Diatom community responses to long-term multiple stressors at Lake Gusinoye, Siberia

Adams, J.K.[a,b], Peng, Y.[c,d], Rose, N.L.[b], Shchetnikov, A.A.[e,f,g,h], Mackay, A.W[b*]

[a] Department of Earth Sciences, University of Toronto, 22 Russell Street, Toronto, Ontario, M5S 3B1, Canada

[b] Environmental Change Research Centre, Department of Geography, Pearson Building, Gower Street, University College London, London WC1E 6BT, United Kingdom

[c] State Key Laboratory of Loess and Quaternary Geology, Institute of Earth Environment, Chinese Academy of Sciences, Xi'an 710075, People's Republic of China

[d] Department of Urban and Rural Construction, Shaoyang University, Shaoyang, 422000, People's Republic of China

[e] Institute of Earth's Crust, Siberian Branch of the Russian Academy of Sciences, 128 ul. Lermontov, Irkutsk, 664033, Russia

[f] Irkutsk State University, 2 Chkalov St., Irkutsk, 664003, Russia

[g] Vinogradov Institute of Geochemistry, Siberian Branch of Russian Academy of Sciences, Irkutsk, 664033, Russia

[h] Irkutsk Scientific Center, Siberian Branch of the Russian Academy of Sciences, Irkutsk, 664033, Russia

*Corresponding author e-mail: ans.mackay@ucl.ac.uk (AWM)

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Abstract

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

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

1. Introduction

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

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

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

The Lake Baikal Basin also contains the second and third largest cities in Siberia, Irkutsk and Ulan Ude, the latter being the hub of economic activity in southeast Siberia, one of Russia's most polluted cities, and through which the Selenga River flows. Smaller industrial centres in southeast Siberia, such as Selenginsk and Gusinoozersk (Figure 1), are also highly polluted, due to open cast mining of brown coal, mining for aluminium and molybdenum, and coal-fired power generation in Gusinoozersk, and pulp and paper manufacturing in Selenginsk. Long range atmospheric transport of sulphur and nitrogen pollutants from these industrial centres are a major source of pollution for Lake Baikal (Obolkin *et al*. 2017).

Lake Gusinoye is the second largest lake in the Lake Baikal Basin, and is the only source of drinking and industrial water in the Gusinoozersk region. However, poor treatment facilities result in the lake being highly polluted from industrial and domestic waste. One of the largest polluters is the coal-fired Gusinoozersk State Regional Power Plant (GSRPP) which discharges about 2M m^3 of heated water into the northern part of the lake every day (UNOPS 2015, p95). Affected waters may be up to 14 °C higher than the rest of the lake, which not only prevents part of the lake freezing over every year (Batueva 2016), but also has a significant impact on lake structure and function. For example, in this region of warmer water, cold adapted fish have disappeared (Pisarksy *et al*. 2005). As well as point source pollution, the ecology of Gusinoye has been impacted by invasions of non-local fish species since the 1950s, followed by the construction of fish farms in the 1980s, which benefit from the warmer waste waters from the GSRPP. Therefore, despite a remote Siberian location, the Gusinoozersk region and Lake Gusinoye are subject to many local stressors.

Local and regional human activities have been well documented in the Lake Gusinoye region in the latter half of the 20th and early 21st centuries, although studies into the impact of such activities on lake environments, and biological responses to anthropogenic activities are much less common, with the response of primary producer communities particularly lacking.

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

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

2. Methods

2.1 Study area and regional setting

Lake Gusinoye is located in southeast Siberia, in the region of Buryatia, and is situated at the foot of the Khamar-Daban ridge at an altitude of 551 m (Figure 1). Lake Gusinoye was formed at the end of Pleistocene as a result of tectonic activities (Bazarov, 1969). It is the second largest lake in southeast Siberia (after Lake Baikal), with a surface area of 164 km^2, and has a coastline which extends over 65 km, and a catchment area of 924 km^2. Lake Gusinoye is morphologically divided into two basins: a southern basin and a northern basin. Lake Gusinoye's maximum depth of 25 m is in the southern basin. Until the early-18th century, two small lakes made up what is currently Lake Gusinoye, with the northern and southern basins separated by land. Increased inflow to the lakes c. 1730 led to increased lake levels, resulting in a merging of the two small lakes into one (Pisarsky *et al*., 2005).

