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

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Abstract

Global freshwater systems are threatened by multiple anthropogenic stressors via impacts on ecological structure and function necessary to maintain their health. In order to properly manage freshwater ecosystems, we must have a better understanding of the ecological response to human-induced stressors, especially 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. 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 (as indicated by spheroidal carbonaceous particle, trace metal and element records) indicate increases in regional and local development c. 1920. Diatom assemblages were initially 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. Significant diatom compositional turnover was observed since the 19th century at Lake Gusinoye. Since the early-20th century, Lake Gusinoye diatom assemblages have changed more profoundly as a result of multiple anthropogenic stressors, including nutrient influx, aquaculture, and wastewater discharge from the Gusinoozersk State Regional Power Plant. Recent diatom assemblages are dominated by *Lindavia ocellata* and nutrient-rich species, including *Fragilaria crotonensis* and *Asterionella formosa*. Evidence of continued nutrient enrichment at Lake Gusinoye is likely due to

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

1. Introduction

Freshwater lakes are under threat globally from interacting stressors (Mills *et al.*, 2017), 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, even remote lakes are no longer truly pristine (Catalan *et al*., 2013; Wolfe *et al*., 2013). Lakes also provide freshwater and protein for human populations, 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 to managing freshwater ecosystems, but because different threats have different causes, pinpointing when they first started to have a 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, including preserved microfossils and chemical constituents, it is possible to reconstruct environmental impacts on lake ecosystems through time, whether they be caused by atmospheric pollutants, disturbance from agriculture and aquaculture, or impacts of global warming, leading to alterations in local ecology and biodiversity. Paleolimnological 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). As 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 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 (Jones *et al*., 2012), leading 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 Selenga River flows through Ulan Ude which is the hub of economic activity in southeast Siberia and one of Russia's most polluted cities.. 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, 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 2 million 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 (Pisarsky *et al*., 2005). In addition to point source pollution, the ecology of Gusinoye has been impacted by invasions of introduced 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 anthropogenic 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 (e.g. Pisarsky *et al*., 2005) 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. Paleolimnological analyses allow us to evaluate ecological sensitivities and thresholds, the nature of ecological responses, as well as evidence for transitions in aquatic ecosystems on account of human activities in the critically important Lake Baikal Basin. Here, we use Lake Gusinoye as a model to study the potential impacts of long-term multiple local and regional stressors on freshwater ecosystems, and utilize multiple components of the Lake Gusinoye sediment record to disentangle recent impacts. The aim is 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, and that the impact of multiple stressors has led to contemporary novel primary producer communities. To test this hypothesis, the following objectives were undertaken:

- Reconstruct geochemical evidence of increased nutrients, catchment erosion, and pollution, and combine these with documentary evidence of local aquaculture;
- Reconstruct diatom assemblages 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 1a). The lake was formed at the end of Pleistocene as a result of tectonic activity (Bazarov, 1969). It is the second largest lake in southeast Siberia (after Lake Baikal), with a surface area of 164 km^2, a coastline that extends over 65 km, and a catchment area of 924 km^2. Lake Gusinoye is morphologically divided into a southern and a northern basin, and has a maximum depth of 25 m (southern basin). Until the early-18th century, the northern and southern basins were two separate, smaller lakes. Increased inflow to the lakes c. 1730 as a result of termination of the Little Ice Age (LIA), 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), which includes 11 currently inflowing streams. 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 only 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 is located on the northeast shore of Lake Gusinoye (Figure 1b), and was founded in 1939 as a settlement for the local coal industry. The settlement grew rapidly, owing to industrialization, and in 1953 was given the status of town. In 1976 the largest coal-fired power plant in southern Siberia was built on the shores of Lake Gusinoye, near the town of Gusinoozersk.

