Assessing the vulnerability of endemic diatom species in Lake Baikal to predicted future climate change: a multivariate approach

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Abstract

Diatoms in Lake Baikal exhibit significant spatial variation, related to prevailing climate, lake morphology and fluvial input into the lake. Here we have assessed the threats to endemic planktonic diatom species (through the development of empirical models), which form a major component of primary production within the lake. Multivariate techniques employed include redundancy analysis (RDA) and Huisman–Olff–Fresco (HOF) models. Our analyses suggest that eight environmental variables were significant in explaining diatom distribution across the lake, and in order of importance these are snow thickness on the ice, water depth, duration of days with white ice, suspended matter in the lake, days of total ice duration, temperature of the water surface in July, concentration of zooplankton and suspended organic matter. Impacts on dominant phytoplankton diatom species are highlighted using t-value biplots. Predictions of future climate change on Lake Baikal are likely to result in shorter periods of ice cover, decreased snow cover across the lake in spring, increased fluvial input into the lake, and an increase in the intensification of surface water stratification during summer months. All these factors are likely to impact negatively on the slow-growing, cold-water endemics such as Aulacoseira baicalensis and Cyclotella minuta, which currently dominate diatom assemblages. Instead, taxa that are only intermittently abundant, at present, in offshore areas (e.g. Stephanodiscus meyerii) are likely to become more frequent. However, given the climatic gradient across the lake, the timing and extent of changes in community structure are likely to vary. Moreover, palaeolimnological records show that Lake Baikal diatom assemblages have been dynamic throughout the Holocene, with both endemic and cosmopolitan species exhibiting periods of dominance. Effects of climate change on the entire lake ecosystem may yet be profound as the structure of the pelagic food web may change from one based on endemic diatom taxa to one dominated by nondiatom picoplankton, and as limnological functioning (e.g. stratification and mixing) affects deepwater oxygen availability, nutrient cycling and trophic linkages.

Keywords: endemic diatoms, environmental controls, future climate change, Lake Baikal, multivariate analysis, multivariate ordination, surface sediments

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Introduction

The magnitude and impact of future climate variability on freshwater ecosystems is uncertain and this is especially the case in central Asia, where there is a paucity of studies compared with, for example, European and North American regions (e.g. Schindler, 2001; Elliott et al., 2005). Gaining more knowledge becomes imperative because in recent decades wintertime warming in central Asia has been greater than any other region of...
the world and this trend is expected to continue, with winter temperatures in central Asia predicted to increase by between 2 and 5 °C over the next 50 years (IPCC, 2001). Uncertainty especially exists with regard to the impacts of changing climate on planktonic communities and the pelagic food web. For example, shifts in dominance between phytoplankton communities are likely to result in shifts between food sources for zooplankton with unknown impacts on other organisms higher up the food chain. This may be due to a number of factors, including changes in autotroph size (e.g. Moline et al., 2004) or disruption to trophic linkages during key limnological periods such as thermal stratification and overturn (Winder & Schindler, 2004).

Lake Baikal in central Asia has long been recognized as one of the world’s most remarkable freshwater ecosystems, especially in terms of its age, depth, volume, continental setting, long sedimentary archive, and the high degree of biological endemism that exists within the lake (Kozhova & Izmest’eva, 1998). Diatoms contribute a major part of primary production (Fietz et al., 2005) especially to the spring crop, which is thought to determine annual productivity in the pelagic lake (Popovskaya, 2000). Monitoring of diatom crops has been carried out for many decades now, but these have been largely restricted to the south basin where pollution impact is greatest. One study suggests that during the 1950s, productive years in the lake were dominated by large celled, endemic species belonging to the genera Aulacoseira (=Melosira) and Cyclotella (Popovskaya, 2000), although Synedra tends to bloom following years of peak Aulacoseira production. In the 1990s, small-celled, cosmopolitan species belonging to the genus Nitzschia were observed in higher numbers in some years, which has been attributed to both increased nutrient input into the lake from economic development in the catchment (Bondarenko, 1999) and to global warming (Popovskaya, 2000). However, diatom-monitoring studies over the last decade have shown that increases in Nitzschia cells have not been maintained in recent years. Moreover, these monitoring studies show that trends in the south basin are different from trends in the north basin, and that species’ responses across the whole lake are complex. Considerable uncertainty, therefore, exists about possible drivers influencing planktonic diatom communities in Lake Baikal. Certainly in records of recently deposited sediments, extracted from pelagic regions of the lake, there is little or no response of diatoms to pollution (Mackay et al., 1998) but there are lake-wide responses to shifts in climate associated with the period coincident with the ‘Little Ice Age’ and subsequent global warming (Mackay et al., 1998, 2005).

Phytoplankton responses to predicted future climate variability may be assessed using a variety of modelling techniques. Recent work by Elliott et al. (2005) linked together a phytoplankton model with a regional climate model developed by the Hadley Centre, UK, to estimate changes in phytoplankton communities and biomass in an English lake up to 2100. However, given the uncertainties of diatom successional trends across the length of Lake Baikal and limited climate modelling in this region of central Asia in general, we have adopted an alternative approach, by developing empirical models from spatially derived data of sedimentary diatom assemblages and environmental data.

In recent years, multivariate techniques have been used to explore the biogeography of diatom species, and relationships with their changing environment in a number of regions prone to intense winter cold (e.g. Laing & Smol, 2000; Lim et al., 2001; Weckstrom & Korhola, 2001; Rühland & Smol, 2002; Ryves et al., 2002; Bouchard et al., 2004). These studies are based on multiple sites/lakes spread across gradients of interest and, therefore, the assumption is made that most, if not all, of the species are cosmopolitan. These data are then used by palaeolimnologists to reconstruct past environmental changes (e.g. in northern and Arctic settings; McGowan et al., 2003; Antoniades et al., 2005; Solovieva et al., 2005). In Lake Baikal, due to its size and heterogenous sedimentary environments, the distribution of diatoms exhibits significant spatial variability (e.g. Bondarenko et al., 1996; Mackay et al., 2003). However, many of the diatoms are endemic, and their ecologies are poorly defined in comparison with some cosmopolitan taxa.

The principal aim of this study is to assess the potential threats from future climate change on endemic diatoms in Lake Baikal, which form a principal component at the base of the food chain (Yoshii et al., 1999). However, this paper is distinctive from other diatom–environment interaction studies in a number of respects. Firstly, we include information derived from remote sensing to expand the range of explanatory variables initially used by Mackay et al. (2003), most notably data on ice, which influences light transmission into the epilimnion for photosynthesis. Secondly, many of the canonical ordination techniques used in previous studies (including Mackay et al., 2003) rely on χ² distances (e.g. canonical correspondence analysis; CCA), which can give undue weight to rare species in the dataset (Legendre & Gallagher, 2001). As diatom assemblages in Lake Baikal tend to be dominated by relatively few species of abundant phytoplankton, the species data are, therefore, transformed in order that Euclidean distance methods, such as redundancy analysis (RDA), can be used to explore relationships between species
and environmental variables (Legendre & Gallagher, 2001). The data generated in this study will improve our knowledge of interactions between Lake Baikal diatom assemblages and environmental variables that influence their growth, thus, providing information for attempts to predict the impacts of future climate change in an aquatic ecosystem whose biodiversity is of global significance.

