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Diatom evidence of 20th Century ecosystem change in Lake Baikal, Siberia

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20	Keywords: Diatoms, climate change, eutrophication, Russia, Siberia					
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22	Highlights:					
23	• This study tests predictions that regional atmospheric warming would result in substantial					
24	shifts in diatom communities in Lake Baikal, characterised by an increase in lighter, littoral					
25	diatom species (including cosmopolitan varieties) at the expense of endemic, heavily silicified					
26	open water species.					
27	• In the south basin of Lake Baikal, we find significant change in diatom assemblages over the					
28	past 40+ years, consistent with predictions of warming surface waters.					
29	• No discernible change is evident in diatom assemblages in the north basin of the lake over the					
30	past 40 years.					
31	• We find no evidence to date for cultural eutrophication in deep water sediments from Lake					
32	Baikal.					

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34 Abstract

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36 Lake Baikal has been experiencing limnological changes from recent atmospheric warming since the 37 1950s, with rising lake water temperatures, reduced ice cover duration and reduced lake water mixing 38 due to stronger thermal stratification. This study uses lake sediment cores to reconstruct recent changes 39 (c. past 20 years) in Lake Baikal's pelagic diatom communities relative to previous 20th century diatom 40 assemblage records collected in 1993 and 1994 at the same locations in the lake. Recent changes 41 documented within the core-top diatom records are in agreement with predictions by Mackay et al 42 (2006) and Moore et al (2009) of diatom responses to warming at Lake Baikal. Sediments in the south 43 basin of the lake exhibit clear temporal changes, with the most rapid occurring in the 1990's with shifts 44 towards higher abundances of the cosmopolitan *Synedra acus* and a decline in endemic species, mainly 45 Cyclotella minuta and Stephanodiscus meyerii and to a lesser extent Aulacoseira baicalensis and 46 Aulacoseira skvortzowii. The north basin, in contrast, shows no evidence of recent diatom response to 47 lake warming despite marked declines in north basin ice cover in recent decades. This study also shows 48 no diatom-inferred evidence of eutrophication from deep water sediments. However, due to the 49 localised impacts seen in areas of Lake Baikal's shoreline from nutrient pollution derived from out-50 dated sewage treatment plants, urgent action is vital to prevent anthropogenic pollution extending into 51 the open waters.

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53 **1. Introduction**

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55 In recent decades, lakes around the world have experienced increased surface water temperatures 56 (O'Reilly et al., 2015; Hampton et al., 2018). The impacts of this warming are numerous but include 57 changes in the vertical thermal structure of the water column and longer ice-free seasons, together with 58 shifts in ecosystem structure and function (Smol et al., 2005; Saros et al., 2012, 2013; O'Reilly et al., 59 2015; Hampton et al., 2017). For example, lakes have experienced community compositional changes 60 such as large-scale shifts in plankton, with increases in taxa (such as picocyanobacteria) which are better 61 adapted to reduced turbulent mixing (Findlay et al., 2001; Bopp et al., 2005; Hampton et al., 2008; 62 O'Beirne et al., 2017; Reavie et al., 2017; Edlund et al., 2017). These changes are not restricted to small 63 - medium sized water bodies. Very large lakes, including the Laurentian Great Lakes, Lake Tahoe 64 (North America) and Lake Tanganyika (East Africa), have also experienced shifts in their biological 65 communities and autochthonous primary production (Winder et al., 2009; Shaw Chraïbi et al., 2014; 66 Cohen et al., 2016; O'Beirne et al., 2017; Reavie et al., 2017; Hampton et al., 2018). At the same time,

67 lake ecosystems are also sensitive to the impacts of climate warming on watershed processes, which

- 68 can lead to alterations of fluvial inputs, including the flux of nutrients to lakes and the browning of lake
- 69 waters from increased dissolved organic matter (DOM) input (Magnuson et al., 2000; Yoshioka et al.,
- 70 2002, Hampton et al., 2008; Edlund et al., 2017; Creed et al. 2018). Such changes can influence
- 71 autotrophic algal and bacterial communities through changes in nutrient cycling and light availability
- 72 (Wrona et al., 2006; Attermeyer et al., 2014).
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74 Lake Baikal, the world's oldest, deepest, and most voluminous lake, is experiencing impacts from 75 climate warming. Atmospheric temperatures in the region around Lake Baikal in southern Siberia have 76 increased significantly in recent decades, with mean annual surface air temperatures in the nearby city 77 of Irkutsk (Figure 1) rising from -5.8°C to 0.3°C over the last 20 years (Shimaraev and Domysheva, 78 2013). Atmospheric temperature data from a climate station in Nizhneangarsk (Figure 1), in the north 79 basin catchment area of Baikal, similarly shows a less pronounced warming trend from -1.27°C to 80 0.48°C between 1952 and 2013 CE (mean annual temperatures; http://climexp.knmi.nl/). The scale of 81 recent atmospheric warming, regionally, is unprecedented for the past 1000 years (Davi et al. 2015). 82 Concordant with recent warming, summer surface lake water temperatures have increased by over 2°C 83 over the past 60 years (Hampton et al., 2008; Moore et al., 2009; Izmest'eva et al. 2016), alongside 84 seasonal changes to ice cover dynamics (Todd and Mackay, 2003; Sizova et al. 2013). Shorter ice cover 85 and warmer water temperatures have led to marked increases in chlorophyll-a concentrations and 86 summer plankton biomass in the south basin of Lake Baikal over the past 60 years (Hampton et al., 87 2008; Moore et al., 2009; Hampton et al., 2014; Hampton et al., 2015; Izmest'eva et al., 2016; Silow et 88 al., 2016).

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90 Further 21st Century warming is predicted to trigger additional plankton community change with a shift 91 from the production of endemic, heavily silicified diatoms towards lighter, littoral diatoms and 92 autotrophic picoplankton (APP) (Popovskaya 2000; Mackay et al., 1998; Fietz et al., 2005; Mackay et 93 al., 2006; Moore et al., 2009). For example, Mackay et al. (2006) predicted that future reductions in ice 94 duration associated with regional warming, would result in enhanced transport of littoral diatoms to 95 pelagic regions, such as Stephanodiscus meyerii and Synedra acus, concomitant with the decline in 96 endemic pelagic species such as Aulacoseira baicalensis and Cyclotella minuta. These changes may be 97 enhanced by elevated spring run-off from increased precipitation (IPCC 2014), increasing silicon and 98 other nutrient delivery to the lake, further encouraging the growth of species such as Synedra acus 99 (Bradbury et al., 1994; Mackay et al., 2006), while also altering carbon cycling in the lake due to 100 enhanced delivery of dissolved organic carbon (DOC) and particulate organic carbon (POC) (Yoshioka 101 et al. 2002; Moore et al. 2009).

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To date, these predictions at Lake Baikal have largely been made from diatom records collected in the early 1990's (Mackay et al. 1998; 2006). In this paper, we test these predictions and assess whether the diatom flora in Lake Baikal has indeed undergone shifts in community composition in response to the major increases in global and regional atmospheric temperatures over the past 20 years (IPCC 2014). In particular we examine whether there has been a transition from a flora dominated by heavily-silicified endemic species to one that is more cosmopolitan with lighter, less-silicified species (Mackay et al., 2006; Hampton et al., 2008, 2014, 2015; Moore et al., 2009; Izmest'eva et al., 2016).

