves were counted in each sample using a Zeiss AXIO Scope.A1 light microscope with a Plan-Apochromat 100×/1.4 Oil Ph3 objective at 1000x magnification. Identification of small diatom species was verified using a scanning electron microscope (SEM) at the GeoForschungsZentrum Potsdam.
During counting of diatom valves, chrysophycean stomatocysts and *Mallomonas* were counted but not further taxonomically identified. Count numbers were used to estimate the chrysophyte cyst to diatom index (C:D) and *Mallomonas* to diatom index (M:D) relative to counted diatom cells (Smol, 1984;Smol and Boucherle, 1985).

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366 Diatom valve preservation was measured and calculated as the f-index (Ryves et al.,
367 2001). Diatom valve concentration was estimated as the number of valves per gram
368 dry sediment following Battarbee and Kneen (1982).
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3.2.5 Oxygen isotopes of diatom silica

371 To analyze the oxygen isotope composition from diatom silica ($\delta^{18}O_{diatom}$) from 9
372 representative surface samples, a purification procedure including wet chemistry (to
373 remove organic matter and carbonates) and heavy liquid separation was applied for
374 the fraction <10 μm following the method described in Chaplligin et al. (2012a). After
375 freeze-drying the samples were treated with H_2O_2 (32%) and HCl (10%) to remove
376 organic matter and carbonates and wet sieved into <10 μm and >10 μm fractions.
377 Four multiple heavy liquid separation (HLS) steps with varying densities (from 2.25 to
378 2.15 g/cm3) were then applied using a sodium polytungstate (SPT) solution before
379 being exposed to a mixture of $HClO_4$ (65%) and HNO_3 (65%) for removing any
380 remaining micro-organics.

381 To remove exchangeable hydrous groups from the diatom valve structure
382 (amorphous silica $SiO_2 * nH_2O$), inert Gas Flow Dehydration was performed
383 (Chaplligin et al., 2010). Oxygen isotope analyses were performed on dehydrated
384 samples using laser fluorination technique (with BrF_5 as reagent to liberate O_2) and
385 then directly measured against an oxygen reference of known isotopic composition
386 using a PDZ Europa 2020 mass spectrometer (MS2020, now supplied by Sercon Ltd.,
387 UK). The long-term analytical reproducibility (1σ) is ±0.25 ‰ (Chaplligin et al., 2010).

388 Every fifth sample was a biogenic working standard to verify the quality of the
389 analyses. For this, the biogenic working standard BFC calibrated within an inter-
390 laboratory comparison was used (Chaplligin, 2011). With a $\delta^{18}O$ value of +29.0±0.3
391 ‰ (1σ) BFC (this study: +28.7±0.17 ‰, n=49) is the closest diatom working standard
392 to the Bolshoe Toko samples ($\delta^{18}O$ values range between +22 and +24 ‰) available.
393 A contamination correction was applied to $\delta^{18}O_{diatom}$ using a geochemical mass-
394 balance approach (Chaplligin et al., 2012a;Swann et al., 2007) determining the
395 contamination end-member by analysing the heavy fractions after the first heavy liquid
396 separation resulting in Al_2O_3=16.2±1.3 % (via EDX; n=9) and $\delta^{18}O$=8.5±0.8 ‰ (n=6).

3.2.6 Chironomids

398 Treatment of 18 sediment samples for chironomid analysis followed standard
399 techniques described in Brooks et al. (2007). Subsamples of wet sediments were
400 deflocculated in 10 % KOH, heated to 70 °C for up to 10 minutes, to which boiling
401 water was added and left to stand for up to another 20 minutes. The sediment was
402 passed through stacked 225 and 90 μm sieves. Chironomid larval head capsules
403 were picked out of a grooved Bogorov sorting tray under a stereomicroscope at 25-

404　40x magnifications and were mounted in Hydromatrix two at a time, ventral side up,
405　under a 6 mm diameter cover slip. From 48 to 117 chironomid larval head capsules
406　were extracted from each sample, to capture the maximum diversity of the chironomid
407　population. Chironomids were identified to the highest taxonomic resolution possible
408　with reference to Wiederholm (1983) and Brooks et al. (2007). Information on the
409　ecology of chironomid taxa and groups was taken from Brooks et al. (2007), Pillot
410　(2009) and Nazarova et al., (2011;2015;2008;2017b)). Ecological information of the
411　taxa associated to biotopes (littoral, profundal), water velocity (standing, running
412　water), and relation to presence of macrophytes were taken from Brooks et al. (2007)
413　and Pillot (2009). T July optima of chironomids were taken from Far East (FE)
414　chironomid-based temperature inference model (Nazarova et al., 2015). The Far East
415　(FE) chironomid-based temperature inference model (WA-PLS, 2 components; r^2
416　boot = 0.81; RMSEP boot = 1.43 °C) was established from a modern calibration data
417　set of 88 lakes and 135 taxa from the Russian Far East (53–75°N, 141–163°E, T July
418　range 1.8 – 13.3 °C). Mean July air temperature for the lakes from the calibration data
419　set was derived from New et al. (2002). All modern and chironomid-inferred
420　temperatures were corrected to 0 m.a.s.l. using a modern July air temperature lapse
421　rate of 6 °C km^{-1} (Livingstone et al., 1999;Heiri et al., 2014).

422　## 3.3　Statistical analyses

423　Detrended Correspondence Analysis (DCA) with detrending by segments was
424　performed on the chironomid and diatom data (rare taxa downweighted) to determine
425　the lengths of the sampled environmental gradients, from which we decided whether
426　unimodal or linear statistical techniques would be the most appropriate for the data
427　analysis (Birks, 1995). For diatom data the gradient lengths of the species scores
428　were 2.07 and 1.49 standard deviation units (SDU) for DCA 1 and 2, respectively,
429　suggesting that lineal numerical methods should be used. A Principal Component
430　Analysis (PCA) was used to explore the main taxonomic variation of the data (ter
431　Braak and Prentice, 1988). The gradient lengths of chironomid species scores were
432　3.78 and 4.12 SDU indicating that numerical methods based on a unimodal response
433　model should be more appropriate to assess the variation structure of the chironomid
434　assemblages (ter Braak, 1995). However, test PCA performed on chironomid data
435　showed that lineal method captures more variance of species data (ESM, Table 2)
436　therefore we further applied lineal methods for both, chironomid and diatom data. In
437　order to summarize the response of lacustrine biota to abiotic, physicochemical
438　explanatory variables, a redundancy analysis (RDA) was performed on diatom and
439　chironomid data in comparison to environmental variables (Fig. 2 and 3).
440　Initially, all environmental variables shown in this paper were tested in a RDA to
441　assess the relationships between the distribution of bioindicator taxa and abiotic
442　habitat parameters. Apart from the chemical and physical parameters of the lake and

443 sediments (Fig. 5), we include in the analysis the presence/absence of the submerged
444 vegetation, distances of the sampling stations from the shore and from the inflowing
445 rivers. All explanatory variables were tested for normality prior to the analyses.
446 Skewness reflects the degree of asymmetry of a distribution around its mean. Normal
447 distributions produce a skewness statistic of about zero. Values that exceeded 2
448 standard errors of skewness were identified as significantly skewed (Sokal and Rohlf,
449 1995). Environmental variables with skewed distributions (gravel, grain-size EM2,
450 smectite-chlorite, mica, K-feldspar) were log transformed and remaining parameters
451 were left untransformed. To reveal intercorrelated parameters, we performed a
452 variance inflation factor (VIF) analysis prior to ordination techniques to only retain
453 non-correlated parameters in further multivariate analysis. Environmental variables
454 with a VIF greater than 20 were eliminated, beginning with the variable with the largest
455 inflation factor, until all remaining variables had values < 20 (ter Braak and Smilauer,
456 2012). A set of RDAs was performed on chironomid and diatom data with each
457 environmental variable as the sole constraining variable. The percentage of the
458 variance explained by each variable was calculated and statistical significance of
459 each variable was tested by a Monte Carlo permutation test with 999 unrestricted
460 permutations. Significant variables (P≤ 0.05) were retained for further analysis. DCA,
461 PCA and RDA were performed using CANOCO 5.04 (ter Braak and Smilauer, 2012).
462   Percentage abundances of the chironomid taxa that are absent or rare in the
463 modern calibration data set were calculated at each sampling site in order to see the
464 distribution of the taxa that could potentially hamper a T July reconstruction in case
465 of palaeoclimatic study that could be done at each of the sampling sites. It is known
466 that less reliability should be placed on the samples in which more than 5% of the
467 taxa are not represented in the modern calibration data or more than 5% of the taxa
468 are rare in the modern calibration dataset (i.e., if the effective number of occurrences
469 in the training set, the Hill's N2, is less than 5) (Heiri and Lotter, 2001;Hill, 1973;Self
470 et al., 2011).
471   Species richness and the Simpson diversity on diatom and chironomid data were
472 estimated after sample-size normalization using a rarefaction analysis of Hill numbers
473 in the iNEXT package in R.
474   To assess the relative contribution of different sedimentary processes to the bulk
475 sediment, such as fluvial or aeolian transport (Wang et al., 2015;Biskaborn et al.,
476 2013b) a statistical end-member analysis on grain-size data was performed using the
477 MATLAB modelling algorithm of Dietze et al. (2012). In this method, individual grain-
478 size populations identified as end-member loadings (vol%, Fig. 4) as well as their
479 contributions to the bulk composition identified as scores (%) were derived by
480 eigenspace analysis, weight transformation, varimax rotations and different scaling
481 procedures.