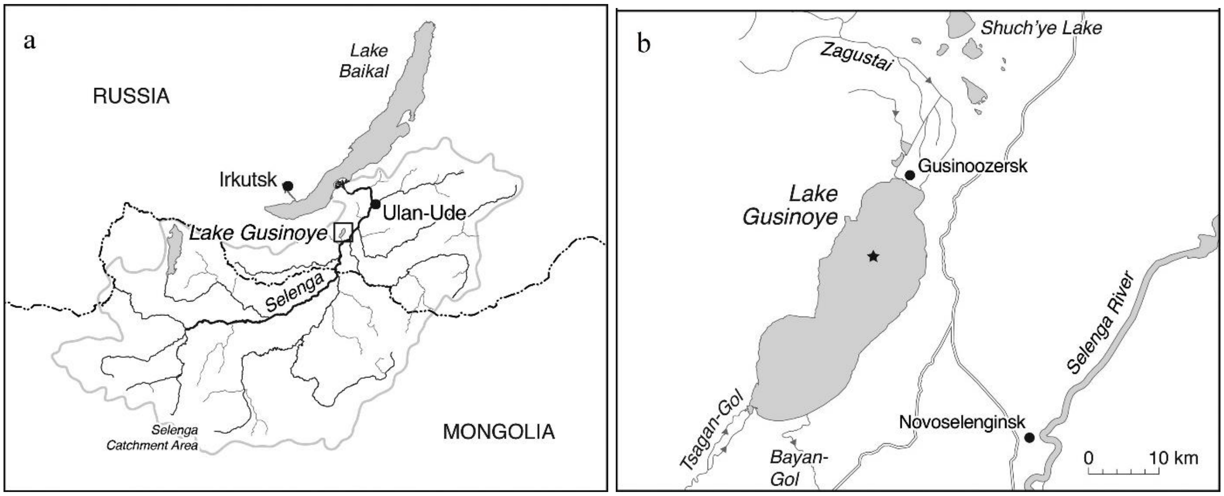

Figure 1: a) Map of Lake Gusinoye and Lake Baikal in southern Siberia; b) Lake Gusinoye with the town of Gusinoozersk and major tributaries indicated. The location of sediment core GSNO is indicated by a star.

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 northern basin was chosen due to its proximity to anthropogenic development in Gusinoozersk. The core was collected from a depth of 22 m, the deepest point in the basin, 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 & Oldfield, 1978; Appleby, 2001), and independently verified using ^{137}Cs.

2.4 Trace elements and metals

Sediment was analyzed for trace and major element concentrations. Following air-drying, dried sediment was subsampled for analysis at 23 intervals within the top 10 cm of the core. 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 (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 (EFs) were calculated for each sample by first normalizing the concentration of an element or metal (M) to the conservative lithogenic element Ti within the sample, and then normalizing to the background ratio within the core. 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. 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).

2.5 Spheroidal carbonaceous particles (SCPs)

Sediment was analyzed for spheroidal carbonaceous particle (SCP) concentrations following Rose (1994). 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 400x magnification. 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). Reference sediment (Rose, 2008) was analyzed concurrently to the samples. SCP concentrations are reported in units of number of particles per gram dry mass of sediment (gDM^{-1}).

2.6 Loss-on-ignition and sediment densities

Combustion 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). It was assumed that organic carbon comprised 58% of the total organic matter determined through LOI550 (e.g. Nelson and Sommers, 1996; Schumacher, 2002). Total organic carbon density was calculated using sediment bulk density and organic carbon content. Carbon accumulation rates were then calculated using total organic carbon density and sedimentation rates (Loisel *et al*., 2014).

2.7 Diatoms

Approximately 0.1g of wet sediment (weighed to four decimal places) was subsampled at approximately 0.5-cm intervals for diatom analysis, and processed following standard procedures according to Battarbee *et al*. (2001). For diatom slide preparation, the final cleaned diatom sample was topped up to 10 ml with distilled water and mixed well. 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. The new diatom sample was then topped up to 10 ml with distilled water and mixed well. 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 following Bacillariophyceae Vol. 1-4 (Krammer & 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 diatom valves counted varied between samples, species richness was determined through rarefaction using 200 valves. Diatom species rarefaction richness was conducted on the diatom raw counts using the vegan package in R (Oksanen *et al.*, 2018; R Core

Team, 2018). Hill's N2, an index of the diversity of very abundant species in a single sample, was calculated on the full diatom dataset using C2 (Juggins, 2014). Diatom valve concentrations were calculated using the microsphere method, and normalized to weight of sediment of the original sample (# valves g^{-1} dry weight) (Battarbee & Kneen, 1982). Diatom valve accumulation rates were calculated using sedimentation rates (# valves cm^{-2} yr^{-1}).

Unconstrained ordinations were employed to detect major patterns of variation in the diatom assemblage data. While the gradient length of axis 1 was shorter than 2.0 SD, unimodal methods (detrended correspondence analysis (DCA)) were used, due to the obvious horseshoe pattern resulting from the use of linear methods (principal components analysis (PCA)). DCA was performed in Canoco5 (ter Braak & 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 by detrended canonical correspondence analysis (DCCA) (Smol *et al.*, 2005; Birks, 2007), using estimated and extrapolated ages obtained from the ^{210}Pb CRS age model as the constraining variable. 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. Monte Carlo permutation tests for temporally ordered data were used to determine significance levels (n = 499).