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111 **2. Methodology**

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113 **2.1. Short cores**

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115 Short cores (< 65 cm) were collected in March and August 2013 from 7 coring stations across the 116 southern and northern basins of Lake Baikal, as well as Maloe More Bay, a relatively isolated bay off 117 the central basin (Figure 1). The codes used to define the locations of these coring sites across Lake 118 Baikal include south basin (SB), nearby the Selenga Delta (SD), at the Buguldieka Saddle (BS), Maloe 119 More bay (MM) and north basin (NB), and these have been applied after the original coring site codes. 120 Cores were collected using a UWITEC corer with PVC-liners (Ø 63 mm), which provided complete 121 and undisturbed recovery of the sediment/water interface. All coring stations were > 5 km from the 122 shore with some sites coinciding with previous short cores taken in 1993 and 1994 - see Table 1 and 123 Mackay et al. (1998) for details. Several cores were collected at each station. One core was sub-sampled in the field at a resolution of 0.2 cm and transported to the UK for diatom analyses and ²¹⁰Pb radiometric 124 125 dating, and at least one other core was transferred to the Institute of the Earth's Crust (Irkutsk) before 126 being cut, photographed and lithologically described, based on smear slide inspection. A Bartington 127 MS2E High Resolution Surface Scanning Sensor (Bartington Instruments, 1995) was used for non-128 destructive measurement of magnetic susceptibility (MS), with a resolution of 1 cm and reproducibility 129 of <5%.

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131 2.2 Diatom Analysis

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Surface sediment samples (upper 2 cm) covering at least the last 30 years were analysed for diatoms,
enabling overlap with published diatom records covering the interval prior to this (Mackay et al., 1998).
Sample preparation followed previous protocols for diatom analysis on Lake Baikal sediment samples

- bumple preparation renowed previous protocols for diatom analysis on Eake Barkar seament samples
- 136 with no chemical treatments in order to minimise valve breakage, especially of lightly silicified diatom

137 species (Flower, 1993; Mackay et al., 1998). To calculate diatom concentrations $(10^4 \text{ valves/g dry}$ 138 weight), a known weight of divinylbenzene microspheres (approximately 1 - 2 g) was added to the 139 cleaned samples (Battarbee and Kneen, 1982). Subsamples of the suspensions were diluted and settled 140 out onto coverslips and fixed onto slides with Naphrax on a hotplate at 130°C. A total of 300 valves 141 were counted at x1000 magnification by using an oil immersion lens and phase contrast under a Zeiss

- 142 Axioskop 2 plus light microscope.
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144 Diatom dissolution also plays a role in shaping sedimentary diatom assemblages, because some species 145 are more heavily silicified (A. baicalensis) than others (S. acus) and consequently more resistant to 146 dissolution (Ryves et al. 2003). Diatom dissolution was estimated by categorising endemic diatom 147 species; Aulacoseira baicalensis (Meyer) Simonsen, Aulacoseira skvortzowii (Edlund, Stoermer and 148 Taylor), Cyclotella baicalensis (Meyer) Skv., and Cyclotella minuta (Skv.) Antipova, into three stages 149 of valve preservation. A diatom dissolution index (DDI) (Flower and Likhoshway, 1993) was then 150 calculated to quantify the extent of diatom preservation in every sample (Ryves et al., 2009). A DDI 151 value of 0 indicates that all diatom valves are affected by dissolution, while a DDI value of 1 indicates 152 that all the diatom valves are in a pristine condition. Indices have been combined to express the index 153 as dissolution per sample. There is possibly a third endemic Cyclotella species, Cyclotella ornata 154 (Flower 1993) of intermediate size between C. baicalensis and C. minuta. However, Jewson et al. 155 (2015) suggest that it most likely belongs to one of the other two species. Either way, in sedimentary 156 material the centre areas of these valves are often indistinguishable from the central areas of C. minuta 157 valves after breakage and dissolution. Here we group potential C. cf. ornata valves in with C. minuta 158 (C. minuta agg.), which also makes comparisons with earlier studies, e.g. Mackay et al. (1998) 159 consistent.

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161 **2.3 Chronology**

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Dried sediments from cores BAIK13-4F_SB, BAIK13-7A_SB, BAIK13-10A_SD, BAIK13-11C_BS, BAIK13-14C_MM, BAIK13-18A_NB and BAIK13-19B_NB (Figure 1) were analysed for ²¹⁰Pb, ²²⁶Ra, ¹³⁷Cs and ²⁴¹Am, by non-destructive direct gamma spectrometry (Appleby et al., 1986) at the UCL Environmental Radiometric Facility, using an ORTEC HPGe GWL series well-type coaxial low background intrinsic germanium detector. Age-depth models were constructed using polynomial regressions fitted to the ²¹⁰Pb data with additional degrees added until no improvement occurred in the fitted model under an ANOVA test at the 95% confidence interval.

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171 2.4 Statistical Analysis

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173 To constrain how diatom assemblages in the core-tops (representing material over the past c. 20 years) have differed through the 19th and 20th Centuries, squared chord distance (SCD) dissimilarity scores 174 175 were determined for cores BAIK13-7A_SB, BAIK13-11C_BS and BAIK13-18A_NB using R (R Core 176 Team, 2013). These cores overlap with previously published cores BAIK38_SB, BAIK19_BS and 177 BAIK29_NB respectively (Table 1), and the results can be used as a baseline to evaluate whether diatom 178 assemblages have significantly altered since the 1990's (Mackay et al., 1998). Ranging between 0 and 179 5, a SCD score of 0 indicates that the diatom assemblages in two samples are identical, whereas a score 180 of 5 indicates samples are completely different in their diatom assemblage composition. Breakpoint 181 analysis was carried out on the SCD scores in R using the segmented library (Muggeo, 2008; R Core 182 Team, 2013). 183 184 Temporal changes in the diatom assemblages were further visualised using principal components

analysis (PCA) of major taxa in all core-top samples collected in 2013 together with data from the
overlapping cores collected in 1993/1994 (Table 1). Following detrended correspondence analysis
(DCA), which demonstrated a linear response based on the gradient length of the first axis, data were
reanalysed using PCA with square root transformation of species abundances using Canoco 4.5 (ter
Braak and Šmilauer, 2002).

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191 **3. Results**

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193 **3.1. Core lithology**

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All cores were dominated by terrigenous material with varying levels of oxidation due to the complete fully oxygenated water column (Figure 2). Turbidites were present in cores BAIK13-4C_SB and BAIK13-18C_NB, but the uppermost turbidites (2.0–5.3 cm in BAIK13-4C_SB; 22.0–49.8 cm in BAIK13-18C_NB) occurred below the samples analysed in this study and are therefore not discussed further.