482   A Pearson correlation matrix of the main important variables (Fig. 5a) was
483 calculated using the basic R core (R Core Team, 2012) and plotted using *corrplot*. To
484 keep false discovery rate below 5% a p-value adjustment was applied prior to
485 assignment of colours using only values that revealed $p < 0.001$ (Colquhoun, 2014).
486 To identify the pattern, the correlation matrix was reordered according to the
487 correlation coefficient. Exceptional sites within the heterogenic lake system lead to
488 disturbance of good correlation coefficients within areas along natural borders, e.g.
489 water depth isobaths. Spatial autocorrelation of variables was estimated using
490 latitudes and longitudes recorded of each sample site and displayed as p values
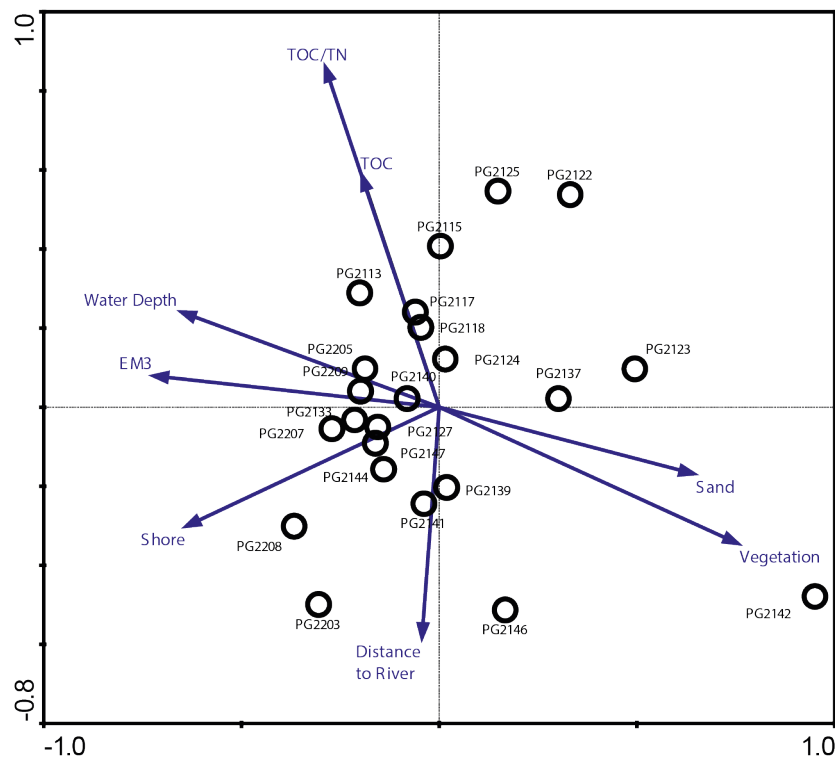491 generated by Moran's Autocorrelation Coefficient (R package "ape").
492   To guarantee the sustained availability of our research (Elger et al., 2016), the data
493 will be uploaded and freely accessible in the PANGAEA repository.
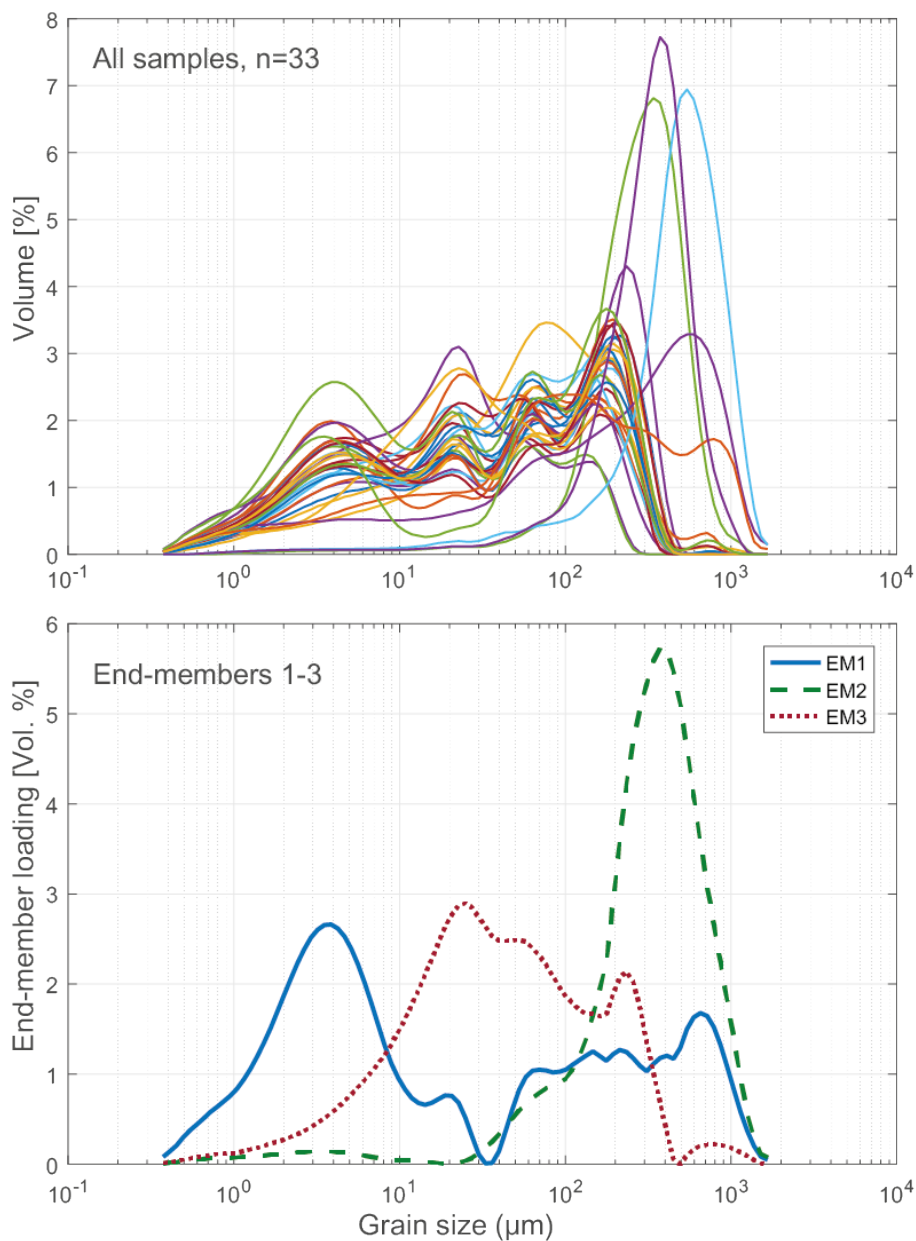494

a. RDA, diatom species scores
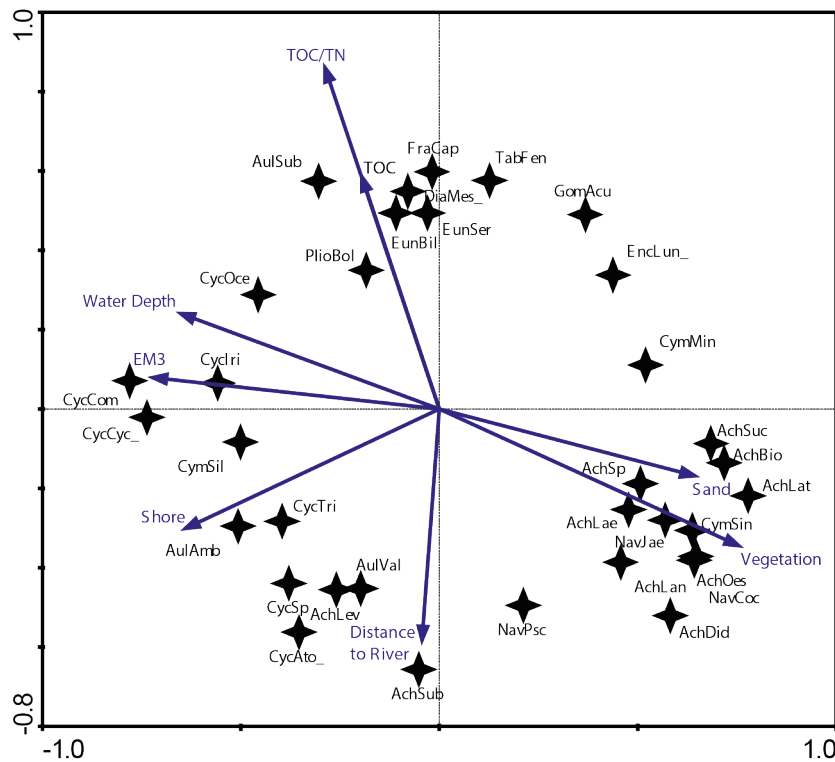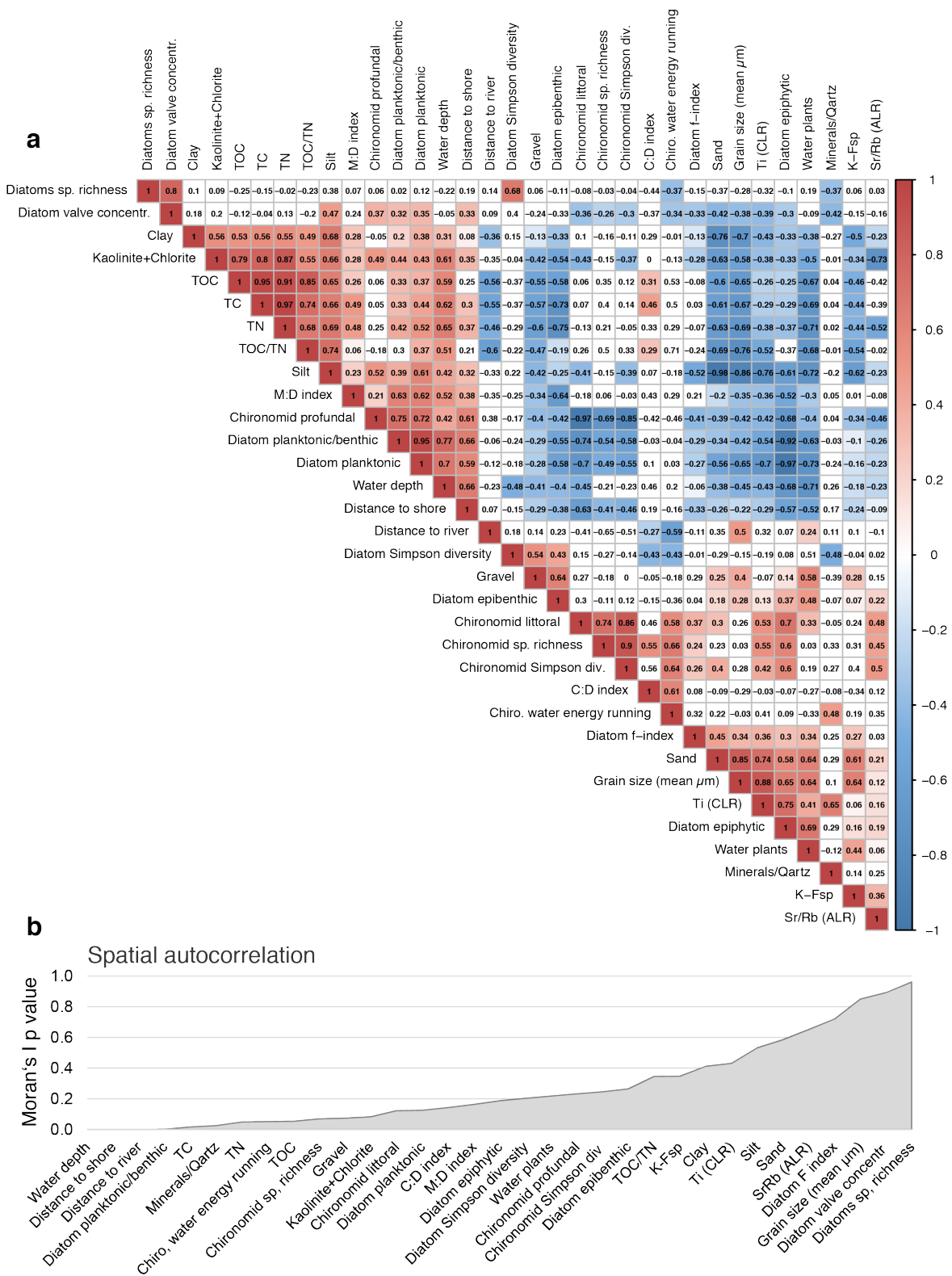

b. RDA, diatom samples scores

495
496 **Fig. 2** RDA biplots of diatoms in the surface sediments of Lake Bolshoe Toko. (a) Common diatom taxa and
497 significant environmental variables. (b) Diatom sampling sites and significant environmental variables. Abbreviated
498 species names: AchBio - *Psammothidium bioretti*; AchDid - *Achnanthes* cf. *didyma*; AchHel - *Psammothidium*
499 *helveticum*; AchLae - *Eucocconeis laevis*; AchLan - *Planothidium lanceolata*; AchLat - *Karayevia laterostrata*;
500 AchLev - *Psammothidium levanderi*; AchOes - *Planothidium oestrupii*; AchSp - *Achnanthes* sp.; AchSub -

15

501 *Psammothidium subatomoides*; AchSuc - *Karayevia suchlandtii*; AmpPed - *Amphora pediculus*; AulAmb -
502 *Aulacoseira ambigua*; AulSub - *Aulacoseira subarctica*; AulVal - *Aulacoseira valida*; CocPla - *Cocconeis*
503 *placentula*; CycAto_ - *Cyclotella* cf. *atomus*; CycCom - *Cyclotella comensis*; CycCyc_ - *Cyclotella cyclopuncta*;
504 CycIri - *Cyclotella iris*; CycSp - *Cyclotella comensis-tripartita*-complex; CymMin - *Encyonema minutum*; CymSin -
505 *Cymbella sinuata*; DiaMes_ - *Diatoma mesodon*; EncLun_ - *Encyonema lunatum*; FraCap - *Fragilaria capucina*;
506 FraConVe - *Staurosira venter*; FraPin - *Fragilaria pinnata*; GomAcu - *Gomphonema acuminatum*; GomIns -
507 *Gomphonema insigne*; HipCos - *Hippodonta costulata*; NavCoc - *Cavinula cocconeiformis*; NavJae - *Cavinula*
508 *jaernefeltii*; NavPsc - *Cavinula pseudoscutiformis*; NitSp - *Nitzschia* sp.; PlioBol – *Pliocaenicus bolshetokoensis*;
509 StaCon_ - *Staurosira construens*.
510
511
512
513

a. RDA, chironomid species scores

b. RDA, chironomid samples scores

514
515 **Fig. 3** RDA biplots of chironomids in the surface sediments of Lake Bolshoe Toko. (a) Common chironomid taxa
516 and significant environmental variables. (b) Chironomid sampling sites and significant environmental variables.
517 Abbreviated species names: ChaetPi - *Chaetocladius piger*-type; ChirLar - *Chironomini larvula*; CladMan -
518 *Cladotanytarsus mancus*-type; Cory arc - *Corynoneura arctica*-type; CoryCor - *Corynoneura coronata*-type; Cricbi
519 - *Cricotopus bicinctus*-type; CricInt - *Cricotopus intersectus*-type; CricoP - *Cricotopus* type P; Cryptoch -
520 *Cryptochironomus*; DIamesi - *Diamesa* sp.; Eukiefe - *Eukiefferiella*; EukiCla - *Eukiefferiella claripennis*-type;

17

Fig. 4 Endmember analysis grain-size distributions in 33 samples from Lake Bolshoe Toko.

Fig. 5 Correlation matrix of selected environmental parameters. a. Pearson correlation. Positive correlations indicated in red, negative correlations indicated in blue. To keep false discovery rate below 5%, only p values of <0.001 were used to assign colours (Colquhoun, 2014). b. Spatial autocorrelation associated to coordinates of sample sites. Shown as p values generated by Moran's Autocorrelation Coefficient (R package "ape").