**Study area**

Lake Baikal (51°28′–55°47′N and 103°43′–109°58′E; Fig. 1) consists of three basins of different ages, separated by interbasin underwater highs: the south and central basins are separated by the Selenga Delta, while the underwater Academician Ridge separates the central and north basins. The age and limnological

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**Fig. 1** Map of Lake Baikal showing location of each of the 92 sampling sites used to develop the training set for multivariate analysis. Geographical locations mentioned in the text are highlighted.
characteristics of Lake Baikal has allowed an ecosystem rich in species endemism to develop, and accordingly it was designated a World Heritage Site in 1996. The region around Lake Baikal is one of the most continental in the world (Lydolph, 1977), with mean daily January air temperatures of approximately $-25^\circ$C, rising to $+19^\circ$C in July. Winters are long, dry and cold, while summers are relatively short, warm and wet. Lake Baikal freezes over every year and there is a distinct north–south gradient in terms of ice duration and thickness, with the south basin freezing later and thawing earlier than the north. The lake is distinct from other deep lakes because its water column is saturated with oxygen throughout, supporting an extensive, and almost wholly endemic deep-water fauna. This is due to both spring and autumnal overturn (i.e. the lake is dimictic, despite strong stratification at 300 m) and deep-water renewal from cold surface water intrusions into deeper waters (Weiss et al., 1991; Wuest et al., 2005).

Methods

Diatom analysis of surface sediments

The dataset used in this study is based on 92 sites from a training set of 126 surface sediment samples collected from across the length of Lake Baikal, between 1992 and 1997 (Fig. 1; see Mackay et al., 2003 for full details). The sedimentary environment of Lake Baikal is heterogeneous, and we have considered the impacts of sediment redeposition, faunal bioturbation and diatom dissolution on the integrity of sites used in this study. Sites were discarded if there was (i) visual evidence of disturbance of the surface sediment–water interface, (ii) visual evidence of turbidite layers present in the upper sediments, when cores were opened longitudinally or (iii) very few diatoms present in the surface sediment (which results in relative abundances not being representative of likely populations). This was the case for one site, BAIK111, hence the number of sites analysed is one less (92) than the 93 sites initially investigated by Mackay et al. (2003). The surface sediments are oxygenated, allowing diverse faunal communities to live at the lake bottom (Martin et al., 2005). Therefore, it follows that bioturbation will always be an issue, and is one of the reasons why the strong seasonal signals in sedimentation are not preserved in annual laminations. Martin et al. (2005) present evidence that concentrations of animal individuals (and therefore bioturbation) are higher in shallow water regions than in the abyssal plains. Moreover, bioturbation probably plays a critical role in the preservation of diatoms in surface sediments, through physical breakage and irradiation of upper sediments, both of which can be expected to enhance silica dissolution (Ryves et al., 2003). However, we know from our own high resolution analyses of surface cores that bioturbation does not affect the overall stratigraphy of the cores, as evidenced from radiometric $^{210}$Pb dating and spheroidal carbonaceous particle analysis (Mackay et al., 1998).

Given recent debates on the concept of ‘cosmopolitanism’ within diatom research (e.g. Kociolek & Spaulding, 2000; Edlund & Jahn, 2001), diatom taxa were identified according to a range of published papers and books, most of which take account of the endemic diatom flora found in Lake Baikal (e.g. Meyer, 1930; Skvortzov, 1937; Zabelina et al., 1951; Skabichevskii, 1960; Gleser, et al., 1988; Khursevich, 1989; Genkal et al., 1992; Flower, 1993; Kozhova & Kobanova, 1995; Edlund et al., 1996). Diatom counts were transformed to percentages before all analyses.

Collation of environmental information

Environmental data in this study come from a number of sources, including previous Russian studies, our own measurements of water depth taken during each expedition, and from remote sensing of snow and ice coverage across the lake. A description of the collation of Russian and water depth data has already been detailed in Mackay et al. (2003), so here we focus on the methodology for the collection of data derived using remote sensing techniques. Remote sensing is a useful tool in the study of environmental variables at high spatial and temporal resolution, especially over large and remote regions such as Lake Baikal. Snow depth on ice has been highlighted as one of the most important variables influencing Lake Baikal diatom species (Mackay et al., 2003). However, remote sensing of snow thickness/depth is problematic. The best results are often obtained from high resolution radar data, combined with an extensive campaign of measuring actual snow depths over the scene to calibrate the inferred snow depths (e.g. Srivastan & Singh, 1991). Owing to the remoteness and size of Lake Baikal and the dangers involved working on the lake during the freeze–thaw cycle, it is too dangerous to collect such ground-truth data. As a result, this study attempts to investigate the seasonal dynamics and duration of various ice-cover types on Lake Baikal based on satellite images in the optical and infrared spectra. Data for classification of Lake Baikal ice cover were collated using the AVHRR meteorological satellite (Morley, 2005). Similar data were also collated in the studies of Lake Baikal by Bolgrien et al. (1995), Le Core (1998), Semovski et al. (2000), Semovski and Mogilev (2000). Kourave et al. (in press). Classification of snow and ice types on Lake Baikal has been...
previously carried out by Le Core (1998) using the normalized difference snow index (NDSI) of Riggs et al. (1994), although this study only exploits general changes in ice cover characteristics and not, for example, ice structure or relative wetness.

Images were chosen between 1996 and 1997, corresponding to the final year in which surface sediments were taken. AVHRR acquires data at a resolution of approximately 1.1 km on the ground for each pixel, and therefore, makes it an ideal tool for studying large sites (such as Lake Baikal) that span several degrees of latitude. Initially, the National Oceanographic Atmospheric Administration’s (NOAA) Satellite Active Archive (SAA) was screened for cloud-free images of Lake Baikal for 1996–1997, and a total of 34 cloud-free images of ice cover were obtained (between 10 December 1996 and 2 June 1997). The average time between images is approximately 5 days, although during May there are intervals of 10–15 days without cloud-free images. The AVHRR data were processed using Imagine 8.5, and the complete multispectral image was classified using an unsupervised classification into groups of pixels using the ISODATA clustering algorithm, which is a centroid-based, iterative approach. Classes according to coverage type were assigned using comparisons with Le Core (1998) and by examining the spectral signatures of certain classes, for example the relatively higher reflectance of snow compared with white ice in the visible channel. Pixels were classed into five categories (open water, white ice, clear ice, wet ice, and snow) and recorded for each diatom sample location (Morley, 2005). From these data, the total number of days of the year when the lake was covered by white ice, clear ice, wet ice, and snow were calculated; a site location was considered to be covered by a certain type of ice up until this coverage changes in a subsequent image. The total time of ice duration was also estimated, as well as the total time of white ice and snow coverage together as these are likely to be most limiting to light penetration. Although only 1 year of data has been used here, similar patterns have been demonstrated to occur across the lake in other years covered by the dates of diatom sample collection (e.g. Bolgrien et al., 1995; Le Core, 1998; Semovski et al., 2000).