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201 **3.2.**²¹⁰Pb age models

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Total ²¹⁰Pb activity reaches equilibrium with supported ²¹⁰Pb at a depth of 9 cm (BAIK13-4F_SB), 4 cm (BAIK13-7A_SB), 13 cm (BAIK13-10A_SD), 10 cm (BAIK13-11C_BS), 7 cm (BAIK13-

205 14C_MM), 3 cm (BAIK13-18A_NB) and 5.5 cm (BAIK13-19B_NB) (Figure 3). At all sites, ²¹⁰Pb

dates were calculated using the constant rate of ²¹⁰Pb supply (CRS) model (Appleby and Oldfield, 206 1978), and where possible, dates independently verified using ¹³⁷Cs and ²⁴¹Am data. For example, a 207 well resolved ¹³⁷Cs activity peak at 5.5-5.7 cm agrees with ²¹⁰Pb dated sediments at BAIK13-4F_SB. 208 At BAIK13-10A_SD, ¹³⁷Cs activity shows a broad peak at 6.7-8.5 cm, and because ²⁴¹Am peaks at 8.3 209 cm, this represents the 1963 CE (common era) peak in radioactive fallout; the ²¹⁰Pb date at 1963 falls 210 in this range. At BAIK13-11C BS, ²¹⁰Pb dating can be confirmed with peaks of ¹³⁷Cs at both 1986 CE 211 and 1963. At BAIK13-14C MM, high ¹³⁷Cs activities in top 4.1cm concur with ²¹⁰Pb dating that these 212 213 sediments were deposited since 1963. At BAIK13-18B_NB, the peak in ¹³⁷Cs activity between 0.7-214 1.1cm concurs with CRS ²¹⁰Pb dating of 1986 being between 0.7-1.1cm, so this peak likely represents 215 Chernobyl accident in 1986. At only two sites, BAIK13-7A SB and BAIK13-19B NB, were ¹³⁷Cs and 216 ²⁴¹Am activities not able to be used to confirm ²¹⁰Pb dating. For all sites, the final age-depth model 217 shows a good fit to the ²¹⁰Pb dates with an adjusted $R^2 > 0.99$ (Figure 3). Mean uncertainty in the 218 individual ²¹⁰Pb dates across all four cores ranges from 2-36 years is: BAIK13-4F SB: $\bar{x} = 8$, range = 219 2-30; BAIK13-7A_SB: $\bar{x} = 3$, range = 2-6, BAIK13-10A_SD: $\bar{x} = 7$, range = 2-20; BAIK13-11C_BS: 220 $\bar{x} = 12$, range = 2-36; BAIK13-14C_MM: $\bar{x} = 8$, range = 2-26; BAIK13-18A_NB: $\bar{x} = 8$, range = 2-15; 221 BAIK13-19B_NB: $\bar{x} = 11$, range = 2-24 (Figure 3).

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223 **3.3. Diatom profiles**

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In the south basin, at BAIK13-4F_SB (Figure 4) *S. acus* increased from 7% to 22% abundance over the
top 2 cm of the core (2006–2013 CE). Over the same interval *A. baicalensis* declined from 26% to 24%,
along with *A. skvortzowii* (decrease from 8% to 5%). *C. minuta* agg. varies between 35% to 51% relative
abundance and *S. meyerii* varied between 2% to 5%. Diatom concentrations in the upper sediments
ranged between 85.1 to 147.1 x 10⁴ valves/g DW over the last decade.

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In the south basin, at site BAIK13-7A_SB (Figure 5) there was a good overlap with the core diatom assemblages from BAIK38_SB in Mackay et al. (1998) between 0.9–1.9 cm. *S. acus* relative abundances in the surface sediment assemblages from BAIK13-7A_SB ranged from 6% to 18%, *A. baicalensis* ranged from 25% to 41% relative abundance over the last c. 40 years between 1975 – 2013, and *Cyclotella minuta* agg. ranged between 38% and 24%. Diatom concentrations ranged between 540.8 to 98.5 x 10⁴ valves/g DW over the last c. 33 years (1980 – 2013 CE). Diatom dissolution index (DDI) values fluctuated between 0.5 to 0.8.

^{225 3.3.1} South basin sites

241 In the south basin, at site BAIK13-10A_SD (Figure 4), in the shallow waters off the coast of the Selenga 242 Delta, the diatom assemblage diversity (> 2% abundance) was higher than the core tops in this study, 243 with Stephanodiscus parvus (1-3% abundance), Staurosira construens var. venter (1-3% abundance), 244 Fragilaria ulna (2-4% abundance), Fragilaria capucina (1-9% abundance), Achnanthidium 245 minutissimum (1-3% abundance), Staurosirella pinnata (1-4% abundance) and Cocconeis placentula 246 (1–2% abundance). Over the top 2 cm (2009-2013 CE), percentage abundances remained relatively 247 consistent for A. baicalensis (range between 9-17%), A. skvortzowii (ranged between 22-31%), C. 248 minuta agg. (ranged between 13-18%) and S. acus (ranged between 10-17%), while S. meyerii ranged 249 from 13% to 2% abundance.

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251 At site BAIK13-11C_BS, in the waters of the Buguldieka Saddle opposite the Selenga Delta (Figure 252 1), there was a good overlap between 2.4–2.6 cm with the diatom assemblages from BAIK19_BS in 253 Mackay et al. (1998) (Figure 5). The upper 2.3 cm in BAIK13-11C BS showed a decreasing trend in 254 A. baicalensis to abundances of c. 14% and C. minuta agg. to abundances of c. 20% and increasing 255 abundances of S. acus to abundances of > 20% over the last c. 20 years (1993-2013 CE). Diatom 256 concentrations showed a decreasing trend towards the surface sediments, from concentrations of 648.5 257 x 10⁴ valves/g DW to 241.1 x 10⁴ valves/g DW over the last c. 80 years (1930-2013). DDI values 258 fluctuated between 0.4 to 0.7.

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260 3.3.2 Maloe More Bay

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In Maloe More bay, off of the central basin, at site BAIK13-14C_MM, in the shallow waters of the Maloe More (Figure 4), *A. baicalensis* (range = 13–20%), *A. skvortzowii* (range = 3-8%), *C. minuta* agg. (range = 19-31%), S. *acus* (range = 9-15%) and *Crateriportula inconspicua* (range = 4-6%) remained relatively consistent in abundance over the 2 cm (2002-2013 CE). However, over the same interval *S. meyerii* ranged from 22-13% abundance, and diatom concentrations ranged between 78.7 to 486.2 x 10^4 valves/g DW.

- 268
- 269 3.3.3 North basin sites
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In the centre of the north basin, at site BAIK13-18A_NB (Figure 1) there was a good overlap between 0.8–1.9 cm with the assemblages from BAIK29_NB in Mackay et al. (1998) (Figure 5). Assemblages within the upper 2 cm of BAIK13-18A_NB showed a decreasing trend in *A. baicalensis* (from c. 60% to c. 50%) and *S. acus* ranged from c. 6% to 1% (Figure 5). *C. minuta* agg. ranged in abundance between c. 20% to 30% over the last c. 80 years (1930–2013 CE). DDI values fluctuated between 0.5 to 0.7 and before the surface sediments, diatom concentrations showed a decreasing trend, from concentrations of

277 129.5 to 12.4 x 10^4 valves/g DW between c. 1876–1992 CE.

