

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*.

44 Species richness and diversity is higher in the northern part of the lake basin,
45 associated with the availability of benthic, i.e. periphytic, niches in shallower waters.
46 $\delta^{18}\text{O}_{\text{diatom}}$ values are higher in the deeper south-western part of the lake probably
47 related to water temperature differences. The highest amount of the chironomid taxa
48 underrepresented in the training set used for palaeoclimate inference was found close
49 to the Utuk river and at southern littoral and profundal sites. Abiotic sediment
50 components are not symmetrically distributed in the lake basin but vary along
51 restricted areas of differential environmental forcing. Grain size and organic matter is
52 mainly controlled by both, river input and water depth. Mineral (XRD) data
53 distributions are influenced by the metamorphic lithology of the Stanovoy mountain
54 range, while elements (XRF) are intermingled due to catchment and diagenetic
55 differences. We conclude that the lake represents a valuable archive for multiproxy
56 environmental reconstruction based on diatoms (including oxygen isotopes),
57 chironomids and sediment-geochemical parameters. Our analyses suggest
58 preferably two correlated coring locations at intermediate depth in the northern basin
59 and the deep part in the central basin, to account for representative bioindicator
60 distributions and higher temporal resolution, respectively.

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63 1 Introduction

64 Over the past few decades, the atmosphere in boreal and high elevation regions
65 has warmed faster than anywhere else on Earth (Pepin et al., 2015;Huang et al.,
66 2017). Dramatic socio-economic and ecological consequences are expected (AMAP,
67 2017) as well as substantial feedbacks from thawing permafrost and the associated
68 release of greenhouse gas into the global climate system (Schuur et al., 2015). Boreal
69 Russia is identified as a global hot-spot where surface air temperature increases have
70 led to substantial ground warming over the past decade (Biskaborn et al., 2019).
71 Accurate estimates of the amplitude of environmental impacts are compounded by an
72 imprecise understanding of ecological indicators of past environmental conditions
73 (Miller et al., 2010). Lake ecosystems, whose development is archived in their
74 sediments, act as sensitive sentinels of environmental changes (Adrian et al., 2009)
75 while even small changes in climate can profoundly deteriorate ecosystem services
76 (Saulnier-Talbot et al., 2014). Assessments of the impact of climate change to lake
77 systems rely on careful interpretation of suitable proxy data. Proxy information on
78 present and past ecological conditions is provided by various biological and
79 physicochemical properties of the sediment components (Meyer et al.,
80 2015;Solovieva et al., 2015;Nazarova et al., 2017a). However, the spatial within-lake
81 distributions of preserved remnants of ecosystem inhabitants and associated
82 sediment-geochemical properties, depend on habitat differences between the

83 epilimnion and the hypolimnion (Raposeiro et al., 2018), and are therefore expected
84 to be non-uniform. Accordingly, precise paleolimnological 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 diatoms ($\delta^{18}\text{O}_{\text{diatom}}$),** grain size distributions,
90 elemental compositions, organic carbon **content**, and mineralogy. Abiotic sediment
91 **properties may** represent signals **resulting from either the** external input of material
92 and lake-internal conditions during deposition, **or** post-sedimentary diagenetic
93 processes near the sediment surface (Biskaborn et al., 2013b; Bouchard et al., 2016).
94 **Hence, our integrated approach enables the identification and distinction between**
95 **internal lake processes and** external forcing (Cohen, 2003).

96 Diatoms (unicellular, siliceous microalgae) **are** major aquatic primary producers.
97 They appear ubiquitous and their opaline frustules ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$) 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; Herzsuh 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

123 between the primary consumer and primary producer trophic levels in benthic
124 ecosystems (Specziar et al., 2018;Zinchenko et al., 2014). Factors influencing the
125 spatial distribution of chironomids within single lakes are water temperature
126 (Nazarova et al., 2011;Luoto and Ojala, 2018), sedimentological habitat
127 characteristics (Heling et al., 2018) and/or water depth and nutrients (Yang et al.,
128 2017), as well as hypolimnetic oxygen (Stief et al., 2005) and the availability of water
129 plants (Raposeiro et al., 2018;Wang et al., 2012b).

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

133 Secondary factors influencing the spatial distribution of subfossil assemblages are
134 selective transitions from living communities to accumulation of dead remains. Both
135 biological remains and physico-chemical properties are influenced by sediment
136 resuspension and redistribution processes described as sediment focusing (Hilton et
137 al., 1986). **These are primarily dependent** on slope steepness (Hakanson, 1977) or,
138 in shallow areas, wind-induced bottom shear stress (Bennion et al., 2010;Yang et al.,
139 2009). Nevertheless, it already has been proven for other lake sites that within-lake
140 bioindicator distributions are laterally non-uniform, contradicting the assumption that
141 mixing processes cause homogenous microfossil assemblages before deposition
142 (Anderson, 1990;Wolfe, 1996;Anderson et al., 1994;Earle et al., 1988;Kingston et al.,
143 1983;Puusepp and Punning, 2011;Stewart and Lamoureux, 2012;Yang et al., 2009).
144 **However, many palaeolimnological studies employ single-site approaches using only**
145 **one sediment core, and hence do not encompass the full spatial extent and natural**
146 **variability of the entire lake sediment archive.** Heggen et al. (2012) report that
147 sediment cores from the deep centre of small and shallow lakes with high spatial
148 proxy variability in the littoral zones contain representative bioindicator assemblages.
149 The authors also conclude, that in larger and deeper lakes similar multi-site studies
150 are necessary to make recommendations about the “ideal” coring positions for multi-
151 proxy palaeolimnological studies.

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

158 An analysis of spatio-temporal within-lake bioindicator distribution requires a
159 suitable and large lake system with an anthropogenically untouched ecosystem and
160 sufficient variability in water depth, catchment setting, and sedimentological regime.
161 **These demands are met by Lake Bolshoe Toko, the deepest lake in Yakutia, Russia**
162 **(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

171 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 km², 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 Rybachiyy ("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

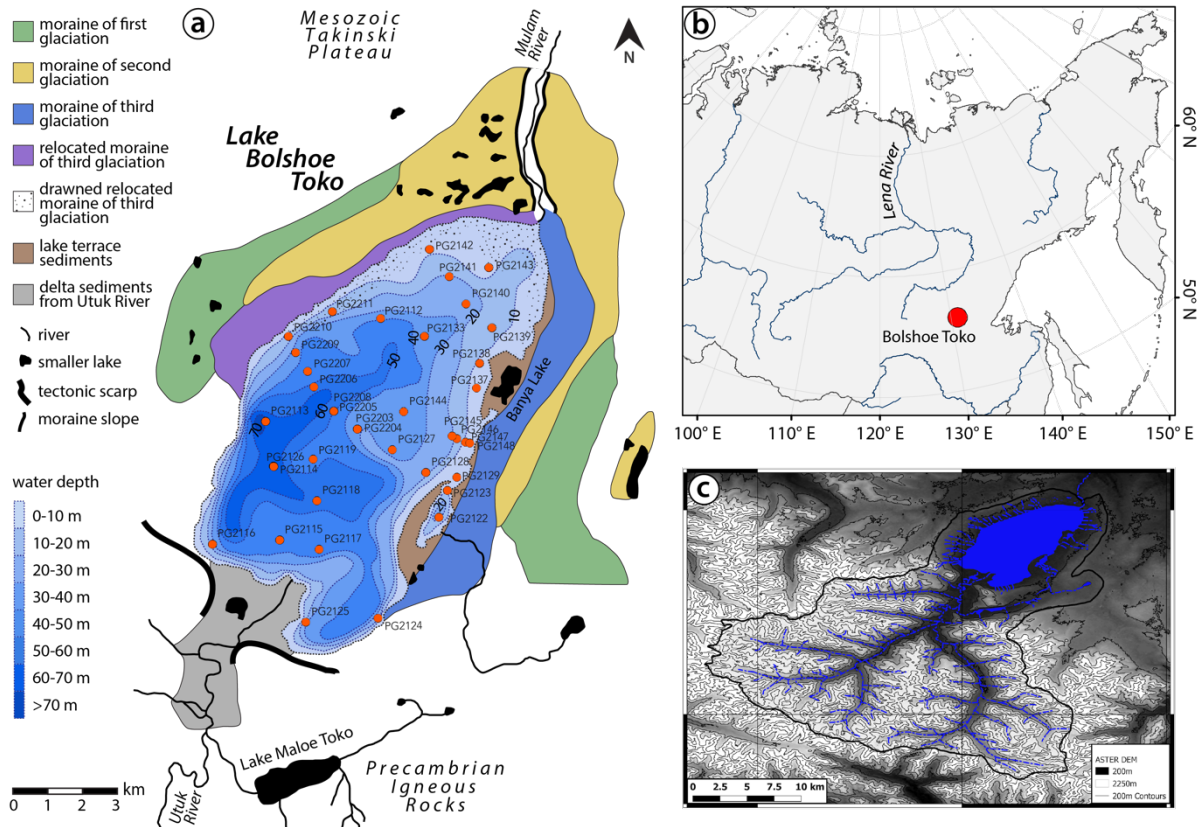
202 from sandstones and mudstones of the Mesozoic Tokinski Plateau in the north. The
203 Stanovoy mountain range in the southern catchment of the lake consists mainly of
204 highly mafic granulites and other high-pressure metamorphic rock types (Rundqvist
205 and Mitrofanov, 1993). At its north-eastern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

207 The study area is situated within the East Siberian continental temperate climate
208 zone exhibiting taiga vegetation (boreal forests) and fragments of steppes and a
209 predominant westerly wind system (Shahgedanova, 2002). The meteorological
210 station in Yakutsk has recorded historical climate data (Gavrilova, 1993). In the 19th
211 Century the mean annual **temperature (Jan-Dec)** was circa -11° to -11.5°C and during
212 the 20th Century **these** temperatures have increased to around -10.2°C, in parallel
213 with an increase in precipitation from 205 to 250 mm per year (Konstantinov, 2000).
214 The meteorological station “Toko” located approximately 10 km northeast of the lake,
215 however, recorded an increase of air temperature of ca. 0.48 °C per decade from the
216 1970’s to 2010 (**calculated from NOAA data, only those years involved that have**
217 **average air T data in 12 months**). Measurements taken directly at the lake were lower,
218 indicating the influence of cold **melt** water from the Stanovoy mountain range in
219 summer and the high volume of ice during wintertime. Since the average air
220 temperature in southern Yakutia increases with height (temperature inversion of ~2°C
221 100 m⁻¹), permafrost can be locally discontinuous where taliks (unfrozen zones)
222 underneath topographically high and deep lakes penetrate the permafrost zone
223 (Konstantinov, 1986). As observed in 1971 (Konstantinov, 2000) ice cover lasts at
224 least partly until mid-July.

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 229 **Fig. 1** Lake Bolshoe Toko study site. **a** Geological map, bathymetry and moraines. Map compiled using data from
 230 Konstantinov (2000) and Kornilov (1962). **b** Overview map of Siberia. World Borders data are derived from
 231 http://thematicmapping.org/downloads/world_borders.php and licensed under CC BY-SA 3.0. **c** Catchment area
 232 around Bolshoe Toko delineated from the ASTER GDEM V2 model between the latitudes N54° and N56° and
 233 longitudes E130° to E131° (1) (Meyer et al., 2011) and a corresponding multispectral Landsat 8 OLI TIRS satellite
 234 image using QGIS (QGIS-Team, 2016). Most of the river catchment is located in the igneous Precambrian
 235 Stanovoy mountain range supplying the southern part of the lake with water and sediment. The shallower
 236 northeastern part of the lake is influenced by the surrounding moraines and Mesozoic sand- and mudstones.
 237

238 3 Materials and methods

239 3.1 Field work

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

251 bottles for subsequent anion and cation analyses in AWI laboratories in autumn 2013.
252 Cation samples were acidified during field work with HNO₃, suprapure (65%) to
253 prevent microbial conversion processes and adsorptive accretion.

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

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

269 3.2 Laboratory analyses

270 3.2.1 Hydrochemistry

271 Water depth profiles were taken during the March 2013 expedition from the
272 deepest part of the lake (PG2208, water depth 70m) and in the lagoon (PG2122, 18
273 m) as well as in August AD 2012 (sample site near the western shoreline, 37 m). The
274 temperature was determined in the field and the samples analysed for isotopes ($\delta^{18}\text{O}$,
275 δD , see Fig. 6). From the water samples anions were analysed using ion
276 chromatography (Dionex DX 320) and cations were determined using inductively
277 coupled plasma–optical emission spectrometry (ICP-OES, Perkin-Elmer Optima
278 8300DV Perkin-Elmer – Optical Emission Spectrometer. Alkalinity was measured by
279 titration with 0.01 M HCl using an automatic titrator (Metrohm 794 Basic Titrino).

280 Stable hydrogen and oxygen isotope analyses were carried out with Finnigan MAT
281 Delta-S mass spectrometers with two equilibration units using common equilibration
282 techniques (Meyer et al., 2000), and given as $\delta^{18}\text{O}$ and δD in ‰ vs. VSMOW
283 (Vienna Standard Mean Ocean Water) with respective analytical errors of better than
284 $\pm 0.1\%$ and 0.8% . The secondary parameter d-excess (d) is calculated as $d = \delta\text{D} - 8\delta^{18}\text{O}$
285 ($\delta^{18}\text{O}$ (Dansgaard, 1964; Merlivat and Jouzel, 1979).

