

1 **Diatom community responses to long-term multiple stressors** 2 **at Lake Gusinoe, Siberia**

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26 deposition

27 **Abstract**

28 The threat of multiple anthropogenic stressors on global freshwater systems impacts ecological
29 structure and function necessary to maintain the welfare of freshwater ecosystems. In order to
30 properly manage freshwater ecosystems, we must have a better understanding of the ecological
31 response to human-induced stressors, and in multiple stressor environments. Where long-term
32 observational records are scarce or non-existent, paleolimnology provides a means to
33 understanding ecological response to long-term stress. Lake Gusinoe is a large, deep lake in
34 continental southeast Siberia, and has been subject to multiple human-induced stressors since the
35 19th century. In the present study, changes in diatom assemblages since the late-17th century were
36 reconstructed from a Lake Gusinoe sediment core, to increase our understanding of the
37 response of primary producer communities to centuries of environmental change. Records of
38 anthropogenic contamination of Lake Gusinoe (including spheroidal carbonaceous particle,
39 trace metal and element records) indicate early increases in regional and local development c.
40 1920. Early diatom assemblages were dominated by *Aulacoseira granulata*, which declined
41 beginning in the 18th century, likely as a response to hydrological change in the Gusinoe basin
42 due to regional climate warming following the termination of the Little Ice Age. Lake Gusinoe
43 diatom assemblages changed more profoundly since the early-20th century, as a result of multiple
44 anthropogenic stressors, including nutrient influx, aquaculture, and wastewater discharge from
45 the Gusinozersk State Regional Power Plant. Current diatom assemblages are dominated by
46 nutrient-rich species, including *Fragilaria crotonensis* and *Asterionella formosa*, and *Lindavia*
47 *ocellata*. Significant diatom compositional turnover was observed at Lake Gusinoe since the
48 19th century. Evidence of continued enrichment at Lake Gusinoe is likely due to continued

49 aquaculture in the lake, and suggests potential interactive effects of warming regional
50 temperatures and increasing nutrients (eutrophication) at Lake Gusinoye.

51 **1. Introduction**

52 Freshwater lakes are under threat globally from interacting stressors, including contamination
53 from human activity (Malaj *et al.* 2014), enrichment from catchment agriculture (Mekonnen &
54 Hoekstra 2018) and aquaculture (Legaspi *et al.* 2015), increased warming of surface waters from
55 climate change (O'Reilly *et al.* 2015), increased deposition of reactive nitrogen (Nr) (Bergstöm
56 & Jansson 2006), increased hypoxia due to human activities (Jenny *et al.* 2016), alterations to
57 local biodiversity from biological introductions and invasions (Gallardo *et al.* 2016),
58 hydrological modifications (Kominoski *et al.* 2018), and falling water levels from abstraction
59 and shifting precipitation patterns (Wurtsbaugh *et al.* 2017). Due to long-range transport of
60 pollutants, it is unlikely that any lake is now truly pristine (e.g. Durnford *et al.* 2010). Lakes also
61 provide freshwater and protein for human populations to survive, and therefore the history of a
62 lake is often intertwined with the regional history of human activity (Dodds *et al.* 2013; Jackson
63 *et al.* 2016a). However, even though the provision of freshwater ecosystem services is
64 fundamental to human well-being, ecosystem functions are often compromised by human
65 activity, threatening the health of the lake itself. Understanding which threats are most important
66 for individual lakes is crucial in managing freshwater ecosystems, but because different threats
67 have different causes, pinpointing when they first started to have major impact on an ecosystem
68 needs a long-term perspective (e.g. see Dubois *et al.* 2018 for a review). While long-term
69 monitoring can provide some of these answers, such records are rather rare and not available for
70 most lacustrine ecosystems. For example, although there are several long-term monitoring
71 networks (e.g. The International Long-term Ecological Research (ILTR) network (Vanderbilt &

72 Gaiser 2017) and the Global Lake Ecological Observatory Network (GLEON) (Rose *et al.*
73 2016), none of these are found in Russia. However, through careful exploitation of lake
74 sedimentary archives, preserved microfossils and chemical constituents, it is possible to
75 reconstruct environmental impacts on lake ecosystems through time, whether they be caused by
76 atmospheric pollutants, point source disturbance from agriculture and aquaculture, or impacts of
77 global warming, leading to alterations to local ecology and biodiversity. Palaeolimnological
78 records can also provide useful insights into natural variability and baseline conditions before
79 human-environment interactions (Dubois *et al.*, 2018).

80 One of the most important river basins in Russia is the Lake Baikal Basin in southeast Siberia,
81 which contains the world's oldest, deepest and most voluminous lake, which is primarily fed by
82 the Selenga River. The Selenga River originates in northern Mongolia and is the largest tributary
83 feeding into Lake Baikal, accounting for over 60% of hydrological flow into the lake (Shimaraev
84 *et al.* 1994). But because over 75% of the plants and animals found in Lake Baikal are endemic,
85 understanding and managing pollution inputs into the lake via rivers such as the Selenga are
86 fundamentally important to its retaining its World Heritage Site status. Geographically, much of
87 the Lake Baikal Basin is positioned along the mountain taiga forest - steppe ecotone, a semi-arid
88 transition zone sensitive to climate change (Wu *et al.* 2012) and fire (Tchebakova *et al.* 2009).
89 The ecotone is underlain by extensive sporadic to semi-permanent permafrost, which together
90 with the taiga forest, represent carbon stores vulnerable to fire and oxidation. The basin sits in
91 one of the most continental regions, but also one of the fastest warming regions on the planet,
92 leading therefore, to the potential for significant ecosystem change.

93 The Lake Baikal Basin also contains the second and third largest cities in Siberia, Irkutsk and
94 Ulan Ude, the latter being the hub of economic activity in southeast Siberia, one of Russia's most

95 polluted cities, and through which the Selenga River flows. Smaller industrial centres in
96 southeast Siberia, such as Selenginsk and Gusinozersk (Figure 1), are also highly polluted, due
97 to open cast mining of brown coal, mining for aluminium and molybdenum, and coal-fired
98 power generation in Gusinozersk, and pulp and paper manufacturing in Selenginsk. Long range
99 atmospheric transport of sulphur and nitrogen pollutants from these industrial centres are a major
100 source of pollution for Lake Baikal (Obolkin *et al.* 2017).

101 Lake Gusinoye is the second largest lake in the Lake Baikal Basin, and is the only source of
102 drinking and industrial water in the Gusinozersk region. However, poor treatment facilities
103 result in the lake being highly polluted from industrial and domestic waste. One of the largest
104 polluters is the coal-fired Gusinozersk State Regional Power Plant (GSRPP) which discharges
105 about 2M m³ of heated water into the northern part of the lake every day (UNOPS 2015, p95).
106 Affected waters may be up to 14 °C higher than the rest of the lake, which not only prevents part
107 of the lake freezing over every year (Batueva 2016), but also has a significant impact on lake
108 structure and function. For example, in this region of warmer water, cold adapted fish have
109 disappeared (Pisarksy *et al.* 2005). As well as point source pollution, the ecology of Gusinoye
110 has been impacted by invasions of non-local fish species since the 1950s, followed by the
111 construction of fish farms in the 1980s, which benefit from the warmer waste waters from the
112 GSRPP. Therefore, despite a remote Siberian location, the Gusinozersk region and Lake
113 Gusinoye are subject to many local stressors.