543

4 Results

4.1 Water chemistry

Sampled surface waters of Bolshoe Toko (Table 1, ESM) were well saturated in O_2 (101-113 %) with a pH-values in the neutral range (6.8 – 7.2). Electrical conductivity was very low for all waters (35.1-39.1 μS/cm), with slightly higher levels in the lagoon (67.8 μS/cm). Traces of Al (mean 72 μg/L), Fe (mean 46.6 μg/L), and Sr (mean 37.1 μg/L) were present but there is no evidence of Pb, Cr, V, Co, Ni, Cu. Mean sulfate concentrations (SO_4^{2-}) was 2.35 mg/l on average, with lower values in the lagoon (0.51 mg/l). The concentrations of nitrate (NO_3^-) was 0.76 mg/l, but lower in the lagoon (0.29 mg/l). HCO_3^- was 37.5 mg/l in the lagoon and 14.9 mg/l on average in the remaining samples. There was no phosphorus in any sample. Overall the water can be characterized as water of the Ca-Mg-HCO_3^- type.

Surface waters were characterized by mean isotope values of –18.7‰, –140.2‰ and 9.5‰ for $\delta^{18}O$, δD and d-excess, respectively (n=6). The isotopic composition was relatively uniform in the main lake basin ($\delta^{18}O$ = –18.58±0.15‰, δD = –139±0.7‰), while the lagoon (PG2122) exhibited slightly lower $\delta^{18}O$ (δD) values of –19.2‰ (–145‰) (Fig. 6).

In March 2013 isotope-depth profiles at PG2208 exhibited a slight isotopic enrichment trend from the surface to ~5 m-depth (~+0.35 ‰ for $\delta^{18}O$), with a relatively uniform isotopic composition ($\delta^{18}O$ = –18.2 ± 0.2 ‰) below 10 m (Fig. 6a). These subtle variations likely reflect minor isotopic fractionation of surface waters during ice formation in spring, and a well-mixed water column below. Conversely, the August 2012 depth profile at the Western Shoreline exhibited a gradual depleting isotope trend below ~6 m depth, with marked variability that closely tracks water temperature changes (Fig. 6a). Meteorological data from the nearby weather station (Toko RS, 10 km northward) recorded heavy rainfall for August 2012 (25 mm above the long term mean of 83 mm). Such precipitation events could cause temporary isotopic stratification or a variation in the isotopic signal throughout the water column. Due to ongoing mixing, these variations were then evened. In conclusion, variations in the isotopic composition throughout the August profile rather represent a temporal phenomenon and not characteristic for Bolshoe Toko. In contrast, the lagoon showed a lighter isotope composition ($\delta^{18}O$ = –18.9 ± 0.2 ‰) than the main lake basin. All samples were positioned close to the Global Meteoric Water Line (GMWL, Fig. 6) indicating negligible evaporative effects on lake water isotope composition, and a dominant influence of meteoric inputs both directly (i.e., precipitation) and indirectly (i.e., river inflows). The Local Meteoric Water Line for Yakutsk (dashed line; δD = 7.59 * $\delta^{18}O$ – 6.8), based on own data (monthly mean precipitation values between 1997

581 and 2006; n=106; from Kloss (2008), is given for comparison, and indicative for more
582 continental climate conditions.
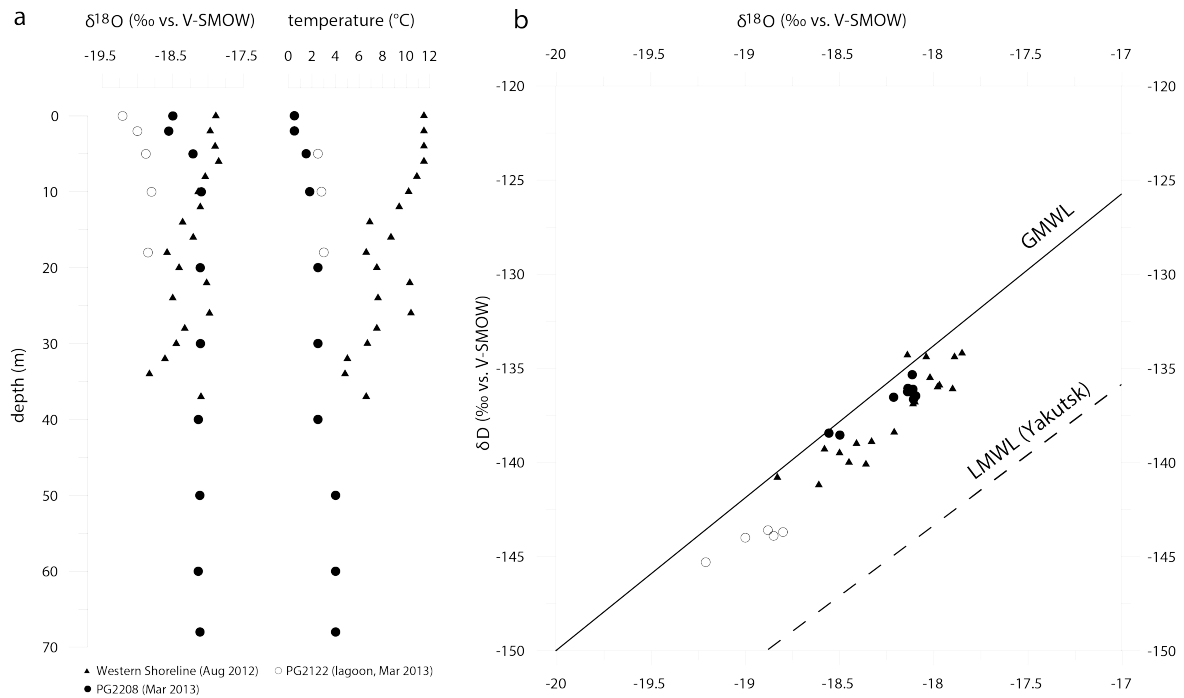
583
584
585 **Fig. 6**: Hydrochemical situation between 2012 and 2013 in lake Bolshoe Toko. a. Profiles of water isotopes ($\delta^{18}O$)
586 and temperature from different locations taken in August 2012 and March 2013. b. $\delta^{18}O/\delta D$ diagram for Bolshoe
587 Toko lake water samples. GMWL is the Global Meteoric Water Line (black line), LMWL is the Local Meteoric Water
588 Line for Yakutsk (dashed line; $\delta D = 7.59 * \delta^{18}O - 6.8$) based on own data (monthly mean precipitation values
589 between 1997 and 2006; n=106; Kloss (2008)).
590

4.2 Physicochemical sediment composition

592 The typical surficial lake bottom sediments consisted of either brown organic-
593 enriched gyttja or sandy, organic-poor siliciclastic material. Sand contents ranged
594 between 10.2 % and 96.2 % (mean 45.9 %, Fig. 7); silt contents ranged from 3.6 %
595 to 83.3 % (mean 47.1 %); clay contents ranged from 0.2 % to 11.3 % (mean 5.8 %).
596 Gravel was found only in four samples at the north eastern near-shore areas with
597 contents of up to 13.1 %. The mean grain size ranged from 12 to 479 μm (mean 72
598 μm). The mean grain size generally correlated negatively with water depth (r -0.45).
599 Mineral grains are composed mainly of quartz (32.7-76.2 %, mean 55.4 %),
600 plagioclase (13.4-39.5 %, mean 26.2 %), K-feldspar (0.0-9.8 %, mean 5.6 %), and, to
601 a smaller degree of pyrite (0.2-5.5 %, mean 3.3 %), hornblende (0.5-10.8 %, mean
602 3.1 %), mica (0.3-2.4 %, mean 1.1 %), and the clay minerals smectite, kaolinite and
603 chlorite (together 0.0-4.6 %, mean 2.0 %). The spatial distribution of minerals (Fig. 7)
604 revealed a generally decreasing gradient of minerals relative to quartz starting from
605 the Utuk river delta (proximal) towards the northern areas (distal).

The CLR transformed XRF data (Fig. 8) revealed high proportions of Zr and intermediate to high Ti near the Utuk river inflow and at the northern and eastern shore proximal areas. Zr values decreased with increasing water depth towards the lake centre with the exception of the shallow lagoon, where low values were observed. Mn values were highest in the lake centre and at the very deep site at the western steep subaquatic slope, and intermediate at shallow areas close to the shore. A minimum in Mn was found in the lagoon. Fe tends to be highest in the southern part of the lake basin, in the very shallow site in the north, and in the lagoon. Br showed a variable distribution; however, high values were found at 2 sites within the eastern lagoon and correspond to high TOC contents.

Additive log ratios (ALR) of Mn/Fe were variable with intermediate values found at sites surrounding the Utuk river inflow and low values within the lagoon and at basin central sites. High values were located at the deepest lake site as well as in the shallow north eastern region. Both Sr/Rb and Zr/Rb ratios showed high values directly in front of the Utuk river inflow, and decreased with distance toward the basin center. Both Sr/Rb and Zr/Rb exhibited intermediate to high values in the north eastern lake region and lower values in the lagoon. Si/Ti ratio values demonstrated an increasing trend from the southern lake region and lagoon to the northern lake region.

The contents of total organic carbon (TOC, Fig. 9) range from 0.1 % to 12.3 % (mean 4.9 %). Maximum values occured in the eastern area, intermediate values in the central basin, and lowest in the northern shallow water areas. The difference between TOC and total carbon is within the error of the devices and hence no inorganic carbon was detected. TOC contents and the TOC/TN ratios were highest near the Utuk river inflow in the southern part of the lake, in the lagoon, and in proximity to the eastern shoreline. $\delta^{13}C$ was measured in 15 samples and showed maximum values at the eastern shore (-25.7 ‰) and minimum values elsewhere (-27.8 ‰).