Data analyses

Multivariate datasets, especially those using compositional data, are often analysed using \( \chi^2 \) distance metrics (such as correspondence analysis and the associated technique of detrended correspondence analysis; DCA), despite some misgivings with the approach (e.g. Faith et al., 1987). An underlying issue with \( \chi^2 \) distance methods is that they are overly influenced by rare species in the dataset, a problem not satisfactorily addressed by often ad hoc methods of downweighting included with some analysis programmes (P. Legendre, personal communication). This is of particular concern where the aim is to assess the significance of relationships between species and environmental variables (Legendre & Gallagher, 2001). An alternative approach, using linear models (Euclidean distance) on suitably transformed species data, has been recently proposed (Legendre & Gallagher, 2001) and can be applied to datasets where gradients of species turnover (as measured by DCA for example) would imply unimodal responses, as here. In the absence of clear criteria for choosing the optimal method a priori, Legendre & Gallagher (2001) suggest selecting the method that explains the highest fraction of the species data in direct ordination. We found a linear model (using RDA) on square-root transformed relative abundance data (the Hellinger transformation; Legendre & Gallagher, 2001) outperformed unimodal models (assessed with CCA), whether or not species downweighting was applied, and thus we have adopted this approach here.

All ordination methods were carried out using the software package CANOCO v. 4.5 (ter Braak & Smilauer, 2002). Additionally, samples and environmental variables were screened within CANOCO v. 4.5 to determine samples with extreme environmental values and to exclude those environmental variables that exhibited high collinearity, which have the effect of destabilizing the dataset. Relationships between diatom distributions and environmental variables were initially examined using the direct gradient technique of RDA, which constrains ordination axes as linear combinations of environmental variables. In order to identify a minimum subset of variables that significantly explain variation in the diatom data, redundant variables were removed through a form of step-wise regression (forward selection) together with Monte Carlo permutation tests \( (P = 0.0001; n = 9999) \) and associated Bonferroni corrections (ter Braak & Smilauer, 2002). Separate RDAs were carried out to determine the explanatory power of each significant environmental variable without considering covariables to confirm each was significant alone. The unique contribution of each of the forward-selected variables was then assessed through a series of partial RDAs with the remaining environmental variables as covariables (Table 1). Significance was again tested using unrestricted Monte Carlo permutation tests \( (P = 0.0001, n = 9999, 9999) \) permutations. Significant positive and negative associations between dominant planktonic taxa and forward selected environmental variables were further explored using t-value biplots and associated Van Dobben circles (ter Braak & Looman, 1994).
Table 1  Limnological, climatic, chemical and biological data used as potential explanatory variables for the distribution of diatoms in surface sediments

<table>
<thead>
<tr>
<th>Category</th>
<th>Explanatory variable</th>
<th>Code</th>
<th>Units</th>
<th>Dates measured</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Mean</th>
<th>Standard deviation</th>
<th>Single variable RDA</th>
<th>% explained</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Limnology</strong></td>
<td>Water depth*</td>
<td>Depth</td>
<td>m</td>
<td>1992–1997</td>
<td>20.0</td>
<td>1678.0</td>
<td>809.6</td>
<td>480.3</td>
<td>10.1</td>
<td>0.0001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Transparency in July†</td>
<td>Transjul</td>
<td>m</td>
<td>1961</td>
<td>9.0</td>
<td>25.0</td>
<td>21.4</td>
<td>5.6</td>
<td>—</td>
<td>—</td>
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<tr>
<td></td>
<td>Transparency in September§</td>
<td>Transsep</td>
<td>m</td>
<td>1961</td>
<td>2.0</td>
<td>11.0</td>
<td>6.0</td>
<td>2.0</td>
<td>—</td>
<td>—</td>
<td></td>
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<tr>
<td></td>
<td>Albedo in July</td>
<td>Albedo</td>
<td>%</td>
<td>n/a</td>
<td>5.0</td>
<td>7.0</td>
<td>5.1</td>
<td>0.4</td>
<td>—</td>
<td>—</td>
<td></td>
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<tr>
<td></td>
<td>Temperature of July water surface‡</td>
<td>Tempws</td>
<td>°C</td>
<td>1896–1959</td>
<td>1.0</td>
<td>13.0</td>
<td>5.9</td>
<td>2.3</td>
<td>5.7</td>
<td>0.0003</td>
<td></td>
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<tr>
<td><strong>Climate</strong></td>
<td>Annual solar radiation†</td>
<td>Solar</td>
<td>mJ m⁻²</td>
<td>n/a</td>
<td>4100.0</td>
<td>4700.0</td>
<td>4478.5</td>
<td>187.6</td>
<td>—</td>
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<tr>
<td></td>
<td>Absorbed radiation in July‡</td>
<td>Absorb</td>
<td>kcal cm⁻²</td>
<td>n/a</td>
<td>13.0</td>
<td>15.0</td>
<td>14.2</td>
<td>1.0</td>
<td>—</td>
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<tr>
<td></td>
<td>Mean July air temperature‡</td>
<td>Julair</td>
<td>°C</td>
<td>Longterm observations††</td>
<td>9.0</td>
<td>15.0</td>
<td>12.2</td>
<td>1.7</td>
<td>—</td>
<td>—</td>
<td></td>
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<tr>
<td></td>
<td>Annual precipitation§</td>
<td>Precip</td>
<td>mm</td>
<td>Longterm observations††</td>
<td>175.0</td>
<td>550.0</td>
<td>257.3</td>
<td>67.7</td>
<td>—</td>
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<tr>
<td></td>
<td>Snow thickness on the lake in March‡</td>
<td>Snow</td>
<td>cm</td>
<td>1972–1973</td>
<td>2.5</td>
<td>12.5</td>
<td>6.2</td>
<td>3.2</td>
<td>11.0</td>
<td>0.0001</td>
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<td></td>
<td>Ice thickness in March§</td>
<td>Icethick</td>
<td>cm</td>
<td>1972–1985</td>
<td>65.0</td>
<td>100.0</td>
<td>82.9</td>
<td>7.2</td>
<td>—</td>
<td>—</td>
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<tr>
<td></td>
<td>Length of ice cover§</td>
<td>Icength</td>
<td>days</td>
<td>Longterm observations††</td>
<td>126.0</td>
<td>168.0</td>
<td>145.3</td>
<td>10.7</td>
<td>—</td>
<td>—</td>
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<tr>
<td></td>
<td>Annual duration of white ice coverage§</td>
<td>DaysWI</td>
<td>days</td>
<td>1996–1997</td>
<td>0</td>
<td>56.0</td>
<td>33.1</td>
<td>7.8</td>
<td>7.8</td>
<td>0.0001</td>
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<tr>
<td></td>
<td>Annual duration of clear ice coverage§</td>
<td>Tclear</td>
<td>days</td>
<td>1996–1997</td>
<td>0</td>
<td>56.0</td>
<td>33.1</td>
<td>7.8</td>
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<tr>
<td></td>
<td>Annual duration of snow coverage§</td>
<td>Tsnow</td>
<td>days</td>
<td>1996–1997</td>
<td>0</td>
<td>63.0</td>
<td>32.4</td>
<td>15.7</td>
<td>—</td>
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<tr>
<td></td>
<td>Annual duration of wet ice coverage§</td>
<td>Twet</td>
<td>days</td>
<td>1996–1997</td>
<td>10</td>
<td>57.0</td>
<td>32.0</td>
<td>11.0</td>
<td>—</td>
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<tr>
<td></td>
<td>Ice cover duration§</td>
<td>DaysIce</td>
<td>days</td>
<td>1996–1997</td>
<td>83</td>
<td>168.0</td>
<td>131.0</td>
<td>24.7</td>
<td>5.7</td>
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<td>Annual duration of white ice and snow cover§</td>
<td>Tws</td>
<td>days</td>
<td>1996–1997</td>
<td>14</td>
<td>131.0</td>
<td>85.5</td>
<td>29.8</td>
<td>—</td>
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<tr>
<td><strong>Chemistry</strong></td>
<td>N – NO₃†</td>
<td>Nitrate</td>
<td>mg m⁻³</td>
<td>July 1978</td>
<td>15.0</td>
<td>70.0</td>
<td>58.17</td>
<td>16.4</td>
<td>—</td>
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<td></td>
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<tr>
<td></td>
<td>P – PO₄†</td>
<td>Phosphate</td>
<td>mg m⁻³</td>
<td>July 1978</td>
<td>4.0</td>
<td>12.0</td>
<td>7.73</td>
<td>2.7</td>
<td>—</td>
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<tr>
<td></td>
<td>Suspended matter**</td>
<td>SuspMat</td>
<td>mg L⁻¹</td>
<td>July 1978</td>
<td>0.8</td>
<td>4.00</td>
<td>2.32</td>
<td>0.6</td>
<td>5.9</td>
<td>0.0004</td>
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<tr>
<td></td>
<td>Suspended organic C**</td>
<td>SuspOrgC</td>
<td>mg L⁻¹</td>
<td>July 1978</td>
<td>0.3</td>
<td>1.50</td>
<td>0.38</td>
<td>0.2</td>
<td>4.1</td>
<td>0.0054</td>
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<tr>
<td></td>
<td>Organic C**</td>
<td>Org C</td>
<td>mg L⁻¹</td>
<td>July 1978</td>
<td>1.1</td>
<td>1.70</td>
<td>1.33</td>
<td>0.2</td>
<td>—</td>
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<td></td>
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<tr>
<td></td>
<td>Organic N**</td>
<td>Org N</td>
<td>µg L⁻¹</td>
<td>July 1978</td>
<td>70.0</td>
<td>175.00</td>
<td>118.38</td>
<td>24.2</td>
<td>—</td>
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<tr>
<td></td>
<td>Organic P**</td>
<td>Org P</td>
<td>µg L⁻¹</td>
<td>July 1978</td>
<td>7.0</td>
<td>16.50</td>
<td>9.96</td>
<td>2.1</td>
<td>—</td>
<td>—</td>
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</tr>
<tr>
<td><strong>Biology</strong></td>
<td>Zooplankton biomass in September§</td>
<td>Zoobio</td>
<td>g m⁻²</td>
<td>1985</td>
<td>5.0</td>
<td>30.0</td>
<td>10.0</td>
<td>8.6</td>
<td>5.5</td>
<td>0.0009</td>
<td></td>
</tr>
</tbody>
</table>