Constrained cluster analysis (based on chord square distance) and breakpoint analysis were performed on the diatom dataset to determine diatom assemblage zones. Broken stick analysis was performed to determine the number of significant zones based on the constrained cluster analysis. Cluster analysis and broken stick analysis were performed in R using the rioja package

(Juggins, 2017), and breakpoint analysis was performed in R using the segmented package (Muggeo, 2008). 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 very gradual increase in the 20th century, also indicated through a constant increase in unsupported ^{210}Pb from 6 cm to 3.5 cm. There was little net change in unsupported ^{210}Pb in the top 2.6 cm, likely to be derived from dilution caused by an increase in sedimentation rates in the 21st century (Figure 2d). Ages from 5.9 to 10 cm were extrapolated assuming constant sedimentation rates.

3.2 Trace metals and elements

Trace elements and metals have the potential to provide information on anthropogenic contamination, and catchment disturbance. Elemental concentrations remained steady and unchanged in Lake Gusinoye prior to the 1930s. Beginning in the late 1930s, Ti-normalized enrichment factors (EFs) of Cu, Zn, and Pb increased above background levels (Figure 3). In the years closely following the end of World War 2, EFs for Cu increased to 2.0, and EFs for Zn and Pb began a continuous increase above background (1.0) (Figure 3). Enrichment factors for Cu, Zn, and Pb peaked between 1970 and 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).

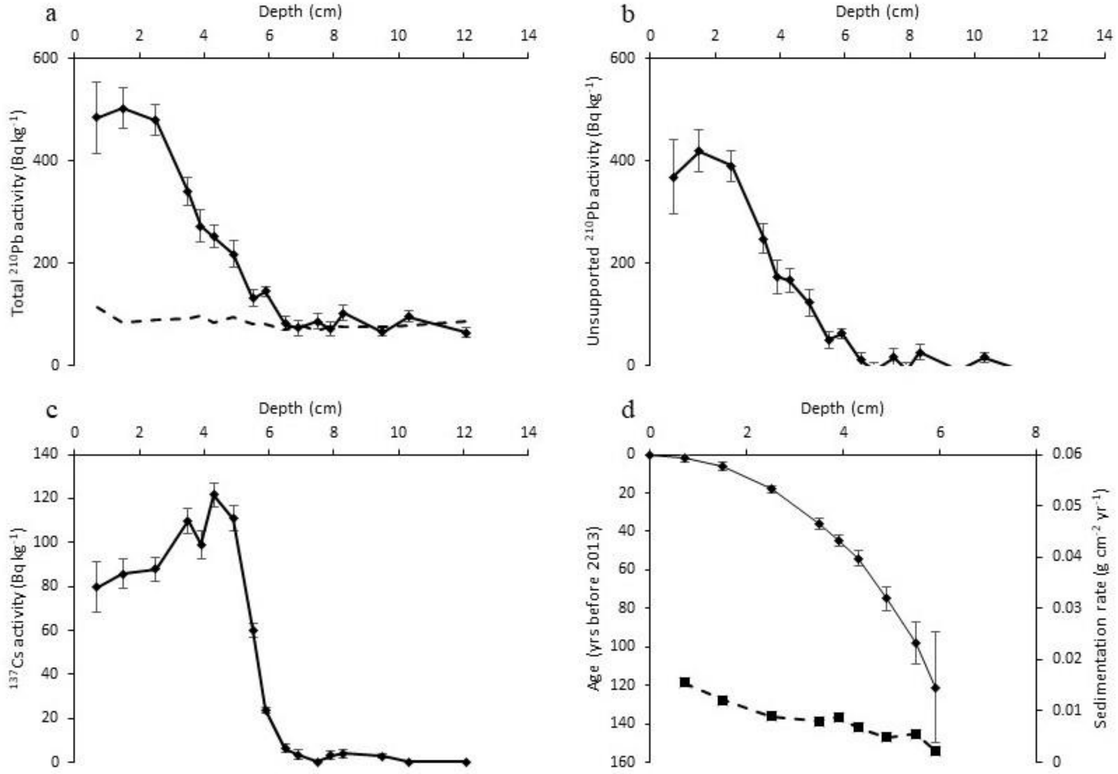

Figure 2. Fallout radionuclide concentrations in core GSNO taken from Lake Gusinoye, Russia, showing (a) total ^{210}Pb, (b) unsupported ^{210}Pb and (c) ^{137}Cs concentrations versus depth. Figure 2d) Radiometric chronology of core GSNO taken from Lake Gusinoye, Russia, showing the CRS model ^{210}Pb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

3.3 Spheroidal carbonaceous particles

SCPs are unambiguous indicators of high-temperature fossil fuel combustion, especially from power stations. 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}. SCP concentrations and fluxes have declined in recent years (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 ~7 g m^{-2} yr^{-1} to a peak of over 30 g m^{-2} yr^{-1} in recent years (Figure 3).