114 Local and regional human activities have been well documented in the Lake Gusinoye region in
115 the latter half of the 20th and early 21st centuries, although studies into the impact of such
116 activities on lake environments, and biological responses to anthropogenic activities are much

117 less common, with the response of primary producer communities particularly lacking.
118 Palaeolimnological analyses allow us to discuss ecological sensitivities and thresholds, and the
119 nature of ecological responses and evidence for transitions in aquatic ecosystems on account of
120 human activities in the critically important Lake Baikal Basin. Using Lake Gusinoe as a model
121 to study the potential impacts of long-term multiple local and regional stressors on freshwater
122 ecosystems, we utilize multiple components of the Lake Gusinoe sediment record to
123 disentangle those that have impacted Lake Gusinoe in the recent past. We aim to test our
124 overarching hypothesis that activities associated with economic development in the former
125 USSR since 1945 have had a major impact on freshwater diversity, even in this remote location,
126 and that the impact of multiple stressors has led to novel primary producer communities. To test
127 this hypothesis, the following objectives were undertaken:

- 128 • Reconstruct evidence of past human impact, including both geochemical evidence of
129 increased nutrients / catchment erosion, pollution, and documentary evidence of local
130 aquaculture;
- 131 • Reconstruct diatom community composition and compositional change (beta-diversity)
132 for the past 200+ years, to place into context any impact from anthropogenic activities
133 with baseline reference conditions, and undertake appropriate statistical analyses to
134 determine if compositional changes observed are important.

135 **2. Methods**

136 **2.1 Study area and regional setting**

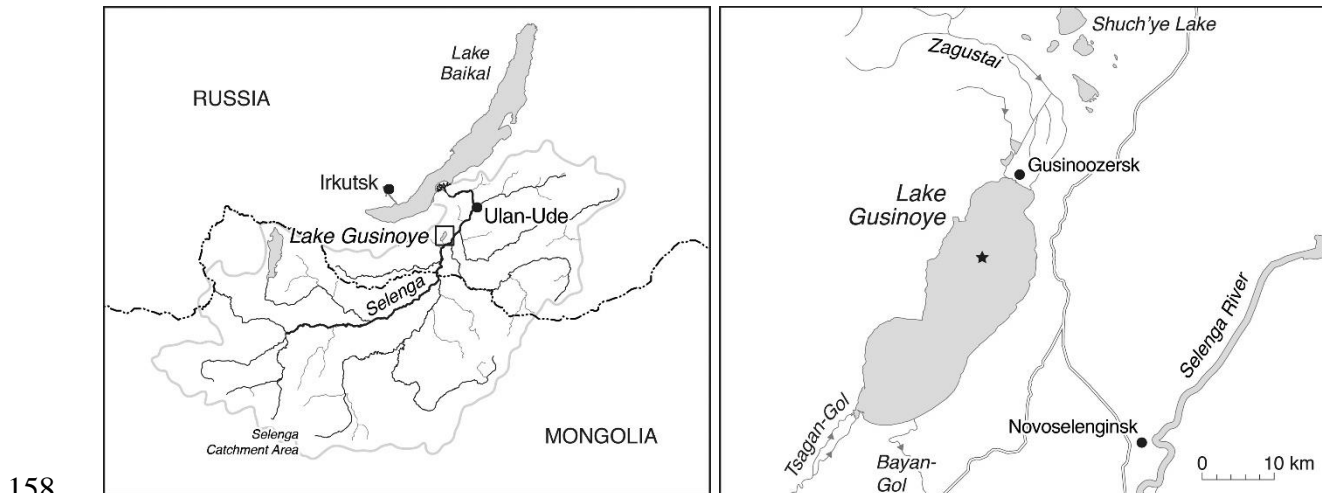
137 Lake Gusinoe is located in southeast Siberia, in the region of Buryatia, and is situated at the
138 foot of the Khamar-Daban ridge at an altitude of 551 m (Figure 1). Lake Gusinoe was formed at

139 the end of Pleistocene as a result of tectonic activities (Bazarov, 1969). It is the second largest
140 lake in southeast Siberia (after Lake Baikal), with a surface area of 164 km², and has a coastline
141 which extends over 65 km, and a catchment area of 924 km². Lake Gusinoe is morphologically
142 divided into two basins: a southern basin and a northern basin. Lake Gusinoe's maximum depth
143 of 25 m is in the southern basin. Until the early-18th century, two small lakes made up what is
144 currently Lake Gusinoe, with the northern and southern basins separated by land. Increased
145 inflow to the lakes c. 1730 led to increased lake levels, resulting in a merging of the two small
146 lakes into one (Pisarsky *et al.*, 2005).

147 The lake-level regime of Lake Gusinoe is dependent on its hydrological inflows (Khardina,
148 2002), and 11 rivers currently flow into the lake. Tsagan-Gol River is the main tributary and
149 enters the southern basin (Figure 1b). The second largest tributary is the Zagustai River, which
150 enters in the northern basin, and on the mouth of which sits the GSRPP. Gusinoe's outflow is
151 located in the southern basin and forms the headwaters of the Bayan-Gol River, a tributary of the
152 Selenga River.

153 The town of Gusinozersk sits on the northeast shore of Lake Gusinoe (Figure 1b).
154 Gusinozersk was founded in 1939 as a settlement for the local coal industry. The settlement
155 grew rapidly, owing to industrialization and increased demand for power, and in 1953 the
156 settlement of Gusinozersk was given the status of town. In 1976 the largest thermal power plant

157 in southern Siberia was built on the shores of Lake Gusinoeye, near the town of Gusinozersk.



159 Figure 1: A) Map of Lake Gusinoeye and Lake Baikal in southern Siberia; B) Lake Gusinoeye with
160 the town of Gusinozersk and major tributaries indicated. The location of sediment core GSNO
161 is indicated by an asterisk (*).

162 2.2 Field sampling/Sediment core collection

163 A sediment core (GSNO) was collected from the northern basin of Lake Gusinoeye in October
164 2013 (Figure 1b). The core was collected from the northern basin, chosen due to proximity to
165 anthropogenic development in Gusinozersk, at the deepest point in the basin, at a depth of 22
166 m, using a *Uwitec* gravity corer fitted with a 6.3 cm internal diameter Perspex[®] tube. The GSNO
167 core was stored intact and upright at the Limnological Institute of the Siberian Branch of the
168 Russian Academy of Sciences (LIN SB-RAS), Irkutsk, RU until extrusion. The GSNO core was
169 sectioned at 0.2 cm intervals using a vertical extruder in September 2014 at LIN SB-RAS. Total
170 core length for the GSNO sediment core was 66.0 cm, however for the purposes of this study we
171 focus on the top 10 cm only. Extruded sediment samples were stored in Whirlpak[®] bags, shipped
172 to University College London (UCL), London, UK and stored at 4°C until processing.