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

The town of Gusinoozersk sits on the northeast shore of Lake Gusinoye (Figure 1b). Gusinoozersk was founded in 1939 as a settlement for the local coal industry. The settlement grew rapidly, owing to industrialization and increased demand for power, and in 1953 the settlement of Gusinoozersk was given the status of town. In 1976 the largest thermal power plant in southern Siberia was built on the shores of Lake Gusinoye, near the town of Gusinoozersk.

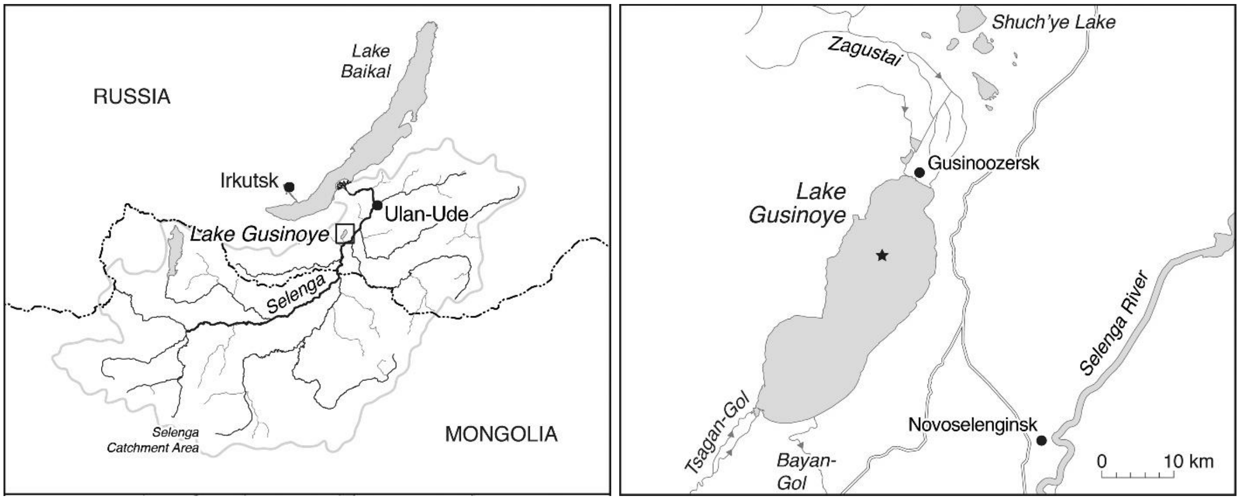

Figure 1: A) Map of Lake Gusinoye and Lake Baikal in southern Siberia; B) Lake Gusinoye with the town of Gusinoozersk and major tributaries indicated. The location of sediment core GSNO is indicated by an asterix (*).

2.2 Field sampling/Sediment core collection

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

2.3 Radioisotope dating

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

2.4 Trace elements and metals

Trace elements and metals have the potential to provide information on anthropogenic contamination, and catchment disturbance. Sediment was analyzed for trace and major element concentrations from the GSNO sediment core. Following air-drying, dried sediment was subsampled for analysis at 23 intervals. Each sample was ground to a fine powder using an agate mortar and pestle. Approximately 1.0 g of dried, finely powdered sediment was weighed into a sample cuvette lined with polypropylene film. Samples were then analyzed for trace and major elements using a Spectro X-Lab 2000 energy dispersive X-ray fluorescence spectrometer (ED-XRF) with a Si(Li) semiconductor detector in the Department of Geography at University College London (UCL). Certified standard reference materials (SRM), Buffalo River sediment (BRS; SRM 2704; Epstein *et al.*, 1989) were analyzed every 10 samples during analysis. Accuracy of standards was within 10%. Trace element and metal enrichment factors were calculated for each sample by normalizing the concentration of an element or metal (M) to the conservative lithogenic element Ti, within the sample, to the background ratio within the core. An enrichment factor of 1 throughout the record is equivalent to background concentrations, values above 1 indicate enrichment, while enrichment factors greater than 3 indicate definite anthropogenic contamination of the metal (Boës *et al.*, 2011). Enrichment factors (EFs) were calculated, using the following equation from Weiss *et al.* (1999):