Radiocarbon dating of surface sample at site PG2139 (0-0.5 cm) indicated an age of 720 ± 30 ^{14}C yrs BP (Lab-ID: Poz-105350, NaOH-SOL), while PG2207 (0-0.5 cm) suggested 1790 ± 130 ^{14}C yrs BP (Lab-ID: Poz-105355, NaOH-SOL. Considering that the carbon concentration dissolved in sample PG2207 was too low (0.03 mgC), we use sample PG2139 as an estimated reservoir effect to the lake caused by the input of old carbon. Given that a hypothetical sediment surface is just a momentum only collectable as a range of past surfaces and there was more time available for radioactive decay at 0.5 cm depth than at 0 cm, the actual reservoir effect will be a little bit lower and should be confirmed by ^{210}Pb and ^{137}Cs measurements of downcore material before establishing an age depth model for sediment cores.
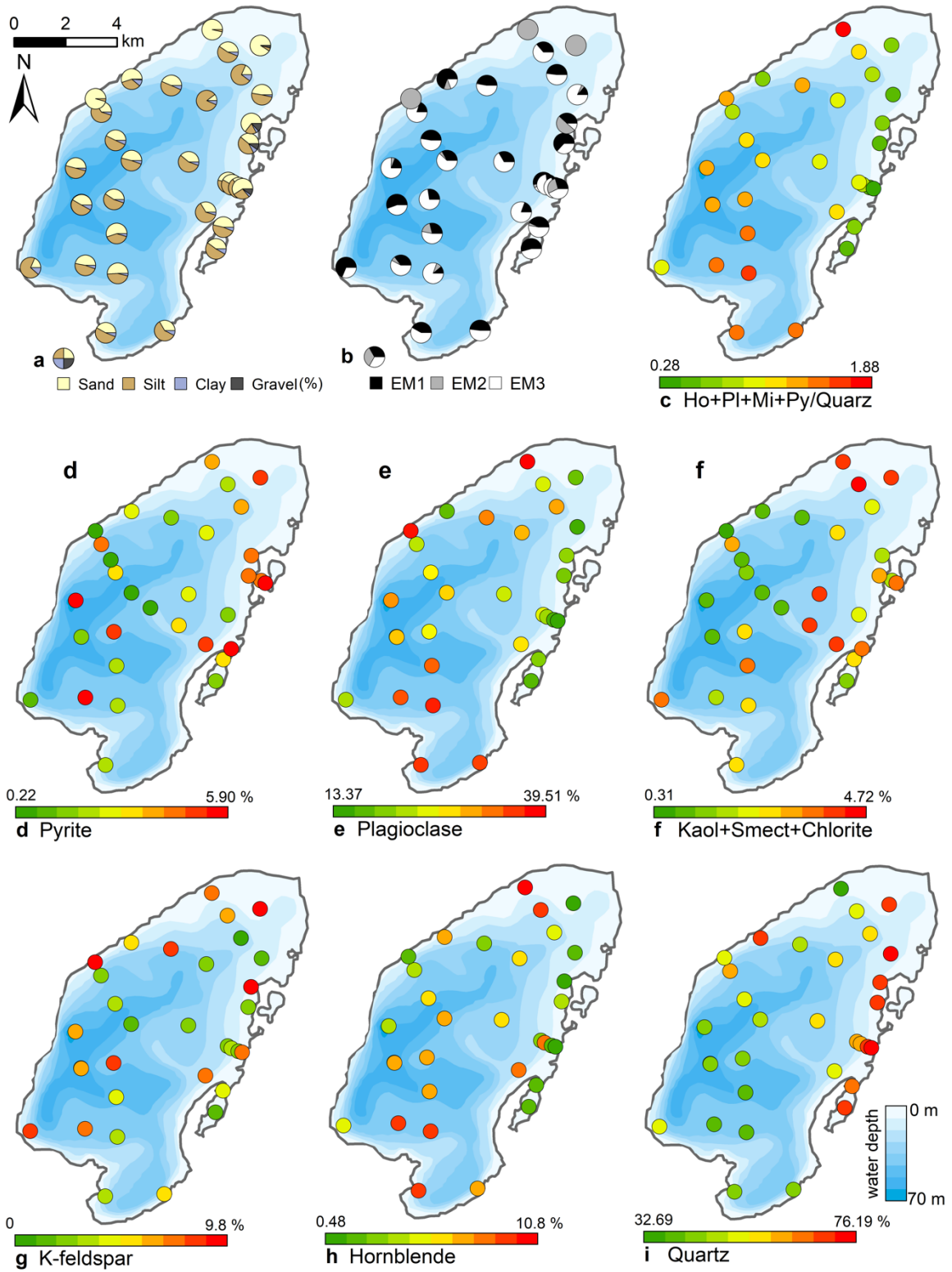
643
644 **Fig. 7** Spatial distribution of the grain-size and mineral compositions of the surface sediments of Lake Bolshoe
645 Toko. Maps compiled in ArcGIS 10.4. Scales chosen as 10 classes with equal intervals.
646
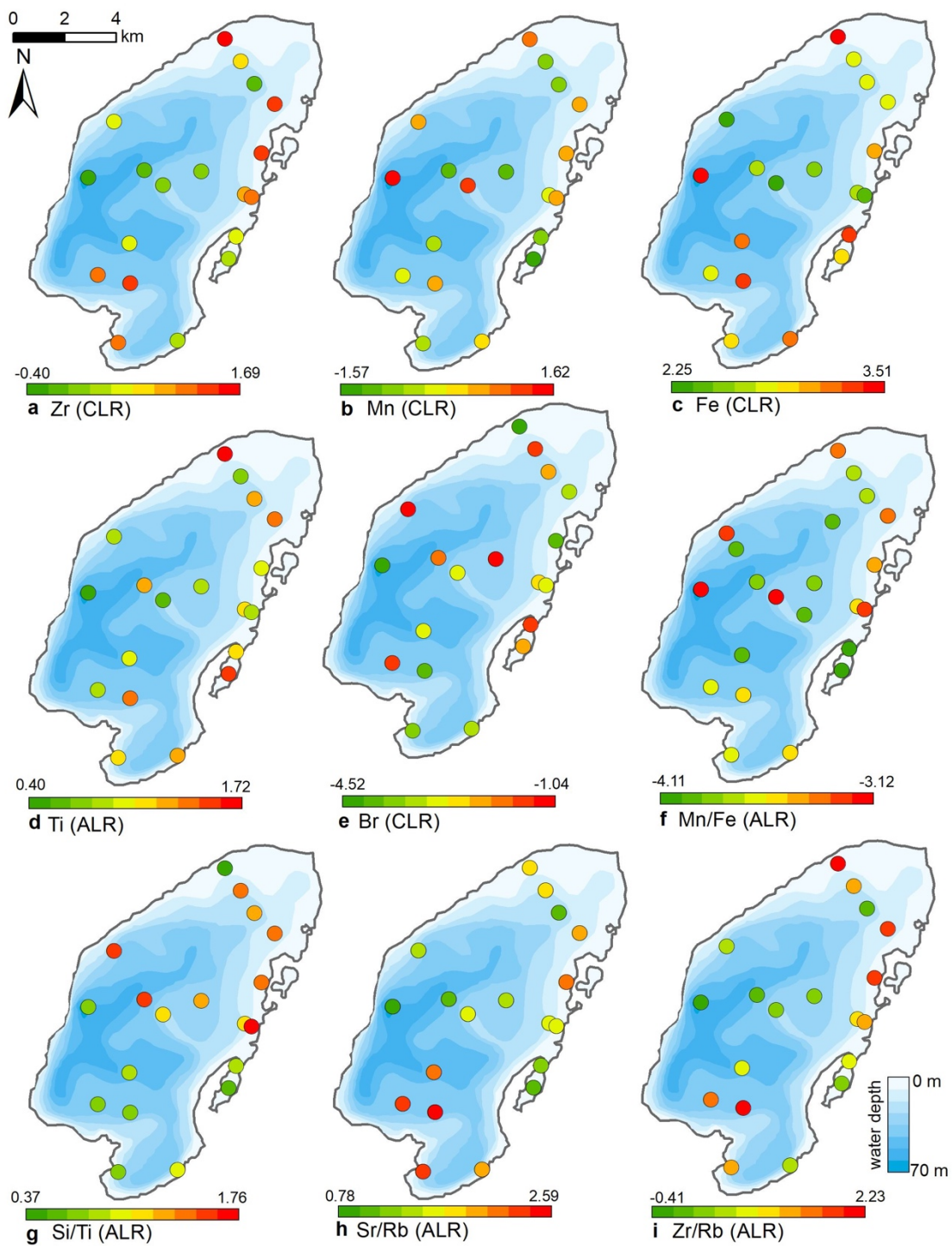
647
648 **Fig. 8** Spatial distribution of elements obtained from XRF measurements of surface sediments of Lake Bolshoe
649 Toko. Maps compiled in ArcGIS 10.4. Scales chosen as 10 classes with equal intervals.
650

4.3 Diatoms

The Bolshoe Toko diatom assemblages were characterized by boreal and arcto-alpine types, and exhibited distinct spatial variations across the lake. In total, 142 different diatom taxa were found at 23 sites, dominated by planktonic species *Pliocaenicus bolshetokoensis (Genkal et al., 2018)* (0.0-27.9 %, mean 14.7 %), *Cyclotella comensis* (0.0-23.1 %, mean 10.9 %), and benthic species *Achnanthidium minutissimum* (0.0-38.0 %, mean 11.8 %). The relative content of planktonic species (Fig. 9) was 2.0-73.7 % (mean 54.2 %), epiphytic species 19.2-83.9 % (mean 36.4 %), and epibenthic species 2.6-23.0 % (mean 9.3 %). The spatial distribution of the main taxa are presented in Fig. 10. Small benthic fragilarioid species were represented by 0.0-27.6 % (mean 7.4 %), Naviculoid species ranged from 3.3 % to 12.9 % (mean 7.2 %), and *Aulacoseira* species ranged from 0.0 % to 10.8 % (mean 4.5 %). *Pliocaenicus bolshetokoensis* maximum abundance occured in areas of deepest water such as the southern part of the lake and in the eastern lagoon. *Cyclotella* species were more abundant in the central lake and were not as strictly bound to water depth as *Pliocaenicus*. *Aulacoseira* species displayed no clear spatial pattern, though were less abundant in the northern shallow water areas. *Tabellaria* species were more abundant in shallow near-shore areas than in central and deep-water areas.

Achnanthoid (monoraphid) species were most abundant in near-shore areas, especially near the eastern lake terrace. Fragilarioid (araphid) species were common in the southernmost part near the inflow, as well as the lagoon. Other benthic species, i.e. *Navicula*, *Cymbella*, and *Eunotia* were generally more abundant in shallow near-shore areas than in deeper water areas.

In pelagic areas planktonic diatoms were generally more abundant than epiphytic and epibenthic species. Epiphytic species, however, predominated in some shallow areas in the north and east parts of the lake. Epibenthic species occurred in smaller abundancies in shallow lake littorals. Together with an increased amount of non-planktonic species, the Simpson diatom species diversity was higher in northern and eastern parts of the lake. The chrysophyte index was high near the river inflow in the south and along the river-like bathymetrical structure, as well as the lagoon where another small river inflowed into the lake. The *Mallomonas* index, reported for high nutrients and low pH (Smol et al., 1984), was highest near the inflow and in the central part, and lowest at near-shore areas in the north and east. The maximum f-index value, representing the highest valve preservation, was found in the near shore areas, whereas lower values were found at the shallow bathymetrical structure in the central part of the lake. Maximum valve concentrations were observed in the central and northern lake basin.

The initial RDA with all environmental variables indicated that axes 1 and 2 explain 39.6 % of variance in diatom species data. After deleting all intercorrelated

691 variables, 13 parameters with VIFs <20 were left for manual selection with Monte-
692 Carlo test. The analysis revealed 8 statistically significant (p≤0.05) explanatory
693 variables: TOC/TN, TOC, water depth, distance from River, distance from the shore,
694 presence of vegetation, sand, and EM3, (ESM diatoms, Fig. 2). Eigenvalues for RDA
695 axes 1 and 2 constrained by eight significant environmental variables constitute 81%
696 and 59%, respectively, of the initial RDA, suggesting that the selected significant
697 variables explain the major variance in the diatoms data. The RDA biplots of the
698 species scores and sample scores (Fig. 2) show that diatom species and sites are
699 grouped according to the main environmental forcing responsible for their spatial
700 distribution. The clearest environmental signals in the RDA are related to water depth,
701 habitat preferences and river influence. The upper left quarter of the biplot is strongly
702 influenced by water depth, grain size (EM3), and the ratio between TOC and TN. The
703 species found next to water depth are planktonic *Cyclotella* taxa, whereas *Aulacoseira*
704 is closer to TOC/TN and the total carbon content. In the lower right quarter epiphytic
705 and benthic taxa prevail, i.e. achnanthoid, naviculoid and cymbelloid taxa, associated
706 to the presence of vegetation and coarser (sand) substrate conditions. The distances
707 to river and to shore are crossing the lower left quarter and are associated to different
708 planktonic *Cyclotella* and achnanthoid taxa, while in the opposite direction, with
709 increasing Utuk river influence, fragilarioid taxa, *Eunotia, Tabellaria, and*
710 *Gomophonema* prevail, next to the high influence of TOC/TN.