173 **2.3 Radioisotope dating**

174 Radiometric dating techniques were used to date the upper sediments from the GSNO core.
175 Approximately 0.5 g of freeze-dried sediment samples were analysed for ^{210}Pb , ^{226}Ra , and ^{137}Cs
176 by direct gamma assay in the Environmental Radiometric Facility at UCL, using ORTEC HPGe
177 GWL series well-type coaxial low background intrinsic germanium detectors. ^{210}Pb chronologies
178 were constructed using the constant rate of supply (CRS) dating model (Appleby and Oldfield,
179 1978; Appleby, 2001), and independently verified using ^{137}Cs .

180 **2.4 Trace elements and metals**

181 Trace elements and metals have the potential to provide information on anthropogenic
182 contamination, and catchment disturbance. Sediment was analyzed for trace and major element
183 concentrations from the GSNO sediment core. Following air-drying, dried sediment was
184 subsampled for analysis at 23 intervals. Each sample was ground to a fine powder using an agate
185 mortar and pestle. Approximately 1.0 g of dried, finely powdered sediment was weighed into a
186 sample cuvette lined with polypropylene film. Samples were then analyzed for trace and major
187 elements using a Spectro X-Lab 2000 energy dispersive X-ray fluorescence spectrometer (ED-
188 XRF) with a Si(Li) semiconductor detector in the Department of Geography at University
189 College London (UCL). Certified standard reference materials (SRM), Buffalo River sediment
190 (BRS; SRM 2704; Epstein *et al.*, 1989) were analyzed every 10 samples during analysis.
191 Accuracy of standards was within 10%. Trace element and metal enrichment factors were
192 calculated for each sample by normalizing the concentration of an element or metal (M) to the
193 conservative lithogenic element Ti, within the sample, to the background ratio within the core.
194 An enrichment factor of 1 throughout the record is equivalent to background concentrations,
195 values above 1 indicate enrichment, while enrichment factors greater than 3 indicate definite

196 anthropogenic contamination of the metal (Boës *et al.*, 2011). Enrichment factors (EFs) were
197 calculated, using the following equation from Weiss *et al.* (1999):

$$198 \quad EFs = (M_{sample}/Ti_{sample}) / (M_{background}/Ti_{background})$$

199 Background was taken as the average of the oldest five samples from the sediment core, as this
200 was assumed to be the most minimally impacted.

201 **2.5 Spheroidal carbonaceous particles (SCPs)**

202 SCPs are unambiguous indicators of high-temperature fossil fuel combustion, especially from
203 power stations. Sediment was analyzed for spheroidal carbonaceous particle (SCP)
204 concentrations following Rose (1994). Reference sediment was analyzed concurrently to the
205 samples (Rose, 2008). Samples underwent a sequential attack of mineral acids to breakdown
206 organic matter, carbonates, and silica components. A sub-sample of the resulting SCP residue
207 was then transferred to a coverslip and allowed to evaporate, mounted onto microscope slides
208 and the SCPs counted under a light microscope at x 400. SCP identification criteria followed
209 Rose (2008). Mean recovery rate for this method is 95.2%, with detection limits of 80-100 SCPs
210 g⁻¹ dry mass (Rose, 1994). The SCP concentration is reported in units of number of particles per
211 gram dry mass of sediment (gDM⁻¹).

212 **2.6 Loss-on-ignition and sediment densities**

213 Burning of sediments (loss-on-ignition) at high temperatures provides a first order estimation of
214 organic matter and carbonates in lake sediments. Loss-on-ignition (LOI) at 550°C and 950°C
215 was conducted on GSNO sediment following Heiri *et al.* (2001). Mass loss between 105°C and
216 550°C, and 550°C and 950°C was calculated and converted to % organic matter (LOI₅₅₀) and %

217 carbonate (LOI₉₅₀) of the dried sediment, respectively (Heiri *et al.*, 2001). Carbon accumulation
218 rates were calculated using bulk density, LOI₅₅₀, and sedimentation rates.

219 **2.7 Diatoms**

220 Diatoms are major primary producers in lakes. Approximately 0.1g of wet sediment (weighed to
221 four decimal places) was subsampled at 0.5-cm intervals for diatom analysis, and processed
222 following standard procedures according to Battarbee *et al.* (2001). One millilitre of the final,
223 cleaned diatom solution was pipetted into a new tube and mixed with 1 ml of 8.0×10^4
224 microsphere ml⁻¹ solution and 8 ml of distilled water. Approximately 1 ml of the diatom and
225 microsphere solution was then pipetted onto a round 19 mm diameter cover slip, and allowed to
226 settle and evaporate overnight. The coverslip was then permanently mounted onto a slide using
227 the resin, Naphrax[®]. Diatoms were observed at 1000X magnification under oil immersion using
228 a Leica DMLB. A minimum of 300 valves were counted for all samples, with the exception of
229 samples 6.5 cm, 7.1 cm, and 7.5 cm depth, in which 200 valves were counted due to low overall
230 concentrations on the slides. Diatom species identification was conducted following Krammer
231 and Lange-Bertalot (1986, 1988, 1991a, b), Diatoms of Europe Vol. 2 (Lange-Bertalot, 2001),
232 Diatoms of Europe Vol. 3 (Krammer, 2002), and Diatoms of Europe Vol. 5 (Levkov, 2009).
233 Diatom raw counts were converted to percent relative abundance per sample.

234 **2.8 Statistical analyses**

235 As the total number of valves counted per sample varied between sites, species richness was
236 determined through rarefaction using 200 valves. Diatom species rarefaction richness was
237 conducted on the diatom raw counts using R, Vegan package (R. v.3.2.4, 2016). Hill's N2, an
238 index of the diversity of very abundant species at a single site, was calculated on the full diatom

239 dataset using C2 (Juggins, 2014). Species concentrations were calculated using the microsphere
240 method, and normalized to weight of sediment of the original sample (# valves g^{-1} dry weight)
241 (Battarbee and Kneen, 1982).

242 Unconstrained ordinations were employed to detect major patterns of variation in the diatom
243 assemblage data. While the gradient length for diatom assemblage axis 1 was shorter than 2.0
244 SD, unimodal methods (detrended correspondence analysis (DCA)) were used, due to the
245 obvious arch pattern resulting from the use of linear methods (principal components analysis
246 (PCA)). DCA was performed in Canoco5 (ter Braak and Šmilauer, 2012), on the untransformed
247 diatom dataset containing only those species present at >2% in a single interval, to eliminate the
248 influence of very rare species and examine only major trends. Compositional change (beta-
249 diversity) in the diatom flora was estimated using detrended canonical correspondence analysis
250 (DCCA) (Smol *et al.* 2005; Birks 2007), using estimated and extrapolated ages obtained from
251 ^{210}Pb analyses. Relative abundance data were square-root transformed to stabilize variances, but
252 rare species were not down-weighted. Detrending was done by segments and non-linear
253 rescaling. Constrained cluster analysis (based on chord square distance) and breakpoint analysis
254 were performed on the diatom dataset to determine major groupings of depths. Broken stick
255 analysis was performed to determine the number of significant zones within diatom assemblages
256 based on the constrained cluster analysis. Cluster analysis and broken stick analysis were
257 performed in R using the rioja package, and breakpoint analysis was performed in R using the
258 segmented package (R. v.3.2.4, 2016). All stratigraphical plots were constructed using C2
259 (Juggins, 2014).