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

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

2.5 Spheroidal carbonaceous particles (SCPs)

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

2.6 Loss-on-ignition and sediment densities

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

carbonate (LOI_{950}) of the dried sediment, respectively (Heiri *et al*., 2001). Carbon accumulation rates were calculated using bulk density, LOI_{550}, and sedimentation rates.

2.7 Diatoms

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

2.8 Statistical analyses

As the total number of valves counted per sample varied between sites, species richness was determined through rarefaction using 200 valves. Diatom species rarefaction richness was conducted on the diatom raw counts using R, Vegan package (R. v.3.2.4, 2016). Hill's N2, an index of the diversity of very abundant species at a single site, was calculated on the full diatom dataset using C2 (Juggins, 2014). Species concentrations were calculated using the microsphere method, and normalized to weight of sediment of the original sample (# valves g^{-1} dry weight) (Battarbee and Kneen, 1982).

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

3. Results

3.1 Radioisotope dating

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

3.2 Trace metals and elements

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

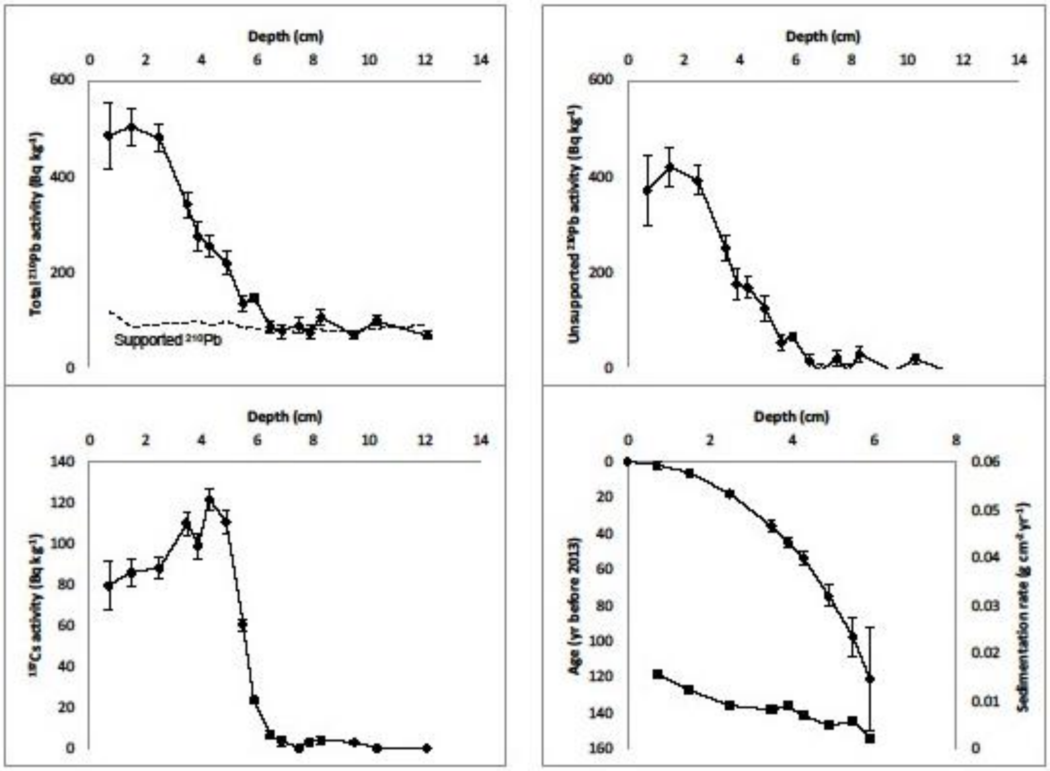

Figure 2. Fallout radionuclide concentrations in core GSNO taken from Lake Gusinoye, Russia, showing (a) total ^{210}Pb, (b) unsupported ^{210}Pb and (c) ^{137}Cs concentrations versus depth. Figure 2d. Radiometric chronology of core GSNO taken from Lake Gusinoye, Russia, showing the CRS model ^{210}Pb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

3.3 Spheroidal carbonaceous particles

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

3.4 Carbon accumulations

LOI_{550} was steady between 13.1 and 14.5 % from the mid-17th century until the mid-1970s, at which point values began to increase, reaching 20.4 in the most recent sample (Figure 3). Carbon mass accumulation rates (CMAR) exhibit a four-fold increase since the late-19th century, from c. 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 increasing sedimentation rates since the 19th century.

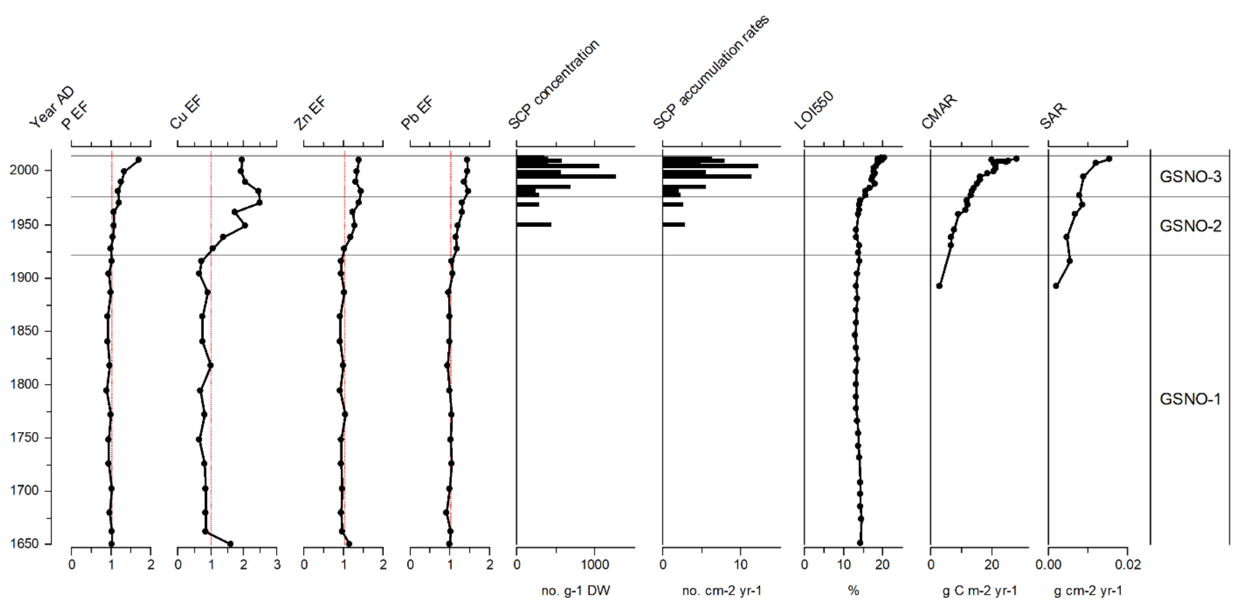

Figure 3. Trace metal and element enrichment factors for P, Cu, Zn, and Pb, SCP concentrations and accumulation rates, carbon mass accumulation rates, and sedimentation rates for sediment core GSNO.