3.5 Diatoms

The diatom assemblages at Lake Gusinoye were dominated throughout the record by planktonic species. Constrained cluster analysis, DCA, breakpoint analysis, and broken stick analysis indicated the presence of three important zones within the diatom assemblages of the past 200 years, and significant shifts occurred c. 1920 AD, and in the late-1970s. Zone 1 of the GSNO sediment record occurred from the base of the record to c.1920. 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 19th and 20th centuries, concurrent with increases in abundance of two other planktonic species, *Fragilaria crotonensis* and *Lindavia ocellata* (Figure 4). *Fragilaria crotonensis* first increased in the early 19th century, reaching abundances of ~20% c. 1820 and again c. 1880 AD. The second increase in *F. crotonensis* is concurrent with the increase in *L. ocellata* to ~5% abundance. Alongside late-19th and early-20th century changes in species abundances, species richness (rarefaction) and Hill’s N2 measure of diversity increased (Figure 4).

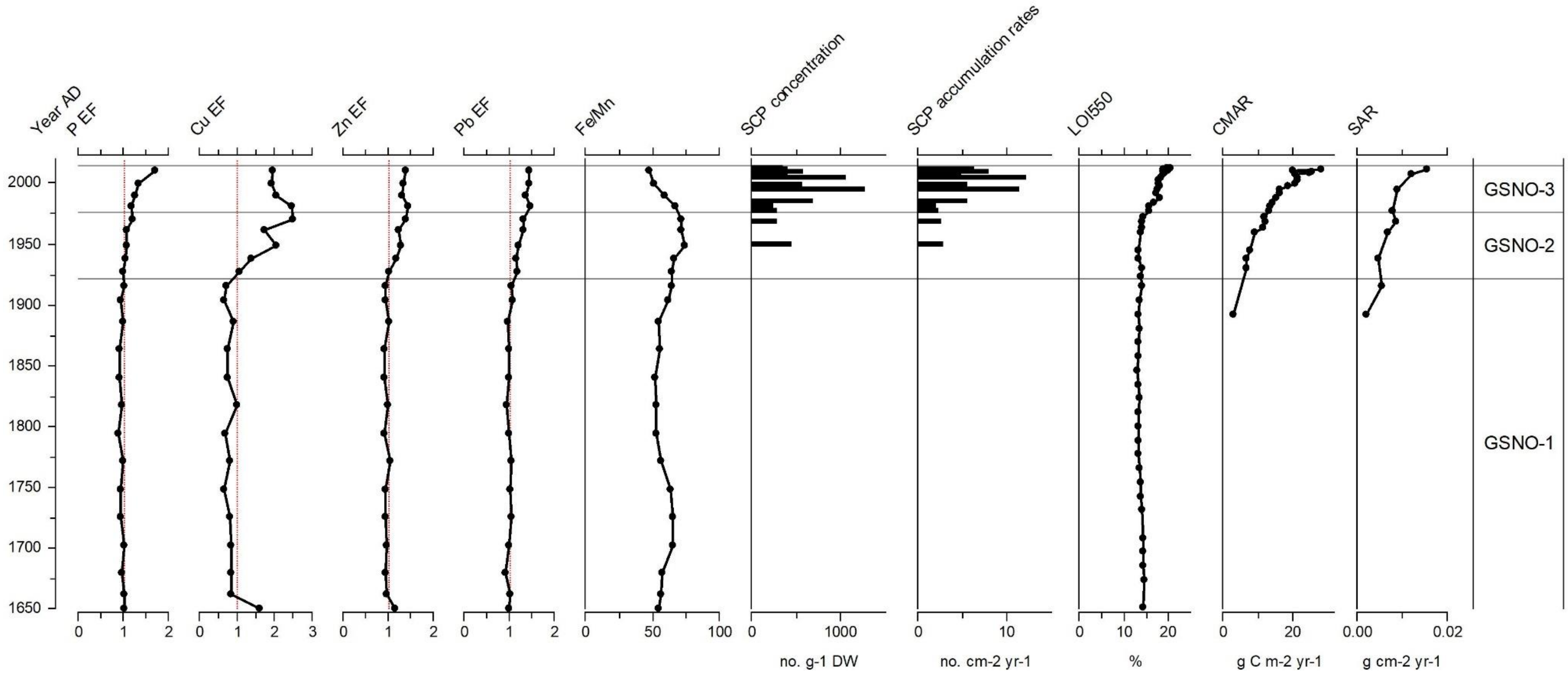

Figure 3. Trace metal and element enrichment factors for P, Cu, Zn, and Pb, Fe/Mn ratios, SCP concentrations and accumulation rates, carbon mass accumulation rates, and sedimentation rates for sediment core GSNO. Zones presented are those from diatom assemblage analyses.