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In the north of the north basin, at site BAIK13-19B_NB (Figure 4), A. baicalensis and C. minuta agg.

varied between 65-74% and 12-17% respectively, while there was little change in both *A. skvortzowii*and *C. inconspicua* (1–4% and 2-3% respectively). *S. meyerii* showed a small decline from 5-1.3% over

- the top 2 cm (1984-2013 CE) with diatom concentrations ranging between 129.5 to 455.6 (10^4 valves/g
- 283 DW) over the last 30 years.
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285 **3.4. Temporal changes in the diatom assemblages**

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287 DDI values are > 0.5 in all samples, suggesting that the majority of the valves, which make it into the 288 sedimentary record are well preserved (Ryves et al., 2003). Squared chord distance (SCD) dissimilarity 289 scores (Figure 5) showed that surface sediment diatom assemblages in the south basin (BAIK13-290 7A_SB) and Buguldieka Saddle (BAIK13-11C_BS) were significantly different from older diatom 291 assemblages determined from BAIK38_SB and BAIK19_BS respectively. In the south basin, the 292 significant change in SCD values occurred at c. 1970 CE (p < 0.001; Figure 5). At the Buguldieka 293 Saddle, breakpoint analysis of the SCD scores showed that a significant shift to the modern-day 294 assemblage occurred later, at c. 2000 CE (p value < 0.001) (Figure 5). In contrast, diatom assemblages 295 have changed very little in the north basin over the past 60 years, with no significant breakpoints found 296 in the SCD scores at BAIK13-18A_NB (Figure 5).

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298 PCA of all diatom assemblages investigated here revealed a difference between the core top samples 299 analysed in this study and all samples in the older, overlapping cores from Mackay et al. (1998). Core 300 tops collected in 2013 contained higher abundances of S. acus, A. skvortzowii and S. meyerii, and lower 301 abundances of A. baicalensis (Figure 6). Axis one explained 47% of the variance in the dataset and is 302 driven largely by the pelagic species A. baicalensis (species score = +0.98) versus species linked to 303 littoral habitats, mainly S. acus, A. skvortzowii, (and to a lesser extent S. meyerii). Axis two explained 304 24% of the variance in the dataset and is driven by a gradient of pelagic C. minuta agg. versus the 305 smaller C. inconspicua species (Figure 6).

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307 **4. Discussion**

- 309 4.1 Diatom ecology and spatial variability
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311 The observed spatial distributions of the most common planktonic diatoms in Lake Baikal surface 312 sediments (summarised by PCA in Figure 6) are linked to complex interactions between lake 313 morphology and chemistry, against a backdrop of a strong climatic gradient associated with the lake 314 spanning over 4 degrees of latitude (Mackay et al., 1998, 2006; Likhoshway et al., 2005). When the 315 lake is frozen (between November and March), and during both spring and autumn turnover periods, 316 siliceous diatoms dominate primary production (Jewson et al., 2009). During summer months however, 317 surface water temperatures increase and lake surface waters stratify, resulting in the seasonal succession 318 to mainly non-siliceous, autotrophic picoplankton. These non-siliceous algae effectively compete for 319 nutrients such as phosphate and nitrate (Belykh & Sorokovikova 2003), making them unavailable for 320 most diatoms growing in the open lake. Picoplankton are well adapted to thrive within summer stratified 321 waters as they are able to adjust their position within the water column, unlike heavy diatoms, and can 322 avoid high solar radiation and move to waters depths with favourable nutrient concentrations and 323 temperatures (Hampton et al., 2008).

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325 PC1 is dominated by the gradient between A. baicalensis (associated with north basin, deep-water 326 surface sediments; species score = +0.98) and A. skvortzowii (-0.72), S. acus (-0.83) & S. meyerii (-327 0.79) (all associated with the shallow water surface sediments of the Buguldieka Saddle, off the Selenga 328 Delta, and in the Maloe More) (Figure 6). Unlike A. baicalensis abundances, Figure 5 reveals that the 329 latter three species have never been abundant in the north basin for at least the last 100 years. Both A. 330 baicalensis and A. skvortzowii thrive in cold water temperatures below 5°C, blooming largely during 331 the spring and decline in abundance when lake waters warm to more than 5-6 °C (Jewson et al., 2008; 332 2010). During the summer therefore as lake stratification commences and surface water warms (Jewson 333 et al., 2009; 2010) and nutrient concentrations decrease (due to the seasonal succession of autotrophic picoplankton), these two species decline. However, each species employs very different adaptations 334 335 that allow them to avoid high surface water temperatures. A. baicalensis grows well in conditions of 336 low light (Jewson et al., 2009), and due to its physiological plasticity competes well under ice through 337 the production of smaller-sized valves, which then sink slowly after ice break up. After ice break up, 338 mixing depths increase and declining light levels induce A. baicalensis to form longer, thicker resting 339 cells full of storage products that allow them to survive throughout the period of summer stratification 340 in cooler waters of intermediate depth (c. 50-100m) (Jewson et al. 2010). Formation of the resting cells 341 requires a lot of silica, which is met through remineralisation of silica from dissolving diatoms at 342 moderate depths in the water column (Callender & Granina 1995; Jewson et al., 2010). A skvortzowii 343 avoids higher surface water temperatures also through the production of resting stages, but unlike A. 344 baicalensis, its cue for the production of resting spores is phosphate utilisation by other algae (e.g. 345 picoplankton) in surface waters (Jewson et al., 2008). Furthermore, A. skvortzowii has evolved 346 planktonic and littoral life history stages, such that viable spores remain in coastal sediments down to a 347 depth of 25 m, where they can be resuspended by strong autumn wind-driven waves into the pelagic 348 zone (ibid.) in time to bloom the following spring. In the north basin of Lake Baikal, generally lower 349 primary production during the spring (e.g. Izmest'eva et al., 2016; Panizzo et al., 2018) means that 350 phosphate concentrations rarely fall below the threshold level of 15-23 µg/L needed to induce spore 351 formation, meaning A. skvortzowii is unable to grow well in this basin (Jewson et al., 2008). Similarly, 352 later ice off dates (compared to the south and central basins) in the north basin can account for the 353 competitive advantage of A. baicalensis species over A skvortzowii.

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355 S. acus is associated with high dissolved silica concentrations (Kilham & Kilham, 1990; Bradbury et 356 al., 1994), which are higher in the south basin than the north basin because of greater river inflow (e.g. 357 the Selenga river), transporting dissolved Si from the catchment to the lake (Bradbury et al., 1994; 358 Shimaraev et al., 2013), and this is reflected in Figure 6 (refer to core BAIK13-10A SD data). However, 359 recent work has shown that increased silicic acid availability is also strongly controlled via population 360 changes in other diatom taxa (Shimaraev and Domysheva, 2013; Jewson et al., 2015). In particular, 361 when populations of A. baicalensis remain high during Melosira years, the availability of silicic acid 362 for other species to uptake (such as S. acus) declines (Jewson et al., 2015). In addition to water 363 temperature dynamics driving high abundances of A. baicalensis populations in north basin sites (see 364 above), it is probable that their high Si demand can also account for the reduced abundances of S. acus 365 in north basin sites (Figures 5 and 6).