Original source references include:
*Data from this study;
†Atlas Baikala (1993);
‡Verbolov et al. (1965);
§Shimaraev et al. (1994);
*Morley (2005);
‖Votinsev et al. (1975);
**Tarasova & Mescheryakova (1992);
††Long term observations over the last century. See text for details.
n/a, not available.
The responses of eight of the main planktonic species (as untransformed, percentage composition data present in at least 10 sites) to the eight significant, modelled environmental variables were determined by fitting Huisman–Off-Fresco (HOF) models (Huisman et al., 1993) with the software HOF (Oksanen & Minchin, 2002; http://cc.oulu.fi/~jarioksa/). This program fits the simplest response model from the five defined by Huisman et al. (1993) to species data using maximum likelihood estimation and a Poisson error distribution. These models are a skewed unimodal response (model V), symmetrical or Gaussian model (model IV), a monotonic model with a fixed plateau (model III), a monotonically increasing or decreasing model (model II) and finally the null model, which is flat with no significant trend (model I). This method is particularly useful when defining the type of species response to an environmental variable (i.e. if there is a linear, unimodal or no response). Here, we explore the responses of the dominant planktonic taxa to each of the significant modelled variables determined by ordination methods, and assess the potential impacts of future climate variability. Gaussian logit regression was used to test the significance of optima of the HOF models that exhibited unimodal responses (VI and V) for each of the common planktonic diatom taxa (GLR version 1.1 Juggins 1994, unpublished program).

Results

Spatial distributions of dominant diatom taxa

Eighty-six diatom species were identified in the surface sediments from 92 sites. Based on number of occurrences and N2 diversity (data not shown), the most abundant taxa in our dataset were endemic plankton, although some littoral species were also common, including Staurosirella pinnata (Ehr.) Williams & Round and Cocconeis placentula var. euglypta (Ehr.) Grun. Proportional abundances of selected diatom species in the training-set surface sediments have been mapped to give an indication of the spatial distribution of species across the lake (Figs 2a and f). These species have also been fitted to HOF models: Aulacoseira baicalensis (Meyer) Simonsen, A. skvortzowii Edlund, Stoermer & Taylor, Cyclotella baicalensis Skv., Crateriportula inconspicua (Mak. & Pom.) Flower & Håkansson, Cyclotella minuta (Skvortzow) Antipova., Synedra acus var. radians Kütz., S. acus var. radians (Kütz.) Hust. fo. pusilla, Stephanodiscus meyerii Genkal & Popovskaya. Mapping in this way provides a useful, visual guide to species distribution across the latitudinal gradient encompassed by the three basins. It is important to note here that dissolution processes affect all taxa to different extents (e.g. Ryves et al., 2003; Battarbee et al., 2005). This is especially the case for Nitzschia acicularis W. Smith, a cosmopolitan species commonly found in the phytoplankton, but which is not recorded in surface sediments due to dissolution processes that occur throughout the water column (see Ryves et al., 2003 for full details).

Highest relative abundances of A. baicalensis are found in the north basin (Fig. 2a), correlated with high values for snow thickness and white ice formation (see Fig. 3b), while the area of low abundance in the central basin (Fig. 2a) occurs in an area of persistent clear ice (Semovski et al., 2000; Morley, 2005). High values are also recorded in the south basin, away from the shallow waters of the Selenga Delta. A. skvortzowii can be found in surface sediments throughout the lake; valves of both vegetative cells and resting spores were found in 90 of 92 sites, but only with moderate N2 diversity; data not shown. However, relative abundances are much greater in the central region of the south basin than elsewhere (i.e. relative abundances are very low in the central region of the central basin, and throughout most of the north basin; Fig. 2b). C. baicalensis and C. inconspicua were found in only very small abundances, with no clear patterns (Figs 2c and d), although it is important to acknowledge that given the size of cells of the former species, its contribution to biovolume will be significant. C. minuta has a similar distribution to A. baicalensis although relative abundances in the very north of the lake are considerably lower (Fig. 2e). S. acus var. radians fo. pusilla has a much more restricted distribution, only occurring in the central region of the south basin, with a couple of occurrences in the central basin (Fig. 2f). Occurrence of the cosmopolitan species S. acus var. radians is restricted to the clear ice region of the central basin (Fig. 2g). There are other occasional occurrences, mainly in shallower, coastal regions influenced by fluvial input (e.g. at the Buguldeika Saddle; Fig. 2g). Taken together, S. acus var. radians agg. is most abundant in the south and central basins, with very little presence at all in the north basin of Lake Baikal. Moreover, maximum abundance of S. acus coincides with either circulation currents crossing between the western shore to the opposite side of the lake in the central basin, or with the convergence of circulation currents in the south basin (see fig. 10.3.2 in Shimaraev et al., 1994). These circulation patterns (which are responsible for the transport of diatom species from shallow waters into the pelagic regions of the lake) are dependent on both whole-lake cyclonic circulation (Verbolov et al., 1965 in Shimaraev et al., 1994) and local circulation patterns influenced by fluvial input. S. meyerii (synonymous with S. binderanus var. baicalensis Popovskaya & Genkal) is most commonly found in shallow waters of the Maloe
More and the Selenga Delta (Fig. 2h). It is possible that dissolution processes have less impact at these shallow sites, although Ryves et al. (2003) in a study in the south basin, could find no evidence to suggest that water depth plays a significant role for species highlighted in this study. It is probable that populations of species such as *S. acus* and *S. meyerii* in the pelagic regions are sustained by innocula originating from shallower areas such as the Selenga Delta. This particularly occurs after ice melt, as water from the Selenga Delta flows down the west shore of the south basin (Heim et al., 2005).