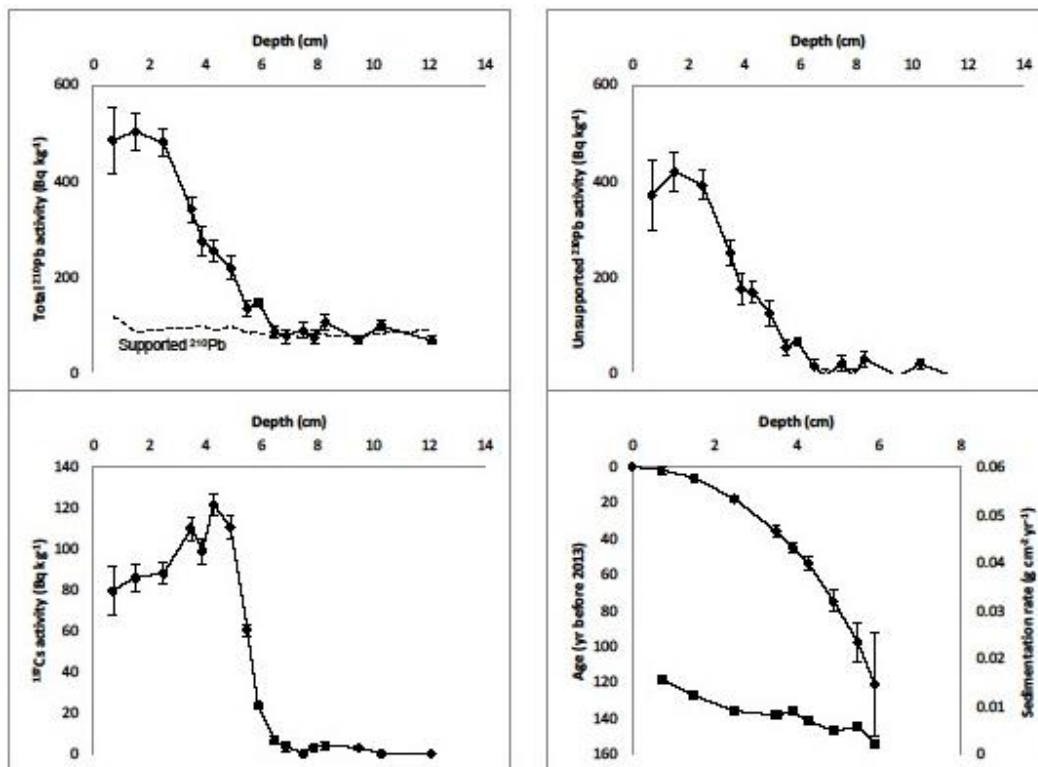
260 **3. Results**

261 **3.1 Radioisotope dating**

262 Total ^{210}Pb activity reached equilibrium with supported ^{210}Pb activity at a depth around 6.5 cm in
263 the GSNO core (Figure 2a). Unsupported ^{210}Pb activities declined irregularly with depth (Figure
264 2b). The CRS dating model placed 1963 at around 4.1 cm, which is in agreement with the depth
265 suggested by the ^{137}Cs record (Figure 2c). Sedimentation rates in the core show a gradual slow
266 increase in the 20th century as indicated through an increase in unsupported ^{210}Pb decline from 6
267 cm to 3.5 cm. There was little net decline in unsupported ^{210}Pb in the top 2.6 cm, likely to be
268 derived from dilution caused by an increase in sedimentation rates, indicating increased
269 acceleration of rates in the 21st century (Figure 2d). Ages beyond 5.9 cm were extrapolated to 10
270 cm assuming constant sedimentation rates.

271 **3.2 Trace metals and elements**

272 Elemental concentrations remained steady and unchanged in Lake Gusinoye prior to the 1930s.
273 Beginning in the late 1930s, increases in Ti-normalized enrichment factors (EFs) of Cu, Zn, and
274 Pb above background levels occurred (Figure 3). In the years closely following the end of World
275 War 2 (WWII), EFs for Cu increased to 2.0, and EFs for Zn and Pb began a continuous increase
276 above 1.0 (Figure 3). Enrichment factors for Cu, Zn, and Pb peaked between 1970 – c. 1980,
277 followed by slight declines but relatively steady values to the surface. Ti-normalized EFs for P
278 showed first signs of an increase post-1940s, with accelerated increase in EFs beginning c. 1970,
279 and peaking at 1.7 at the surface (Figure 3).



280

281 Figure 2. Fallout radionuclide concentrations in core GSNO taken from Lake Gusinoe, Russia,
 282 showing (a) total ^{210}Pb , (b) unsupported ^{210}Pb and (c) ^{137}Cs concentrations versus depth. Figure
 283 2d. Radiometric chronology of core GSNO taken from Lake Gusinoe, Russia, showing the CRS
 284 model ^{210}Pb dates and sedimentation rates. The solid line shows age, while the dashed line
 285 indicates sedimentation rate.

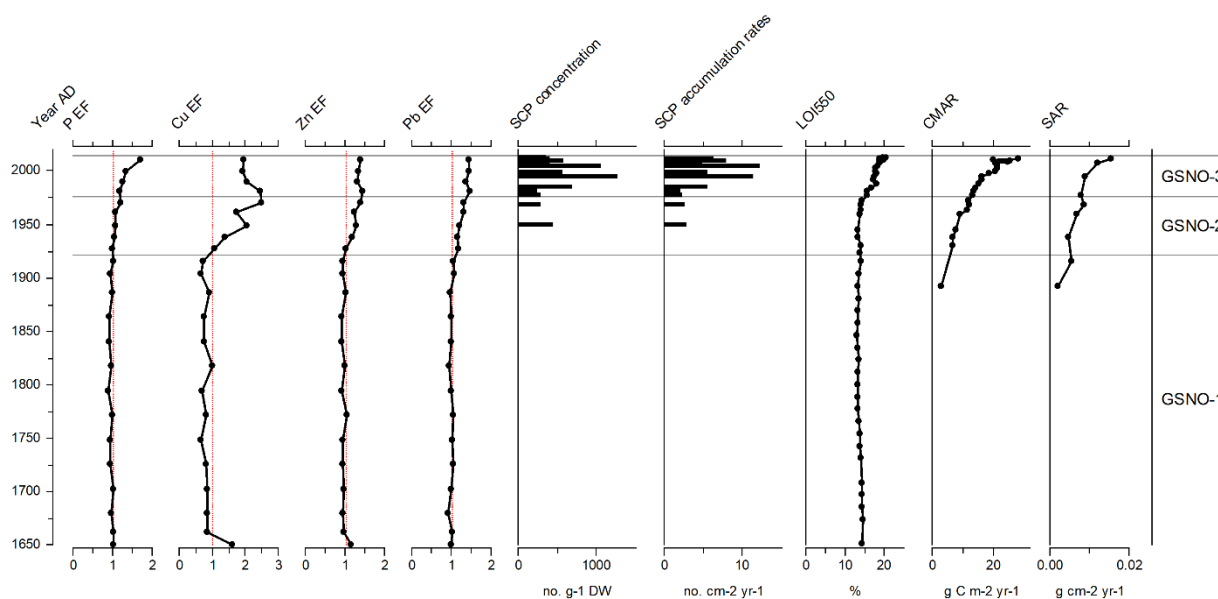
286 3.3 Spheroidal carbonaceous particles