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367 S. meyerii is a small endemic diatom which has a high temperature optimum of 15 - 17.5 °C (Jewson et al., 2015), and like other *Stephanodiscus* species likely has a high affinity for phosphorus (Bradbury et al., 1994), although its autecology is poorly known. These adaptations likely account for the observed distributions in the surface sediments of Lake Baikal (Figure 6), especially in regions which have high phosphorus loadings (Mackay et al., 2006), such as the shallow waters of the Maloe More and off the coast of the Selenga Delta (Müller et al., 2005).

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C. minuta is a co-dominant of the pelagic community in both the north and south basins, although it mainly occupies a different temporal niche than the spring blooming diatoms, which accounts for it being positioned orthogonal to taxa associated with PCA axis 1 (Figure 6). Populations of *C. minuta* also grow under ice during spring, but their main growth occurs during autumn overturn (Jewson et al., 2015). Indeed, they are the only pelagic diatom to bloom in substantial numbers in autumn; they persist in the upper water column for longer because they can tolerate water temperatures up to 11 °C, so that when stratification breaks down at the end of the summer, and nutrient overturn occurs in the photic

- 381 zone, cells are retrained first, giving them a competitive advantage (Jewson et al., 2015). However, at 382 the finer scale, C. minuta abundances are not truly independent of spring blooming species. For 383 example, when A. baicalensis blooms are particularly large (e.g. "Melosira bloom years"), dissolved 384 silica becomes depleted for all other diatoms, causing the subsequent autumnal crop of C. minuta to be 385 much smaller (Jewson et al., 2015). Unfortunately, we know very little about the ecology of the endemic 386 *C. inconspicua*, and currently can only describe its spatial distribution here as being present in very low 387 relative abundances (< 2%) in the south basin and in the shallow waters off the Selenga Delta, but is 388 persistent (> 2%) in the north basin and the Buguldieka Saddle, which accounts for its strong negative 389 association with axis 2 in Figure 6.
- 390

391 4.2. Environmental trends and temporal variability

392

393 Spring (March to April) air temperatures, from the KNMI Climate Explorer database 394 (http://climexp.knmi.nl/) for Irkutsk, close to the south basin of Lake Baikal (World Meteorological 395 Organisation station 30710; 52°16'20''N, 104°18'29''E; elevation = 467 m) increased between 1950-396 2013 CE (Figure 7). Air temperatures in the south basin of Lake Baikal have increased by c. 1.2 °C per 397 year, significantly higher than global trends, with greatest warming occurring during winter months, 398 especially at the start of the 1950s and again since the early 1970s (Shimaraev & Domysheva, 2013). 399 Increasing air temperatures have resulted in increases in average annual surface water temperatures of 400 c. 2°C across the entire lake between 1977-2003 (Izmest'eva et al., 2016), with warming in the south 401 basin, reaching increases of over 2.4 °C during late summer months (Hampton et al., 2008) and warming 402 also reported in the north basin from 1977 to 2003 CE (Izmest'eva et al., 2016). Warmer atmospheric 403 temperatures have also resulted in marked changes in ice dynamics across the lake; annual ice duration 404 in the south and north basins has declined, as has ice thickness since the start of the 1970s in the south 405 basin (Todd and Mackay 2003; Shimaraev and Domysheva, 2013). Since the 1950s, increased surface 406 water temperatures have resulted in extended summer stratification (Hampton et al., 2014), and 407 increased chlorophyll-a concentrations (Moore et al., 2009; Izmest'eva et al., 2016). Total annual river 408 inflow into the lake has increased over the past 100 years due to increased precipitation, bringing with 409 it supplies of nutrients and dissolved silica (Shimaraev and Domysheva, 2013). A key question 410 therefore, is whether this significant and unprecedented regional warming in southern Siberia (Davi et 411 al., 2015; Shimaraev and Domysheva, 2013), led to a measurable impact, either directly or indirectly, 412 on diatom community composition in Lake Baikal in particular.

413

414 Breakpoint analyses reveal that a significant change in diatom assemblage composition in the south 415 basin was already underway by the early 1970s (Figure 5a). Although this trend was initially identified 416 in the diatom record by Mackay et al. (1998), the more recent records show the disappearance of S. 417 meyerii altogether from (BAIK13-7A_SB) in the south basin. At the Buguldieka Saddle (BAIK13-11C BS), significant changes occurred c. 2000 CE, a few decades later than the more southern site. 418 419 Here, the increase in *S. acus* is accompanied by wider changes in the diatom flora (Figure 5b); again *S.* 420 meyerii declines to low relative abundance (although it persists in record), while C. inconspicua almost 421 disappears from the record. Both sites also show declines in heavily silicified species such as A. 422 baicalensis and C. minuta. These changes are in contrast to no significant changes in the diatom flora 423 from the north basin over the past 100 years (BAIK13-18A_NB).

424

425 Significant change in diatom SCD scores in the south basin core BAIK13-7A SB (Figure 5a) at c.1970 426 CE occurs soon after significant change in rising summer (July to August) surface water temperatures 427 in the south basin (Figure 7; breakpoint at 1966 CE in the temperature record; p value < 0.001) and the 428 start of declining ice thickness in the south basin (Todd and Mackay, 2003; Sizova et al., 2013). 429 Phytoplankton monitoring studies from the south basin show major changes in the diatom flora 430 consistent with those observed in the stratigraphic record. For example, within phytoplankton samples 431 from the south basin, A. baicalensis concentrations have declined from c. 5 to 3 cells L⁻¹ between 1950– 432 2010 (Silow et al., 2016). These changes are likely related to ice cover dynamics and increasing surface 433 water stratification (Hampton et al., 2014). For example, Hampton et al. (2014) demonstrate that 434 monitored diatoms now occur deeper in the water column, likely due to increased surface water 435 temperature, stratification and reduced mixing, causing cells to sink further. For C. minuta, this would 436 mean fewer cells being entrained back up into the photic zone during the autumnal overturn, hence the 437 declining valve numbers observed in the south basin (Figure 5a).

438

439 Factors causing the heavily silicified diatoms to decline in abundance may also contribute to observed 440 increases in S. acus. S. acus is non-endemic to Lake Baikal and has a high temperature optima and fast 441 growth rates (Mackay et al., 1999), so can take advantage of rapidly warming surface waters after ice 442 break-up. It is also able to grow through the summer months (e.g. Ryves et al., 2003; Panizzo et al., 443 2018) due to its low biovolume and higher surface – volume ratio, enabling it to stay in the photic zone 444 longer than heavily silicified endemic species. So as endemic diatom species find growth in increasingly 445 warmer waters of southern Lake Baikal challenging, S. acus is able to flourish under these conditions, 446 especially if availability of dissolved silica also increases (Jewson et al., 2015).

447

An additional, notable, finding of this study is the disappearance in the endemic *S. meyerii* off the
Vydrino Shoulder (BAIK13-7A_SB) and its marked decline at the Buguldieka Saddle (BAIK1311C_BS) post c. 2003 CE (Figure 1 and Figure 5). Its decline may be linked to changes towards reduced

451 nutrient availability (including silicon and phosphorus concentrations). As mentioned above, S. meyerii 452 may be indicative of more nutrient rich waters. However, in core BAIK13-10A_SD (Figure 4) within 453 the shallow waters off the Selenga Delta, *Stephanodiscus parvus*, a cosmopolitan diatom which is often 454 indicative of cultural enrichment, remains only at low abundance while S. meyerii declines in abundance 455 over the past 10 years. High abundances of S. acus are seen within the BAIK13-10A_SD core top 456 sediments, which are similar to those observed in BAIK13-4F SB, BAIK13-7A SB, BAIK13-11C BS 457 and BAIK13-14C MM core tops (Figure 4 and 5). We conclude therefore that S. acus may be out-458 competing S. meyerii at these locations.