**Multivariate analyses**

Environmental variables used in this study are summarized in Table 1. Constrained RDA found eight variables significant in explaining diatom distributions, accounting for approximately 44% of the variation in the diatom dataset (Table 2). In order of importance, these are snow thickness on the ice, water depth, duration of days with white ice, suspended matter in the lake, days of total ice duration, temperature of the water surface in July, concentration of zooplankton and suspended organic matter. Each variable explains between approximately 2–5% of the diatom data, independent of the other seven significant parameters (Table 3). Together, the unique contribution of these eight variables is approximately 25% of the total variance in diatom data, with approximately 19% of the variation accounted for by covariance between two or more of the eight variables.

The correlations between these variables and the distribution of major diatom taxa across the lake (species and core locations) can be seen in the RDA biplots (Figs 3a and b). In terms of species composition, the lake regions show distinct differences (Fig. 3a). For example, the shallow water sites towards the centre and north of Lake Baikal (the Maloe More and the Academician Ridge) are characterized by the endemic *S. meyerii*, and very little snow cover. Sites in the south basin are dominated by the endemic *A. skvortzowii* and the cosmopolitan taxon *S. acus* var. *radians fo. pusilla*. These two taxa are highly correlated with increasing numbers in zooplankton, and periods of short ice duration on the

![Fig. 2](image-url)  
**Fig. 2** Spatial distributions of the percentage abundance of eight of the most abundant diatom phytoplankton found in the full training set (a–h).
lake (Fig. 3b). The north basin is most characterized by *A. baicalensis* and *C. minuta*. *A. baicalensis* is highly correlated with increasing snow thickness estimates on the lake, which in turn suggests that this taxon is more tolerant of low irradiances than other taxa in the dataset. Culture studies show that this species is also intolerant of high irradiances (D. Jewson, unpublished data), which contrasts with reports of Richardson et al. (2000). However, their estimates of growth were based on filament length; this can be misleading because with *A. baicalensis* longer than normal vegetative cells can be produced under light stress. Conversely, *C. minuta* is highly correlated with ice duration on the lake – (i.e. longer ice on the lake in spring promotes high abundance of *C. minuta* during the following autumn turnover; Fig. 3b). The shallow waters of the Selenga Delta are dominated by cosmopolitan plankton, including *S. acus* var. *radians*, *Stephanodiscus minutulus* (Kütz.) Cleve & Möller (not shown) and *Stephanodiscus parvus* Stoermer & Håkansson (not shown). These latter two taxa are more commonly found growing during the summer in more nutrient-rich waters.

Results suggest that climatically controlled variables (especially during spring, with the presence of ice on the lake) are important in influencing diatom floristic variation. Table 4 summarizes the distribution of HOF models amongst the eight significant environmental variables. More than half of the models show a significant trend. Table 5 shows summary responses of the eight main taxa to each of the significant environmental variables, together with the corresponding fitted HOF model. However, to assess which of these responses are significant (both positively and negatively) *t*-value bi-plots and Van Dobben circles have been constructed and are shown in Figs 4a and h; ter Braak & Looman, 1994). Species that fall within the Van Dobben circles are significantly (linearly) correlated (at *P* = 0.05) to the environmental variable, either positively (solid circles) or negatively (dashed circles).

Snow depth on the lake has a positive, significant effect on *A. baicalensis* and *C. minuta*, but a negative impact on *S. meyerii* (Fig. 4a). Thus, we would expect that, should future climate impacts result in a decline in snow cover on the lake (see Discussion), then there is...
Fig. 3 Redundancy analysis (RDA) biplots showing (a) species and coded site locations and (b) species, abbreviated significant explanatory variables and coded site locations. The coded site locations are previously outlined in Fig. 1. There are too many species to identify individually in one diagram, and so in (b) all species other than the eight highlighted above are suppressed from view.

Table 2 Redundancy analysis (RDA) of species data (86 taxa) with eight forward selected variables using Hellinger’s distance (Legendre & Gallagher 2001)

<table>
<thead>
<tr>
<th>RDA Axes</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>Total variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eigenvalue</td>
<td>0.210</td>
<td>0.112</td>
<td>0.051</td>
<td>0.029</td>
<td>1.000</td>
</tr>
<tr>
<td>P</td>
<td>0.0001</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cumulative % variance of explanatory data</td>
<td>21.0</td>
<td>32.2</td>
<td>37.4</td>
<td>40.3</td>
<td></td>
</tr>
<tr>
<td>Sum of all eigenvalues</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sum of all canonical eigenvalues; P = 0.0001</td>
<td>0.437</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 3 Unique contributions to diatom variation of each of the eight significant environmental variables as determined using RDA, with the remaining seven variables as co-variables, in order

<table>
<thead>
<tr>
<th>No.</th>
<th>Variable</th>
<th>Eigenvalue</th>
<th>% explained</th>
<th>P value for unique explanation (n = 9999)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Snow</td>
<td>0.048</td>
<td>4.8</td>
<td>0.0001</td>
</tr>
<tr>
<td>2</td>
<td>Depth</td>
<td>0.044</td>
<td>4.4</td>
<td>0.0001</td>
</tr>
<tr>
<td>3</td>
<td>DaysWI</td>
<td>0.034</td>
<td>3.4</td>
<td>0.0001</td>
</tr>
<tr>
<td>4</td>
<td>SuspMat</td>
<td>0.026</td>
<td>2.6</td>
<td>0.0004</td>
</tr>
<tr>
<td>5</td>
<td>DaysIc</td>
<td>0.025</td>
<td>2.5</td>
<td>0.0005</td>
</tr>
<tr>
<td>5</td>
<td>Tempws</td>
<td>0.025</td>
<td>2.5</td>
<td>0.0003</td>
</tr>
<tr>
<td>7</td>
<td>Zoobio</td>
<td>0.024</td>
<td>2.4</td>
<td>0.0009</td>
</tr>
<tr>
<td>8</td>
<td>SuspOrgC</td>
<td>0.018</td>
<td>1.8</td>
<td>0.0054</td>
</tr>
<tr>
<td>Total</td>
<td>8 vars</td>
<td>0.018</td>
<td>24.4 (combined)</td>
<td></td>
</tr>
</tbody>
</table>