Zone 2 of the diatom assemblages occurred from c. 1920 to the late-1970s, with the first significant breakpoint in the diatom DCA c. 1920 AD. By the start of Zone 2, the previously dominant *A. granulata* had declined to ~20% relative abundance, replaced as dominant species by both *F. crotonensis* and *L. ocellata*. Relative abundances of *A. granulata* remained between 20-30% through Zone 2. Between c. 1920 and the 1970s, both *L. ocellata* and *F. crotonensis* continued to increase in abundance, seemingly at the expense of small Fragilarioids (Figure 4). *Lindavia ocellata* abundances increased to ~15% c. 1930 AD, and remained steady throughout Zone 2, while *F. crotonensis* increased through Zone 2, to an abundance of 35% at the end of the zone. As species richness and Hill's N2 diversity began to decline c. 1950 AD, diatom concentrations and fluxes began to increase.

Zone 3 of the diatom assemblages occurred from the late-1970s until 2013 AD. Beginning in the 1970s and concurrent with the second breakpoint in the diatom DCA analyses c. 1977 AD, increased abundances of planktonic *Asterionella formosa*, were observed, while abundances of *Lindavia praetermissa* and *Stephanodiscus hantzschii* began to increase c. 1990 AD. Abundances of *F. crotonensis* and *L. ocellata* increased at the onset of Zone 3 to ~40% and 20%, respectively. Since the onset of Zone 3, abundances of *F. crotonensis* and *L. ocellata* have remained relatively steady, and the assemblages have since been dominated by these two planktonic species, peaking at almost 50% and 30%, respectively (Figure 4). At the beginning of Zone 3, abundances of *A. granulata* declined once again to fluctuate between 5 and 15% through the zone. Diatom accumulation rates peaked c. 2000 AD valves cm^{-2} yr^{-1}, however total diatom concentrations and fluxes, and all species 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, species composition was stable, with little change in beta-diversity during this time. Beginning c. 1930 AD, at the onset of diatom Zone 2, greater species turnover was observed with declines in beta-diversity through diatom Zones 2 and 3.

4. Discussion

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 changes to the zooplankton community occurred concurrently to fish diversification, but also loss of native fish species (Borisenko *et al*., 1994). The new contaminant and diatom sedimentary records from Lake Gusinoye provide important insights into 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 the lake (Pisarsky *et al*., 2005). The increases in trace metal and SCP concentrations between 1950 and the 1980s reflect the intensification of both local and regional 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