711   Mean surface sediment $\delta^{18}O_{diatom}$ was 22.8 ‰ (min. 21.9 ‰, max. 23.6 ‰, n=9,
712 Fig. 9) with a standard deviation of ± 0.6 ‰ (1σ). The spatial distribution indicated
713 higher values ~23.3 ‰ in the deeper south-western part of lake (PG2113, 2115, 2005)
714 and lower values ~22.3 ‰ in the shallower northern lake basin (PG2139, 2140, 2147,
715 2209). The two samples from the lagoon exhibited values of 22.2 ‰ in the shallower
716 northern area and 23.6 ‰ in the deeper part. Four samples from the southern part
717 could not be purified well enough and had contamination corrections >2 ‰.
718
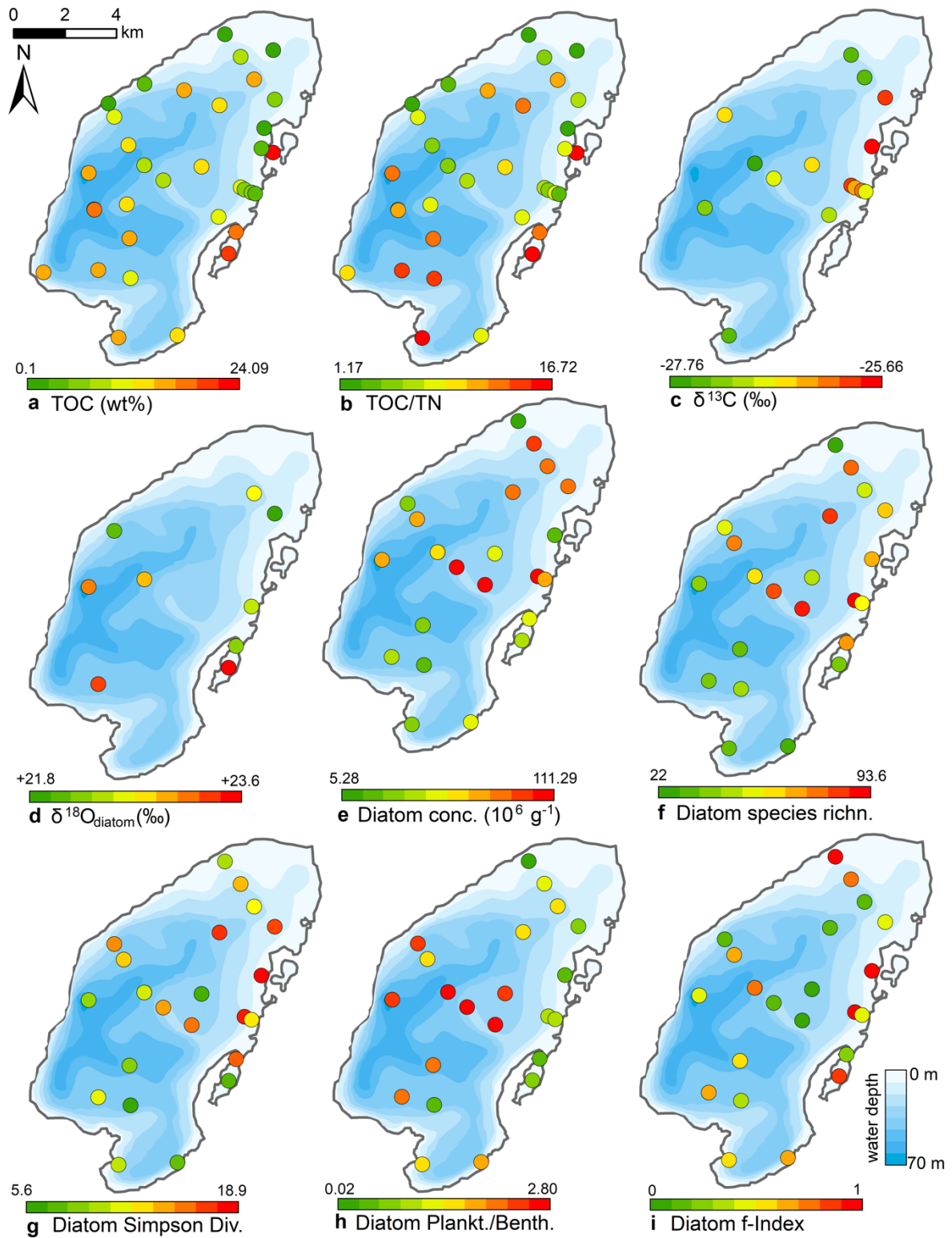
719
720 **Fig. 9** Spatial distribution of organic properties and statistical parameters inferred from diatom assemblages in the
721 surface sediments of Lake Bolshoe Toko. Maps compiled in ArcGIS 10.4. Scales chosen as 10 classes with equal
722 intervals.
723
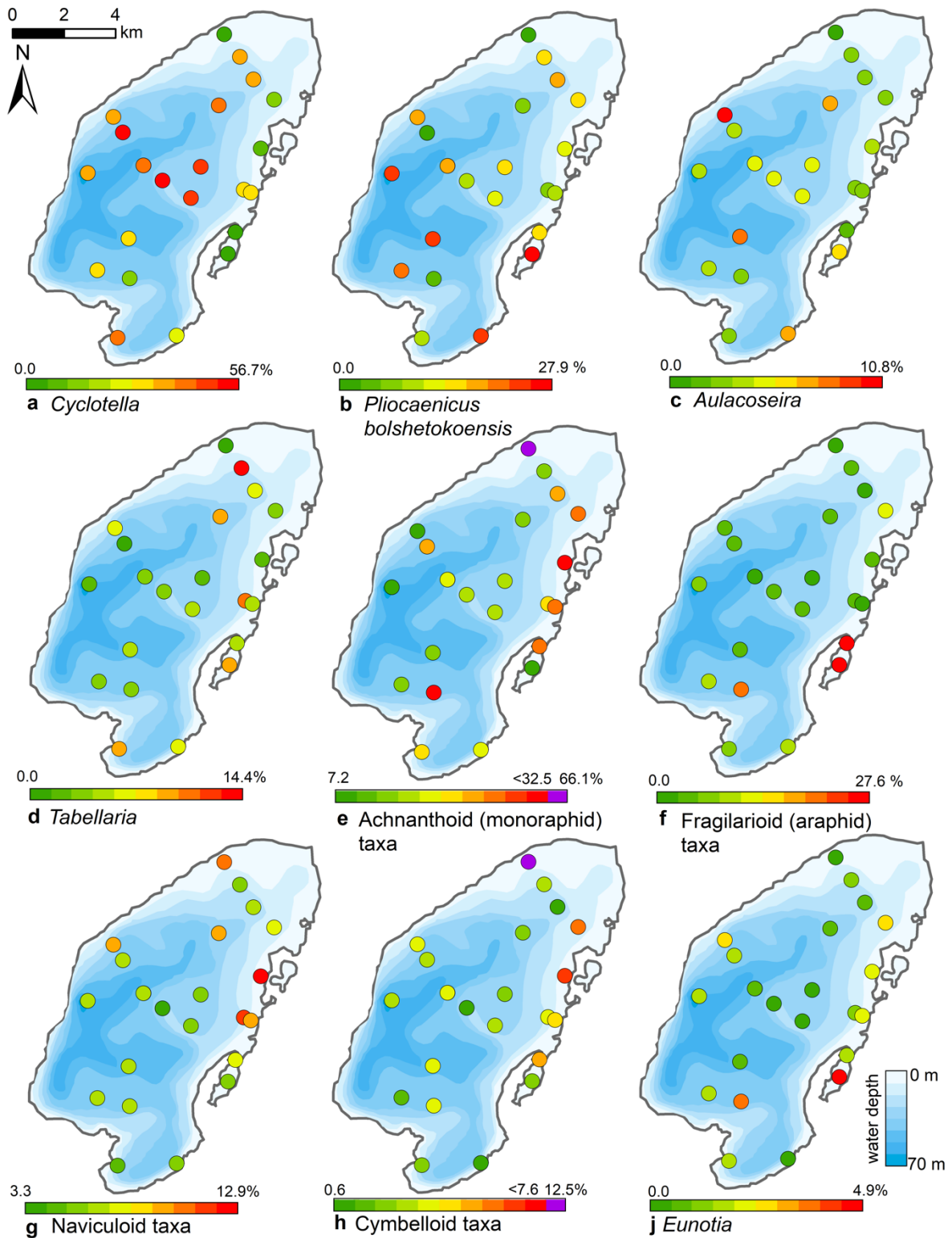
724
725 **Fig. 10** Spatial distribution of main diatom taxa in the surface sediments of Lake Bolshoe Toko. Maps compiled in
726 ArcGIS 10.4. Scales chosen as 10 classes with equal intervals. Maps e and h had exceptionally high values of
727 achnanthoid and cymbelloid taxa only in the very shallow (0.5 m) site PG2142. These values are shown in purple,
728 indicated separately at the right side of the scales.

729

4.4 Chironomids

A total 79 different chironomid taxa were present in the surface sediment samples, of which 48 belong to the subfamily Orthocladiinae, 25 to Chironominae (15 from the triba Tanitarsini and 10 from the triba Chironomini), four taxa were from subfamily Diamesinae, and 2 from Tanypodinae.
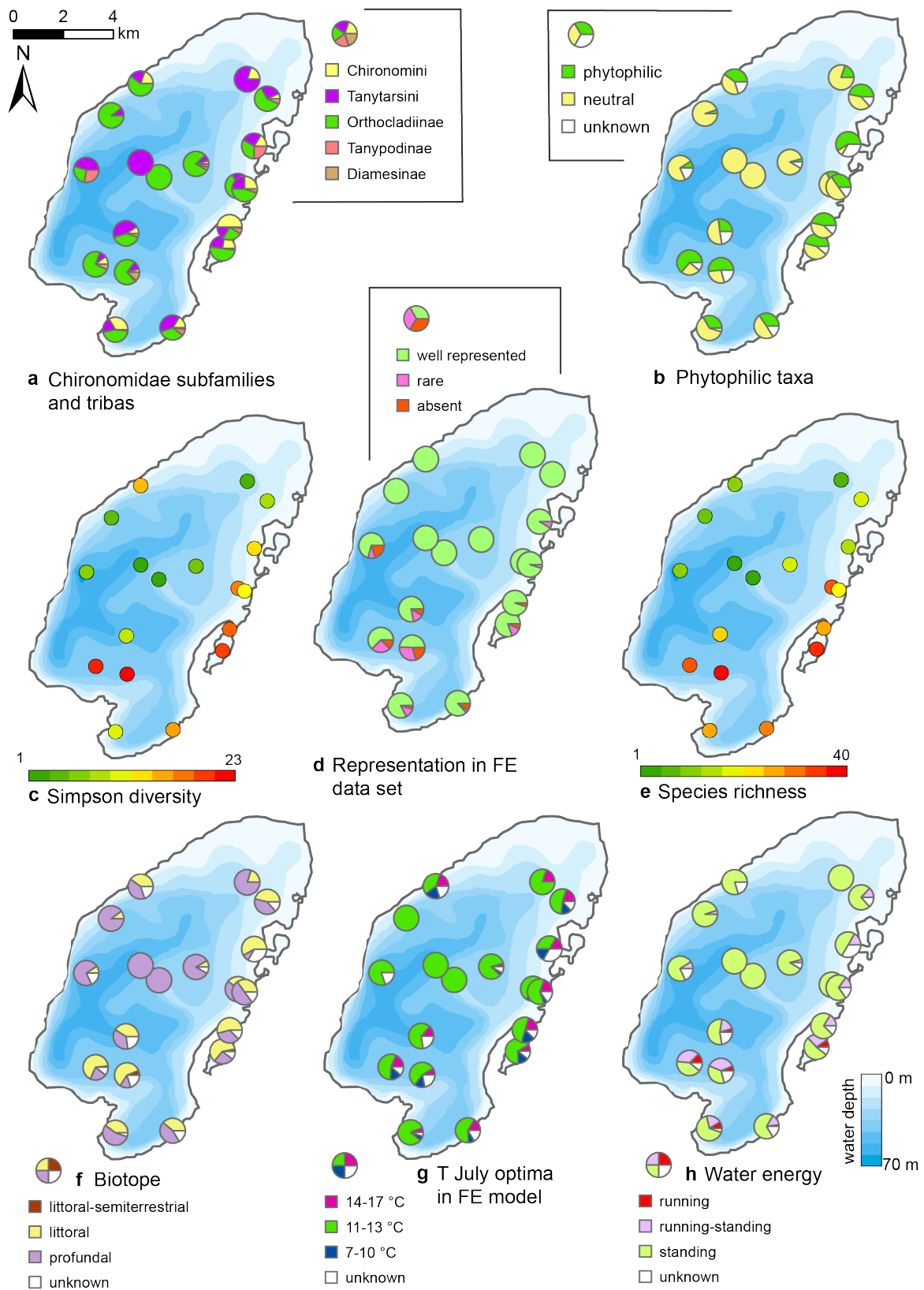
The initial RDA with all environmental variables shows that axes 1 and 2 explain 46.7% of variance in the taxon data. Most of the environmental parameters were intercorrelated, and following sequential deletion of all redundant variables, eight parameters with VIFs <20 remained for the further analysis. The manual Monte-Carlo test selection demonstrates four statistically significant ($p \leq 0.05$) explanatory variables: TOC/N, water depth (WD), distance from River, and presence of vegetation (Table 2). Distance from the river and presence of vegetation showed lower than TOC/N and WD level of significance. However, we still use these parameters for interpretation of the chironomid data as there was a clear gap between the 4 chosen parameters ($p = 0.001$ to 0.059) and much higher p values (>0.25) of the following tested parameters (TC, distance to the shore, silt, clay). Eigenvalues for RDA axes 1 and 2 constrained by four significant environmental variables were 0.200 and 0.150, respectively, and constituted 70 and 85 % of the RDA performed on all environmental variables (0.289 and 0.177, respectively). This minor difference suggests that the four selected variables sufficiently explain the major gradients in the chironomid data.

The RDA biplot of the sample scores shows that sites are grouped by their location in relation to the major environmental variables (Fig. 11), and distribution of chironomid taxa along the RDA axes reflects their ecological spectra. Fig. 11 and Table 6 in the ESM show median values of eco-taxonomical chironomid groups and their relation to environmental parameters.

Sites most strongly influenced by the inflowing rivers grouped in the lower left quadrant of the biplot, as the vector in the upper right quarter shows increasing distance from the river mouth. In total 64 chironomid taxa were found in this group of sites, and of these 33 were only found here. Chironomid fauna were chiefly represented by phytophilic littoral taxa from the Orthocladiinae genera *Cricotopus, Orthocladius, Eukiefferiella,* and *Parakiefferiella* etc. (Fig. 11). Another important feature is the presence of a relatively high amount of lotic environmental taxa, among which are several *Diamesa* taxa, *Rheocricotopus effusus*-type, *Synorthocladius, Brillia*, and for lotic-lentic environments *Parakiefferiella bathophila*-type, P*. triguetra*-type, *Nanocladius rectinervis*-type, *N. branchicolus*-type, several *Eukiefferiella* taxa, and *Stictochironomus*.