459

Temporal changes in sedimentary diatom assemblages in the north basin (BAIK13-18A_NB) contrast with those from the south (BAIK13-7A_SB and BAIK13-11C_BS) (Figure 7). Hydro-physical parameters in the north basin, such as ice cover, are clearly responding to a warming in global mean temperatures (Jewson et al. pers comm), yet we detected no discernible effect on sedimentary diatom assemblages. We conclude that the magnitude of change in ice cover duration, open water stratification and ice thickness has not yet been sufficient to induce changes in these endemic populations in the north basin, which are uniquely adapted to these cold, low-light environments.

467

468 In addition to direct climate change, changes in the Lake Baikal diatom community may also be driven 469 by changes within the lake's food-web. Since the 1950s, increased surface water temperatures have 470 resulted in changes to zooplankton numbers, including declining abundances of planktonic rotifers, but 471 increased abundances of cladocera (Hampton et al., 2008) and copepods (Izmest'eva et al., 2016). With 472 shorter ice cover duration on the lake, a rise in summer zooplankton biomass (copepods and Bosmina/ 473 Daphnia) has been seen over the last 60 years (Hampton et al., 2008) (Figure 7), with many of these 474 groups also shifting to more shallow waters in the water column for reasons not yet fully understood 475 (Hampton et al., 2014). Increasing zooplankton biomass (largely the endemic copepod Epischura 476 *baicalensis*) in the upper 50 m of the water column have also been determined (Silow et al., 2016) from 477 1950 - 2010 CE. The diatom assembly shifts seen in the south basin and Buguldieka sediment core 478 (BAIK13-11C_BS) (Figure 5) could therefore also be affected by increased grazing pressures, both 479 from increasing zooplankton numbers and their shift to shallow water positions, but also an increase in 480 the spatial overlap between phytoplankton and copepods (Yoshii et al., 1999; Hampton et al., 2014). 481 For example, C. minuta is a key food source for the zooplankton Epischura baicalensis (e.g. Mackay 482 et al., 2006; Hampton et al., 2014; Jewson et al., 2015), while the larger endemic Cyclotella baicalensis 483 although too large to be consumed by *E. baicalensis* is instead an important food source for the larger 484 endemic gammarid Macrohectopus brankcii (Jewson et al, 2015).

486 Finally, we find no evidence in our recent palaeolimnological records to suggest that local 487 anthropogenic pollution has had a detectable effect on planktonic diatom communities. Nevertheless, 488 in the past decade, evidence of cultural eutrophication of benthic and littoral regions of Lake Baikal 489 near towns and tourist resorts is clear (Kravtsova et al., 2014; Timoshkin et al., 2016). Very poor or 490 non-existent sewage treatment has resulted in localised high levels of nutrients (phosphorus & nitrogen) 491 and organic matter (Khodzer et al., 2017). Such eutrophication is causing large blooms of filamentous 492 green algae to form, often far from local sources of pollution (including Spirogyra spp. and 493 Stigeoclonium tenue), which then rot along the coastlines (Kravtsova et al., 2014; Timoshkin et al., 494 2016; Ozerksy et al., 2018). As yet there is no chemical monitoring evidence to suggest that littoral 495 eutrophication has spread into the pelagic regions of lake (e.g. Khodzer et al., 2017), nor of a biological 496 impact in the form of increased chlorophyll concentrations or decline in water transparency (Izmest'eva 497 et al., 2016). However, near-shore nutrient pollution can act as a precursor of off-shore disturbance, 498 especially food-web dynamics (Rosenberger et al., 2008). Improvements to water treatment facilities in 499 Lake Baikal are essential as soon as possible to ensure that eutrophication does not reinforce the 500 negative impacts of global warming (Moss et al., 2011) on the Lake Baikal ecosystem.

501

502 **5. Conclusions**

503

504 Palaeolimnological records of changing diatom assemblages over recent decades agree well with 505 phytoplankton monitoring studies; numbers of heavily silicified diatom species in the south basin of 506 Lake Baikal are in decline at the expense of increasing cosmopolitan, lighter, littoral species. These 507 changes are consistent with previous predictions as to what might happen to diatoms in Lake Baikal as 508 global mean temperature continue to increase (Mackay et al., 2006; Moore et al., 2009). Warmer surface 509 waters and increased period of stratification are very inhospitable for endemic taxa such as A. 510 baicalensis, A. skvortzowii and C. minuta, while changes in nutrient availability may be restricting the 511 growth of smaller, lighter endemics such as S. meyerii. Interactions with increasing numbers of primary 512 consumers, especially endemic copepods such as Epischura baicalensis and amphipods such as 513 Macrohectopus, are as yet undefined, but likely to be important. S. acus on the other hand may be 514 benefiting from a combination of different impacts including shorter ice duration, longer periods of 515 summer stratification, and increased dissolved silica availability from both increased river discharge, 516 but also declining numbers of heavily silicified diatoms. At the moment these changes are confined to 517 the south basin of Lake Baikal, and we have no evidence of warming impacts on sedimentary diatom 518 assemblages in the north basin, despite a marked decline in ice duration in both basins over recent 519 decades. We also have no evidence in our records of increased impact from littoral eutrophication -520 however, given that littoral regions can act as early indicators of future wide-spread change, urgent

521	action is still needed to stop nutrient pollution from entering the lake. Observed changes in the diatom
522	flora are likely to be affected by several interacting factors which are still in play today, and much more
523	work still needs to be done to unravel these multiple stressors.
524	
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526	
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533	
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Figure 1: Map of Lake Baikal showing coring station sites across the south and north basin, and within Maloe More Bay, off the central basin. [SB: South basin, SD: Selenga Delta, BS: Buguldieka Saddle, MM: Maloe More and NB: North basin].

Figure 2: Core lithology and magnetic susceptibility profiles for BAIK13-4C_SB, BAIK13-7B_SB, BAIK13-10B_SD, BAIK13-11A_BS, BAIK13-14B_MM BAIK13-18C_NB and BAIK13-19A_NB sediment cores. Lithology key: 1 - pelagic mud, 2 - turbidite, 3 - sandy sediment, 4 - diatoms, 5 - clay, 6 - silt, 7 - sand, 8 - land plant remains. Right column: 9 - oxidized sediment, 10 - Fe/Mn crust, 11 - fragments of Fe/Mn crust, 12 e O2 reduced sediment. Boundaries between layers: 13 - distinct boundaries between layers, 14 - indistinct boundaries between layers. The lithology for cores BAIK13-4C_SB and BAIK13-7B_SB have previously been published in Swann et al (2018). [SB: South basin, SD: Selenga Delta, BS: Buguldieka Saddle, MM: Maloe More and NB: North basin].