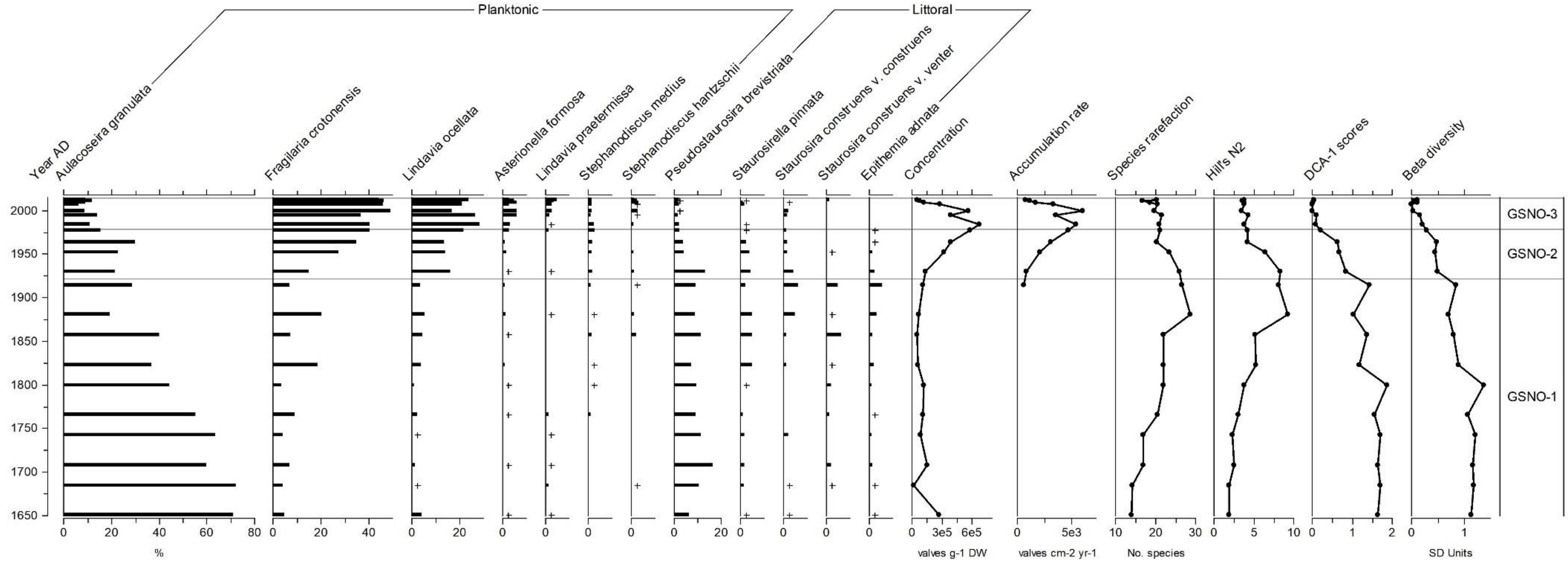

Figure 4. Diatom assemblages of Lake Gusinoye from 17th century to present day. Relative abundances (%) of all diatoms present at >5% at any one time in the sediment record. (+) indicates species present in sample at <1% relative abundance. Diatom concentrations (no. valves g^{-1} dry weight) and diatom accumulation rates (no. valves cm^{-2} yr^{-1}) are plotted, along with species rarefaction, Hill's N2 diversity, DCA axis 1 scores, and DCCA (beta-diversity) axis 1. Zones are based on DCA, breakpoint, broken stick and constrained cluster analyses.

Lake Baikal (BAIK6) (Rose *et al*., 1998), and from shallow lakes in the Selenga Delta (SLNG04), and Black Lake, a small lake adjacent to Lake Gusinoye (Adams, 2017; Adams *et al*., 2018) (Figure 5). 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 (Shirapova *et al*., 2013; Adams *et al*., 2018). 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 (BAIK6), the Selenga Delta (SLNG04), 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 sediment P may reflect the gradual, long-term increase in P inputs to Lake Gusinoye, initially as a result of early agricultural practices in the region (Bazhenova & 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 were established in the lake the 1980s (Pisarsky *et al*., 2005). While P chemistry is complex, making it difficult to interpret sedimentary changes in P as directly related to changes in P in the water column, there is little evidence for changing sedimentary redox conditions at this time in Lake Gusinoye (Figure 3), which may indicate that changes in sedimentary P in the 20th century provides an indication of directional change in P inputs to the lake. The sedimentary enrichment of P since the 1940s coincides with the measured increases in phosphate observed by Borisenko *et al*. (1994) between the mid-20th century and early 1990s in Lake Gusinoye.

4.2 Biological responses

Over the past 150 years, undisturbed, temperate lakes show little change in diatom beta-diversity (only ~1 standard deviation units (SD)) (Smol *et al*., 2005). These sites 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, Lake Gusinoye 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). However, Lake Gusinoye beta-diversity is lower than found in impacted lakes in Svalbard (Holmgren *et al*., 2010) and permafrost thaw slump-affected lakes in the Canadian Arctic (Thienpont *et al*., 2013). Prior to the 1800s, diatom assemblages were very stable in Lake Gusinoye (Figure 4) which we suggest represents reference conditions and baseline assemblages for the lake prior to anthropogenic development in the region. 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 the limnological impacts of climate change, we argue that in Lake Gusinoye, species turnover is driven by multiple factors, notably impacts of 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).