286 3.2.2 X-ray fluorescence and X-ray diffractometry

287 **To gain information on the variability of the elemental sediment composition, 20**
288 **freeze-dried and milled surface samples were** semi-quantitatively analysed by X-ray
289 fluorescence (XRF) using a novel single sample modification for the AVAATECH XRF
290 core scanner at AWI Bremerhaven. A Rhodium X-ray tube was warmed up to 1.75mA
291 and 3 mA with a detector count time of 10s and 15s for elemental analysis at 10kV
292 (No filter) and 30kV (Pd-Thin filter) respectively. The average modelled chi square
293 values (χ^2) of measured peak intensity curve fitting for the relevant elements were
294 variable, but generally low (Zr = 0.92, Mn = 1.49, Fe = 2.32, Ti = 1.53, Br = 3.65, Sr =
295 4.79, Rb = 4.98, Si = 16.11). Values above 3 were ascribed to suspiciously high count
296 rates from sample PG2133 which was subsequently excluded from XRF
297 interpretation. The relatively low amount of total sample material available did not
298 facilitate the removal of organic matter **prior** to sample measurement and may have
299 contributed to the variable modelled chi square values.

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

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

316

317 3.2.3 Grain-size, carbon and nitrogen analyses

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

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

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

334 To gain additional bioproductivity information we analysed the stable carbon
335 isotope composition $\delta^{13}\text{C}$ of the total organic carbon fraction in 15 samples using a
336 Finnigan Delta-S mass spectrometer. Dried, milled and carbonate-free (HCl treated)
337 samples were combusted in tin capsules to CO₂. Results are expressed as $\delta^{13}\text{C}$
338 values relative to the PDB standard in parts per thousand (‰) with an error of $\pm 0.15\%$.

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

343

344 3.2.4 Diatoms

345 23 samples were prepared for diatom analysis following the standard procedure
346 (Battarbee et al. (2001)). To calculate the diatom valve concentration (DVC) 5×10^6
347 microspheres were added to each sample following organic removal with hydrogen
348 peroxide. Diatom slides were prepared on a hot plate using Naphrax mounting
349 medium. For the identification of diatoms to the lowest possible taxonomic level we
350 used several diatom flora including Lange-Bertalot et al. (2011), Lange-Bertalot and
351 Metzeltin (1996), Krammer and Lange-Bertalot (1986-1991) and Lange-Bertalot and
352 Genkal (1999). For rare taxa (i.e. *Pliocaenicus*) literature research was applied in
353 scientific papers, including Cremer and Van de Vijver (2006) and Genkal et al. (2018).
354 A minimum of 300 (and up to 400) diatom valves were counted in each sample using
355 a Zeiss AXIO Scope.A1 light microscope with a Plan-Apochromat 100 \times /1.4 Oil Ph3
356 objective at 1000x magnification. Identification of small diatom species was verified
357 using a scanning electron microscope (SEM) at the GeoForschungsZentrum
358 Potsdam.

359 During counting of diatom valves, chrysophycean stomatocysts and *Mallomonas*
360 were counted but not further taxonomically identified. Count numbers were used to
361 estimate the chrysophyte cyst to diatom index (C:D) and *Mallomonas* to diatom index
362 (M:D) relative to counted diatom cells (Smol, 1984; Smol and Boucherle, 1985).

363 Diatom valve preservation was measured and calculated as the f-index (Ryves et al.,
364 2001). Diatom valve concentration was estimated as the number of valves per gram
365 dry sediment following Battarbee and Kneen (1982).
366

367 3.2.5 Oxygen isotopes of diatom silica

368 To analyze the oxygen isotope composition from diatom silica ($\delta^{18}\text{O}_{\text{diatom}}$) from 9
369 representative surface samples, a purification procedure including wet chemistry (to
370 remove organic matter and carbonates) and heavy liquid separation was applied for
371 the fraction $<10\ \mu\text{m}$ following the method described in Chaplignin et al. (2012a). After
372 freeze-drying the samples were treated with H_2O_2 (32%) and HCl (10%) to remove
373 organic matter and carbonates and wet sieved into $<10\ \mu\text{m}$ and $>10\ \mu\text{m}$ fractions.
374 Four multiple heavy liquid separation (HLS) steps with varying densities (from 2.25 to
375 2.15 g/cm^3) were then applied using a sodium polytungstate (SPT) solution before
376 being exposed to a mixture of HClO_4 (65%) and HNO_3 (65%) for removing any
377 remaining micro-organics.

378 To remove exchangeable hydrous groups from the diatom valve structure
379 (amorphous silica $\text{SiO}_2 \cdot n\text{H}_2\text{O}$), inert Gas Flow Dehydration was performed
380 (Chaplignin et al., 2010). Oxygen isotope analyses were performed on dehydrated
381 samples using laser fluorination technique (with BrF_5 as reagent to liberate O_2) and
382 then directly measured against an oxygen reference of known isotopic composition
383 using a PDZ Europa 2020 mass spectrometer (MS2020, now supplied by Sercon Ltd.,
384 UK). The long-term analytical reproducibility (1σ) is $\pm 0.25\ \text{‰}$ (Chaplignin et al., 2010).

385 Every fifth sample was a biogenic working standard to verify the quality of the
386 analyses. For this, the biogenic working standard BFC calibrated within an inter-
387 laboratory comparison was used (Chaplignin, 2011). With a $\delta^{18}\text{O}$ value of $+29.0 \pm 0.3$
388 ‰ (1σ) BFC (this study: $+28.7 \pm 0.17\ \text{‰}$, $n=49$) is the closest diatom working standard
389 to the Bolshoe Toko samples ($\delta^{18}\text{O}$ values range between $+22$ and $+24\ \text{‰}$) available.
390 A contamination correction was applied to $\delta^{18}\text{O}_{\text{diatom}}$ using a geochemical mass-
391 balance approach (Chaplignin et al., 2012a; Swann et al., 2007) determining the
392 contamination end-member by analysing the heavy fractions after the first heavy liquid
393 separation resulting in $\text{Al}_2\text{O}_3=16.2 \pm 1.3\ \%$ (via EDX; $n=9$) and $\delta^{18}\text{O}=8.5 \pm 0.8\ \text{‰}$ ($n=6$).

394 3.2.6 Chironomids

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

401 40x magnifications and were mounted in Hydromatrix two at a time, ventral side up,
402 under a 6 mm diameter cover slip. From 48 to 117 chironomid larval head capsules
403 were extracted from each sample, to capture the maximum diversity of the chironomid
404 population. Chironomids were identified to the highest taxonomic resolution possible
405 with reference to Wiederholm (1983) and Brooks et al. (2007). Information on the
406 ecology of chironomid taxa and groups was taken from Brooks et al. (2007), Pillot
407 (2009) and Nazarova et al., (2011;2015;2008;2017b)). Ecological information of the
408 taxa associated to biotopes (littoral, profundal), water velocity (standing, running
409 water), and relation to presence of macrophytes were taken from Brooks et al. (2007)
410 and Pillot (2009). T July optima of chironomids were taken from Far East (FE)
411 chironomid-based temperature inference model (Nazarova et al., 2015). The Far East
412 (FE) chironomid-based temperature inference model (WA-PLS, 2 components; r^2
413 boot = 0.81; RMSEP boot = 1.43 °C) was established from a modern calibration data
414 set of 88 lakes and 135 taxa from the Russian Far East (53–75°N, 141–163°E, T July
415 range 1.8 – 13.3 °C). Mean July air temperature for the lakes from the calibration data
416 set was derived from New et al. (2002). All modern and chironomid-inferred
417 temperatures were corrected to 0 m.a.s.l. using a modern July air temperature lapse
418 rate of 6 °C km⁻¹ (Livingstone et al., 1999;Heiri et al., 2014).

419 3.3 Statistical analyses

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

437 Initially, all environmental variables shown in this paper were tested in a RDA to
438 assess the relationships between the distribution of bioindicator taxa and abiotic
439 habitat parameters. Apart from the chemical and physical parameters of the lake and

440 sediments (Fig. 5), we include in the analysis the presence/absence of the submerged
441 vegetation, distances of the sampling stations from the shore and from the inflowing
442 rivers. All explanatory variables were tested for normality prior to the analyses.
443 Skewness reflects the degree of asymmetry of a distribution around its mean. Normal
444 distributions produce a skewness statistic of about zero. Values that exceeded 2
445 standard errors of skewness were identified as significantly skewed (Sokal and Rohlf,
446 1995). Environmental variables with skewed distributions (gravel, grain-size EM2,
447 smectite-chlorite, mica, K-feldspar) were log transformed and remaining parameters
448 were left untransformed. To reveal intercorrelated parameters, we performed a
449 variance inflation factor (VIF) analysis prior to ordination techniques to only retain
450 non-correlated parameters in further multivariate analysis. Environmental variables
451 with a VIF greater than 20 were eliminated, beginning with the variable with the largest
452 inflation factor, until all remaining variables had values < 20 (ter Braak and Smilauer,
453 2012). A set of RDAs was performed on chironomid and diatom data with each
454 environmental variable as the sole constraining variable. The percentage of the
455 variance explained by each variable was calculated and statistical significance of
456 each variable was tested by a Monte Carlo permutation test with 999 unrestricted
457 permutations. Significant variables ($P \leq 0.05$) were retained for further analysis. DCA,
458 PCA and RDA were performed using CANOCO 5.04 (ter Braak and Smilauer, 2012).

459 Percentage abundances of the chironomid taxa that are absent or rare in the
460 modern calibration data set were calculated at each sampling site in order to see the
461 distribution of the taxa that could potentially hamper a T July reconstruction in case
462 of palaeoclimatic study that could be done at each of the sampling sites. It is known
463 that less reliability should be placed on the samples in which more than 5% of the
464 taxa are not represented in the modern calibration data or more than 5% of the taxa
465 are rare in the modern calibration dataset (i.e., if the effective number of occurrences
466 in the training set, the Hill's N2, is less than 5) (Heiri and Lotter, 2001; Hill, 1973; Self
467 et al., 2011).

468 Species richness and the Simpson diversity on diatom and chironomid data were
469 estimated after sample-size normalization using a rarefaction analysis of Hill numbers
470 in the iNEXT package in R.

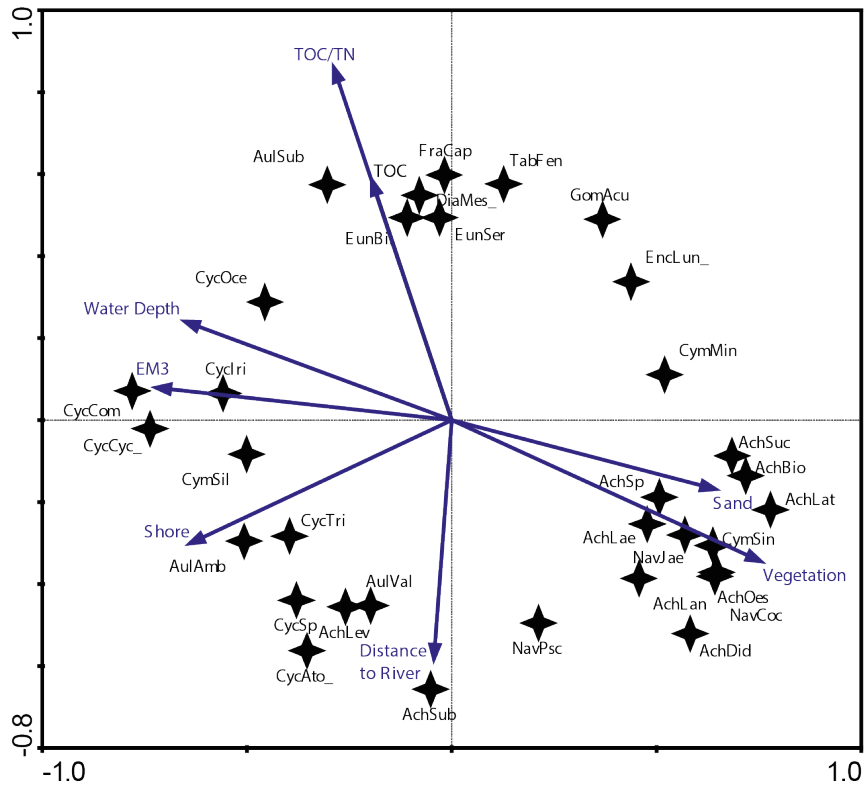
471 To assess the relative contribution of different sedimentary processes to the bulk
472 sediment, such as fluvial or aeolian transport (Wang et al., 2015; Biskaborn et al.,
473 2013b) a statistical end-member analysis on grain-size data was performed using the
474 MATLAB modelling algorithm of Dietze et al. (2012). In this method, individual grain-
475 size populations identified as end-member loadings (vol%, Fig. 4) as well as their
476 contributions to the bulk composition identified as scores (%) were derived by
477 eigenspace analysis, weight transformation, varimax rotations and different scaling
478 procedures.

479 A Pearson correlation matrix of the main important variables (Fig. 5a) was
480 calculated using the basic R core (R Core Team, 2012) and plotted using *corrplot*. To
481 keep false discovery rate below 5% a p-value adjustment was applied prior to
482 assignment of colours using only values that revealed $p < 0.001$ (Colquhoun, 2014).
483 To identify the pattern, the correlation matrix was reordered according to the
484 correlation coefficient. Exceptional sites within the heterogenic lake system lead to
485 disturbance of good correlation coefficients within areas along natural borders, e.g.
486 water depth isobaths. Spatial autocorrelation of variables was estimated using
487 latitudes and longitudes recorded of each sample site and displayed as p values
488 generated by Moran's Autocorrelation Coefficient (R package "ape").