The group in the opposite upper right quadrant represents the northern part of the lake situated far from the inflowing rivers. Here, mainly profundal taxa prevail, i.e. *Procladius*, *Polypedilum nubeculosum*-type, *Cryptochironomus* (eurytopic*),* and *Heterotrissocladius maeaeri*-type 1 (acidophilic).

770   The lower right group of sites represent eastern shallow littoral with presence of
771 macrophytes. Species richness and proportion of semiterrestrial and littoral taxa in
772 this group is generally low. Littoral taxa were generally phytophilic: *Cricotopus*
773 *intersectus*-type, *C. cylindraceus*-type, *Dicrotendipes nervosus*-type (mesotrophic),
774 and *Cladotanytarsus mancus*-type and *Psectrocladius sordidellus*-type (acid-tolerant
775 mesotrophic). Most abundant profundal taxa here belong to the acid-tolerant
776 *Heterotrissocladius* genera represented by *H. macridus*-type, *H. maeaeri*-type 1 and
777 2, *H. grimschawi*-type (acidophilic), and to the subfamily Tanypodinae represented by
778 *Procladius*. The sites grouped in the opposing upper left quadrant represent lotic and
779 lotic-lentic taxa (*Diamesinae, Thenimaniella clavicornis*-type, *Eukiefferiella*
780 *claripennis*-type, *Eukiefferiella fittkaui*-type, several *Orthocladius* taxa).
781

a Chironomidae subfamilies and tribas

Chironomini
Tanytarsini
Orthocladiinae
Tanypodinae
Diamesinae

b Phytophilic taxa

phytophilic
neutral
unknown

c Simpson diversity

1   23

d Representation in FE data set

well represented
rare
absent

e Species richness

1   40

f Biotope

littoral-semiterrestrial
littoral
profundal
unknown

g T July optima in FE model

14-17 °C
11-13 °C
7-10 °C
unknown

h Water energy

running
running-standing
standing
unknown

water depth
0 m
70 m

0 2 4
km

N

782
783 **Fig. 11** Spatial distribution of chironomid taxa and inferred statistical parameters in the surface sediments of Lake
784 Bolshoe Toko. Maps compiled in ArcGIS 10.4. Scales chosen as 10 classes with equal intervals.
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5 Discussion

5.1 Spatial control of abiotic and biogeochemical sediment components

Sediment-geochemical and physical properties of the uppermost surface of the sediment basin in Bolshoe Toko are spatially variable. Physical properties of particles within the surface sediments depend chiefly on transportation processes and the characteristics and availability of clastic compounds in the lake catchment. The main catchment comprises the Stanovoy mountain range in the south channelled through the Utuk river into Bolshoe Toko. Accordingly, the lake experiences annual input of suspended material through a single source at the Utuk river mouth that likely is at its maximum during spring snow melt (Bouchard et al., 2013). The grain-size data and its end-members (Fig. 4 and 7) indicate that the relative proportions of sand, silt, and clay are somewhat constant in proximity to the Utuk river inflow but change towards the north and at the lake shoreline. Whereas in the central northern lake basin the amount of silt increases, the proportions of sand increase along the northern shoreline on top of the drowned moraine. Gravel is only present in samples near the lake terraces in the east. The constant distribution in the south-central lake basin reflects the river input. Decreasing river influence and hence decreasing water transport energy with increasing distance from the river mouth leads to the observed predominance of finer grain-sizes (silt dominated) samples in the northern central parts of the lake. Sandy samples along the shoreline reflect direct input from the moraines around the northern part of the lake. Other relevant within-lake sedimentary processes include shore-erosion and inwash and winnowing of fine sediment grains by surface currents as well as alluvial processes and debris flows which continue basin ward as subaquatic flows. The restriction of gravel at the eastern shore can be attributed to the availability of source material and suitable transport pathways of coarser clasts from the third moraine. In consequence to the described lateral transport trajectories and local control factors within the lake, there is only weak negative correlation between mean grain size and water depth (r -0.45, Fig. 7 and 12).

The modelled end-member loadings of the observed grain-size classes (Fig. 4 and 7) indicate an EM1 major peak in fine silt that represents fluvial sediment input. EM2 has peak values in fine to medium sandy grain-size fractions and in the northern part of the lake indicative of depositional processes associated with the erosion of moraines distal from the river inflow, where the hydrological dynamics in the lake basin are weak. The weak positive correlation between EM3 and the concentration of diatom valves (r 0.44) likely represents both *in-situ* diatom valves that could not be removed from allochthonous sediment particles during sample processing, and possibly redistributed ice-rafted debris (Wang et al., 2015).

824 Intermediate concentrations of TOC and high ratios of TOC/TN in the south as
825 compared to the north suggest differences in catchment characteristics, i.e. a
826 considerable allochthonous contribution of terrestrial plant material from the Utuk
827 river. This assumption is supported by previous findings that show non-vascular
828 plants, i.e. phytoplankton and other algae, with TOC/TN ratios between ca. 5 and 10
829 while organic matter from vascular land plants has higher values of about 20 (Meyers
830 and Teranes, 2002). High values of TOC/TN in lake sediment surfaces at river inflows
831 have also been observed in other studies (Vogel et al., 2010). $\delta^{13}C$ is generally low
832 on average (-26.8‰) and only slightly higher at the eastern shore (-25.7‰),
833 suggesting a strong overall dominance of C_3 plants and phytoplankton in the bulk
834 organic matter fraction (Meyers, 2003). It remains unclear as to the degree of old and
835 reworked organic carbon, e.g. from charcoal deposits, transported to the lake.

836   The distribution of elements from the XRF scanning data suggests strong abiotic
837 relationships to grain-size and mineral distributions. We focus on heavier elements
838 because lighter elements, even though commonly in higher concentrations, show
839 potential contribution from multiple sources. Sr/Rb ratios and Zr are negatively
840 correlated with Kaolinite/Chlorite (r -0.73 and -0.85, respectively). As described in
841 Kalugin et al. (2007), Rb substitutes for K in clay minerals. The Sr/Rb ratios do not
842 however show a significant correlation with grain-size parameters, as found in other
843 studies (Biskaborn et al., 2013b). We assume therefore that Sr, as substituent for Ca,
844 is influenced by multiple minerals represented in different grain-size fractions, i.e. K-
845 feldspar (r 0.45) and Hornblende (r 0.24). Associated to high metamorphic grades in
846 the Stanovoy mountains, Sr is preferentially taken into the K-feldspar phase (Virgo,
847 1968). Conversely, the Zr/Rb ratio correlates well with the sand fraction (r 0.50) and
848 with the mean grain size (r 0.49), but negatively with silt (r -0.54) and clay (r -0.39).
849 We account for this effect by a higher diversity of minerals in the input of the Utuk
850 river supplying the lake basin with mafic Ca-rich metamorphic rocks from the
851 Stanovoy mountains. The strong influence of the Utuk river in the spatial distribution
852 of physicochemical sediment components is further demonstrated by the decreasing
853 gradient of minerals relative to quartz starting from the Utuk river towards the northern
854 lake basin (Fig. 7). The most representative indicator of grain size variations in surface
855 sediments is given by clr transformed values of Ti, which correlate well with the sand
856 fraction (r 0.74) and the mean grain size (r 0.88).

857   Si/Ti ratios have traditionally been used as a proxy for the biogenic silica content
858 of sediments (Melles et al., 2012). This stems from the fact that Ti is generally
859 attributed to detrital influx and Si to both detrital and biogenic (diatom) origins. At
860 Bolshoe Toko positive correlations between Si/Ti ratios, diatom valve concentrations
861 (r 0.36) and the ratio of planktonic to benthic diatoms (r 0.42) suggests that Si/Ti may
862 be useful to trace the relative portion of diatom valves in intermediate grain-size
863 fractions. Moreover, the Si/Ti ratio correlates significantly with silt (r 0.81).

864   Mn/Fe ratios have been ascribed to redox dynamics associated to bottom water
865   oxygenation processes (Naeher et al., 2013). In Bolshoe Toko, however, the detrital
866   input of ferrous minerals, i.e. pyrite, suggests that Mn/Fe ratios cannot be directly
867   attributed to redox processes in the surface sediments. This is supported by the
868   correlation of Fe with the sand fraction (r 0.6) and grain-size (r 0.59). Accordingly, we
869   found no significant correlations between Mn/Fe and other abiotic or biotic proxies.
870   Lastly, there is an uncertainty in the spatial distribution of elements measured by
871   XRF techniques. We attribute this lack of clear patterns to: (1) methodological hurdles
872   to apply XRF techniques to surface sediments commonly rich in water and organic
873   material, and (2) multiple sources of the same elements coming from minerogenic
874   input, grain-size differences in individual samples and different intensities of redox
875   processes at different habitat settings. The high variance of elements are therefore
876   representative of the high complexity of this lake system, rather than unequivocal
877   validations or falsifications of the applicability of XRF scanner data as an
878   environmental proxy at Bolshoe Toko.
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880

881   ## 5.2 Factors explaining the spatial diatom distribution

882   Diatom communities in Yakutia respond rapidly to environmental changes
883   including hydrochemical parameters, water depth, nutrients, and catchment
884   vegetation type (Pestryakova et al., 2018). Planktonic diatom species are ubiquitous
885   across Bolshoe Toko, with a distinct tendency of the ratio between planktonic and
886   benthic species to greater water depths (r 0.77, Fig. 5 and 12), due to the limited
887   availability of light for benthic species (Gushulak et al., 2017;Raposeiro et al., 2018).
888   Especially *Aulacoseira* species were never abundant along the shallower northern
889   and eastern shorelines. The primary difference between the two most abundant
890   genera in the lake is that *Pliocaenicus* exhibits highest abundancies proximal to the
891   inflow and in the southeastern lagoon, whereas *Cyclotella* are more abundant in the
892   lake center and absent in the lagoon. Little is yet known about the new species
893   *Pliocaenicus bolshetokoensis (Genkal et al., 2018).* Our findings suggest factors other
894   than water depth (r 0.39), such as proximity (e.g. nutrient supply) to the Utuk river and
895   small streams, as controlling parameters for bloom intensities of this species.
896   *Cyclotella*, however, is restricted to stratification of the water column and hence more
897   abundant at distance from the river mouth, where incoming water causes turbulence
898   (Rühland et al., 2003;Smol et al., 2005). *Cyclotella* is therefore also believed to benefit
899   from recent air temperature warming trends and will likely increase in abundance
900   (Paul et al., 2010). *Aulacoseira* is a dense, rapidly-sinking tychoplanktonic group of
901   species requiring water turbulence to remain in the photic zone (Rühland et al.,
902   2008;Rühland et al., 2015), which explains the lower abundancies in the northern and

hydrologically less dynamic zones within the lake. Lightly silicified *Tabellaria* species are known to occur in zigzag planktonic colonies, yet, they also appear as short-valved populations in the benthos (Lange-Bertalot et al., 2011;Biskaborn et al., 2013a;Krammer and Lange-Bertalot, 1986-1991). In Bolshoe Toko, the spatial distribution of *Tabellaria* indicates benthic habitats are more favourable than planktonic.

The most common non-planktonic species in Bolshoe Toko belong to achnanthoid (monoraphid) genera, of which most species are epiphytic. Epiphytic species exhibit a stronger negative correlation to water depth (r -0.68) than epibenthic species (r -0.4), indicating that aquatic plants, in turn controlled by water transparency, pH, water depth and nutrient status (Valiranta et al., 2011), have an important function in the lake ecosystem (Fig. 12). The highest abundance of achnanthoid and cymbelloid valves occurs at 400 m distance to the northern shore at a water depth of 0.5 m.

Fragilarioid species are adapted to rapidly changing environments and are thus good indicators of ecosystem variability (Wischnewski et al., 2011). The peak occurrences of *Staurosira* species, which are pioneering small benthic fragilarioids (Biskaborn et al., 2012), therefore indicates the formation of a new ecosystem habitat type in the lagoon at the south-eastern lake basin. We assume this basin is successively separated from the main basin and will eventually form a small isolated remnant lake, similar to "Banya" lake (Fig. 1). High productivity of epiphytic species and low detrital input suggested by elemental and grain-size data, together with higher organic content (High TOC and Br), indicate a calm sedimentological regime with high bioproductivity. Similar neutral pH values measured in water samples from the central basin and the lagoon (Table 1) questions pH as a main driving factor of the *Eunotia* peak in the lagoon. However, Barinova et al. (2011) suggest 5.0-5.8 pH range for the identified *Eunotia* species, which rather indicates that the pH values obtained during April in 2013 are not representative for the annual average and the specific catchment of the lagoon, which likely will differ from this point measurement. The ice break-up during spring and transport of water from the catchment restricted to the lagoon likely leads to milieu differences in the lagoon relative to the main basin.