3.5 Diatoms

The diatom assemblages at Lake Gusinoye were dominated throughout the record by planktonic species. Cluster analysis, DCA, breakpoint analysis, and broken stick indicated the presence of three important zones within the diatom assemblages of the past 200 years, and significant shifts occurred c. 1920, and from the mid-1970s to c. 1980. The diatom assemblages from the earliest part of the record were dominated (up to 70%) by *Aulacoseira granulata*, while subordinate species included small benthic Fragilarioids of the *Pseudostaurosira-Staurosira-Staurosirella* complex, particularly *Pseudostaurosira brevistriata* (Figure 4). Declines in the relative abundance of *A. granulata* began in the 18th century (Figure 4). A steady decline in *A. granulata* continued into the 20th century, concurrent with increases in abundance of two other planktonic species, *Fragilaria crotonensis* and *Lindavia ocellata* (Figure 4). Alongside late-19th and early-20th century changes in species abundances, species richness (rarefaction) and Hill's N2 measure of diversity increased (Figure 4).

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

Beginning in the 1970s and concurrent with the second breakpoint in the diatom DCA analyses, increased abundances of planktonic *Asterionella formosa*, were observed, while abundances of *Lindavia praetermissa* and *Stephanodiscus hantzschii* began to increase c. 1990. Since the late-1970s/early-1980s, abundances of *F. crotonensis* and *L. ocellata* have remained relatively steady, and the assemblages have since been dominated by these two planktonic species, occurring at almost c. 50% and c. 30%, respectively (Figure 4). Diatom accumulation rates peaked c. 2000 valves cm^2 yr^{-1}, and both concentrations and fluxes have declined in the past two decades. Significant diatom compositional turnover was observed from Lake Gusinoye (beta-diversity = 1.300 SD; $p = 0.002$). Between the mid-17th century and early-19th century, beta-diversity was stable, but then has steadily declined to very low values at the present day.