287 SCPs appear in the sediment record at Lake Gusinoe c. 1950 at ~500 SCPs g $^{-1}$ DW, and are
 288 fairly steady in concentration and flux until c. 1980 (Figure 3). Post-1980, SCP concentration
 289 and flux increased, and peaked between the mid-1990s and early 2000s at ~1200 SCPs g $^{-1}$ DW
 290 and 12 SCPs cm $^{-2}$ yr $^{-1}$. Declines in SCP concentrations and fluxes occurred in recent years. The
 291 decline in SCPs since c. 2005 occurred separately from sedimentation rates (Figure 3).

292 **3.4 Carbon accumulations**

293 LOI₅₅₀ was steady between 13.1 and 14.5 % from the mid-17th century until the mid-1970s, at
 294 which point values began to increase, reaching 20.4 in the most recent sample (Figure 3). Carbon
 295 mass accumulation rates (CMAR) exhibit a four-fold increase since the late-19th century, from c.
 296 7 g m⁻² yr⁻¹ to a peak of over 30 g m⁻² yr⁻¹ in recent years (Figure 3). CMAR are similar to
 297 increasing sedimentation rates since the 19th century.

298



299 Figure 3. Trace metal and element enrichment factors for P, Cu, Zn, and Pb, SCP concentrations
 300 and accumulation rates, carbon mass accumulation rates, and sedimentation rates for sediment
 301 core GSNO.

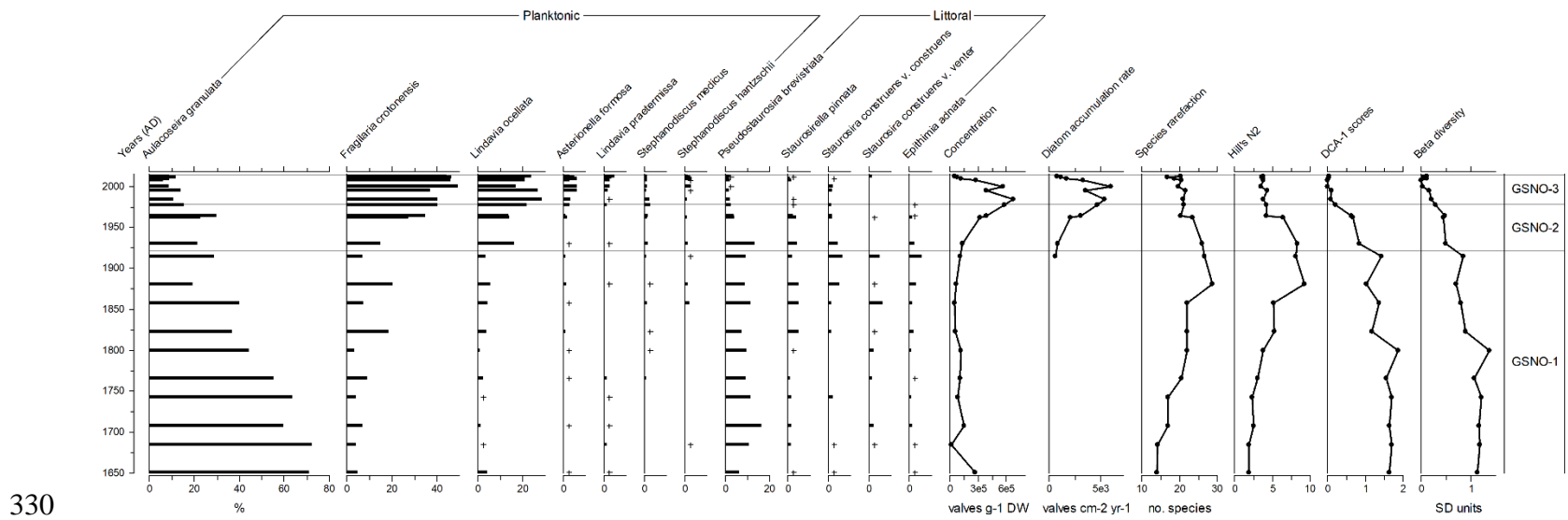
302 **3.5 Diatoms**

303 The diatom assemblages at Lake Gusinoye were dominated throughout the record by planktonic
 304 species. Cluster analysis, DCA, breakpoint analysis, and broken stick indicated the presence of
 305 three important zones within the diatom assemblages of the past 200 years, and significant shifts
 306 occurred c. 1920, and from the mid-1970s to c. 1980. The diatom assemblages from the earliest
 307 part of the record were dominated (up to 70%) by *Aulacoseira granulata*, while subordinate

308 species included small benthic Fragilarioids of the *Pseudostaurosira-Staurosira-Staurosirella*
309 complex, particularly *Pseudostaurosira brevistriata* (Figure 4). Declines in the relative
310 abundance of *A. granulata* began in the 18th century (Figure 4). A steady decline in *A. granulata*
311 continued into the 20th century, concurrent with increases in abundance of two other planktonic
312 species, *Fragilaria crotonensis* and *Lindavia ocellata* (Figure 4). Alongside late-19th and early-
313 20th century changes in species abundances, species richness (rarefaction) and Hill's N2 measure
314 of diversity increased (Figure 4).

315 The first significant breakpoint in the diatom DCA occurred c. 1920, as the previously dominant
316 *A. granulata* declined to ~20% relative abundance, replaced as dominant species by both *F.*
317 *crotonensis* and *L. ocellata*. Between the 1920 and the 1970s, both *L. ocellata* and *F. crotonensis*
318 continued to increase in abundance (Figure 4). As species richness and Hill's N2 diversity began
319 to decline c. 1950, diatom concentrations and fluxes began to increase.