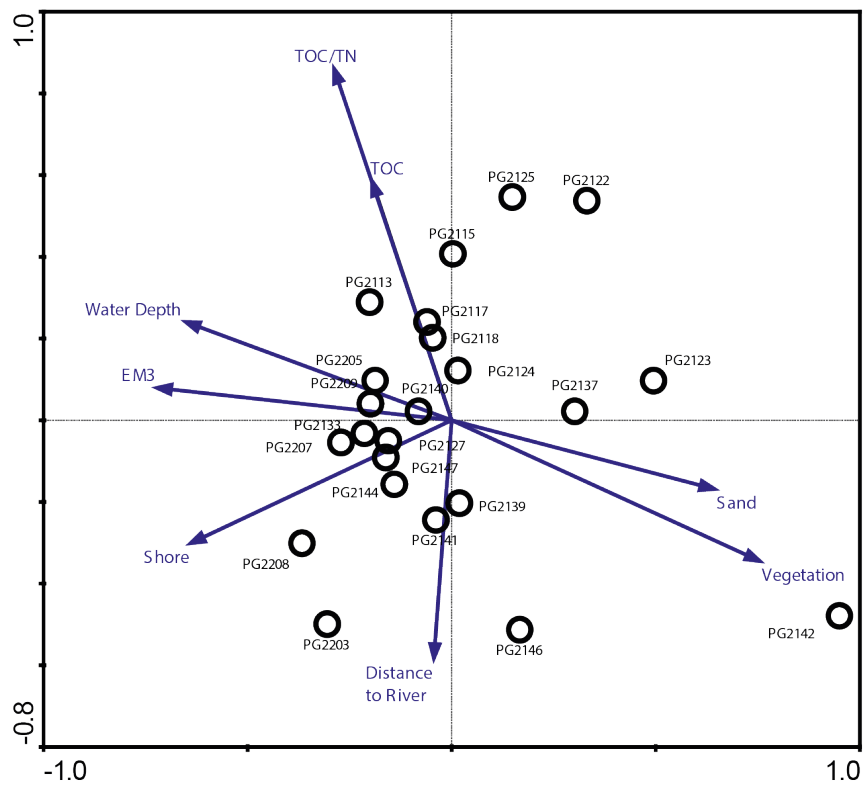
489 To guarantee the sustained availability of our research (Elger et al., 2016), the data
490 will be uploaded and freely accessible in the PANGAEA repository.

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a. RDA, diatom species scores



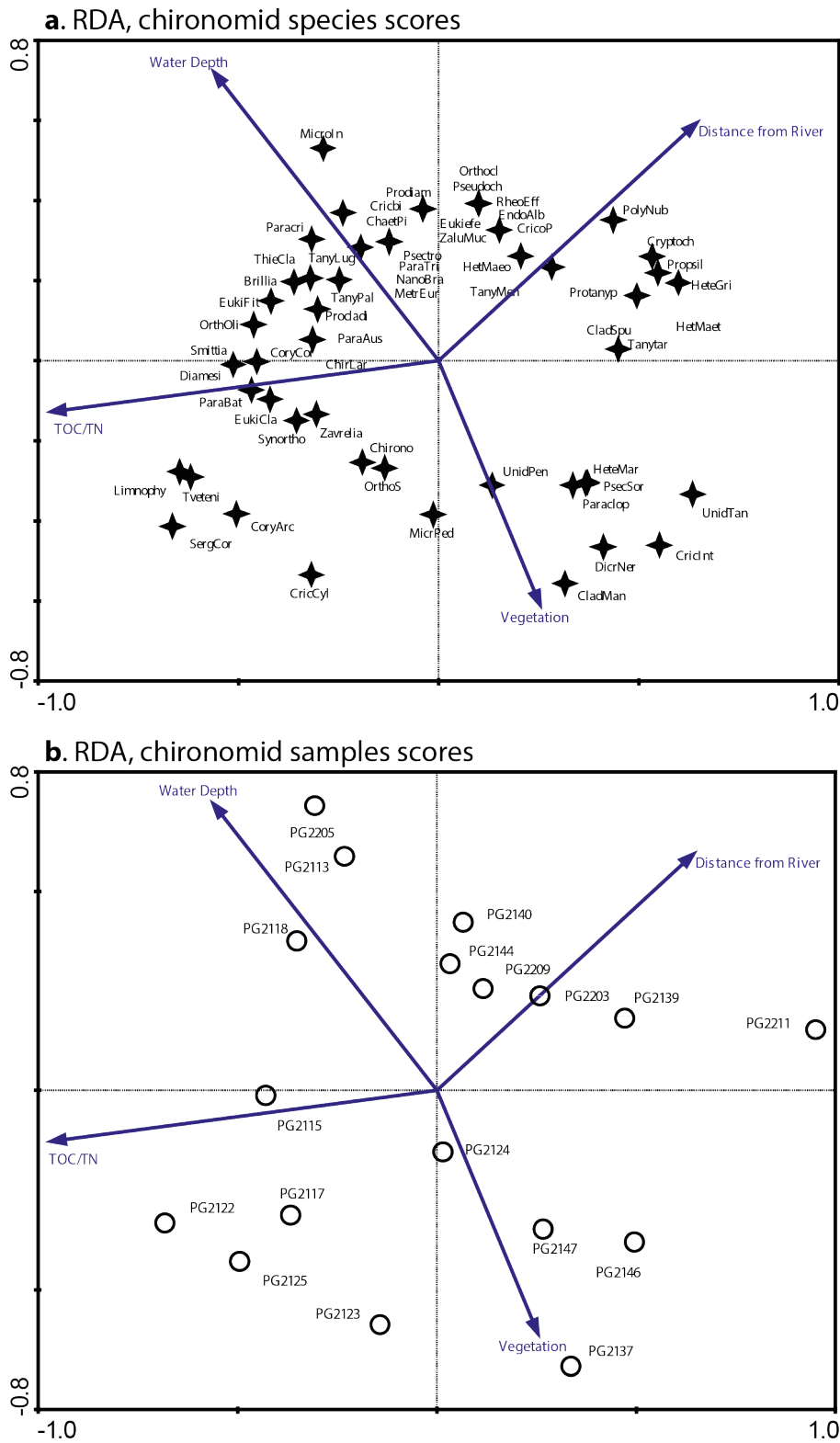
b. RDA, diatom samples scores



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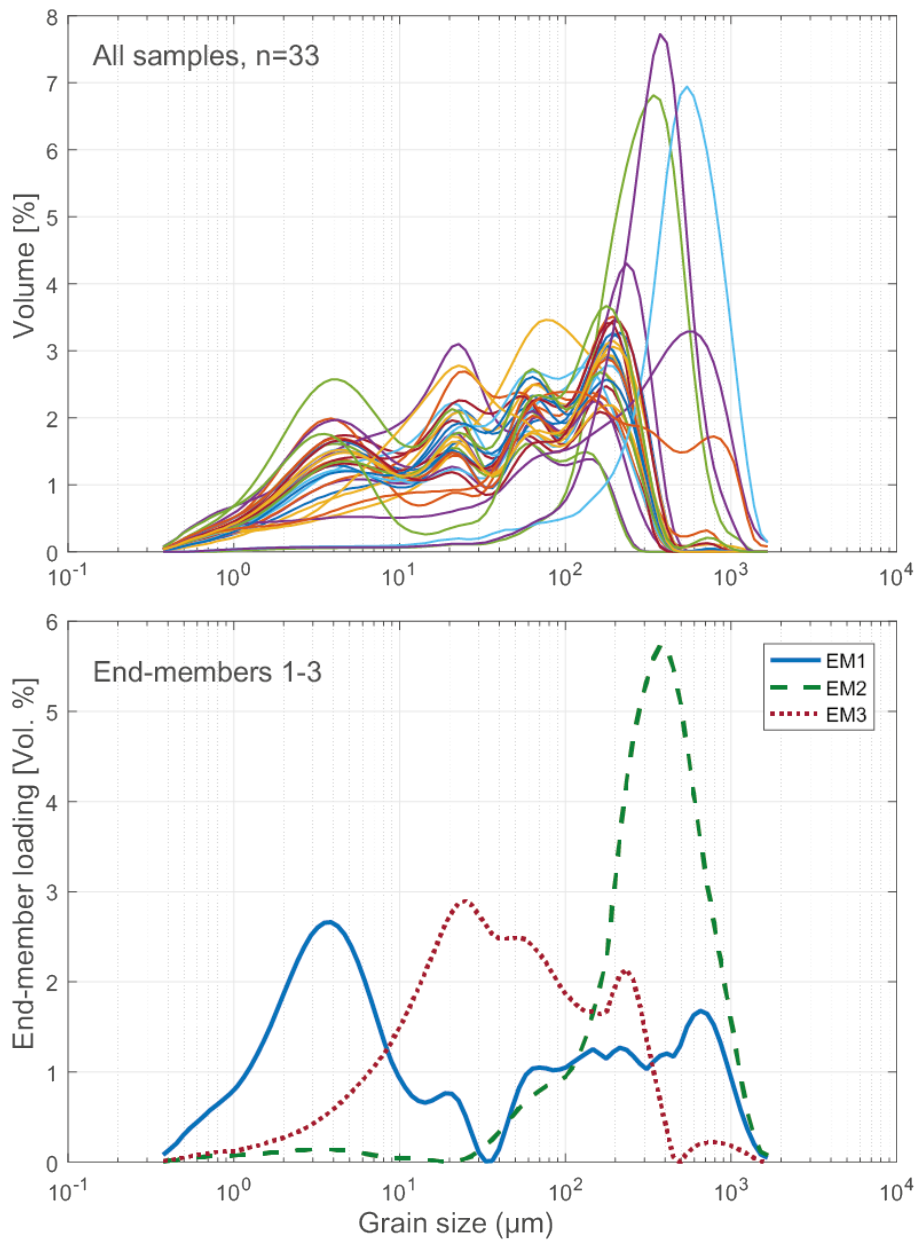
Fig. 2 RDA biplots of diatoms in the surface sediments of Lake Bolshoe Toko. (a) Common diatom taxa and significant environmental variables. (b) Diatom sampling sites and significant environmental variables.

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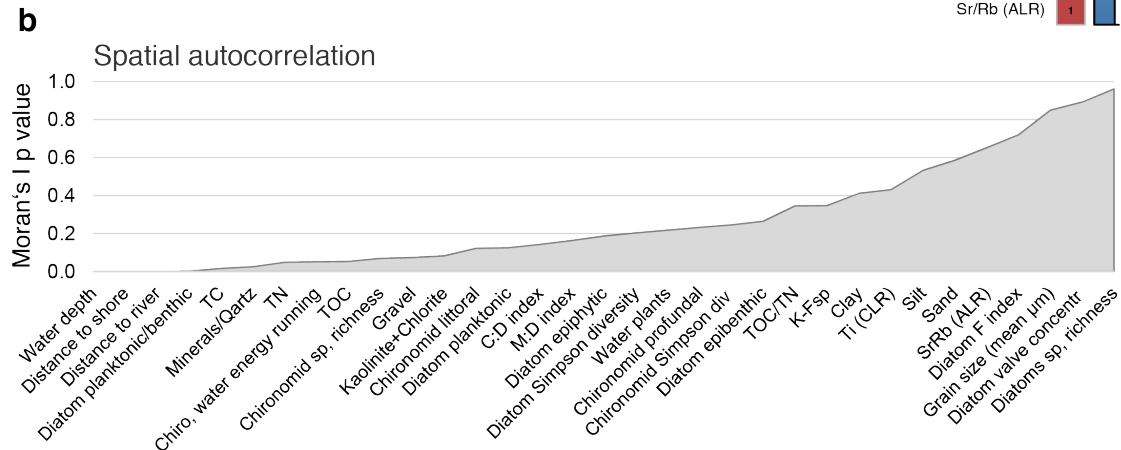
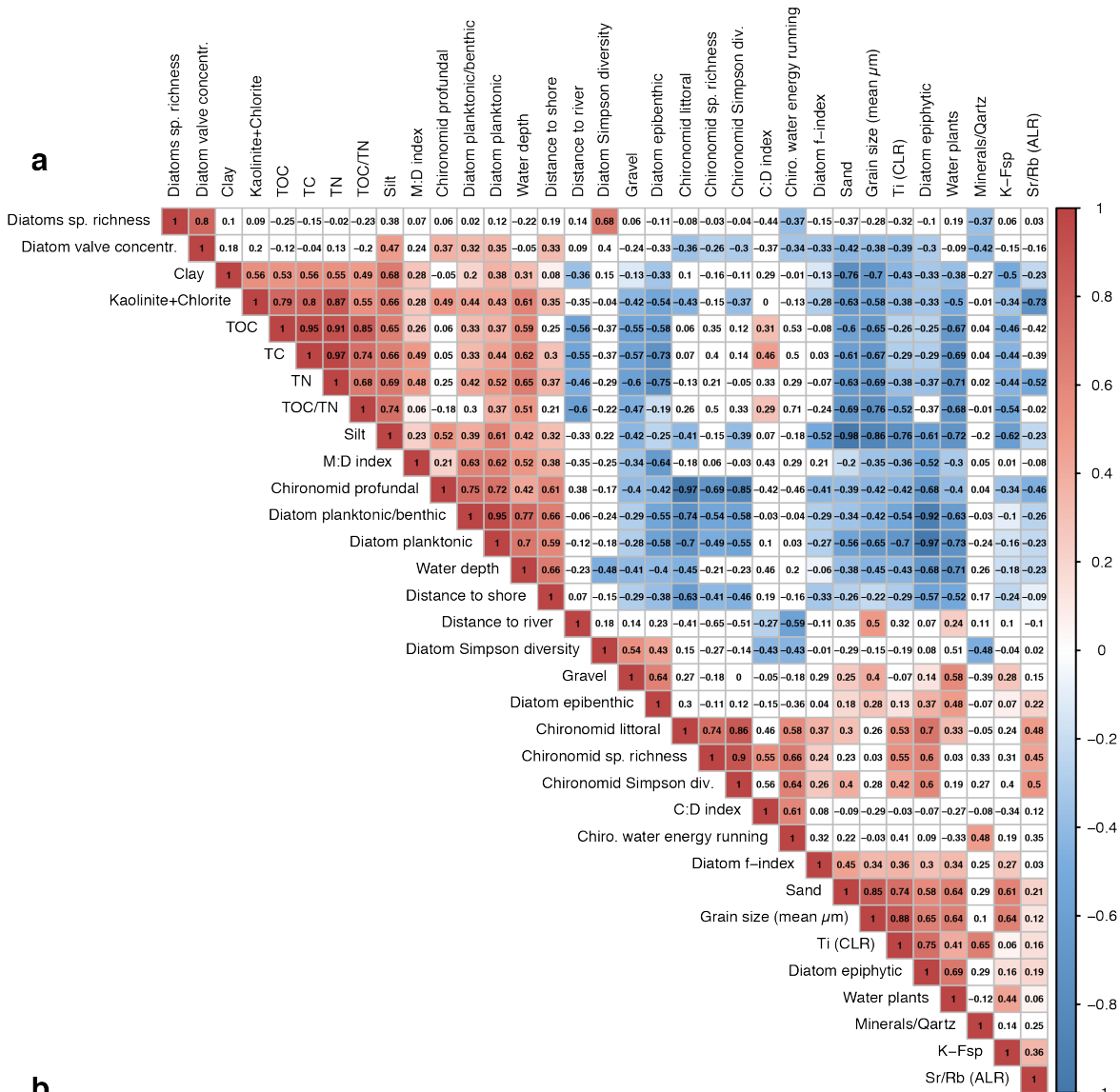
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Fig. 3 RDA biplots of chironomids in the surface sediments of Lake Bolshoe Toko. (a) Common chironomid taxa and significant environmental variables. (b) Chironomid sampling sites and significant environmental variables.