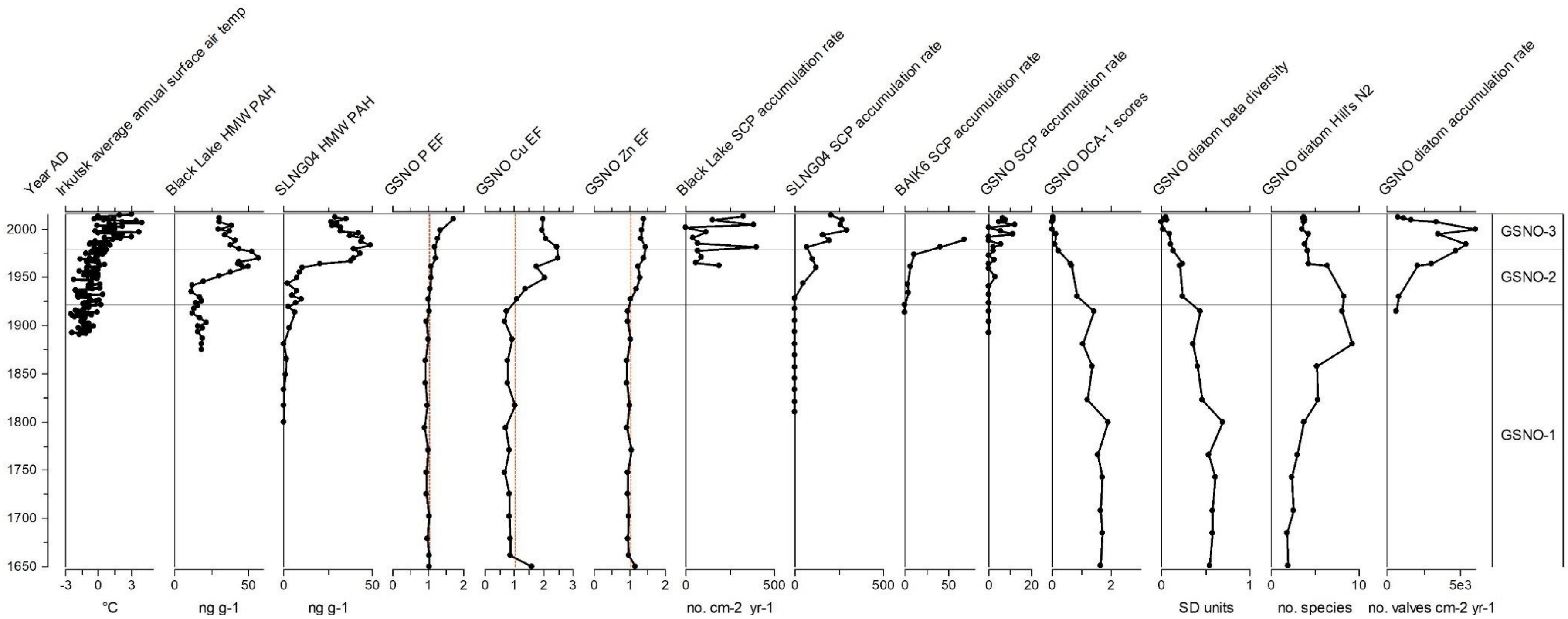

Figure 5. A comparison of anthropogenic contamination and diatom records from Lake Gusinoye with regional and local lake sediment records of anthropogenic contamination from Lake Baikal south basin (BAIK6), Selenga Delta lakes #4 (SLNG04) and neighbouring Black Lake, and Irkutsk, RU temperature change since the late-19th century.

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 entrained 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 the late 19th century (Figure 4). 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 AD, 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 Lake Gusinoye occurred, which allowed regeneration of nutrients such as silica for *A. granulata* to take up. Elsewhere in the region, paleolimnological records indicate that climate was very cold at this time, linked to the latter stages of the LIA (Mackay *et al*., 2005; 2012). After ice break up in spring on Lake Gusinoye, cold waters would have been easy to mix, so supporting *A. granulata*. Additionally, growing season at the time would have been shorter, leading to shorter and weaker periods of stratification.

Increasing river flow and flooding of the lake after 1750 AD was likely caused by warming, as the region came out of the LIA, causing widespread hydrological instability (Pisarsky *et al*., 2005). Regional warming will also have caused the growing season and period of surface water stratification in lakes to lengthen. In Lake Gusinoye, this may have limited upwelling of nutrients,resulting in the decline in *A. granulata*. *Fragilaria 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 both flooding of Lake Gusinoye, and earliest agricultural expansion and widespread deforestation in the Selenga River basin, likely leading to increased mobility and delivery of nutrients (Bazhenova & Kobylkin, 2013). 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 & Kilham, 2001), likely brought in with meltwater floods.

Prior to the end of the 19th century, shifts in diatom communities, between *A. granulata* and *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 AD (Figure 4). 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 & Kobylkin, 2013) and mining (Pisarsky *et al*., 2005) resulting in increased soil erosion, against a backdrop of increasing regional temperatures (Figure 5). *Fragilaria 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. *Lindavia ocellata* may indicate a response to continued warming temperatures, weaker lake turnover and strengthened stratification (Malik & 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 and nutrient enrichment from N, against a background of warmer temperatures in the early-20th century (Figure 5).