Figure 3: ²¹⁰Pb age models for BAIK13-4F_SB, BAIK13-7A_SB, BAIK13-10A_SD, BAIK13-11C_BS, BAIK13-14C_MM, BAIK13-18A_NB and BAIK13-19B_NB sediment cores. In the upper sediments, turbidites are present between 2.0 – 5.3 cm in the BAIK13-4F_SB sediment core. [SB: South basin, SD: Selenga Delta, BS: Buguldieka Saddle, MM: Maloe More and NB: North basin].

Figure 4: Stratigraphic plots of core top diatom assemblages are shown for [A] BAIK13-4F_SB, [B] BAIK13-18A_NB, [C] BAIK13-10A_SD and [D] BAIK13-14C_MM. Diatom fluxes are shown alongside diatom abundances (species with > 2% abundance). [SB: South basin, SD: Selenga Delta, BS: Buguldieka Saddle, MM: Maloe More and NB: North basin].

Figure 5: Stratigraphic plot of diatom assemblages at [A] BAIK13-7A_SB, [B] BAIK13-11C_BS, [C] BAIK13-18A_NB with core top samples (represented by grey bars) overlapping with diatoms records from Mackay et al (1998) [A] BAIK38_SB, [B] BAIK19_BS and [C] BAIK29_NB (represented by black bars). Diatom Dissolution Index (DDI) and diatom fluxes are shown alongside diatom abundances (species with > 2% abundance). SCD dissimilarity scores are shown for the diatom dataset. The timings of significant breakpoints in the SCD scores are highlighted in grey for BAIK13-7A_SB and BAIK13-11C_BS diatom assemblages. No significant breakpoints were found in the BAIK13-18A_NB diatom assemblage data. [SB: South basin, SD: Selenga Delta, BS: Buguldieka Saddle, MM: Maloe More and NB: North basin].

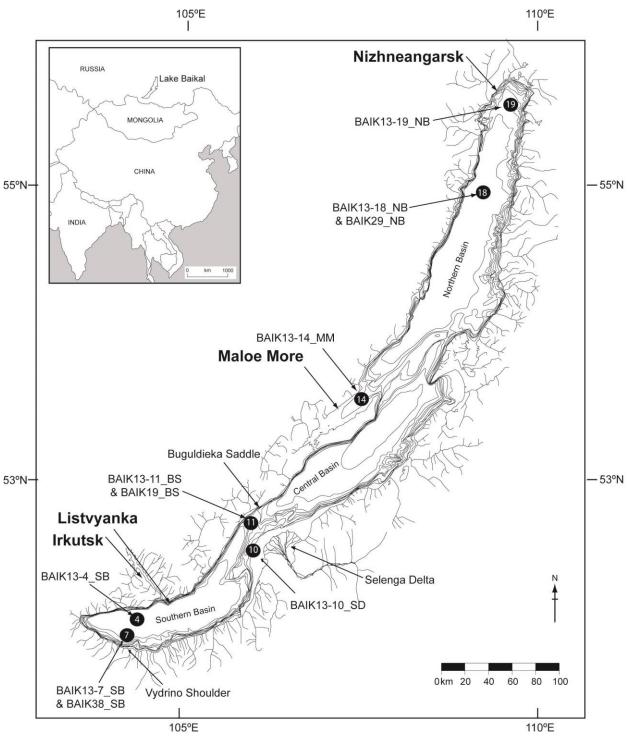
Figure 6: PCA of diatom species from all core samples. Core top samples (upper 2 cm) are from BAIK13-4F_SB, BAIK13-7A_SB, BAIK13-10A_SD, BAIK13-11C_BS, BAIK13-14C_MM, BAIK13-18A_NB and BAIK13-19B_NB sediment cores collected in 2013. The older sediments (20th century sediments) are from cores BAIK19_BS, BAIK29_NB and BAIK38_SB (Mackay et al.,

1998). Axis one eigenvalue is 0.47 and axis two eigenvalue is 0.24. [SB: South basin, SD: Selenga Delta, BS: Buguldieka Saddle, MM: Maloe More and NB: North basin].

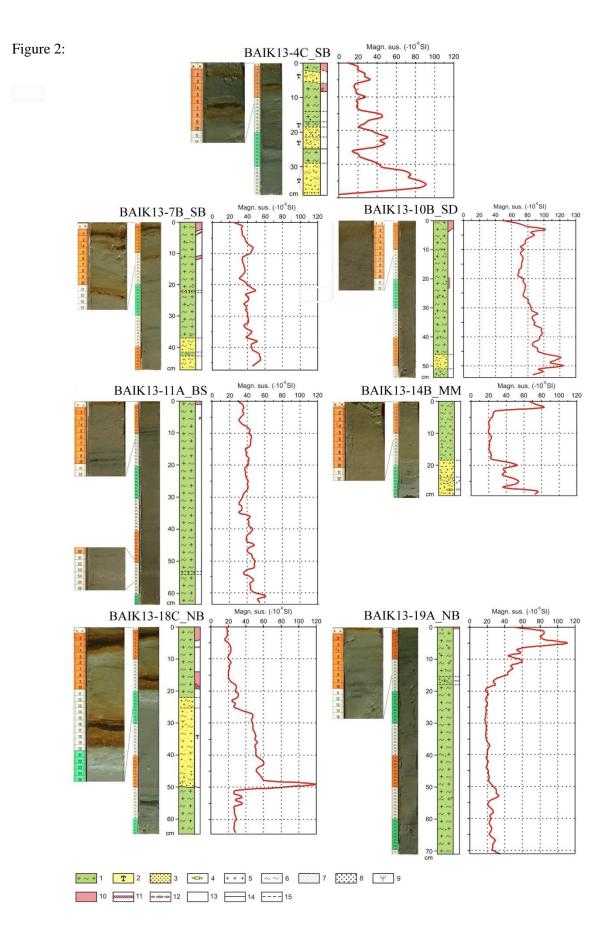
Figure 7: Regional spring Irkutsk air temperatures (March and April average) from a climate station next to the south basin of Lake Baikal (World Meteorological Organisation station 30710; $52^{\circ}16'20''N$, $104^{\circ}18'29''E$; elevation = 467 m) are shown over the period 1950 CE to 2013 CE. Summer surface water temperatures and water temperatures in the upper 25m of the water column (July to August average) are shown for the south basin over the period 1948 CE to 2002 CE (Hampton et al., 2008). Ice cover duration data for the south basin of Lake Baikal is shown between the period 1869 CE to 1996 CE (Todd and Mackay, 2003). Zooplankton summer abundance (1000 cells L⁻¹) for copepods, rotifers and bosmina/daphnia are shown for the period 1950 CE to 2002 CE (data provided by S. Hampton). The stratigraphic plot includes SCD dissimilarity scores, comparing upper core top samples to all samples below in the same core. Timings of significant breakpoints in the SCD scores are also highlighted in grey for BAIK13-7A_SB and BAIK13-11C_BS diatom assemblages. No significant breakpoints were found in the BAIK13-18A_NB diatom assemblage data. [SB: South basin, BS: Buguldieka Saddle and NB: North basin].