High autocorrelation coefficients (Moran's I p values) for species richness and valve concentration indicate strong local influence of biotic processes, i.e. reproduction, leading to spatial autocorrelation (Legendre et al., 2005). The lowest observed autocorrelation for the diatom planktonic/benthic ratio confirms the strong relationship between diatom species assemblage composition and water depth. A strong relationship between diatom diversity and water depth is supported by a study comparing morphological count data and phylogenetic species data gained by next-generation sequencing DNA analysis (Stoof-Leichsenring et al., in review).

The RDA biplot of diatoms (Fig. 2) suggests that both water depth and distance to river are important lake attributes accounting for the species distributions across the

lake. Especially *Eunotia*, fragilarioids, *Tabellaria*, and also *Aulacoseira subarctica* appear more frequently at sites that are close to the Utuk river mouth (e.g. PG2113, PG2115, PG2117, PG2118). The high TOC/TN ratios in these samples illustrates the strong riverine input of allochthonous material. In the biplots, high water depth is primarily associated to *Cyclotella* species (and *Aulacoseria*), while *Aulacoseira* species tend to be additionally influenced by incoming rivers and also thrive closer to the shorelines. Areas close to river mouths are usually dominated by river taxa and species that prefer higher nutrient content related to river input and associated early ice cover melting (Kienel and Kumke, 2002). Accordingly, the influx of diatoms from wetlands in the lake catchment is an important additional factor influencing the spatial diatom distribution (Earle et al., 1988). Compared to direct conductivity, water depth and nutrient controls, the link between temperature and diatom species is poorly understood in Yakutian lake systems (Pestryakova et al., 2018) and should be avoided.

Our RDA also shows that a high diversity of benthic, and particularly epiphytic diatom species, i.e. several achnanthoid species and some naviculoid taxa, plot in the opposite direction from water depth together with vegetation and the coarse grain-size fraction. Kingston et al. (1983) revealed spatial diatom variability in the Laurentian Great Lakes, where the stability of diatom assemblages increased with water depth. In shallower marginal waters of the Great Lakes, the availability of diverse habitats, including benthic and periphytic niches, leads to high species diversity. According to our data in Bolshoe Toko, the Simpson diversity index suggests higher effective numbers of dominant species associated to increased habitat complexity (Kovalenko et al., 2012), i.e. availability of water plants and benthic substrates in shallower depths along the eastern and northern shore. Thus, higher diversity in this area is facilitated by differential catchment preferences. However, it can be assumed that due to lesser water supply rates from the small northern part of the catchment (Fig. 1), a single location at the north eastern lake margin will likely not receive significantly higher loadings of nutrients as compared to the Utuk river coming from the igneous mountain range. Nevertheless, moraine deposits typically contain high amounts of silt and clay which can more easily be weathered and altered to fertilizing substances that are transported into the calm and shallower northern part of the basin.

The indices of chrysophyte cysts and *Mallomonas* relative to diatom cells exhibit indistinct patterns in spatial distributions, but a slight tendency towards proximity to river input and high water depths. Although chrysophyte cysts commonly represent planktonic algae (Smol, 1988b), periphytic taxa are also common in boreal regions (Douglas and Smol, 1995) with cool and oligotrophic conditions (Gavin et al., 2011). *Mallomonas* was reported as an indicator of lake eutrophication and acidification (Smol et al., 1984).

982   Taphonomic effects on the preservation of subfossil assemblages are generally
983   influenced by clastic transport mechanisms depending on the lake morphology
984   (Raposeiro et al., 2018). The preservation of diatom valves in Bolshoe Toko is found
985   to be lowest in samples from a plateau-like feature at the central part of the lake
986   bottom, which indicates increased re-working associated to bottom currents and/or
987   increased dissolution of diatom valves due to lesser accumulation rates, and/or
988   increased grazing activity of herbivorous organisms (Flower and Ryves, 2009;Ryves
989   et al., 2001).

990   The spatial distribution of $\delta^{18}O_{diatom}$ from the sediment surface indicates higher
991    $\delta^{18}O_{diatom}$ values at the deeper, south-western part of the lake with a difference of app.
992   1‰ compared to lower $\delta^{18}O_{diatom}$ values in the shallower northern part. This could
993   reflect a combination of spatial $\delta^{18}O_{water}$ variations, water temperatures, and/or a
994   potential species-driven fractionation effect. However, existing studies demonstrate
995   no apparent species composition effects on lacustrine $\delta^{18}O_{diatom}$ (Bailey et al.,
996   2014;Chapligin et al., 2012b). Additionally, the sieving step reduces the assemblage
997   before the isotope analysis to a small size interval resulting in a similar species-
998   composition. Furthermore, dissolution effects in nature and during sample preparation
999   could have an impact on $\delta^{18}O_{diatom}$. However, we suppose differential dissolution to
1000   have minor influence on the spatial variability of $\delta^{18}O_{diatom}$ at BT samples tackled in
1001   our study as these are (1) of similar age, (2) have been treated with wet chemistry at
1002   low temperatures and (3) after preparation do not show any microscopical signs of
1003   dissolution effects, i.e. a low diatom dissolution index (Smith et al., 2016).

1004   Regarding $\delta^{18}O_{water}$ variability, waters sampled at the same time in different parts
1005   of the lake show a uniform isotopic composition (within ±0.15‰) and indicate an
1006   isotopically well-mixed lake. Considering this is a one-time recording, slight seasonal
1007   variation between shallower and deeper parts (for example due to evaporation)
1008   cannot be excluded and could account for some differences in ^{18}O. However, lake
1009   surface evaporation would result in isotopic enrichment and overall higher $\delta^{18}O_{diatom}$
1010   values.

1011   Alternatively, the lake temperature in which the diatoms grow has an impact of ca.
1012   -0.2‰/°C on $\delta^{18}O_{diatom}$ (Brandriss et al., 1998;Dodd et al., 2012;Moschen et al., 2005).
1013   Shallower areas heat up faster especially in the photic zone. The temperature profile
1014   near to the western shoreline taken in August 2012 (Fig. 6) shows 12°C at the surface
1015   with an average of app. 10°C in the first 15m of the water column decreasing to app.
1016   6°C in 30m depth. Although a spatial difference of 5°C in the photic zone for causing
1017   a 1‰ shift is rather unlikely, this could account for part of the variation in surface
1018 $\delta^{18}O_{diatom}$.

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5.3 Factors explaining the spatial chironomid distribution

The chironomid RDA indicates that spatial variations are primarily influenced by the distribution of tributary rivers. For example, high species diversity is found adjacent to the Utuk river inflow (2117), and in the SE lagoon fed from a small inflowing stream (PG2122). Semiterrestrial taxa, like *Smittia-Parasmittia, Pseudosmittia, Limnophies-Paralimnophies*, have been found only here with the highest abundancies of 6 and 3.2% at the sites opposite of the inflowing rivers (PG2117 and PG2122) suggesting these taxa were transported from marshy river deltas.

Species at lentic sites with no tributary influence are primarily controlled by water depth. Deep profundal sites of the lake have much lower taxonomic richness of chironomid communities. Higher taxonomic richness at site PG2118 can be explained by an enriching riverine influence. High proportions of lotic and lotic-lentic taxa lead to a high taxonomic similarity of this profundal site to littoral sites in the S and SE. Similarly, in relation to temperature, sublittoral and profundal sites both have much higher representation of the taxa characteristic of semi-warm conditions and lower abundancies of the taxa preferring warm and cold conditions. However, high depths of the sublittoral and profundal sites lead to the development of a poor chironomid fauna at these sites. High distance from the shore and presumably only weak transportation of chironomid remains of littoral fauna to the profundal zone could be another limiting factor for diversity of chironomid communities in the profundal.

Eastern relatively shallow littorals are inhabited by more diverse, phytophilic, mesotrophic and partly acidophilic fauna with absence of lotic taxa, related to a less disturbed and turbulent environments and presence of macrophytes. This fauna has higher abundance of the semi-warm and warm taxa. The presence of meso- to eutrophic and acidophilic taxa can be attributed to paludification of the shore zone and decomposition of macrophytes and submerged vegetation in the shallow littoral (Nazarova et al., 2017b).

It is still debated how spatial and local environmental processes influence the distribution of chironomids at a small spatial scale in a lake (Luoto and Ojala, 2018;Yang et al., 2017). It is known that within one water body the concentration of chironomid head capsules can vary from zero to several thousand per 1 cm^3 of sediments (Kalinkina and Belkina, 2018;Walker et al., 1997) depending on factors such as water depth, rate of sediment accumulation, the hydrological conditions, or anthropogenic influence. Water depth in particular is a major driving factor of chironomid assemblages (Ali et al., 2002;Luoto, 2012;Vemeaux and Aleya, 1998) with depth optima of several species consistent across broad spatial scales (Nazarova et al., 2011). Chironomid remains from the deepest zones of Bolshoe Toko represents an assemblage of elements of profundal necrocenosis (Hofmann, 1971) mixed with secondary components of littoral fauna transported with in-lake hydrological and

sedimentary processes into the profundal from outside. Thus, the re-deposition of littoral taxa into the profundal zone is an important factor that affects the final composition and abundance of subfossil assemblages. While in small lakes, subfossil assemblages from the profundal zone quite adequately reflect the fauna of the entire water body (Brooks and Birks, 2001;Walker and Mathewes, 1990), our findings support the hypothesis that in large lakes the taphonomy of chironomid communities seems to be more complex (Yang et al., 2017;Árva et al., 2015).
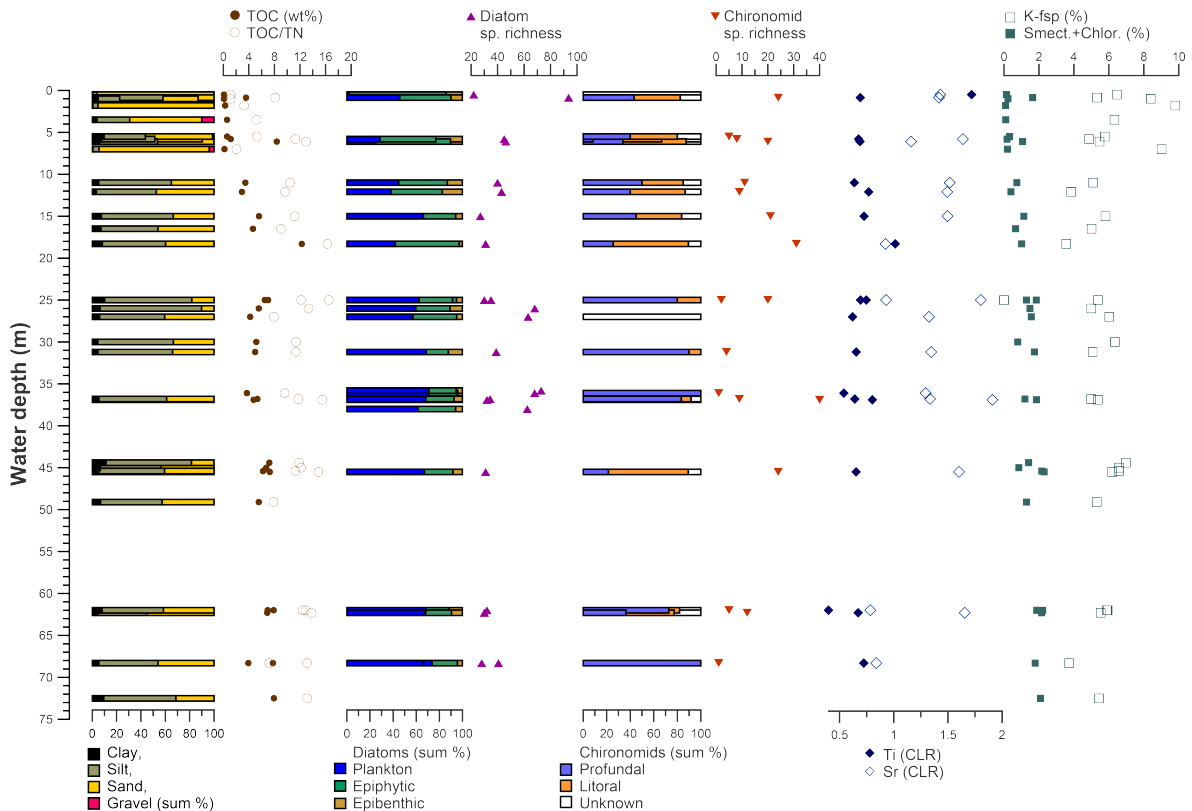
Fig. 12 Distribution of grain size, organic carbon and nitrogen indices, diatom and chironomid parameters, and selected elements and minerals in dependence to water depth in lake Bolshoe Toko.