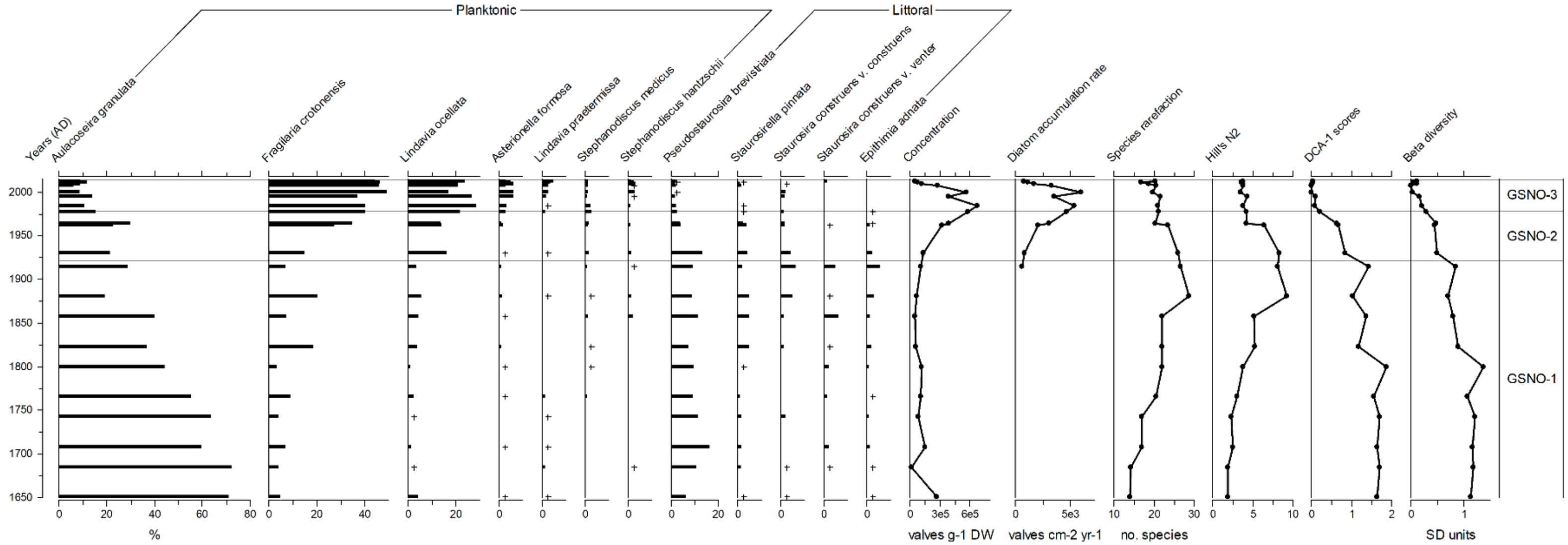

Figure 4. Diatom assemblages of Lake Gusinoye, breakpoint analysis results define zonations, and breakpoint analysis results shown along plot of DCA axis 1 scores.

4. Discussion

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

4.1 Anthropogenic contamination of Lake Gusinoye

Enrichment of trace metals started during the early-20th century, concurrent with known historical records of increasing local economies, including the development of coal mining operations around Lake Gusinoye (Pisarsky *et al*., 2005). The concurrent increases in trace metal and SCP concentrations between 1950 and the 1980s reflect the intensification of both local and regional increases in economic activity, including the construction of the Gusinoozersk State Regional Power Plant (GSRPP) (*ibid*.). Other regional lake sediment records of anthropogenic contamination indicate similar timing of events, including organic pollutants and SCP records from the south basin of Lake Baikal, from shallow lakes in the Selenga Delta, as well as Black Lake, a small lake adjacent to Lake Gusinoye (Adams *et al*., 2018; Adams, 2017; Rose *et al*., 1998). Rapid increases in SCP concentrations in the south basin of Lake Baikal in the 1950s/1960s reflected local increases in industrialization across southeast Siberia (Rose *et al*., 1998), while small increases in Baikal's north basin reflected regional sources because they were of a similar magnitude to hemispherical background increases. Increased concentrations of polycyclic aromatic hydrocarbons (PAHs) in the Lake Baikal Basin in the 1940s to 1960s also indicate a high likelihood of atmospherically deposited contaminants to Lake Gusinoye from both local and regional sources in the mid-20th century (Adams *et al*., 2018; Shirapova *et al*., 2013). Close temporal matches between the Lake Gusinoye SCP record and SCP and PAH concentrations from lake sediment cores from the south basin of Lake Baikal, the Selenga Delta, and neighbouring Black Lake indicates the primary period of anthropogenic contamination from industrialization occurred between the 1940s and 1990s (Figure 5). Post-1940, increases in P, indicative of enrichment, reflects the gradual, long-term eutrophication of Lake Gusinoye, as a result initially of early agricultural practices in the region (Bazheniva & Kobylkin, 2013), then of increases in wastewater effluent into the lake from the GSRPP and the town of Gusinoozersk, and the impacts of fish farming, which began in Lake Gusinoye in the 1980s (Pisarsky *et al*., 2005).