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



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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").

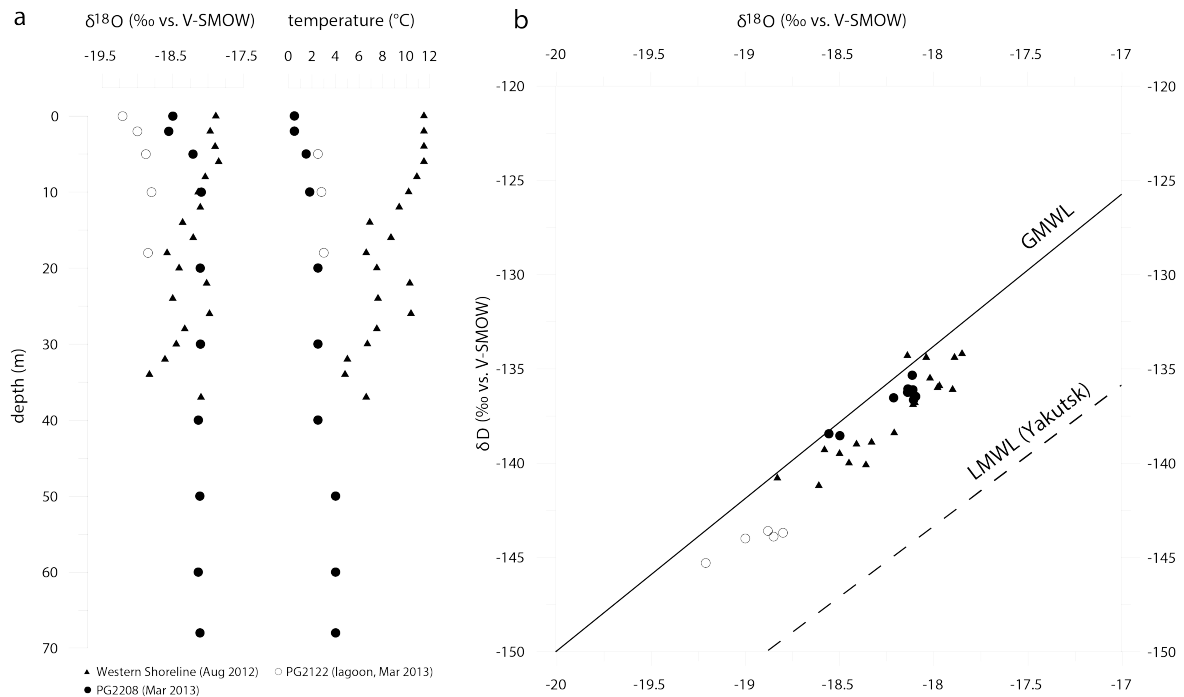
514 4 Results

515 4.1 Water chemistry

516 Sampled surface waters of Bolshoe Toko (Table 1, ESM) were well saturated in O₂
517 (101-113 %) with a pH-values in the neutral range (6.8 – 7.2). Electrical conductivity
518 was very low for all waters (35.1 – 39.1 μS/cm), with slightly higher levels in the lagoon
519 (67.8 μS/cm). Traces of Al (mean 72 μg/L), Fe (mean 46.6 μg/L), and Sr (mean 37.1
520 μg/L) were present but there is no evidence of Pb, Cr, V, Co, Ni, Cu. Mean sulfate
521 concentrations (SO₄²⁻) was 2.35 mg/l on average, with lower values in the lagoon (0.51
522 mg/l). The concentrations of nitrate (NO₃⁻) was 0.76 mg/l, but lower in the lagoon (0.29
523 mg/l). HCO₃⁻ was 37.5 mg/l in the lagoon and 14.9 mg/l on average in the remaining
524 samples. There was no phosphorus in any sample. Overall the water can be
525 characterized as water of the Ca-Mg-HCO₃⁻ type.

526 Surface waters were characterized by mean isotope values of -18.7‰, -140.2‰
527 and 9.5‰ for δ¹⁸O, δD and d-excess, respectively (n=6). The isotopic composition
528 was relatively uniform in the main lake basin (δ¹⁸O = -18.58±0.15‰, δD = -139±0.7‰),
529 while the lagoon (PG2122) exhibited slightly lower δ¹⁸O (δD) values of -19.2‰ (-
530 145‰) (Fig. 6).

531 In March 2013 isotope-depth profiles at PG2208 exhibited a slight isotopic
532 enrichment trend from the surface to ~5 m-depth (~+0.35 ‰ for δ¹⁸O), with a relatively
533 uniform isotopic composition (δ¹⁸O = -18.2 ± 0.2 ‰) below 10 m (Fig. 6a). These
534 subtle variations likely reflect minor isotopic fractionation of surface waters during ice
535 formation in spring, and a well-mixed water column below. Conversely, the August
536 2012 depth profile at the Western Shoreline exhibited a gradual depleting isotope
537 trend below ~6 m depth, with marked variability that closely tracks water temperature
538 changes (Fig. 6a). Meteorological data from the nearby weather station (Toko RS, 10
539 km northward) recorded heavy rainfall for August 2012 (25 mm above the long term
540 mean of 83 mm). Such precipitation events could cause temporary isotopic
541 stratification or a variation in the isotopic signal throughout the water column. Due to
542 ongoing mixing, these variations were then evened. In conclusion, variations in the
543 isotopic composition throughout the August profile rather represent a temporal
544 phenomenon and not characteristic for Bolshoe Toko. In contrast, the lagoon showed
545 a lighter isotope composition (δ¹⁸O = -18.9 ± 0.2 ‰) than the main lake basin. All
546 samples were positioned close to the Global Meteoric Water Line (GMWL, Fig. 6)
547 indicating negligible evaporative effects on lake water isotope composition, and a
548 dominant influence of meteoric inputs both directly (i.e., precipitation) and indirectly
549 (i.e., river inflows). The Local Meteoric Water Line for Yakutsk (dashed line; δD = 7.59
550 * δ¹⁸O – 6.8), based on own data (monthly mean precipitation values between 1997
551 and 2006; n=106; from Kloss (2008), is given for comparison, and indicative for more
552 continental climate conditions.



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Fig. 6: Hydrochemical situation between 2012 and 2013 in lake Bolshoe Toko. a. Profiles of water isotopes ($\delta^{18}\text{O}$) and temperature from different locations taken in August 2012 and March 2013. b. $\delta^{18}\text{O}/\delta\text{D}$ diagram for Bolshoe Toko lake water samples. GMWL is the Global Meteoric Water Line (black line), LMWL is the Local Meteoric Water Line for Yakutsk (dashed line; $\delta\text{D} = 7.59 \cdot \delta^{18}\text{O} - 6.8$) based on own data (monthly mean precipitation values between 1997 and 2006; $n=106$; Kloss (2008)).

561 4.2 Physicochemical sediment composition

562 The typical surficial lake bottom sediments consisted of either brown organic-
563 enriched gyttja or sandy, organic-poor siliciclastic material. Sand contents ranged
564 between 10.2 % and 96.2 % (mean 45.9 %, Fig. 7); silt contents ranged from 3.6 %
565 to 83.3 % (mean 47.1 %); clay contents ranged from 0.2 % to 11.3 % (mean 5.8 %).
566 Gravel was found only in four samples at the north eastern near-shore areas with
567 contents of up to 13.1 %. The mean grain size ranged from 12 to 479 μm (mean 72
568 μm). The mean grain size generally correlated negatively with water depth ($r -0.45$).
569 Mineral grains are composed mainly of quartz (32.7-76.2 %, mean 55.4 %),
570 plagioclase (13.4-39.5 %, mean 26.2 %), K-feldspar (0.0-9.8 %, mean 5.6 %), and, to
571 a smaller degree of pyrite (0.2-5.5 %, mean 3.3 %), hornblende (0.5-10.8 %, mean
572 3.1 %), mica (0.3-2.4 %, mean 1.1 %), and the clay minerals smectite, kaolinite and
573 chlorite (together 0.0-4.6 %, mean 2.0 %). The spatial distribution of minerals (Fig. 7)
574 revealed a generally decreasing gradient of minerals relative to quartz starting from
575 the Utuk river delta (proximal) towards the northern areas (distal).

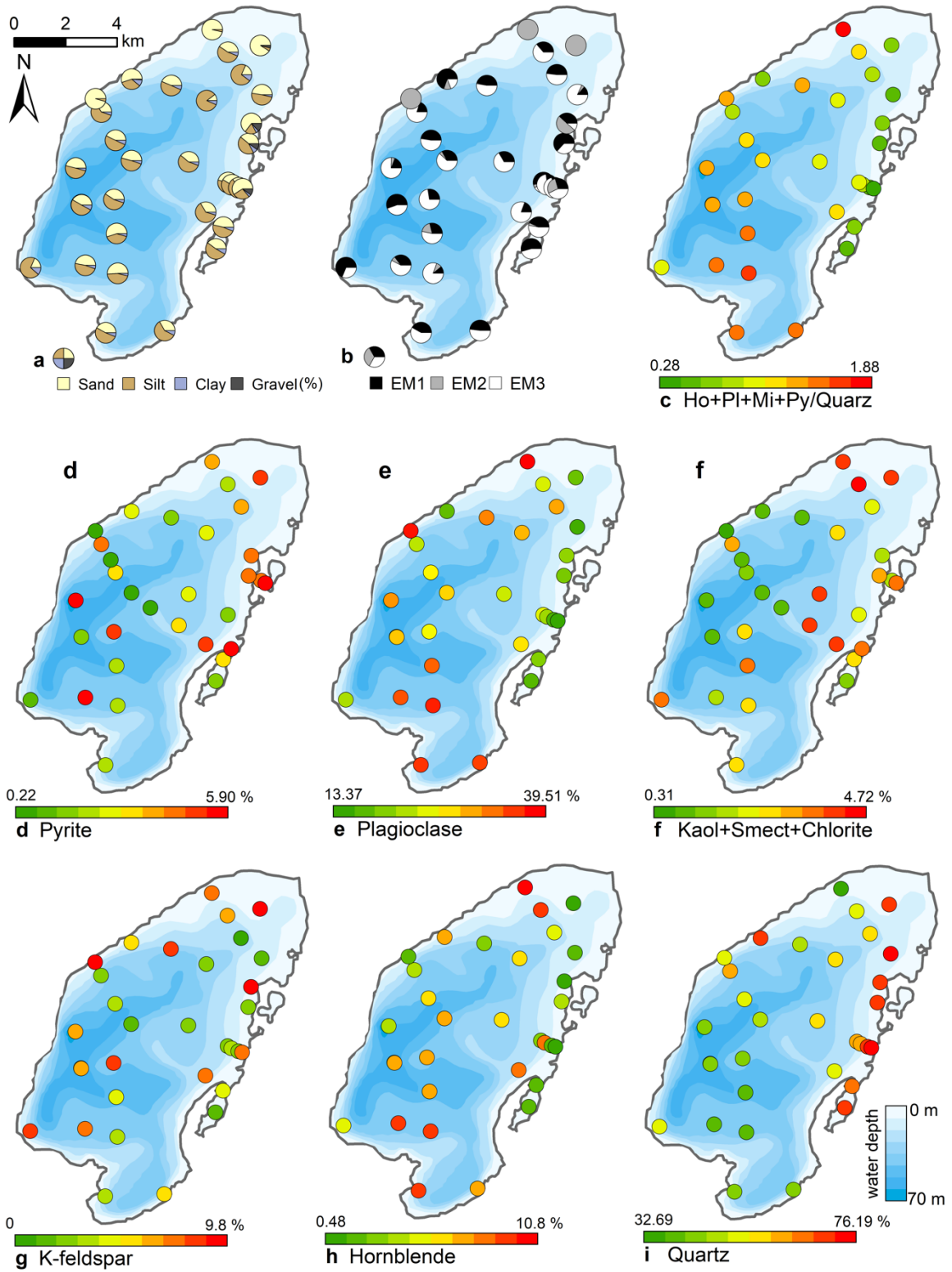
576 The CLR transformed XRF data (Fig. 8) revealed high proportions of Zr and
577 intermediate to high Ti near the Utuk river inflow and at the northern and eastern

578 shore proximal areas. Zr values decreased with increasing water depth towards the
579 lake centre with the exception of the shallow lagoon, where low values were observed.
580 Mn values were highest in the lake centre and at the very deep site at the western
581 steep subaquatic slope, and intermediate at shallow areas close to the shore. A
582 minimum in Mn was found in the lagoon. Fe tends to be highest in the southern part
583 of the lake basin, in the very shallow site in the north, and in the lagoon. Br showed a
584 variable distribution; however, high values were found at 2 sites within the eastern
585 lagoon and correspond to high TOC contents.