Including covariances, % explained of eight variables = 43.7% (P = 0.0001, n = 9999).
likely to a be a decline in deep water, pelagic, endemic diatoms. Depth of water in the lake elicits a similar response to snow cover (Fig. 4b), but predictions of future climate change are not likely to have a significant effect on water depths across the lake in the time scale of 100 years, as precipitation is greater than evaporation in all models. Days of white ice duration on the lake have a positive impact on *A. baicalensis* but negative impact on *S. meyerii* (Fig. 4c; i.e. low irradiances under the ice favour *A. baicalensis*). Suspended matter has a significantly positive impact on *A. skvortzowii* only (Fig. 4d), which in the south basin is mainly derived from Selenga River input (Heim et al., 2005). Ice duration (Fig. 4e) on the lake positively affects *C. minuta*, and this is likely to be related to the fact that net increase in cells of this species occurs during autumn overturn (see ‘Discussion’). The temperature of the water surface during July also impacts significantly on several species (Fig. 4f). Higher water temperatures have a negative impact on diatom distribution on both the endemic *Aulacoseria* species. However, warmer temperatures are associated with significantly higher abundances of *S. meyerii*, and it may be expected that predicted changes in climate will result in higher abundances of this species across the lake. Concentrations of zooplankton, especially the endemic mesozooplankton *Epischura baicalensis* Sars. are associated with lower abundances of *C. minuta*, because these animals track populations of *C. minuta* as a food source (Fig. 4g). Finally, within our datasets, suspended organic matter in the lake does not significantly impact on any of the eight species highlighted here (Fig. 4h), and only explains under 2% of total diatom variation (Table 3).

### Discussion

**Ecological responses of dominant diatom taxa**

*A. baicalensis* is most productive in areas of opaque ice (e.g. because of snow cover or white ice) rather than clear ice, which appears to be detrimental to growth. This implies that increasing light penetration (e.g. through clear ice) inhibits growth of this taxon. However, unlike *C. minuta*, there is only a weak correlation with ice duration on the lake (Fig. 3b), which will have implications for spatial responses within Lake Baikal to future climate change (i.e. between the north and south basins). In the north basin, ice break-up occurs later in the spring, and subsequent warming of the lake water delayed, compared with the south basin. In some years in the north basin, spring turnover period can be consequently shorter too (Shimaraev et al., 1994). Importantly, summer stratification is shorter in the north basin, during which time there is a shift from diatom-

### Table 4 Distribution of HOF models amongst the eight significant environmental variables

<table>
<thead>
<tr>
<th>Model</th>
<th>Snow</th>
<th>Depth</th>
<th>White ice</th>
<th>SuspMat</th>
<th>Ice dur</th>
<th>Tempws</th>
<th>Zoobio</th>
<th>SuspOrgC</th>
<th>Total</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>V</td>
<td>1</td>
<td>6</td>
<td>0</td>
<td>1</td>
<td>4</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>17</td>
<td>4.5</td>
</tr>
<tr>
<td>IV</td>
<td>9</td>
<td>7</td>
<td>10</td>
<td>8</td>
<td>6</td>
<td>6</td>
<td>3</td>
<td>9</td>
<td>70</td>
<td>18.5</td>
</tr>
<tr>
<td>III</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0.2</td>
</tr>
<tr>
<td>II</td>
<td>15</td>
<td>16</td>
<td>11</td>
<td>18</td>
<td>14</td>
<td>8</td>
<td>19</td>
<td>13</td>
<td>119</td>
<td>31.4</td>
</tr>
<tr>
<td>I</td>
<td>17</td>
<td>13</td>
<td>20</td>
<td>15</td>
<td>20</td>
<td>25</td>
<td>20</td>
<td>19</td>
<td>172</td>
<td>45.4</td>
</tr>
</tbody>
</table>

Note that the majority of the models are linear (II + I), 291/379 = 77%.  

### Table 5 HOF responses for each of the common planktonic taxa in Lake Baikal

<table>
<thead>
<tr>
<th></th>
<th>Snow</th>
<th>Depth</th>
<th>White ice</th>
<th>SuspMat</th>
<th>Ice dur</th>
<th>Tempws</th>
<th>Zoobio</th>
<th>Susp OrgC</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Aulacoseira baicalensis</em></td>
<td>II+</td>
<td>V*</td>
<td>II+</td>
<td>IV*</td>
<td>II+</td>
<td>IV*</td>
<td>I</td>
<td>IV*</td>
</tr>
<tr>
<td><em>A. skvortzowii</em></td>
<td>IV*</td>
<td>II+</td>
<td>IV*</td>
<td>V</td>
<td>II+</td>
<td>V</td>
<td>II+</td>
<td>I</td>
</tr>
<tr>
<td><em>Stephanodiscus meyerii</em></td>
<td>II–</td>
<td>IV*</td>
<td>II–</td>
<td>II–</td>
<td>V*</td>
<td>I</td>
<td>II–</td>
<td>II–</td>
</tr>
<tr>
<td><em>Cyclotella minuta</em></td>
<td>II+</td>
<td>V*</td>
<td>II+</td>
<td>I</td>
<td>II+</td>
<td>IV*</td>
<td>II–</td>
<td>I</td>
</tr>
<tr>
<td><em>Syneina acus</em> v. radians*</td>
<td>II–</td>
<td>I</td>
<td>II–</td>
<td>IV*</td>
<td>IV*</td>
<td>I</td>
<td>I</td>
<td>IV*</td>
</tr>
<tr>
<td><em>Crateriportula inconspicua</em></td>
<td>I</td>
<td>I</td>
<td>I</td>
<td>I+</td>
<td>I</td>
<td>I</td>
<td>I</td>
<td>I</td>
</tr>
<tr>
<td><em>S. acus</em> v. radians f. pusilla*</td>
<td>I</td>
<td>II+</td>
<td>IV*</td>
<td>IV</td>
<td>IV*</td>
<td>II–</td>
<td>II+</td>
<td>II–</td>
</tr>
<tr>
<td><em>Cyclotella baicalensis</em></td>
<td>II+</td>
<td>I</td>
<td>I</td>
<td>I</td>
<td>II+</td>
<td>IV*</td>
<td>I</td>
<td>I</td>
</tr>
</tbody>
</table>

Where unimodal models are apparent (i.e. IV and V), significant optima determined using GLR are indicated with an asterisk.
dominated phytoplankton to dominance by autotrophic picoplankton, especially the cyanobacteria *Synechocystis limnetica* Popovskaya (Popovskaya, 2000; Fietz et al., 2005).

*A. skvortzowii* populations can develop both in spring in pelagic regions of the lake, and during autumn turnover in shallow-water bays (e.g. Bolshiye Koty and Barguzin Bay; Fig. 1) (Kozhova & Izmes'eva, 1998). According to the HOF models, growth of *A. skvortzowii* under increasing snow and ice cover is inhibited when compared with the deep-water endemics, *A. baicalensis* and *C. minuta.* Thus a combination of environmental factors, including earlier ice out time and warmer waters in the south basin (as suggested by RDA, Fig. 3b) are likely to be responsible for the spatial distributions observed here.