Table 1: Location of both the sediment cores collected in August 2013 and the published diatom records at the same coring sites in Lake Baikal collected in 1993/1994 (Mackay et al., 1998). Water depths at each coring site is shown, along with the basin which they were collected from in Lake Baikal. [SB: South basin, BS: Buguldieka Saddle and NB: North basin].

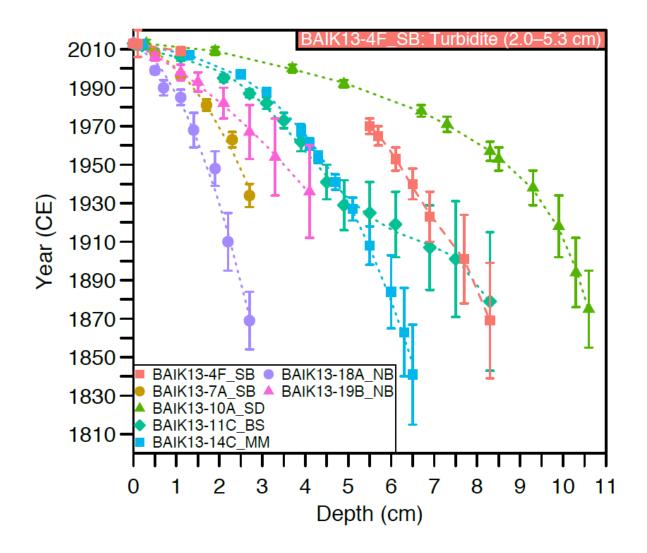




Scale1:2,500,000

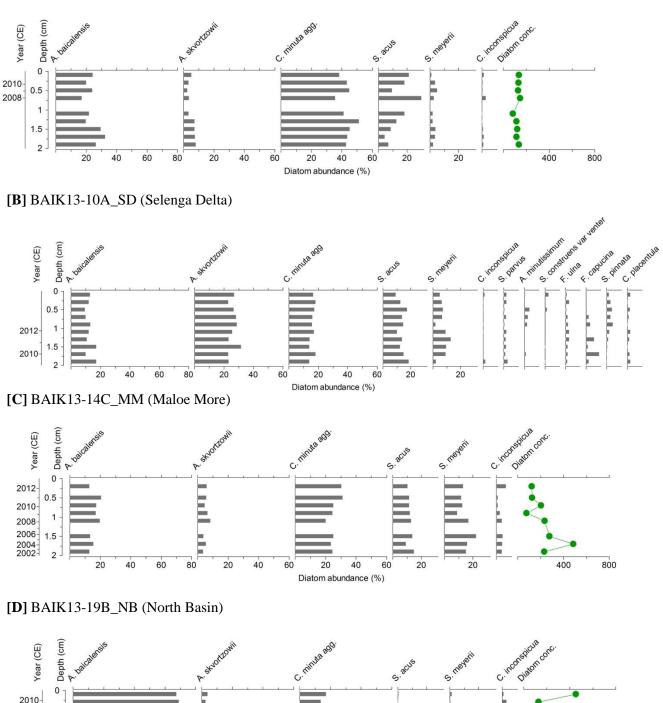


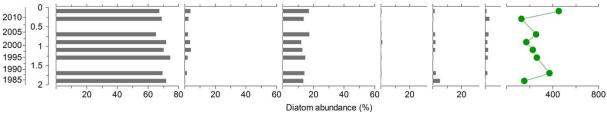






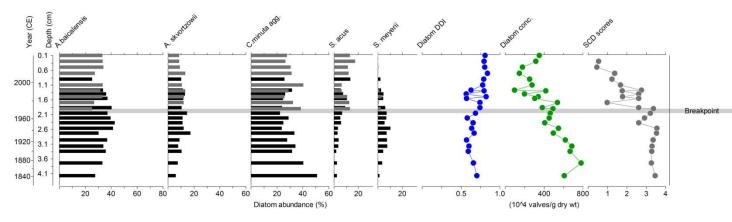
[A] BAIK13-4F_SB (South Basin)



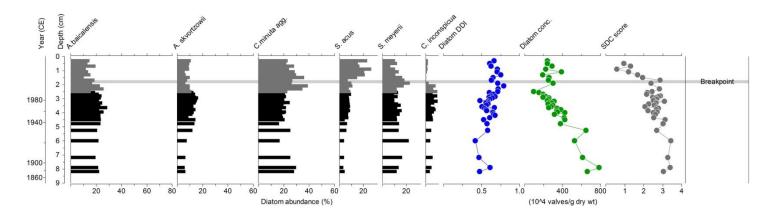




[A] BAIK13-7A_SB (South Basin)



[B] BAIK13-11C_BS (Buguldieka Saddle)



[C] BAIK13-18A_NB (North Basin)

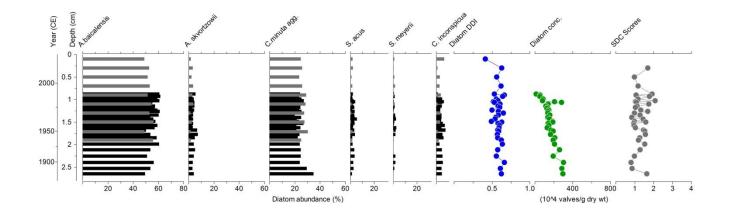
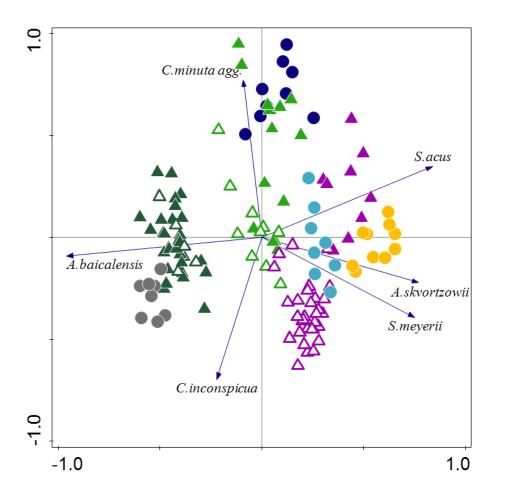


Figure 6:







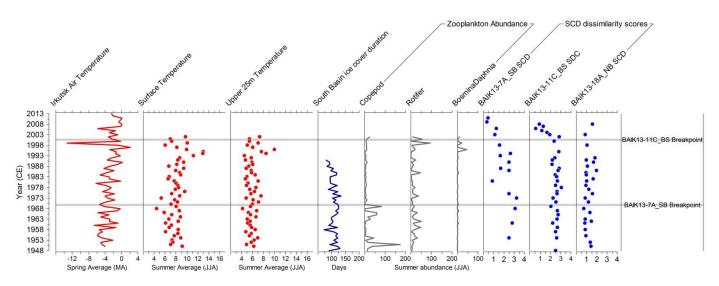


Table 1:

Sediment cores collected in August 2013	Sediment cores published in Mackay et al (1998)	Basin	Ν	E	Water depth (m)
BAIK13-7A_SB	BAIK38_SB	South	51°34'06"	104°31'43"	1080
BAIK13-11C_BS	BAIK19_BS	South/Selenga	52°27'00"	106°07'32"	345
BAIK13-18A_NB	BAIK29_NB	North	54°47'31.4"	109°14'15.3"	890