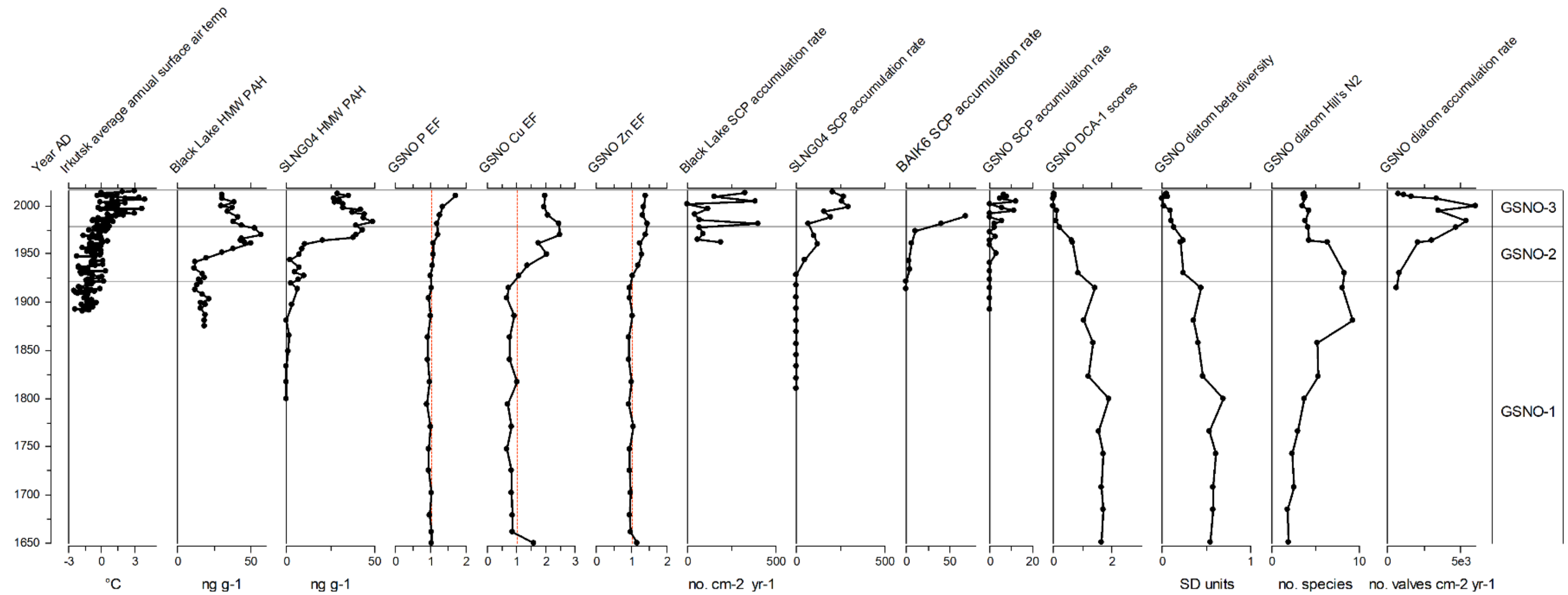

Figure 5. A comparison of anthropogenic contamination and diatom records from Lake Gusinoye with regional and local lake sediment records of anthropogenic contamination and Irkutsk, RU temperature change since the late-19th century.

4.2 Biological responses

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

The early part of our record is dominated by the heavily silicified diatom, *Aulacoseira granulata*. (Figure 4). It is a meroplanktonic species which means it is adapted to being suspended in the water column during periods of turnover (Kilham 1990). When lakes stratify, *A. granulata* sinks out of the photic zone, but because it forms resting spores from which it can regenerate (Schelske *et al*. 1995) once mixing recommences, e.g. due to strong autumnal winds, it can become retrained back into the water column. One of the most striking features of the diatom record is the gradual decline in abundance of *A. granulata* from approximately 1750 AD to just before the start of the 20th century (Figure 4). Despite its remote location, there are good historical records for 18th century development of Lake Gusinoye. When *A. granulata* dominated the sequence, the lake was divided into two separated, smaller lakes. However, after 1730, water levels in the region rose and the basin was flooded. So prior to 1750 AD, conditions in the region must have been such that deep mixing of Gusinoye occurred, which allowed regeneration of nutrients such as silica for *A. granulata* to take up. Elsewhere in the region, palaeolimnological records indicate that climate was very cold at this time, linked to the latter stages of the Little Ice Age (LIA; Mackay *et al*. 2005; 2012). After ice break up in spring on Gusinoye, cold waters would have been easy to mix, so supporting *A. granulata*.