Like *A. baicalensis*, *C. minuta* is exclusively pelagic. Although this species can be found growing under the ice in spring (when it usually auxosporulates; Kozhova & Kobanova, 1995), the main period of net increase in cell numbers occurs during autumn turnover when nutrients become available again and concomitant water transparency is low (confirmed by RDA and the high correlation with increased suspended matter in the water column; Fig. 3b). High relative abundance of this species may be related to periods of warmer waters and a dominance of autummal over spring productivity, due to either longer summers (Bradbury et al., 1994) or restriction of the size of the spring crop relative to the autumn crop, due to long, cold winters, with concomitant increased ice duration on the lake. The latter reason has been invoked by Mackay et al. (2005) to explain the dominance of this species in the sediment record during the period commonly referred to as the ‘Little Ice Age’ (approximately AD 1200–1840). At this time, there was a weakening of the North Atlantic Oscillation (NAO; Shindell et al., 2001) and the expansion of the Siberian High (SH) across central Asia (Krenke & Chernavskaya, 2002). Our data suggest, therefore, that factors that promote a decline in ice and snow cover during spring (or variables that are linearly related to these factors), will also have a negative impact on populations of *C. minuta* the following autumn.

In palaeoecological studies, abundance of both forms of *S. acus* is interpreted as being associated with increased concentrations of silica, related to increased catchment run-off and river discharge (Kilham & Kilham, 1990; Bradbury et al., 1994). The distribution of *S. acus* observed here reflects these parameters. For example, biogeochemical silica mass balance (Callender & Granina, 1995) shows that the production of diatoms in Lake Baikal is supported mostly by remineralization processes in the water column, accompanied by significant contribution from fluvial inputs of dissolved silica, especially from the Selenga River which flows into the central and south basins. Very low relative abundances of *S. acus* agg. in the north basin are likely, therefore, to be related to increased snow and ice cover (as suggested by RDA, Fig. 3b), together with lower concentrations of silica input via rivers than in the other two basins (Shimaraev et al., 1994). It is also worth noting that the valves of *S. acus* suffer considerable breakage and dissolution in the water column at the surface sediment–water interface (Ryves et al., 2003; Battarbee et al., 2005). It is likely, therefore, that the distribution of this species is under-represented in the sediment record.

In agreement with the Kilham & Kilham (1990) hypothesis for Si : P ratios for cosmopolitan diatoms in African Great Lakes (i.e. *Synechocystis* > *Nitzschia* > *Stephanodiscus*), Bradbury et al. (1994) suggested from palaeoecological studies that phosphorus concentrations are likely to be important for growing populations of *S. meyerii*. This will occur when nutrient dynamics are dominated by circulation, promoting a long period of spring overturn and large release of nutrients from bottom sediments. A recent study by Muller et al. (2005) demonstrated that flux rates for phosphorus (between the surface sediment–water interface) were significantly higher in the Maloe More than elsewhere in the lake during the period investigated (1994–2003), agreeing with the assertion by Bradbury et al. (1994) that high phosphorus supply is an important factor for this species. *S. meyerii* exhibits a linear response to snow depth over the gradient sampled, with highest abundance at minimum snow depths (Fig. 4a; Table 5). RDA also shows that *S. meyerii* is found in highest abundances in shallow regions of Lake Baikal with low levels of snow cover when the lake is frozen. The Maloe More is subjected to high winds (Shimaraev et al., 1994), while the region is also semi-arid, receiving less than 200 mm of precipitation annually compared with the 300–400 mm falling annually in the south basin (Atlas Baikala, 1993). Both these factors result in low levels of snow accumulation on the ice of frozen Maloe More during spring. This fits with the assumption of Bradbury et al. (1994) that this species is indicative of

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**Fig. 4** *t*-Value biplots, showing relationships between the eight highlighted species and each of the significant explanatory variables (a = Snow; b = Depth; c = DaysWL; d = SuspMat; e = DaysIce; f = Tempws; g = Zoobio; h = SuspOrgC). Species that fall within the Van Dobben circles are significantly (linearly) correlated (*at* *P* = 0.05) to the environmental variable, either positively (solid circles) or negatively (dashed circles).

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Future climate impacts will result in:

(i) **Shorter ice duration**: Using scenarios of anthropogenic greenhouse gas emissions, model predictions of climate variability over the next 100 years show pronounced warming during winter in the Lake Baikal region (IPCC, 2001). For example, under conditions of a 1% annual increase in CO₂, model simulations suggest that, during the period 2071–2100, mean winter temperature changes over the Northern Asian region range from +4.8 to +9.3 °C, relative to the 1961–1990 period (IPCC, 2001). Todd & Mackay (2003) calculated that, assuming a linear dependence of Lake Baikal ice duration on winter temperature, ice duration in the south basin may decrease by a further 15–28 days by 2071–2100. This decrease is rather less than that estimated by Shimaraev et al. (2002) who calculated that ice duration may decrease by as much as 2 months in the south basin. Our analyses suggest that shorter ice duration will favour growth of species which presently develop in shallow and coastal water regions (e.g. *A. skvortzowii*, *S. meyerii* and *S. acus*; Fig. 4e), whose cells are then transported into the open water through circulation processes in the lake. Conversely, populations of the pelagic, endemic species *C. minuta* are likely to decline, as ice duration gets shorter (Fig. 4e).

(ii) **Reduced snow cover extent**: Snow cover extent in central Asia is controlled by a number of factors, most notably the availability of precipitation (Clarke et al., 1999) linked to changes in e.g. Atlantic sea surface anomalies and the associated NAO (Ye, 2001). Snow cover on frozen Lake Baikal is the strongest single variable in explaining variation in diatom assemblages (Tables 1 and 3). Light is important because it has a direct influence on algal photosynthesis (and primary production) and provides the energy needed for convective mixing to keep diatom cells suspended in the photic zone (Granin et al., 2000). On Lake Baikal, depth of surface snow often exceeds 10 cm, which results in light becoming limiting for diatom cells in the water, and mixing processes to weaken, causing heavier diatoms to sink out of the photic zone (Granin et al., 2000). *A. baikalensis* is adapted to low light conditions and, therefore, snow cover offers this species a competitive advantage over other taxa, which partly explains its dominance in the north basin of Lake Baikal. However, should snow cover impede too much light, then growth of this taxon too is inhibited (Mackay et al., 2005). Regional analysis of snow cover extent indicates that between the 1970s to the middle of the 1980s snow cover over Eurasia was more extensive than between late 1980s to late 1990s (Robinson & Frei, 2000), while model predictions of future global warming suggests that there will be less overall winter snow accumulation.
Our models suggest a decline in snow cover associated with global warming will have a negative impact on deep-water pelagic species such as *A. baicalensis* and *C. minuta*, while promoting net growth of more opportunistic, high-irradiance tolerant species (both cosmopolitan and endemic), including *S. meyerii* (Table 5; Figs 3b and 4a).