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

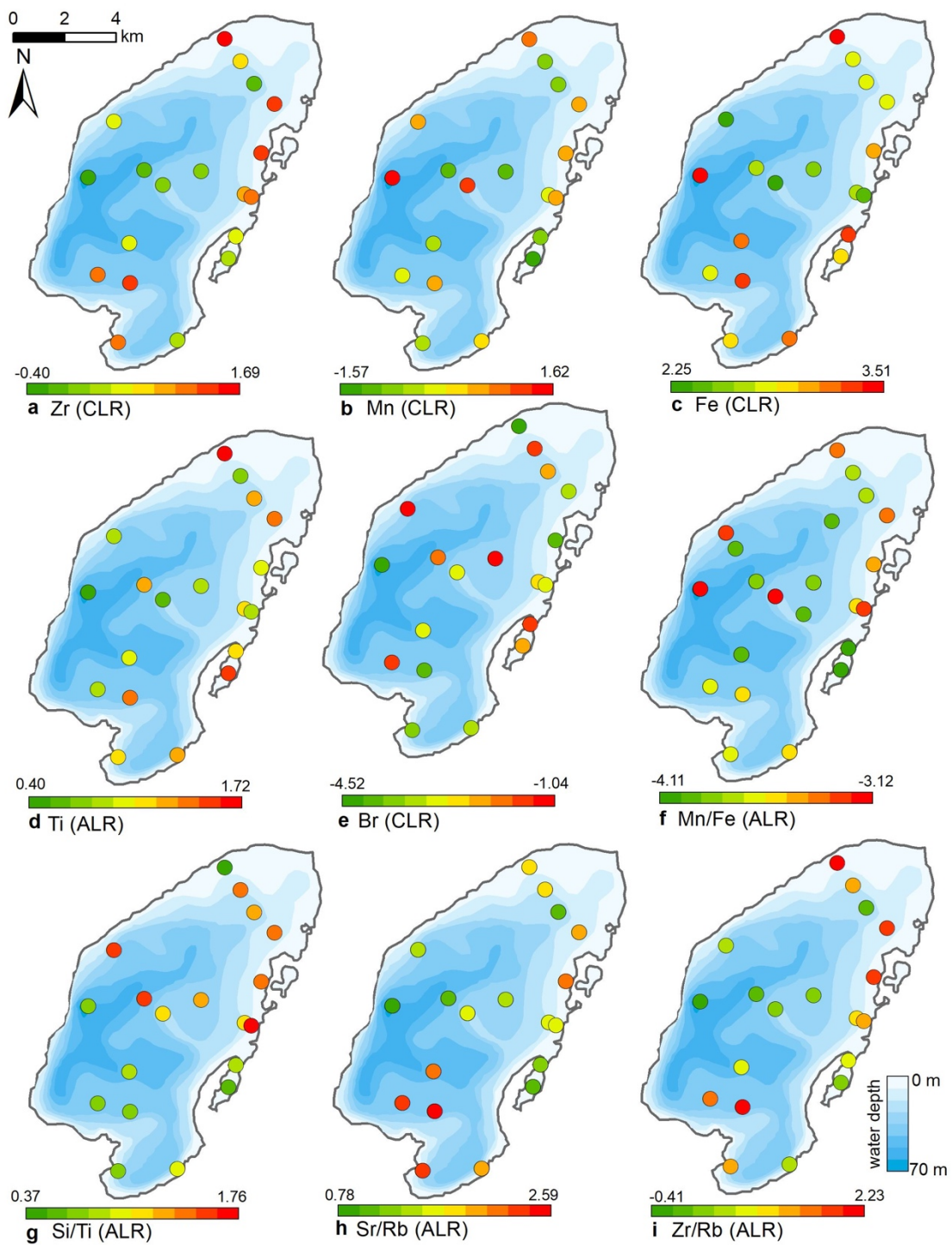
594 The contents of total organic carbon (TOC, Fig. 9) range from 0.1 % to 12.3 %
595 (mean 4.9 %). Maximum values occurred in the eastern area, intermediate values in
596 the central basin, and lowest in the northern shallow water areas. The difference
597 between TOC and total carbon is within the error of the devices and hence no
598 inorganic carbon was detected. TOC contents and the TOC/TN ratios were highest
599 near the Utuk river inflow in the southern part of the lake, in the lagoon, and in
600 proximity to the eastern shoreline. $\delta^{13}\text{C}$ was measured in 15 samples and showed
601 maximum values at the eastern shore (-25.7 ‰) and minimum values elsewhere (-
602 27.8 ‰).

603 Radiocarbon dating of surface sample at site PG2139 (0-0.5 cm) indicated an age
604 of 720 ± 30 ^{14}C yrs BP (Lab-ID: Poz-105350, NaOH-SOL), while PG2207 (0-0.5 cm)
605 suggested 1790 ± 130 ^{14}C yrs BP (Lab-ID: Poz-105355, NaOH-SOL. Considering that
606 the carbon concentration dissolved in sample PG2207 was too low (0.03 mgC), we
607 use sample PG2139 as an estimated reservoir effect to the lake caused by the input
608 of old carbon. Given that a hypothetical sediment surface is just a momentum only
609 collectable as a range of past surfaces and there was more time available for
610 radioactive decay at 0.5 cm depth than at 0 cm, the actual reservoir effect will be a
611 little bit lower and should be confirmed by ^{210}Pb and ^{137}Cs measurements of downcore
612 material before establishing an age depth model for sediment cores.



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Fig. 7 Spatial distribution of the grain-size and mineral compositions of the surface sediments of Lake Bolshoe Toko. **Maps compiled in ArcGIS 10.4. Scales chosen as 10 classes with equal intervals.**



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Fig. 8 Spatial distribution of elements obtained from XRF measurements of surface sediments of Lake Bolshoe Toko. **Maps compiled in ArcGIS 10.4. Scales chosen as 10 classes with equal intervals.**

621 4.3 Diatoms

622 The Bolshoe Toko diatom assemblages were characterized by boreal and arcto-
623 alpine types, and exhibited distinct spatial variations across the lake. In total, 142
624 different diatom taxa were found at 23 sites, dominated by planktonic species
625 *Pliocaenicus bolshetokoensis* (Genkal et al., 2018) (0.0-27.9 %, mean 14.7 %),
626 *Cyclotella comensis* (0.0-23.1 %, mean 10.9 %), and benthic species *Achnantheidium*
627 *minutissimum* (0.0-38.0 %, mean 11.8 %). The relative content of planktonic species
628 (Fig. 9) was 2.0-73.7 % (mean 54.2 %), epiphytic species 19.2-83.9 % (mean 36.4
629 %), and epibenthic species 2.6-23.0 % (mean 9.3 %). The spatial distribution of the
630 main taxa are presented in Fig. 10. Small benthic fragilarioid species were
631 represented by 0.0-27.6 % (mean 7.4 %), Naviculoid species ranged from 3.3 % to
632 12.9 % (mean 7.2 %), and *Aulacoseira* species ranged from 0.0 % to 10.8 % (mean
633 4.5 %). *Pliocaenicus bolshetokoensis* maximum abundance occurred in areas of
634 deepest water such as the southern part of the lake and in the eastern lagoon.
635 *Cyclotella* species were more abundant in the central lake and were not as strictly
636 bound to water depth as *Pliocaenicus*. *Aulacoseira* species displayed no clear spatial
637 pattern, though were less abundant in the northern shallow water areas. *Tabellaria*
638 species were more abundant in shallow near-shore areas than in central and deep-
639 water areas.

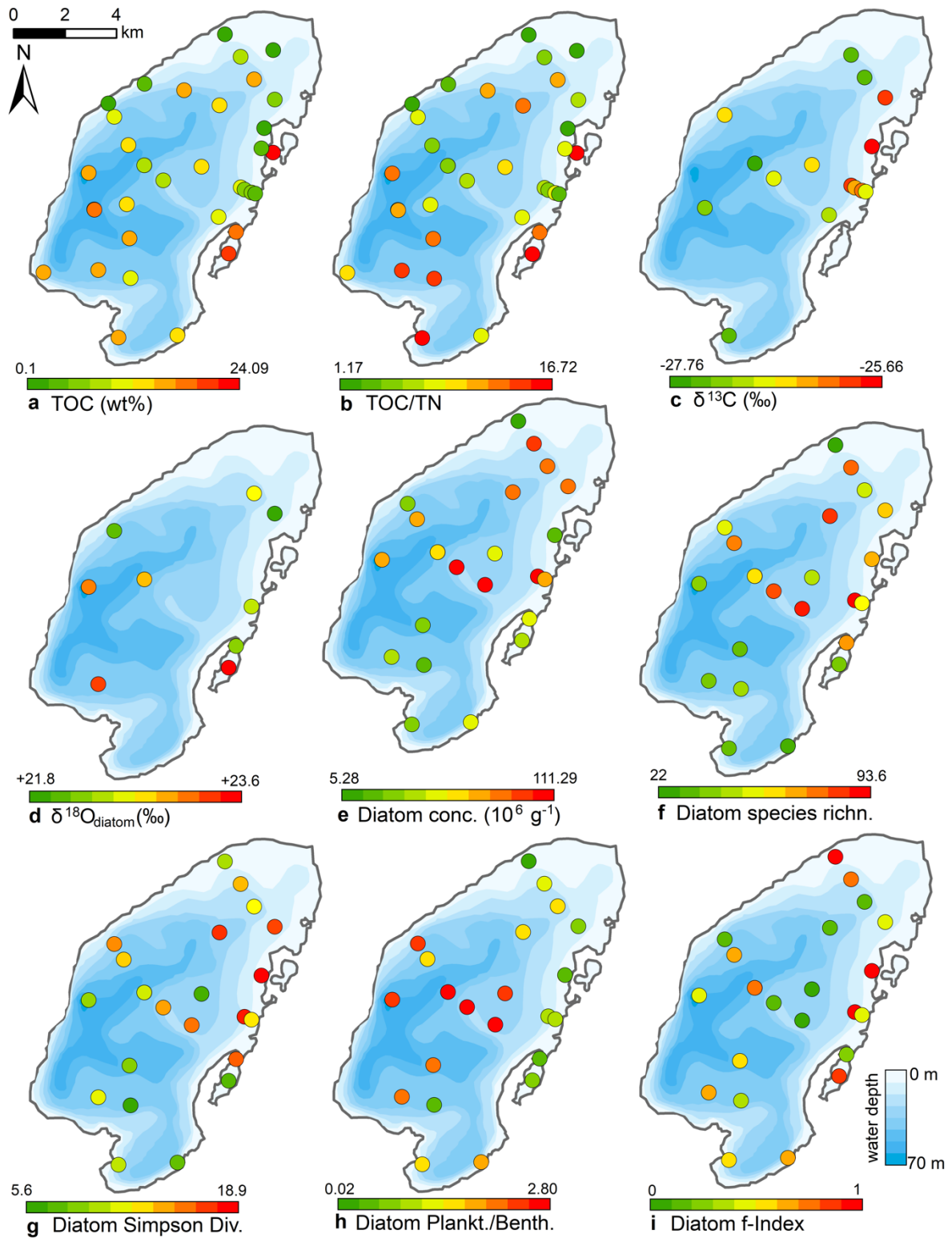
640 Achnantheid (monoraphid) species were most abundant in near-shore areas,
641 especially near the eastern lake terrace. Fragilarioid (araphid) species were common
642 in the southernmost part near the inflow, as well as the lagoon. Other benthic species,
643 i.e. *Navicula*, *Cymbella*, and *Eunotia*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