5.4 Lake Bolshoe Toko as a site for palaeoclimate reconstructions

Compared to small lowland lakes of Central and Northern Yakutia, sedimentary processes are quite different in Bolshoe Toko. One reason is the lack of thaw slumps, subsidence, and other permafrost related phenomena (Biskaborn et al., 2013b) that are typical for shallow thermokarst lake settings across northern permafrost regions (Biskaborn et al., 2016;Bouchard et al., 2016;Biskaborn et al., 2012;Schleusner et al., 2015;Biskaborn et al., 2013a;Subetto et al., 2017;Biskaborn et al., 2013b).

The Bolshoe Toko mineral composition is primarily influenced by the Utuk river, and only samples in extremely shallow areas are influenced by direct shoreline input.

1083 The grain-size signal is influenced by dissolution effects associated with organic
1084 matter and *in situ* growth of diatom valves. Conversely, the coarser fractions parallel
1085 minerogenic compositions and water depth. Accordingly, the grain-size distribution
1086 originated from multiple processes and should only be considered as an
1087 environmental proxy when combined with biotic indicators.
1088   Diatoms are spatially distributed according to their preferred habitat. Aside from
1089 the spatial habitat conditions associated with basin morphology, an additional
1090 consideration is the annual duration and thickness of lake ice-cover (Keatley et al.,
1091 2008;Smol, 1988a). For instance, planktonic communities in Lake Baikal, including
1092 *Aulacoseira* species, are found to grow under the ice if the surface snow properties
1093 (i.e. thickness, density) allow sufficient light penetration (Jewson et al., 2009;Mackay
1094 et al., 2005). Generally, planktonic and benthic diatom species have strategies to
1095 survive in ice-covered lakes by growing in benthic mode, forming resting spores, or
1096 attaching to the ice-cover substrate (D'souza, 2012). Hence, the duration and
1097 presence of ice-cover can significantly impact both changes in assemblage
1098 composition and spatial distribution, particularly including the ratio of planktonic to
1099 benthic diatoms (Wang et al., 2012a;Bailey et al., 2018).
1100   The applicability of chironomids for temperature reconstructions reveals clear
1101 spatial constraints. 22% of the taxa in sites with riverine influence are absent or rare
1102 from the FE mean July chironomid-based temperature inference model (Nazarova et
1103 al., 2015), whereas fewer of these rare/absent taxa occur in the central and northern
1104 littoral, sublittoral and profundal part of the lake (Fig. 4). However, low taxonomic
1105 richness of the profundal zone also hampers palaeoclimatic inferences. Also the
1106 number of chironomid head capsules are generally lower here relative to littoral sites.
1107 Maximum taxonomic diversity in areas influenced by lake tributaries can be explained
1108 by both a taxonomic enrichment from the lake catchment, as well by more favorable
1109 oxygen and nutrient conditions.
1110   The applicability of $\delta^{18}O_{diatom}$ as a proxy of past hydroclimate conditions at
1111 Bolshoe Toko is facilitated by the main controls influencing on $\delta^{18}O_{diatom}$, which are
1112 here found to be: (1) lake water temperature (T_{lake}) and (2) lake water isotope
1113 composition ($\delta^{18}O_{lake}$) (Dodd and Sharp, 2010;Leng and Barker, 2006;Labeyrie,
1114 1974;Leclerc and Labeyrie, 1987). The fractionation between lake water and biogenic
1115 opal can be calculated when comparing $\delta^{18}O_{lake}$ (mean: −18.7‰) with recent surface
1116 sediments of Bolshoe Toko lake and their respective mean $\delta^{18}O_{diatom}$ (of +22.8‰)
1117 using this isotope fractionation correlation between sedimentary diatom silica and
1118 water as determined by Leclerc and Labeyrie (1987). The mean T_{lake} can be estimated
1119 to ca. 6°C for the photic zone/diatom bloom. This estimate is at the lower end of
1120 summer temperatures between 4.8 and 12°C. The corresponding derived mean
1121 isotope fractionation factor for the system diatom silica–water α = 1.0424 matches the

1122 fractionation factor for sediments proposed by Juillet-Leclerc and Labeyrie (1987) well
1123 ($\alpha_{(silica-water)}$ = 1.0432).

1124   Additionally, as lacustrine $\delta^{18}O_{diatom}$ also reflects the isotopic composition of the
1125 water where the diatoms grow ($\delta^{18}O_{lake}$), $\delta^{18}O_{diatom}$ typically reflects meteoric inputs
1126 associated with precipitation and riverine inflows (Fig. 6b). For example, existing
1127 studies have used lacustrine $\delta^{18}O_{diatom}$ to reconstruct past changes in precipitation
1128 amount and seasonality, the precipitation/evaporation balance, spring snow melt
1129 inputs, and synoptic-scale shifts in atmospheric circulation (Bailey et al., 2015;Meyer
1130 et al., 2015;Bailey et al., 2018;Kostrova et al., 2013;Mackay et al., 2013). It is
1131 envisaged that changes in $\delta^{18}O_{diatom}$ through time at a single site in Bolshoe Toko will
1132 yield insights into the long-term air temperature and palaeohydrological history of the
1133 region.

1134   Positive feedback mechanisms between benthic algae and chironomid larvae in
1135 benthic ecosystems are well-documented (Herren et al., 2017). Chironomids in
1136 Bolshoe Toko, however, showed less significant correlations with benthic diatom
1137 species, but weak correlations with planktonic species and lake attributes associated
1138 to benthic habitats and water depth, highlighting the potential of chironomids for
1139 independent water depth and temperature reconstruction in future sediment core
1140 studies (Nazarova et al., 2011).

1141   High correlation coefficients between organic carbon and *Pliocaenicus*
1142 *bolshetokoensis* (0.66) and silt (0.65) suggest that the accumulation of organic matter
1143 and intermediate grain-size fraction is, to a certain degree, controlled by the
1144 productivity of siliceous microalgae (Biskaborn et al., 2012). A strong contribution of
1145 plankton indicates that TOC/TN ratios can provide insights in the relative influx
1146 between land and water plants (Meyers and Teranes, 2002). The relatively weak
1147 correlation between TOC/TN ratios and water depth (0.51 r), demonstrates the
1148 accuracy limits of TOC/TN as a proxy for relative lake level changes. This is caused
1149 by transport and accumulation of allochthonous organic matter in proximity to the Utuk
1150 river. Furthermore, correlations between TOC/TN and TOC, as well as negative
1151 correlations with grain size indicators suggest diagenetic alteration (i.e. loss) of
1152 nitrogen in the surface sediments (Galman et al., 2008).

1153   The distinct difference between two samples along the subaquatic slope near the
1154 western shore (diatoms, minerals, organics) indicates redistribution of sediment.
1155 Downslope transport of surface layers over the time could lead to redistribution of old
1156 material into the deepest parts of the basin. Due to higher accumulation rates, a
1157 sediment core from the deepest part of the basin would potentially provide a higher
1158 temporal resolution, but also a higher risk of repositioned sediment layers. On top of
1159 redistribution processes, hump-shaped relations between lake depth and species
1160 diversity observed in other studies suggest that the total subfossil species
1161 assemblages is better represented at intermediate depths than at the maximum depth

1162 (Raposeiro et al., 2018). A coring site at intermediate depth in the shallow northern
1163 and sedimentologically calm sector of the basin would enable the tracking of different
1164 river and glacial influences, and offers greater chances of undisturbed successions of
1165 bioindicator time series.
1166

6 Conclusions

1168   Our study on the within-lake variance of environmental indicator data and its
1169 attribution to habitat factors improves the understanding of lake-internal filters
1170 between environmental forcing and the resulting sediment parameters of Lake
1171 Bolshoe Toko and comparable boreal, cold, and deep lakes. We found that the spatial
1172 variabilities of biotic ecosystem components are mainly explained by static habitat
1173 preferences as water depth and river distance. Abiotic sediment features are not
1174 symmetrically distributed in the basin but vary along restricted areas of differential
1175 environmental forcings (e.g. river input, rocky shore, steep shore, shallow shore).
1176 They depend, in addition to water depth and riverine activity, to multiple interacting
1177 factor, such as catchment characteristics, geochemical sediment diagenesis and
1178 hydrochemical dynamics. Our main findings can be highlighted as follows:
1179

1180 • The lake water of Bolshoe Toko can be characterized as Ca-Mg-HCO3-Type
1181   water. It is well saturated in O2, neutral to slightly acidic, showing a low
1182   conductivity and corresponding ion concentrations suggesting unpolluted
1183   freshwater conditions. Lake Bolshoe Toko is a cold, polymictic, oligotrophic,
1184   open through-flow lake system and can be regarded as an undisturbed
1185   ecosystem.
1186 • Water depth is a strong factor explaining the spatial variability of diatoms and
1187   chironomids. The proportions of planktonic to benthic diatoms and profundal
1188   to littoral chironomids serve as a reliable lake level proxy.
1189 • The diatom assemblage is dominated by planktonic species, i.e. *Pliocaenicus*
1190   *bolshetokoensis*, which is unique for this lake, and more common plankton
1191   such as *Cyclotella* and *Aulacoseira*, as well as non-planktonic taxa, such as
1192   *Achnanthidium*. Diatom species richness and diversity is higher in surface
1193   sediments in the northern part of the basin, associated to shallower waters and
1194   the availability of benthic and periphytic niches.
1195 • The $\delta^{18}O_{diatom}$ values (22.8±0.6‰) show slight spatial variations with higher
1196   values in the deeper south-western part of the lake probably related to water
1197   temperature differences in the photic zone during the main diatom bloom. The
1198   silica–water isotope fractionation is suitable for further downcore investigations
1199   for assessing palaeohydrological information and potential air-temperature
1200   changes in the region.

- The water of Bolshoe Toko is well mixed and does not show significant isotopic stratification apart from lake ice-cover formation where thermal stratification prevents mixing. The isotopic lake water composition ($\delta^{18}O = 18.2 \pm 0.2$ ‰) correspond with the GMWL and do not show evaporative enrichment. Both isotopic and hydrochemical data indicate atmospheric precipitation (and meltwater run-off) as the main water source. Accordingly, $\delta^{18}O_{lakewater}$ is directly linked to $\delta^{18}O_{precipitation}$.

- The highest amount of the chironomid taxa underrepresented in the FE training set used for regional palaeoclimate inference was found close to the Utuk river and at southern littoral and profundal sites. Poor chironomid communities from the deep profundal zone would also hamper palaeoclimate reconstruction. Cold-stenotherm chironomid taxa were influenced by river proximity while taxa preferring warm conditions were more frequent at shallow littorals of the lake.

- Weak negative correlation between mean grain size and water depth is explain by end-members revealing influences of river input and diatom valves in the grain-size composition.

- Observed TOC values (mean 4.9 %) and TOC/TN ratios indicate strong allochthonous supply of organic matter from the Utuk river. $\delta^{13}C$ (mean -26.8 ‰) indicate dominance of C_3 plants and phytoplankton in the bulk organic matter fraction. Radiocarbon dating suggests that there is a reservoir effect caused by input of old organic carbon by max. 720 ± 30 ^{14}C yrs BP.

- Elemental (XRF) data and mineral (XRD) distribution is influenced by the methamorphic lithology of the Stanovoy mountain range. Ratios of minerals relative to quartz decrease from the Utuk river towards the northern lake basin. Ti correlates well with mean grain size. There is no clear pattern in Mn/Fe ratios, due to mixture of allochthonous elements and differential intensities of redox processes in the lake basin.

- The observed proxy variabilities in the surface sediments suggest at least two locations for sediment coring: (1) at intermediate depth in the northern basin to account for representative bioindicator distributions, and (2) the deep part in the central basin to potentially receive higher temporal resolution in the sedimentary record.

Data Availability

All data used in this study will be available online at PANGAEA.

Supplement

The supplementary material related to this study will be available online at Copernicus.

Author contributions

BKB conceived the study, led the laboratory analyses and the writing of the manuscript. LN conducted statistical analyses and contributed with ecological chironomid expertise. LAP led the Russian team during field work and contributed with ecological diatom expertise. LS conducted chironomid analysis. KF conducted diatom analyses. HM conducted water chemistry analyses. BC and HLB analysed diatom opal oxygen isotopes. SV conducted the XRF analysis. RG and EZ retrieved surface samples during field work and helped with translation of Russian literature and geographical expertise of the study area. RW conducted grain-size analyses including end-member modelling. GS conducted XRD analyses. BD was the leader of German expedition team and contributed with sedimentological expertise.

Competing interests

The authors declare that they have no conflict of interest.

Acknowledgements

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