The second significant change in diatom community composition occurred in the late-1970s (Figure 4), when livestock populations and concomitant soil erosion in the region were at their highest (Bazhenova & Kobylkin, 2013). *Aulacoseira granulata* abundances decline reaching 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, all of which may be indictive of increasing nutrient levels, both N and P, in Lake Gusinoye. Total 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 (Figure 5). *Asterionella 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 & Jansson, 2006), and competes well for 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 & Wakeman, 2000; Forrest *et al*., 2002; Wolin & 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). Therefore, the combined high abundances of *F. crotonensis* and *A. formosa*, alongside low abundances of *Stephanodiscus* spp. may represent low but increasing P conditions and moderately abundant N and Si (Michel *et al*., 2006). Indeed, spot measurements from Lake Gusinoye indicate concentration increases for several nutrients between the mid-20th century and the early-1990s, including phosphate (from 0.003-0.03 up to 0.09 mg l^{-1}), sulphate (from 8 to 68 mg l^{-1}), nitrate (from 0-035 to 0.9 mg l^{-1}), and ammonium (from 0.001 to 2.4 mg l^{-1}) (Borisenko *et al*., 1994; Khakhinov *et al*., 2005). Furthermore, *Epithemia adnata*, which contains endosymbiotic cyanobacteria in its cells to assist in nitrogen fixation, completely disappears from the Lake Gusinoye sediment record at this time, lending 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 AD. Aquaculture 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, and phosphate (San Diego-McGlone *et al*., 2008). Primary producers have been observed to respond strongly to increasing nutrient levels related to fish farming activities, manifested, for example, as transitions to new primary producer communities, and increased occurrences of harmful algal blooms (e.g. San Diego-McGlone *et al*., 2008; Wang *et al*., 2009; Jiang *et al*., 2013). Thermal effluent from the GSRPP in recent decades provided excellent conditions for aquaculture to thrive (Pisarsky *et al*., 2005). The presence of thermal discharge from the GSRPP and the onset of aquaculture in Lake Gusinoye coincided with further declines in *A. granulata*, and our recorded increase in *A. formosa*, *L. praetermissa* and *S. hantzschii*, and peaks in diatom flux. However, declines in fluxes of all diatoms since c. 2000 may be evidence for either their decline in the water column linked to increasing stratification, increased grazing, or increased competition for resources from other algal groups. 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 significant shifts in diatom assemblages during the past several centuries.

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 significant shifts relative to pre-industrial assemblages. 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*., 1994). Therefore, rapid and extensive 20th century anthropogenic development in and around the Gusinoozersk region resulted in whole-ecosystem shift of Lake Gusinoye to historically novel ecological communities for the lake. 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 and trajectories (Sala *et al*., 2000; Christensen *et al*., 2006; Bogan & Lytle, 2011; Jackson *et al*., 2016b), promoting more extensive and/or rapid change, as well as unexpected or unprecedented response to stressors. At Lake Gusinoye, this includes an assessment that the record of diatom assemblages since the mid-17th century provide evidence for a current novel trajectory for algal communities. This includes significant shifts in the planktonic diatom community and declines in the littoral community, with no evidence for recovery, and overall decline in diatom flux since c. 2000, likely due to shifts in trophic dynamics or stronger stratification regimes.

Overall, diatom community changes indicate that increasing nutrient loadings to Lake Gusinoye since the early-20th century, 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 other lakes in cold regions, which primarily experience increases in small *Discotella/Lindavia* species as a result of reduced ice cover and/or enhanced thermal stratification due to increasing temperatures (e.g. Sorvari *et al*., 2002; Rühland *et al*., 2003; Smol *et al*., 2005; Rühland *et al*., 2008). This dominant 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 and nutrient upwelling with plentiful silica supply to a lake with high nitrogen levels, abundant silica, 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 AD 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 AD, concurrent with the onset of increasing livestock numbers and deforestation 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 with significant shifts in community structure to the multitude of developments in the Lake Gusinoye region. Diatoms first underwent assemblage shifts as a result of hydrological changes, including increased river flow and flooding, and regional warming leading to lengthening growing season and strengthening of stratification, due to the termination of the Little Ice Age in southern Siberia. Since the early-20th century, diatom communities have 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 significant ecological change in the second largest lake in southern Siberia, 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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