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

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

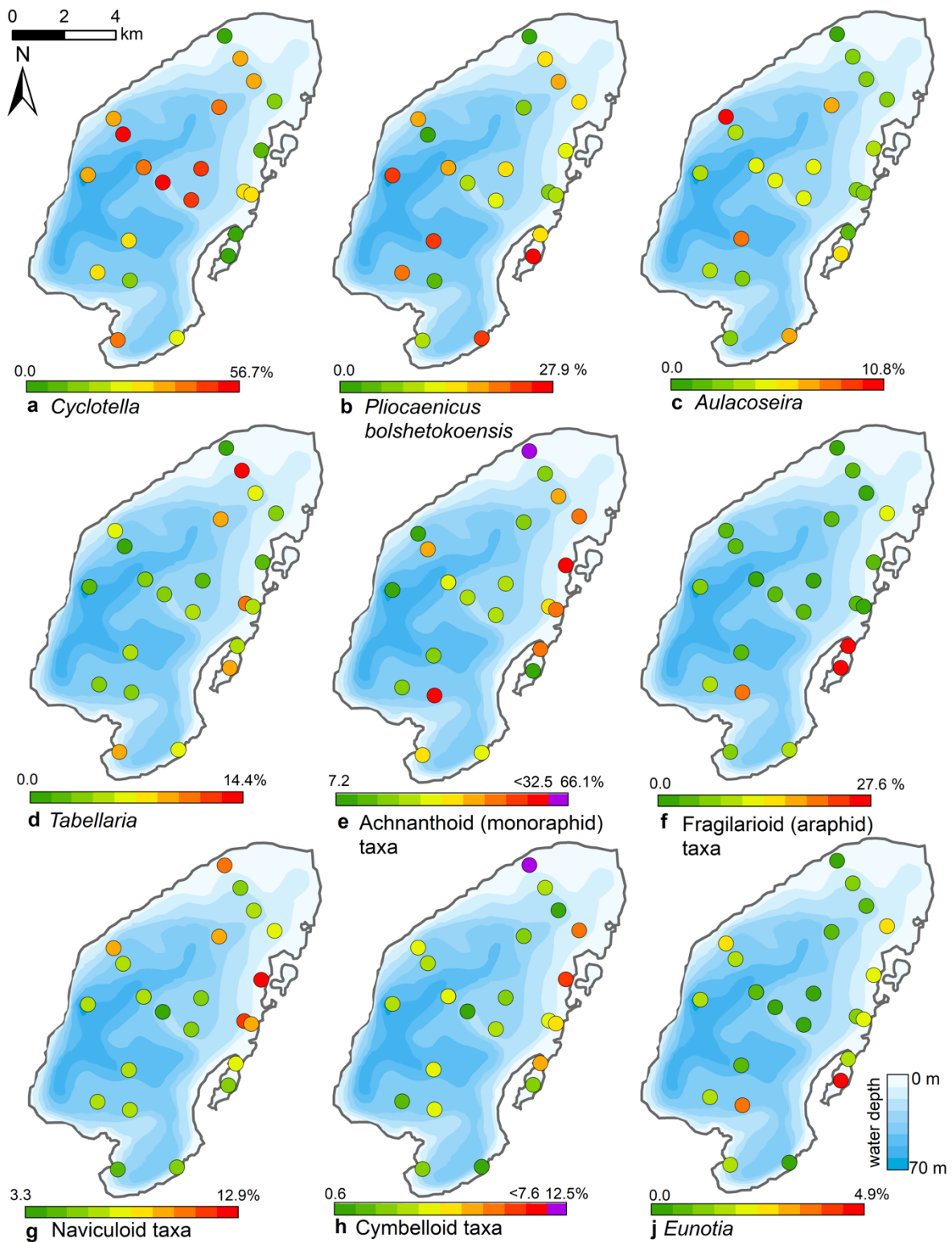
661 variables, 13 parameters with VIFs <20 were left for manual selection with Monte-
662 Carlo test. The analysis revealed 8 statistically significant ($p \leq 0.05$) explanatory
663 variables: TOC/TN, TOC, water depth, distance from River, distance from the shore,
664 presence of vegetation, sand, and EM3, (ESM diatoms, Fig. 2). Eigenvalues for RDA
665 axes 1 and 2 constrained by eight significant environmental variables constitute 81%
666 and 59%, respectively, of the initial RDA, suggesting that the selected significant
667 variables explain the major variance in the diatoms data. The RDA biplots of the
668 species scores and sample scores (Fig. 2) show that diatom species and sites are
669 grouped according to the main environmental forcing responsible for their spatial
670 distribution. The clearest environmental signals in the RDA are related to water depth,
671 habitat preferences and river influence. The upper left quarter of the biplot is strongly
672 influenced by water depth, grain size (EM3), and the ratio between TOC and TN. The
673 species found next to water depth are planktonic *Cyclotella* taxa, whereas *Aulacoseira*
674 is closer to TOC/TN and the total carbon content. In the lower right quarter epiphytic
675 and benthic taxa prevail, i.e. achnanthoid, naviculoid and cymbelloid taxa, associated
676 to the presence of vegetation and coarser (sand) substrate conditions. The distances
677 to river and to shore are crossing the lower left quarter and are associated to different
678 planktonic *Cyclotella* and achnanthoid taxa, while in the opposite direction, with
679 increasing Utuk river influence, fragilarioid taxa, *Eunotia*, *Tabellaria*, and
680 *Gomphonema* prevail, next to the high influence of TOC/TN.

681 Mean surface sediment $\delta^{18}\text{O}_{\text{diatom}}$ was +22.8 ‰ (min. +21.9 ‰, max. +23.6 ‰, $n=9$,
682 Fig. 9) with a standard deviation of ± 0.6 ‰ (1σ). The spatial distribution indicated
683 higher values ~23.3 ‰ in the deeper south-western part of lake (PG2113, 2115, 2005)
684 and lower values ~22.3 ‰ in the shallower northern lake basin (PG2139, 2140, 2147,
685 2209). The two samples from the lagoon exhibited values of 22.2 ‰ in the shallower
686 northern area and 23.6 ‰ in the deeper part. Four samples from the southern part
687 could not be purified well enough and had contamination corrections >2 ‰.
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Fig. 9 Spatial distribution of organic properties and statistical parameters inferred from diatom assemblages in the surface sediments of Lake Bolshoe Toko. **Maps compiled in ArcGIS 10.4. Scales chosen as 10 classes with equal intervals.**



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Fig. 10 Spatial distribution of main diatom taxa in the surface sediments of Lake Bolshoe Toko. Maps compiled in ArcGIS 10.4. Scales chosen as 10 classes with equal intervals. Maps e and h had exceptionally high values of achnantheid and cymbelloid taxa only in the very shallow (0.5 m) site PG2142. These values are shown in purple, indicated separately at the right side of the scales.

700 4.4 Chironomids

701 A total 79 different chironomid taxa were present in the surface sediment samples,
702 of which 48 belong to the subfamily Orthoclaadiinae, 25 to Chironominae (15 from the
703 triba Tanitarsini and 10 from the triba Chironomini), four taxa were from subfamily
704 Diamesinae, and 2 from Tanypodinae.

705 The initial RDA with all environmental variables shows that axes 1 and 2 explain
706 46.7% of variance in the taxon data. Most of the environmental parameters were
707 intercorrelated, and following sequential deletion of all redundant variables, eight
708 parameters with VIFs <20 remained for the further analysis. The manual Monte-Carlo
709 test selection demonstrates four statistically significant ($p \leq 0.05$) explanatory
710 variables: TOC/N, water depth (WD), distance from River, and presence of vegetation
711 (Table 2). Distance from the river and presence of vegetation showed lower than
712 TOC/N and WD level of significance. However, we still use these parameters for
713 interpretation of the chironomid data as there was a clear gap between the 4 chosen
714 parameters ($p = 0.001$ to 0.059) and much higher p values (>0.25) of the following
715 tested parameters (TC, distance to the shore, silt, clay). Eigenvalues for RDA axes 1
716 and 2 constrained by four significant environmental variables were 0.200 and 0.150,
717 respectively, and constituted 70 and 85 % of the RDA performed on all environmental
718 variables (0.289 and 0.177, respectively). This minor difference suggests that the four
719 selected variables sufficiently explain the major gradients in the chironomid data.

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

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

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

740 The lower right group of sites represent eastern shallow littoral with presence of
741 macrophytes. Species richness and proportion of semiterrestrial and littoral taxa in
742 this group is generally low. Littoral taxa were generally phytophilic: *Cricotopus*
743 *intersectus*-type, *C. cylindraceus*-type, *Dicrotendipes nervosus*-type (mesotrophic),
744 and *Cladotanytarsus mancus*-type and *Psectrocladius sordidellus*-type (acid-tolerant
745 mesotrophic). Most abundant profundal taxa here belong to the acid-tolerant
746 *Heterotrissocladius* genera represented by *H. macridus*-type, *H. maeaeri*-type 1 and
747 2, *H. grimschawi*-type (acidophilic), and to the subfamily Tanypodinae represented by
748 *Procladius*. The sites grouped in the opposing upper left quadrant represent lotic and
749 lotic-lentic taxa (*Diamesinae*, *Thenimaniella clavicornis*-type, *Eukiefferiella*
750 *claripennis*-type, *Eukiefferiella fittkaui*-type, several *Orthocladius* taxa).
751

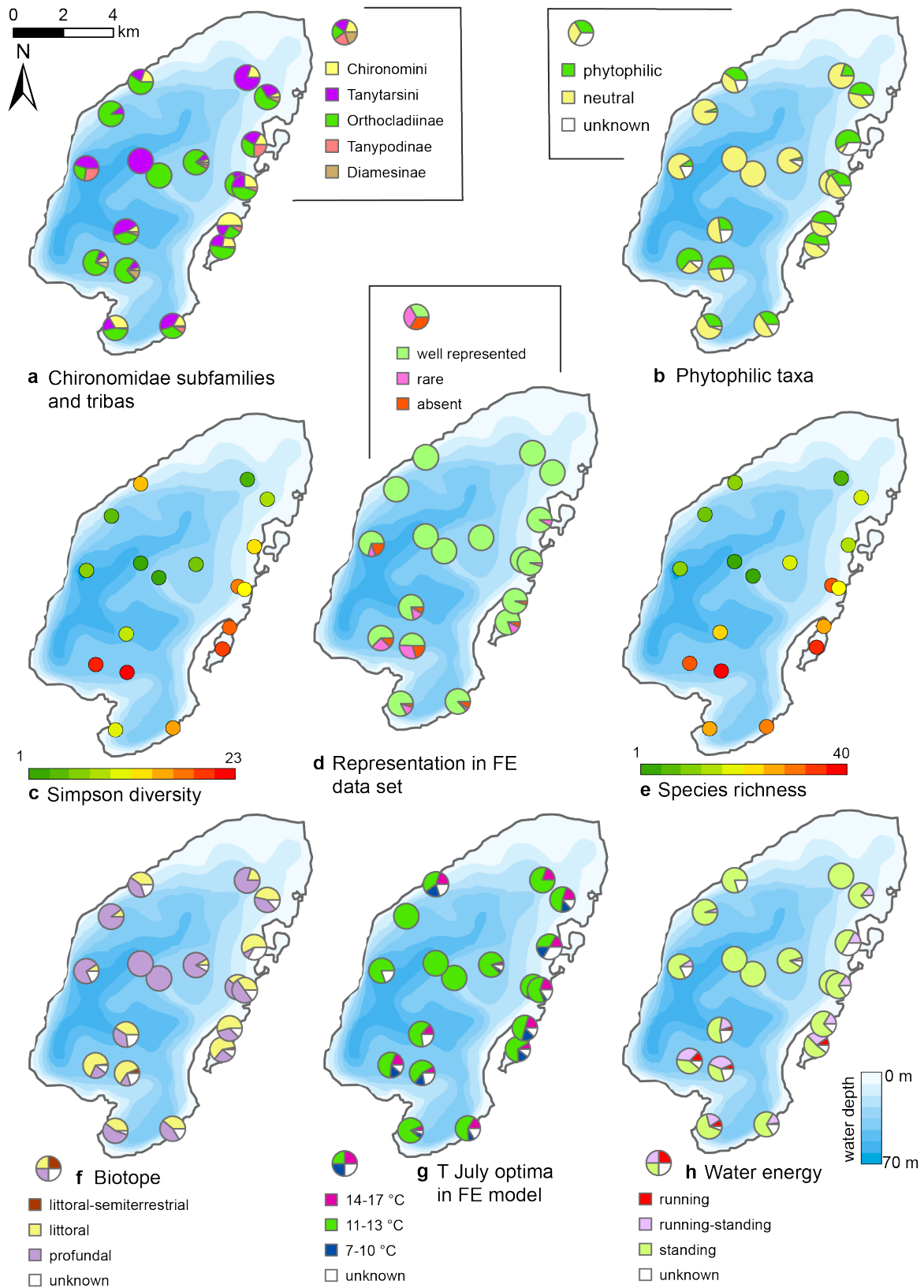


Fig. 11 Spatial distribution of chironomid taxa and inferred statistical parameters in the surface sediments of Lake Bolshoe Toko. **Maps compiled in ArcGIS 10.4. Scales chosen as 10 classes with equal intervals.**

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756 5 Discussion

757 5.1 Spatial control of abiotic and biogeochemical sediment components

758 Sediment-geochemical and physical properties of the uppermost surface of the
759 sediment basin in Bolshoe Toko are spatially variable. Physical properties of particles
760 within the surface sediments depend chiefly on transportation processes and the
761 characteristics and availability of clastic compounds in the lake catchment. The main
762 catchment comprises the Stanovoy mountain range in the south channelled through
763 the Utuk river into Bolshoe Toko. Accordingly, the lake experiences annual input of
764 suspended material through a single source at the Utuk river mouth that likely is at its
765 maximum during spring snow melt (Bouchard et al., 2013). The grain-size data and
766 its end-members (Fig. 4 and 7) indicate that the relative proportions of sand, silt, and
767 clay are somewhat constant in proximity to the Utuk river inflow but change towards
768 the north and at the lake shoreline. Whereas in the central northern lake basin the
769 amount of silt increases, the proportions of sand increase along the northern shoreline
770 on top of the drowned moraine. Gravel is only present in samples near the lake
771 terraces in the east. The constant distribution in the south-central lake basin reflects
772 the river input. Decreasing river influence and hence decreasing water transport
773 energy with increasing distance from the river mouth leads to the observed
774 predominance of finer grain-sizes (silt dominated) samples in the northern central
775 parts of the lake. Sandy samples along the shoreline reflect direct input from the
776 moraines around the northern part of the lake. Other relevant within-lake sedimentary
777 processes include shore-erosion and inwash and winnowing of fine sediment grains
778 by surface currents as well as alluvial processes and debris flows which continue
779 basin ward as subaquatic flows. The restriction of gravel at the eastern shore can be
780 attributed to the availability of source material and suitable transport pathways of
781 coarser clasts from the third moraine. In consequence to the described lateral
782 transport trajectories and local control factors within the lake, there is only weak
783 negative correlation between mean grain size and water depth ($r = -0.45$, Fig. 7 and
784 12).