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

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

The second significant change in diatom community composition occurred between the mid-1970s to c. 1980 (Figure 4), when livestock populations and concomitant soil erosion in the region were at their highest (Bazhenova and Kobylkin 2013). *A. granulata* abundances decline to their lowest levels for the whole record, *L. ocellata* and *F. crotonensis* reach their highest abundances, and taxa including *A. formosa*, *L. praetermissa* and *S. hantzschii* become persistent in the record. Diatom fluxes reach their highest values for the whole record, before declining in the most recently deposited sediments. The significant changes occurring in the late-20th century occur concurrently with peak SCP concentrations and P enrichment above background levels, indicative of high economic and agricultural activity in the region, respectively (Figure 5). *A. formosa* in particular has been linked in large freshwater lakes to increasing anthropogenic development and associated nutrient enrichment, particularly nitrogen (Stoermer *et al*. 1991; Wolin *et al*. 1991; Bergstöm and Jansson 2006), and competes well for increasing P in high Si environments (Bradbury, 1988; Saros *et al* 2005). The concurrent high abundances of *F. crotonensis* and *A. formosa* have been used previously to infer increased nutrient loadings and anthropogenic disturbances in lake catchments (Fritz *et al*. 1993; Anderson *et al*., 1995; Garrison and Wakeman 2000; Forrest *et al*. 2002; Wolin and Stoermer 2005; Hobbs *et al*. 2010). Further, both *F. crotonensis* and *A. formosa* have been shown to respond primarily to increases in silica and nitrogen in both temperate and alpine lakes (Saros *et al* 2005; Bennion *et al* 2011). Furthermore, *Epithemia adnata* contains endosymbiotic cyanobacteria in its cells to assist in nitrogen fixation, and that this species completely disappears from the Gusinoye sediment record at this time lends support to our suggestion that nitrogen supply was plentiful (Deyoye *et al*. 1992).

Ecological changes in the late-20th century are also likely a response to the onset of aquaculture economies (primarily *Cyprinus carpio* and *Acipenser baeri baicalensis*) in the northern basin of Lake Gusinoye c. 1980. Fish farming is known to result in increases in organic matter deposition in aquatic systems due to fish food deposition and increased fecal matter, and inorganic nutrient enrichment, particularly ammonium, nitrate, nitrite, phosphate (San Diego-McGlone *et al*., 2008). Primary producer communities have been observed to respond strongly to fish farming activities (e.g. San Diego-McGlone *et al*., 2008; Wang *et al*., 2009; Jiang *et al*., 2013). Thermal effluent from the GSRPP likely also contributed to eutrophication in recent years (e.g. Jiang *et al*., 2013), providing excellent conditions for aquaculture to thrive (Pisarsky *et al*. 2005), and coinciding with our recorded increase in *A. formosa*, *L. praetermissa* and *S. hantzschii*, peaks in diatom flux, and increasing P enrichment factors. Therefore aquaculture and thermal pollution from the GSRPP are the latest in the multitude of 20th century anthropogenic stressors impacting the ecology of Lake Gusinoye, which resulted in unprecedented shifts in diatom assemblages.

4.3 The nature of ecological shifts in multi-stressor systems

Diatom assemblage changes at Lake Gusinoye during the 20th century now indicate that primary producer communities have undergone unprecedented shifts. Our findings of primary producer changes correspond with previous studies of increasing zooplankton biomass and change in zooplankton community structure and fish diversification since the mid- to late-20th century (Borisenko *et al*., 2004). Therefore, rapid and extensive 20th century anthropogenic development in and around the Gusinoozersk region resulted in whole-ecosystem shift of Lake Gusinoye to novel ecological communities. Major shifts at all trophic levels in Lake Gusinoye have come as a result of the multiple anthropogenic stressors impacting the lake ecosystem. In multi-stressors environments, it is possible that the ecological effect of multiple disturbances may be individual, with each stressor inciting an individual response, with an overall additive effect of all stressors. However, the interaction between multiple stressors may result in exceptional ecological shifts and novel ecological communities (Sala *et al*., 2000; Christensen *et al*., 2006; Jackson *et al*., 2016b), promoting more extensive and/or rapid change, as well as unexpected or unprecedented response to stressors.

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

5. Conclusion

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

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