320 Beginning in the 1970s and concurrent with the second breakpoint in the diatom DCA analyses,
321 increased abundances of planktonic *Asterionella formosa*, were observed, while abundances of
322 *Lindavia praetermissa* and *Stephanodiscus hantzschii* began to increase c. 1990. Since the late-
323 1970s/early-1980s, abundances of *F. crotonensis* and *L. ocellata* have remained relatively
324 steady, and the assemblages have since been dominated by these two planktonic species,
325 occurring at almost c. 50% and c. 30%, respectively (Figure 4). Diatom accumulation rates
326 peaked c. 2000 valves cm² yr⁻¹, and both concentrations and fluxes have declined in the past two
327 decades. Significant diatom compositional turnover was observed from Lake Gusinoye (beta-
328 diversity = 1.300 SD; p = 0.002). Between the mid-17th century and early-19th century, beta-
329 diversity was stable, but then has steadily declined to very low values at the present day.



330

331 Figure 4. Diatom assemblages of Lake Gusinoye, breakpoint analysis results define zonations, and breakpoint analysis results shown
332 along plot of DCA axis 1 scores.

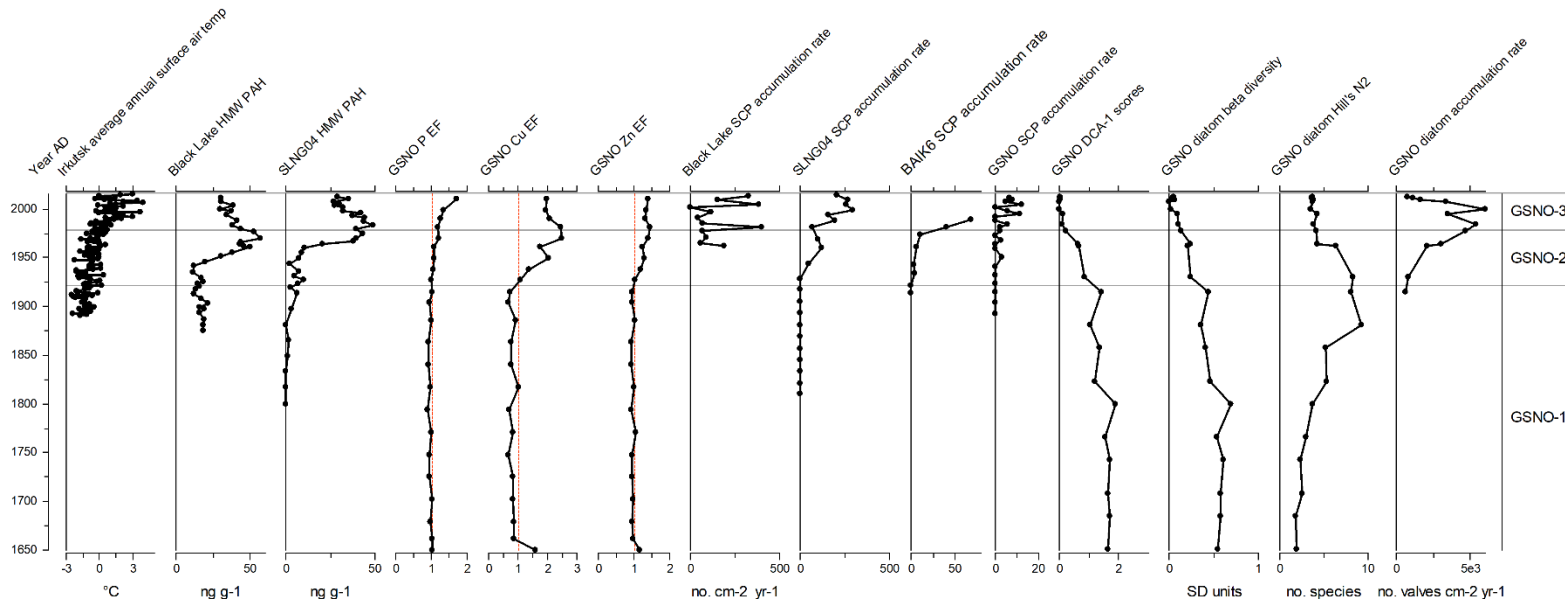
333 **4. Discussion**

334 As a large, deep lake in southern Siberia, Lake Gusinoe has undergone several ecological shifts
335 in response to multiple regional and local stressors in the past 100 years. Previous research has
336 indicated increases in zoobenthic biomass from annual average of 18.97 g m⁻² in the 1940s to
337 32.78 g m⁻² by the 1990s, and unprecedented changes in the structure of the zooplankton
338 community at Lake Gusinoe since the 1980s from large cladocera and copepods to
339 predominantly rotifers and small *Daphnia* (Borisenko *et al.* 1994; Pisarsky *et al.*, 2005). These
340 unprecedented changes to the zooplankton community occurred concurrently to fish
341 diversification, but also loss of native fish species (Borisenko *et al.* 1994). Combining these
342 existing records of zooplankton and fish communities with new records from Lake Gusinoe of
343 contaminants and primary producers, would allow for a more representative analysis of
344 ecosystem change to multiple anthropogenic stressors on this economically and ecologically
345 important freshwater ecosystem in southern Siberia.

346 **4.1 Anthropogenic contamination of Lake Gusinoe**

347 Enrichment of trace metals started during the early-20th century, concurrent with known
348 historical records of increasing local economies, including the development of coal mining
349 operations around Lake Gusinoe (Pisarsky *et al.*, 2005). The concurrent increases in trace metal
350 and SCP concentrations between 1950 and the 1980s reflect the intensification of both local and
351 regional increases in economic activity, including the construction of the Gusinozersk State
352 Regional Power Plant (GSRPP) (*ibid.*). Other regional lake sediment records of anthropogenic
353 contamination indicate similar timing of events, including organic pollutants and SCP records
354 from the south basin of Lake Baikal, from shallow lakes in the Selenga Delta, as well as Black
355 Lake, a small lake adjacent to Lake Gusinoe (Adams *et al.*, 2018; Adams, 2017; Rose *et al.*,

356 1998). Rapid increases in SCP concentrations in the south basin of Lake Baikal in the
357 1950s/1960s reflected local increases in industrialization across southeast Siberia (Rose *et al.*,
358 1998), while small increases in Baikal's north basin reflected regional sources because they were
359 of a similar magnitude to hemispherical background increases. Increased concentrations of
360 polycyclic aromatic hydrocarbons (PAHs) in the Lake Baikal Basin in the 1940s to 1960s also
361 indicate a high likelihood of atmospherically deposited contaminants to Lake Gusinoe from
362 both local and regional sources in the mid-20th century (Adams *et al.*, 2018; Shirapova *et al.*,
363 2013). Close temporal matches between the Lake Gusinoe SCP record and SCP and PAH
364 concentrations from lake sediment cores from the south basin of Lake Baikal, the Selenga Delta,
365 and neighbouring Black Lake indicates the primary period of anthropogenic contamination from
366 industrialization occurred between the 1940s and 1990s (Figure 5). Post-1940, increases in P,
367 indicative of enrichment, reflects the gradual, long-term eutrophication of Lake Gusinoe, as a
368 result initially of early agricultural practices in the region (Bazheniva & Kobylkin, 2013), then of
369 increases in wastewater effluent into the lake from the GSRPP and the town of Gusinozersk,
370 and the impacts of fish farming, which began in Lake Gusinoe in the 1980s (Pisarsky *et al.*,
371 2005).