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

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

806 The distribution of elements from the XRF scanning data suggests strong abiotic
807 relationships to grain-size and mineral distributions. We focus on heavier elements
808 because lighter elements, even though commonly in higher concentrations, show
809 potential contribution from multiple sources. Sr/Rb ratios and Zr are negatively
810 correlated with Kaolinite/Chlorite (r -0.73 and -0.85, respectively). As described in
811 Kalugin et al. (2007), Rb substitutes for K in clay minerals. The Sr/Rb ratios do not
812 however show a significant correlation with grain-size parameters, as found in other
813 studies (Biskaborn et al., 2013b). We assume therefore that Sr, as substituent for Ca,
814 is influenced by multiple minerals represented in different grain-size fractions, i.e. K-
815 feldspar (r 0.45) and Hornblende (r 0.24). Associated to high metamorphic grades in
816 the Stanovoy mountains, Sr is preferentially taken into the K-feldspar phase (Virgo,
817 1968). Conversely, the Zr/Rb ratio correlates well with the sand fraction (r 0.50) and
818 with the mean grain size (r 0.49), but negatively with silt (r -0.54) and clay (r -0.39).
819 We account for this effect by a higher diversity of minerals in the input of the Utuk
820 river supplying the lake basin with mafic Ca-rich metamorphic rocks from the
821 Stanovoy mountains. The strong influence of the Utuk river in the spatial distribution
822 of physicochemical sediment components is further demonstrated by the decreasing
823 gradient of minerals relative to quartz starting from the Utuk river towards the northern
824 lake basin (Fig. 7). The most representative indicator of grain size variations in surface
825 sediments is given by clr transformed values of Ti, which correlate well with the sand
826 fraction (r 0.74) and the mean grain size (r 0.88).

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

834 Mn/Fe ratios have been ascribed to redox dynamics associated to bottom water
835 oxygenation processes (Naeher et al., 2013). In Bolshoe Toko, however, the detrital
836 input of ferrous minerals, i.e. pyrite, suggests that Mn/Fe ratios cannot be directly
837 attributed to redox processes in the surface sediments. This is supported by the
838 correlation of Fe with the sand fraction (r 0.6) and grain-size (r 0.59). Accordingly, we
839 found no significant correlations between Mn/Fe and other abiotic or biotic proxies.

840 Lastly, there is an uncertainty in the spatial distribution of elements measured by
841 XRF techniques. We attribute this lack of clear patterns to: (1) methodological hurdles
842 to apply XRF techniques to surface sediments commonly rich in water and organic
843 material, and (2) multiple sources of the same elements coming from minerogenic
844 input, grain-size differences in individual samples and different intensities of redox
845 processes at different habitat settings. The high variance of elements are therefore
846 representative of the high complexity of this lake system, rather than unequivocal
847 validations or falsifications of the applicability of XRF scanner data as an
848 environmental proxy at Bolshoe Toko.

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851 5.2 Factors explaining the spatial diatom distribution

852 Diatom communities in Yakutia respond rapidly to environmental changes
853 including hydrochemical parameters, water depth, nutrients, and catchment
854 vegetation type (Pestryakova et al., 2018). Planktonic diatom species are ubiquitous
855 across Bolshoe Toko, with a distinct tendency of the ratio between planktonic and
856 benthic species to greater water depths (r 0.77, Fig. 5 and 12), due to the limited
857 availability of light for benthic species (Gushulak et al., 2017; Raposeiro et al., 2018).
858 Especially *Aulacoseira* species were never abundant along the shallower northern
859 and eastern shorelines. The primary difference between the two most abundant
860 genera in the lake is that *Pliocaenicus* exhibits highest abundancies proximal to the
861 inflow and in the southeastern lagoon, whereas *Cyclotella* are more abundant in the
862 lake center and absent in the lagoon. Little is yet known about the new species
863 *Pliocaenicus bolshetokoensis* (Genkal et al., 2018). Our findings suggest factors other
864 than water depth (r 0.39), such as proximity (e.g. nutrient supply) to the Utuk river and
865 small streams, as controlling parameters for bloom intensities of this species.
866 *Cyclotella*, however, is restricted to stratification of the water column and hence more
867 abundant at distance from the river mouth, where incoming water causes turbulence
868 (Rühland et al., 2003; Smol et al., 2005). *Cyclotella* is therefore also believed to benefit
869 from recent air temperature warming trends and will likely increase in abundance
870 (Paul et al., 2010). *Aulacoseira* is a dense, rapidly-sinking tycho planktonic group of
871 species requiring water turbulence to remain in the photic zone (Rühland et al.,
872 2008; Rühland et al., 2015), which explains the lower abundancies in the northern and

873 hydrologically less dynamic zones within the lake. Lightly silicified *Tabellaria* species
874 are known to occur in zigzag planktonic colonies, yet, they also appear as short-
875 valved populations in the benthos (Lange-Bertalot et al., 2011; Biskaborn et al.,
876 2013a; Krammer and Lange-Bertalot, 1986-1991). In Bolshoe Toko, the spatial
877 distribution of *Tabellaria* indicates benthic habitats are more favourable than
878 planktonic.

879 The most common non-planktonic species in Bolshoe Toko belong to achnantheid
880 (monoraphid) genera, of which most species are epiphytic. Epiphytic species exhibit
881 a stronger negative correlation to water depth ($r = -0.68$) than epibenthic species ($r =$
882 0.4), indicating that aquatic plants, in turn controlled by water transparency, pH, water
883 depth and nutrient status (Valiranta et al., 2011), have an important function in the
884 lake ecosystem (Fig. 12). The highest abundance of achnantheid and cymbelloid
885 valves occurs at 400 m distance to the northern shore at a water depth of 0.5 m.

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

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

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

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

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

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

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

960 The spatial distribution of $\delta^{18}\text{O}_{\text{diatom}}$ from the sediment surface **indicates** higher
961 $\delta^{18}\text{O}_{\text{diatom}}$ values at the deeper, south-western part of the lake with a difference of app.
962 1‰ compared to lower $\delta^{18}\text{O}_{\text{diatom}}$ values in the shallower northern part. This **could**
963 **reflect a combination of spatial $\delta^{18}\text{O}_{\text{water}}$ variations, water temperatures, and/or a**
964 **potential species-driven fractionation effect. However, existing studies demonstrate**
965 **no apparent species composition effects on lacustrine $\delta^{18}\text{O}_{\text{diatom}}$ (Bailey et al.,**
966 **2014; Chaplignin et al., 2012b).** Additionally, the sieving step reduces the assemblage
967 before the isotope analysis to a small size interval resulting in a similar species-
968 composition. **Furthermore, dissolution effects in nature and during sample preparation**
969 **could have an impact on $\delta^{18}\text{O}_{\text{diatom}}$. However, we suppose differential dissolution to**
970 **have minor influence on the spatial variability of $\delta^{18}\text{O}_{\text{diatom}}$ at BT samples tackled in**
971 **our study as these are (1) of similar age, (2) have been treated with wet chemistry at**
972 **low temperatures and (3) after preparation do not show any microscopical signs of**
973 **dissolution effects, i.e. a low diatom dissolution index (Smith et al., 2016).**

974 Regarding **$\delta^{18}\text{O}_{\text{water}}$ variability,** waters sampled at the same time in different parts
975 of the lake show a uniform isotopic composition (within $\pm 0.15\text{‰}$) and indicate an
976 **isotopically well-mixed lake. Considering** this is a one-time recording, slight seasonal
977 variation between shallower and deeper parts (for example due to evaporation)
978 cannot be excluded and could account for **some** differences in ^{18}O . **However, lake**
979 **surface evaporation would result in isotopic enrichment and overall higher $\delta^{18}\text{O}_{\text{diatom}}$**
980 **values.**

981 **Alternatively, the** lake temperature in which the diatoms grow has an impact of ca.
982 $-0.2\text{‰}/^{\circ}\text{C}$ on $\delta^{18}\text{O}_{\text{diatom}}$ (Brandriss et al., 1998; Dodd et al., 2012; Moschen et al., 2005).
983 Shallower areas heat up faster especially in the photic zone. The temperature profile
984 near to the western shoreline taken in August 2012 (Fig. 6) shows 12°C at the surface
985 with an average of app. 10°C in the first 15m of the water column decreasing to app.
986 6°C in 30m depth. Although a spatial difference of 5°C in the photic zone for causing
987 a 1‰ shift is rather unlikely, this could account for part of the variation in surface
988 $\delta^{18}\text{O}_{\text{diatom}}$.

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991 5.3 Factors explaining the spatial chironomid distribution

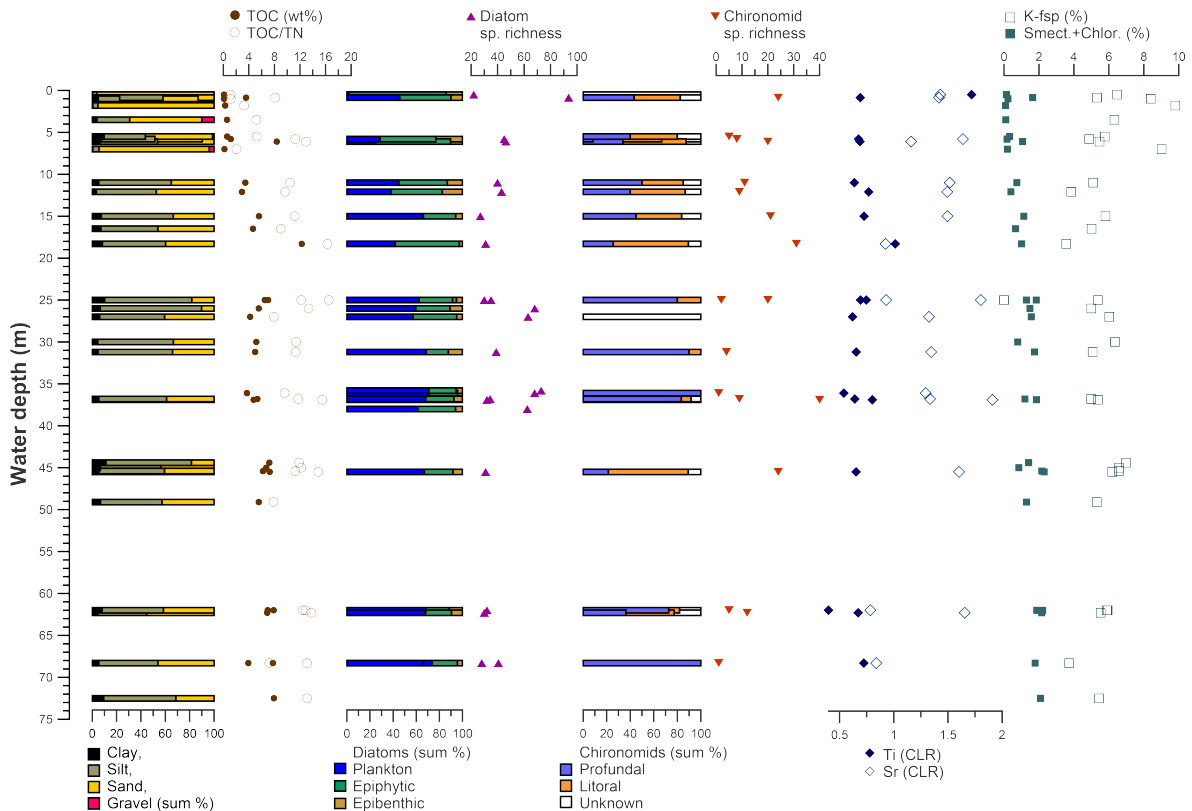
992 The chironomid RDA indicates that spatial variations are primarily influenced by
993 the distribution of tributary rivers. For example, high species diversity is found
994 adjacent to the Utuk river inflow (2117), and in the SE lagoon fed from a small
995 inflowing stream (PG2122). Semiterrestrial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

1000 Species at lentic sites with no tributary influence are primarily controlled by water
1001 depth. Deep profundal sites of the lake have much lower taxonomic richness of
1002 chironomid communities. Higher taxonomic richness at site PG2118 can be explained
1003 by an enriching riverine influence. High proportions of lotic and lotic-lentic taxa lead
1004 to a high taxonomic similarity of this profundal site to littoral sites in the S and SE.
1005 Similarly, in relation to temperature, sublittoral and profundal sites both have much
1006 higher representation of the taxa characteristic of semi-warm conditions and lower
1007 abundancies of the taxa preferring warm and cold conditions. However, high depths
1008 of the sublittoral and profundal sites lead to the development of a poor chironomid
1009 fauna at these sites. High distance from the shore and presumably only weak
1010 transportation of chironomid remains of littoral fauna to the profundal zone could be
1011 another limiting factor for diversity of chironomid communities in the profundal.