372

373 Figure 5. A comparison of anthropogenic contamination and diatom records from Lake Gusinoye with regional and local lake
 374 sediment records of anthropogenic contamination and Irkutsk, RU temperature change since the late-19th century.

375 **4.2 Biological responses**

376 Undisturbed, temperate lakes show little diatom change, with a beta-diversity over the past 150
377 years of c. 1 standard deviation units (SD) (Smol *et al.* 2005). These lakes act as good reference
378 points for comparing diatom beta-diversity in lakes in other regions with contrasting impact
379 histories. Diatom composition in Lake Gusinoe shows significant change over the past few
380 hundred years (Figure. 4). Overall, beta-diversity (1.3 SD) exceeds mean reference conditions
381 from unimpacted lakes in North America and northern Europe (Smol *et al.* 2005; Hobbs *et al.*
382 2010), western Greenland (Hobbs *et al.* 2010), the Tibetan Plateau (Wischnewski *et al.* 2011)
383 and nearby East Sayan Mountains (Mackay *et al.* 2012). Prior to the 1800s, diatom assemblages
384 were very stable in Lake Gusinoe (Figure 4) which we suggest represents baseline reference
385 conditions for the lake. Evidence for diatom compositional turnover starts in the early decades of
386 the 19th century, and accelerates in the lake after 1950 AD. Whereas in polar regions increased
387 beta-diversity is attributed to climate change, we argue that in Lake Gusinoe, high beta-
388 diversity is driven by multiple factors, notably economic development around the lake and its
389 catchment over the past 100 years, alongside global warming in the past few decades. It is
390 interesting to note that high beta-diversity was also observed in alpine lakes in the American
391 Cordillera linked to increased Nr availability (Hobbs *et al.* 2010).

392 The early part of our record is dominated by the heavily silicified diatom, *Aulacoseira granulata*.
393 (Figure 4). It is a meroplanktonic species which means it is adapted to being suspended in the
394 water column during periods of turnover (Kilham 1990). When lakes stratify, *A. granulata* sinks
395 out of the photic zone, but because it forms resting spores from which it can regenerate (Schelske
396 *et al.* 1995) once mixing recommences, e.g. due to strong autumnal winds, it can become
397 retrained back into the water column. One of the most striking features of the diatom record is

398 the gradual decline in abundance of *A. granulata* from approximately 1750 AD to just before the
399 start of the 20th century (Figure 4). Despite its remote location, there are good historical records
400 for 18th century development of Lake Gusinoye. When *A. granulata* dominated the sequence, the
401 lake was divided into two separated, smaller lakes. However, after 1730, water levels in the
402 region rose and the basin was flooded. So prior to 1750 AD, conditions in the region must have
403 been such that deep mixing of Gusinoye occurred, which allowed regeneration of nutrients such
404 as silica for *A. granulata* to take up. Elsewhere in the region, palaeolimnological records indicate
405 that climate was very cold at this time, linked to the latter stages of the Little Ice Age (LIA;
406 Mackay *et al.* 2005; 2012). After ice break up in spring on Gusinoye, cold waters would have
407 been easy to mix, so supporting *A. granulata*.

408 Increasing river flow and flooding of the lake after 1750 was likely caused by warming, as the
409 region come out of the LIA, causing widespread hydrological instability (Pisarsky *et al.* 2005).
410 Regional warming will also have caused the period of surface water stratification to lengthen in
411 Gusinoye, and deeper water would have meant that it would have been more difficult for *A.*
412 *granulata* valves to become re-entrained again once out of the photic zone, hence causing the
413 decline in the species. *F. crotonensis* is a common indicator of increasing nutrient influx and
414 increasing trophic level in freshwater lakes (Saros *et al.*, 2005; Akcaalan *et al* 2007), and the
415 early increase in *F. crotonensis*, especially after 1800 AD is concordant with flooding of
416 Gusinoye. Increased diatom turnover after 1800 AD therefore is a response to regional warming
417 after the cool conditions of the LIA. Hill's N2 diversity values also increase at this time,
418 indicative of increases in available resources (Interlandi & Kilhman 2001), likely brought in with
419 meltwater floods.

420 Prior to the end of the 19th century, shifts in diatom communities, between heavier *A. granulata*
421 and lighter *F. crotonensis* were gradual but persistent, as highlighted by DCA axis 1 scores
422 (Figure 4). It was not until the start of the 20th century that we start to see critical ecological
423 transitions occurring in the diatom record. The first transition marks the stabilisation of *A.*
424 *granulata*, but rapid increases in two other planktonic taxa, *F. crotonensis* and *Lindavia ocellata*
425 c. 1920 (Figure 4), leading to accelerated compositional turnover. This switch in community is
426 concurrent with increases in diatom fluxes, trace metal enrichment, and SAR (Figure 3). These
427 early-20th century changes in the diatom communities are likely an ecological response to land-
428 use change from increasing livestock populations (Bazhenova and Kobylkin, 2013) and mining
429 (Pisarsky *et al.* 2005) resulting in increased soil erosion, against a backdrop of increasing
430 regional temperatures (Figure 5). *F. crotonensis* is known to respond to increases in nitrogen,
431 and has been considered as an indicator of increasing Nr in previously oligotrophic lakes in the
432 western United States, as a result of increased nitrogen deposition (Saros *et al.* 2005, Wolfe *et al.*
433 2006; Hobbs *et al.* 2010), as well as rising nitrate concentrations (Stoermer *et al.* 1978; Wolin *et*
434 *al.* 1991), and therefore may be indicative of increasing nutrient flux to the lake. *L. ocellata* may
435 indicate a response to continued warming temperatures, weaker lake turnover and strengthened
436 stratification (Malik and Saros, 2016; Liu *et al.*, 2017). Although it may also represent a switch
437 in the lake from N to P limitation (Winder & Hunter 2008). Therefore, the first significant
438 change in the diatom community of Lake Gusinoye, post baseline conditions, was likely a
439 response to intensifying anthropogenic activities against a background of warmer temperatures in
440 the early-20th century (Figure 5).

441 The second significant change in diatom community composition occurred between the mid-
442 1970s to c. 1980 (Figure 4), when livestock populations and concomitant soil erosion in the

443 region were at their highest (Bazhenova and Kobylkin 2013). *A. granulata* abundances decline
444 to their lowest levels for the whole record, *L. ocellata* and *F. crotonensis* reach their highest
445 abundances, and taxa including *A. formosa*, *L. praetermissa* and *S. hantzschii* become persistent
446 in the record. Diatom fluxes reach their highest values for the whole record, before declining in
447 the most recently deposited sediments. The significant changes occurring in the late-20th century
448 occur concurrently with peak SCP concentrations and P enrichment above background levels,
449 indicative of high economic and agricultural activity in the region, respectively (Figure 5). *A.*
450 *formosa* in particular has been linked in large freshwater lakes to increasing anthropogenic
451 development and associated nutrient enrichment, particularly nitrogen (Stoermer *et al.* 1991;
452 Wolin *et al.* 1991; Bergstöm and Jansson 2006), and competes well for increasing P in high Si
453 environments (Bradbury, 1988; Saros *et al.* 2005). The concurrent high abundances of *F.*
454 *crotonensis* and *A. formosa* have been used previously to infer increased nutrient loadings and
455 anthropogenic disturbances in lake catchments (Fritz *et al.* 1993; Anderson *et al.*, 1995; Garrison
456 and Wakeman 2000; Forrest *et al.* 2002; Wolin and Stoermer 2005; Hobbs *et al.* 2010). Further,
457 both *F. crotonensis* and *A. formosa* have been shown to respond primarily to increases in silica
458 and nitrogen in both temperate and alpine lakes (Saros *et al.* 2005; Bennion *et al.* 2011).
459 Furthermore, *Epithemia adnata* contains endosymbiotic cyanobacteria in its cells to assist in
460 nitrogen fixation, and that this species completely disappears from the Gusinoye sediment record
461 at this time lends support to our suggestion that nitrogen supply was plentiful (Deyoye *et al.*
462 1992).

463 Ecological changes in the late-20th century are also likely a response to the onset of aquaculture
464 economies (primarily *Cyprinus carpio* and *Acipenser baeri baicalensis*) in the northern basin of
465 Lake Gusinoye c. 1980. Fish farming is known to result in increases in organic matter deposition

466 in aquatic systems due to fish food deposition and increased fecal matter, and inorganic nutrient
467 enrichment, particularly ammonium, nitrate, nitrite, phosphate (San Diego-McGlone *et al.*,
468 2008). Primary producer communities have been observed to respond strongly to fish farming
469 activities (e.g. San Diego-McGlone *et al.*, 2008; Wang *et al.*, 2009; Jiang *et al.*, 2013). Thermal
470 effluent from the GSRPP likely also contributed to eutrophication in recent years (e.g. Jiang *et*
471 *al.*, 2013), providing excellent conditions for aquaculture to thrive (Pisarsky *et al.* 2005), and
472 coinciding with our recorded increase in *A. formosa*, *L. praetermissa* and *S. hantzschii*, peaks in
473 diatom flux, and increasing P enrichment factors. Therefore aquaculture and thermal pollution
474 from the GSRPP are the latest in the multitude of 20th century anthropogenic stressors impacting
475 the ecology of Lake Gusinoeye, which resulted in unprecedented shifts in diatom assemblages.

476 **4.3 The nature of ecological shifts in multi-stressor systems**

477 Diatom assemblage changes at Lake Gusinoeye during the 20th century now indicate that primary
478 producer communities have undergone unprecedented shifts. Our findings of primary producer
479 changes correspond with previous studies of increasing zooplankton biomass and change in
480 zooplankton community structure and fish diversification since the mid- to late-20th century
481 (Borisenko *et al.*, 2004). Therefore, rapid and extensive 20th century anthropogenic development
482 in and around the Gusinozersk region resulted in whole-ecosystem shift of Lake Gusinoeye to
483 novel ecological communities. Major shifts at all trophic levels in Lake Gusinoeye have come as a
484 result of the multiple anthropogenic stressors impacting the lake ecosystem. In multi-stressors
485 environments, it is possible that the ecological effect of multiple disturbances may be individual,
486 with each stressor inciting an individual response, with an overall additive effect of all stressors.
487 However, the interaction between multiple stressors may result in exceptional ecological shifts
488 and novel ecological communities (Sala *et al.*, 2000; Christensen *et al.*, 2006; Jackson *et al.*,

489 2016b), promoting more extensive and/or rapid change, as well as unexpected or unprecedented
490 response to stressors.

491 Overall, diatom community changes indicate that increasing nutrient loadings to Lake Gusinoye
492 since the early-20th century, and the subsequent shift from an oligotrophic to eutrophic lake, have
493 had a greater impact on primary producer communities than increasing regional temperatures.
494 This is in contrast to recent shifts observed in diatom communities from many lakes in cold
495 regions, which primarily experience increases in small *Cyclotella* species as a result of reduced
496 ice cover and/or increases in stratification due to increasing temperatures (e.g. Sorvari *et al.*,
497 2002; Ruhland *et al.*, 2003; Smol *et al.*, 2005; Ruhland *et al.*, 2008). Such a shift was not
498 observed at Lake Gusinoye. Therefore, Lake Gusinoye appears to either be more sensitive to
499 nutrient increases than other northern lakes, or, indicates that, where the opportunity allows due
500 to local or regional sources, diatom responses to nutrient increases will dominate over responses
501 to warming temperatures. However, the rate of compositional turnover (β -diversity; 1.3 SD), and
502 major shifts in diatom assemblages, i.e. concurrent increase in *F. crotonensis* and *L. ocellata*
503 with declines in *A. granulata*, Fragilarioids and *E. adnata*, followed by concurrent increases in *A.*
504 *formosa* and *L. praetermissa*, may indicate a simultaneous response to increasing nutrients and
505 temperature, with a switch from deep mixing with plentiful silica supply to a lake with high
506 nutrient status, and longer stratification times. Moreover, temperature and nutrients may interact
507 with each other at several ecological levels, from individual to whole-ecosystem, resulting in
508 feedbacks (Cross *et al.*, 2015). Therefore, the post-1920 diatom assemblage shifts observed may
509 be the result of synergistic effects of increasing nutrients and temperature at Lake Gusinoye.

510 **5. Conclusion**

511 Lake Gusinoye is a multi-stressor environment, and numerous human-related changes in the
512 Gusinozersk region have been documented through the 20th century, all with the potential to
513 impact ecological community structure and function. Trace metal and element records combined
514 with SCP concentrations indicate early impacts of regional and local development c. 1920, with
515 the onset of increasing livestock numbers resulting in increased regional soil erosion. Previous
516 studies have indicated shifts in zooplankton and fish communities since the 1980s as a response
517 to human-related stressors. Now, we show that primary producers have also responded in
518 exceptional ways to the multitude of developments in the Lake Gusinoye region. Diatoms first
519 underwent assemblage shifts as a result of hydrological changes due the termination of the Little
520 Ice Age in southern Siberia, but have, since the early-20th century, changed more profoundly as a
521 result of multiple anthropogenic stressors, including nutrient influx, aquaculture, and wastewater
522 discharge from the Gusinozersk State Regional Power Plant. Lake Gusinoye is an economically
523 and ecologically important freshwater system in southern Siberia. These records of
524 unprecedented ecological change in the second largest lake in southern Russia, reveal that
525 anthropogenic stressors have had a significant impact on primary producers within the lake.
526 However, despite declines in animal husbandry over the past few decades, diatom assemblages
527 remain indicative of a persistent enriched system, which is likely related to increasing
528 dependency on local aquaculture in the lake, and potential interactive effects between increasing
529 regional temperatures and nutrients.

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