1012 Eastern relatively shallow littorals are inhabited by more diverse, phytophilic,
1013 mesotrophic and partly acidophilic fauna with absence of lotic taxa, related to a less
1014 disturbed and turbulent environments and presence of macrophytes. This fauna has
1015 higher abundance of the semi-warm and warm taxa. The presence of meso- to
1016 eutrophic and acidophilic taxa can be attributed to paludification of the shore zone
1017 and decomposition of macrophytes and submerged vegetation in the shallow littoral
1018 (Nazarova et al., 2017b).

1019 It is still debated how spatial and local environmental processes influence the
1020 distribution of chironomids at a small spatial scale in a lake (Luoto and Ojala,
1021 2018; Yang et al., 2017). It is known that within one water body the concentration of
1022 chironomid head capsules can vary from zero to several thousand per 1 cm³ of
1023 sediments (Kalinkina and Belkina, 2018; Walker et al., 1997) depending on factors
1024 such as water depth, rate of sediment accumulation, the hydrological conditions, or
1025 anthropogenic influence. Water depth in particular is a major driving factor of
1026 chironomid assemblages (Ali et al., 2002; Luoto, 2012; Vemeaux and Aleya, 1998) with
1027 depth optima of several species consistent across broad spatial scales (Nazarova et
1028 al., 2011). Chironomid remains from the deepest zones of Bolshoe Toko represents
1029 an assemblage of elements of profundal necrocenosis (Hofmann, 1971) mixed with
1030 secondary components of littoral fauna transported with in-lake hydrological and

1031 sedimentary processes into the profundal from outside. Thus, the re-deposition of
 1032 littoral taxa into the profundal zone is an important factor that affects the final
 1033 composition and abundance of subfossil assemblages. While in small lakes, subfossil
 1034 assemblages from the profundal zone quite adequately reflect the fauna of the entire
 1035 water body (Brooks and Birks, 2001; Walker and Mathewes, 1990), our findings
 1036 support the hypothesis that in large lakes the taphonomy of chironomid communities
 1037 seems to be more complex (Yang et al., 2017; Árvá et al., 2015).
 1038
 1039



1040
 1041 **Fig. 12** Distribution of grain size, organic carbon and nitrogen indices, diatom and chironomid parameters, and
 1042 selected elements and minerals in dependence to water depth in lake Bolshoe Toko.
 1043

1044 **5.4 Lake Bolshoe Toko as a site for palaeoclimate reconstructions**

1045 Compared to small lowland lakes of Central and Northern Yakutia, sedimentary
 1046 processes are quite different in Bolshoe Toko. One reason is the lack of thaw slumps,
 1047 subsidence, and other permafrost related phenomena (Biskaborn et al., 2013b) that
 1048 are typical for shallow thermokarst lake settings across northern permafrost regions
 1049 (Biskaborn et al., 2016; Bouchard et al., 2016; Biskaborn et al., 2012; Schleusner et al.,
 1050 2015; Biskaborn et al., 2013a; Subetto et al., 2017; Biskaborn et al., 2013b).

1051 The Bolshoe Toko mineral composition is primarily influenced by the Utuk river,
 1052 and only samples in extremely shallow areas are influenced by direct shoreline input.

1053 The grain-size signal is influenced by dissolution effects associated with organic
1054 matter and *in situ* growth of diatom valves. Conversely, the coarser fractions parallel
1055 minerogenic compositions and water depth. Accordingly, the grain-size distribution
1056 originated from multiple processes and should only be considered as an
1057 environmental proxy when combined with biotic indicators.

1058 Diatoms are spatially distributed according to their preferred habitat. Aside from
1059 the spatial habitat conditions associated with basin morphology, an additional
1060 consideration is the annual duration and thickness of lake ice-cover (Keatley et al.,
1061 2008;Smol, 1988a). For instance, planktonic communities in Lake Baikal, including
1062 *Aulacoseira* species, are found to grow under the ice if the surface snow properties
1063 (i.e. thickness, density) allow sufficient light penetration (Jewson et al., 2009;Mackay
1064 et al., 2005). Generally, planktonic and benthic diatom species have strategies to
1065 survive in ice-covered lakes by growing in benthic mode, forming resting spores, or
1066 attaching to the ice-cover substrate (D'souza, 2012). Hence, the duration and
1067 presence of ice-cover can significantly impact both changes in assemblage
1068 composition and spatial distribution, particularly including the ratio of planktonic to
1069 benthic diatoms (Wang et al., 2012a;Bailey et al., 2018).

1070 The applicability of chironomids for temperature reconstructions reveals clear
1071 spatial constraints. 22% of the taxa in sites with riverine influence are absent or rare
1072 from the FE mean July chironomid-based temperature inference model (Nazarova et
1073 al., 2015), whereas fewer of these rare/absent taxa occur in the central and northern
1074 littoral, sublittoral and profundal part of the lake (Fig. 4). However, low taxonomic
1075 richness of the profundal zone also hampers palaeoclimatic inferences. Also the
1076 number of chironomid head capsules are generally lower here relative to littoral sites.
1077 Maximum taxonomic diversity in areas influenced by lake tributaries can be explained
1078 by both a taxonomic enrichment from the lake catchment, as well by more favorable
1079 oxygen and nutrient conditions.

1080 The applicability of $\delta^{18}\text{O}_{\text{diatom}}$ as a proxy of past hydroclimate conditions at
1081 Bolshoe Toko is facilitated by the main controls influencing on $\delta^{18}\text{O}_{\text{diatom}}$, which are
1082 here found to be: (1) lake water temperature (T_{lake}) and (2) lake water isotope
1083 composition ($\delta^{18}\text{O}_{\text{lake}}$) (Dodd and Sharp, 2010;Leng and Barker, 2006;Labeyrie,
1084 1974;Leclerc and Labeyrie, 1987). The fractionation between lake water and biogenic
1085 opal can be calculated when comparing $\delta^{18}\text{O}_{\text{lake}}$ (mean: -18.7‰) with recent surface
1086 sediments of Bolshoe Toko lake and their respective mean $\delta^{18}\text{O}_{\text{diatom}}$ (of $+22.8\text{‰}$)
1087 using this isotope fractionation correlation between sedimentary diatom silica and
1088 water as determined by Leclerc and Labeyrie (1987). The mean T_{lake} can be estimated
1089 to ca. 6°C for the photic zone/diatom bloom. This estimate is at the lower end of
1090 summer temperatures between 4.8 and 12°C . The corresponding derived mean
1091 isotope fractionation factor for the system diatom silica–water $\alpha = 1.0424$ matches the

1092 fractionation factor for sediments proposed by Juillet-Leclerc and Labeyrie (1987) well
1093 ($\alpha_{(\text{silica-water})} = 1.0432$).

1094 Additionally, as lacustrine $\delta^{18}\text{O}_{\text{diatom}}$ also reflects the isotopic composition of the
1095 water where the diatoms grow ($\delta^{18}\text{O}_{\text{lake}}$), $\delta^{18}\text{O}_{\text{diatom}}$ typically reflects meteoric inputs
1096 associated with precipitation and riverine inflows (Fig. 6b). For example, existing
1097 studies have used lacustrine $\delta^{18}\text{O}_{\text{diatom}}$ to reconstruct past changes in precipitation
1098 amount and seasonality, the precipitation/evaporation balance, spring snow melt
1099 inputs, and synoptic-scale shifts in atmospheric circulation (Bailey et al., 2015; Meyer
1100 et al., 2015; Bailey et al., 2018; Kostrova et al., 2013; Mackay et al., 2013). It is
1101 envisaged that changes in $\delta^{18}\text{O}_{\text{diatom}}$ through time at a single site in Bolshoe Toko will
1102 yield insights into the long-term air temperature and paleohydrological history of the
1103 region.

1104 Positive feedback mechanisms between benthic algae and chironomid larvae in
1105 benthic ecosystems are well-documented (Herren et al., 2017). Chironomids in
1106 Bolshoe Toko, however, showed less significant correlations with benthic diatom
1107 species, but weak correlations with planktonic species and lake attributes associated
1108 to benthic habitats and water depth, highlighting the potential of chironomids for
1109 independent water depth and temperature reconstruction in future sediment core
1110 studies (Nazarova et al., 2011).

1111 High correlation coefficients between organic carbon and *Pliocaenicus*
1112 *bolshetokoensis* (0.66) and silt (0.65) suggest that the accumulation of organic matter
1113 and intermediate grain-size fraction is, to a certain degree, controlled by the
1114 productivity of siliceous microalgae (Biskaborn et al., 2012). A strong contribution of
1115 plankton indicates that TOC/TN ratios can provide insights in the relative influx
1116 between land and water plants (Meyers and Teranes, 2002). The relatively weak
1117 correlation between TOC/TN ratios and water depth (0.51 r), demonstrates the
1118 accuracy limits of TOC/TN as a proxy for relative lake level changes. This is caused
1119 by transport and accumulation of allochthonous organic matter in proximity to the Utuk
1120 river. Furthermore, correlations between TOC/TN and TOC, as well as negative
1121 correlations with grain size indicators suggest diagenetic alteration (i.e. loss) of
1122 nitrogen in the surface sediments (Galman et al., 2008).

1123 The distinct difference between two samples along the subaquatic slope near the
1124 western shore (diatoms, minerals, organics) indicates redistribution of sediment.
1125 Downslope transport of surface layers over the time could lead to redistribution of old
1126 material into the deepest parts of the basin. Due to higher accumulation rates, a
1127 sediment core from the deepest part of the basin would potentially provide a higher
1128 temporal resolution, but also a higher risk of repositioned sediment layers. On top of
1129 redistribution processes, hump-shaped relations between lake depth and species
1130 diversity observed in other studies suggest that the total subfossil species
1131 assemblages is better represented at intermediate depths than at the maximum depth

1132 (Raposeiro et al., 2018). A coring site at intermediate depth in the shallow northern
1133 and sedimentologically calm sector of the basin would enable the tracking of different
1134 river and glacial influences, and offers greater chances of undisturbed successions of
1135 bioindicator time series.
1136

1137 6 Conclusions

1138 Our study on the within-lake variance of environmental indicator data and its
1139 attribution to habitat factors improves the understanding of lake-internal filters
1140 between environmental forcing and the resulting sediment parameters of Lake
1141 Bolshoe Toko and comparable boreal, cold, and deep lakes. We found that the spatial
1142 variabilities of biotic ecosystem components are mainly explained by static habitat
1143 preferences as water depth and river distance. Abiotic sediment features are not
1144 symmetrically distributed in the basin but vary along restricted areas of differential
1145 environmental forcings (e.g. river input, rocky shore, steep shore, shallow shore).
1146 They depend, in addition to water depth and riverine activity, to multiple interacting
1147 factor, such as catchment characteristics, geochemical sediment diagenesis and
1148 hydrochemical dynamics. Our main findings can be highlighted as follows:
1149

- 1150 • The lake water of Bolshoe Toko can be characterized as Ca-Mg-HCO₃-Type
1151 water. It is well saturated in O₂, neutral to slightly acidic, showing a low
1152 conductivity and corresponding ion concentrations suggesting unpolluted
1153 freshwater conditions. Lake Bolshoe Toko is a cold, polymictic, oligotrophic,
1154 open through-flow lake system and can be regarded as an undisturbed
1155 ecosystem.
- 1156 • Water depth is a strong factor explaining the spatial variability of diatoms and
1157 chironomids. The proportions of planktonic to benthic diatoms and profundal
1158 to littoral chironomids serve as a reliable lake level proxy.
- 1159 • The diatom assemblage is dominated by planktonic species, i.e. *Pliocaenicus*
1160 *bolshetokoensis*, which is unique for this lake, and more common plankton
1161 such as *Cyclotella* and *Aulacoseira*, as well as non-planktonic taxa, such as
1162 *Achnanthydium*. Diatom species richness and diversity is higher in surface
1163 sediments in the northern part of the basin, associated to shallower waters and
1164 the availability of benthic and periphytic niches.
- 1165 • The $\delta^{18}\text{O}_{\text{diatom}}$ values ($22.8 \pm 0.6\text{‰}$) show slight spatial variations with higher
1166 values in the deeper south-western part of the lake probably related to water
1167 temperature differences in the photic zone during the main diatom bloom. The
1168 silica–water isotope fractionation is suitable for further downcore investigations
1169 for assessing paleo-hydrological information and potential air-temperature
1170 changes in the region.

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- 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 ($\delta^{18}\text{O} = 18.2 \pm 0.2 \text{ ‰}$) 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, $\delta^{18}\text{O}_{\text{lakewater}}$ is directly linked to $\delta^{18}\text{O}_{\text{precipitation}}$.
 - 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. $\delta^{13}\text{C}$ (mean -26.8 ‰) indicate dominance of C₃ 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. $720 \pm 30 \text{ }^{14}\text{C}$ 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.

1204 Data Availability

1205 All data used in this study will be available online at PANGAEA.
1206

1207 **Supplement**

1208 The supplementary material related to this study will be available online at
1209 Copernicus.

1210 **Author contributions**

1211 BKB **conceived the study**, led the laboratory analyses and the writing of the
1212 manuscript. LN conducted statistical analyses and contributed with ecological
1213 chironomid expertise. LAP led the Russian team during field work and contributed
1214 with ecological diatom expertise. LS conducted chironomid analysis. KF conducted
1215 diatom analyses. HM conducted water chemistry analyses. BC **and HLB** analysed
1216 diatom opal oxygen isotopes. SV conducted the XRF analysis. RG and EZ retrieved
1217 surface samples during field work and helped with translation of Russian literature
1218 and geographical expertise of the study area. RW conducted grain-size analyses
1219 including end-member modelling. GS conducted XRD analyses. BD was the leader
1220 of German expedition team and contributed with sedimentological expertise.

1221

1222 **Competing interests**

1223 The authors declare that they have no conflict of interest.

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