(iii) Increased amounts of precipitation: Shimaraev et al. (2002) report that over the last 100 years, there has been a positive relationship between increasing temperatures and hydrological inflow into the lake, which also correlate to observed trends in increasing levels of precipitation in central Asia (Aizen et al., 2001). As precipitation levels at the latitude of Lake Baikal are estimated to increase by 5–10%, Shimaraev et al. (2002) further estimate that water inflow via Lake Baikal tributaries will increase by 5–10% too. It is likely, therefore, that there will be an increase in more generalist species with wider tolerances being transported into the pelagic regions of the lake. For example, t-value biplots (e.g. Fig. 4d) highlight that increases in suspended matter are significantly associated with the endemic *A. skvortzowii*, although resuspension of this taxon from littoral regions during autumn turnover will be important too. Increased fluvial input into Lake Baikal will also result in increased silica and nutrient input into the lake, which in turn will encourage growth of species such as *S. acus* even in the north basin, because of its higher requirement for silica (Bradbury et al., 1994). There is considerable palaeolimnological evidence that *S. acus* was in the past a dominant component of the diatom flora across the length of Lake Baikal, linked to prevailing warmer and wetter climates (e.g. Bradbury et al., 1994; Karabanov et al., 2000; Mackay et al., 2005; Morley, 2005). Other cosmopolitan species, such as *Asterionella formosa* Hassall, *A. subarctica* (O. Müller) Haworth, *A. granulata* (Ehrenberg) Simonsen, which can be relatively abundant locally in coastal areas, would also likely benefit from such changes, and evidence is growing that these increases may already be underway (e.g. Kozhova & Izmes’t’eva, 1998; Mackay et al., 1998).

(iv) An increased period of summer stratification: Predicted increases in temperature are also likely to have an important impact on the length (i.e. longer, and increased stability) and depth of summer and autumn surface-water stratification. An increase in the stratification period will have a negative impact on the success of the resting stages produced by *A. baicalensis* and *C. minuta*, as they slowly sink through the water column to avoid warmer conditions and nutrient depletion (D. Jewson & N. Granin, unpublished data). If turnover during autumn is delayed, then the resting cells of these species will sink further in the water column during stratification, making their resuspension less likely, resulting in a smaller number of cells being entrained back into the photic zone for the following years in oculum. Thus, under a warmer climate, populations of autumnal taxa such as the slow growing *C. minuta* will decline.

We acknowledge, however, that there is a considerable amount of uncertainty, especially with respect to the extent of increasing summer and autumn storminess in the Lake Baikal region, which may actually increase resuspension of cells from deeper waters or from littoral regions. Another major impact resulting from increased stratification will be a shift in balance between large phytoplankton (i.e. diatoms) and autotrophic picoplankton (especially *Synechocystis limnetica*; Fietz et al., 2005). Picoplankton dominate Lake Baikal stratified waters, and because compared with diatoms relative cell-size is small, mass growth occurs due to high rates of nutrient assimilation and high rates of cell division (Popovskaya, 2000). The distribution of picoplankton in the lake varies greatly with region, thereby again ensuring a complex lake-wide response to global warming (Fietz et al., 2005). Nevertheless, such shifts are likely to have important implications for trophic interactions in the Lake Baikal aquatic ecosystem, especially between primary producers and consumers. Our analyses suggest that increases in zooplankton biomass are linked to a decline in *C. minuta*, and a relative increase in coastal species, including *A. skvortzovii* and *S. acus v. radians* fo. *pusilla*. We are not at a stage yet to assess how such changes will impact on complex consumers such as the endemic gammarids (e.g. *Macrohectopus branickii*), or how these changes will be propagated up the food chain. However, the effects are likely to be important for many endemic fish and may have consequences at all trophic levels over time, even affecting the endemic freshwater seal, *Phoco sibirica* (Yoshii et al., 1999). Thus, although the magnitude and nature of the impacts of such changes on Lake Baikal’s biodiversity and ecological functioning are uncertain, there may be major consequences for the conservation and economic value of the lake. For example, a recent study on another deep rift-lake rich in biodiversity, Lake Tanganyika, has shown that recent climate warming has strengthened lake stratification, which has had a negative impact on nutrient recycling, causing a decline in algal biomass and subsequent fish stocks (O’Reilly et al., 2003).

Confounding factors and limitations of study

Linked to variations in diatom assemblages caused by climate change, are confounding factors such as potential increases in pollutant input. Pollutant input occurs
especially through poorly regulated land-use in the catchment of Lake Baikal, most notably around the southern basin and the Maloe More region, west of the central basin (Fig. 1). For example, Popovskaya (2000) highlights how in the shallow waters of the Selenga Delta region, standing crops of phytoplankton are approximately eight times higher in the 1980s than they were in the 1960s, and that this figure is still increasing. These large increases are attributed to anthropogenic eutrophication of the Selenga River and associated shallow waters of the Selenga Delta. Evidence of eutrophication is also borne out by the palaeolimnological record; increases in relative abundances of small centric taxa more commonly associated with nutrient rich waters (e.g. _S. minutulus_ and _A. formosa_) were found in a short core extracted from the shallow waters of the Selenga Delta (fig. 11 in Mackay et al., 1998). Recent attempts have been made to model the impact of anthropogenic disturbance on the lake’s biota using an ecosystem disturbance model (Silow et al., 2001). Initial results suggest all components of the planktonic communities become disturbed, especially under-ice diatom communities, together with an overall increase in nutrient concentration and increase in summer phytoplankton biomass. These changes are similar to those predicted by future climate variability and, therefore, it is now important that refined models are developed to take account of interactions between localized eutrophication and climate change impacts on the lake’s ecosystem.

In Lake Baikal, diatom growth is only limited by Si every third or fourth year, when there is a high abundance of _A. baikalensis_ (so-called _Melosira_ years). While the specific causes for _Melosira_ years are still uncertain, their occurrence is influenced by the interaction between its life cycle and factors that influence population growth, such as nutrients and grazing. We acknowledge, therefore, the likelihood that our interpretations underestimate the full complexity in the Lake Baikal ecosystem. For example, we have not considered responses to Si in our training set, which other diatom-based studies have found to be important (e.g. Rühland & Smol, 2002). Furthermore, phosphate and nitrate are drawn down (by nondiatomaceous phytoplankton) each year to undetectable concentrations in the upper layers during summer stratification. Changes in future climate will undoubtedly affect the availability and use of nutrients, such as phosphate and nitrate, by aquatic algae in the lake, and these responses have not as yet been taken into account. This is partly because our knowledge of the interactions between Lake Baikal phytoplankton and nutrients is still relatively poor, but also because we have not yet been able to compile modern values for many of these nutrients, including Si. Moreover, although diatoms responses will vary spatially between the three lake basins, a single lake-wide response is unlikely, confounded with the knowledge that for some species in our dataset (e.g. cosmopolitan taxa such as _S. acus_), we will not have captured full environmental gradient responses.

As highlighted above, dissolution of diatom valves is a significant process in both the water column and the surface sediment–water interface (Ryves et al., 2003). Dissolution causes differential preservation of diatom species in Lake Baikal – for example, _C. minuta_ is relatively resistant to dissolution, whereas other taxa, including _N. acicularis, S. meyerii_ and _S. acus_ are very susceptible to dissolution (Battarbee et al., 2005). _N. acicularis_ is a common diatom found in Lake Baikal, especially in the south basin. However, because virtually no valves preserve in the surface sediments, we are unable to model impacts of climate change on this species, and we acknowledge that this is a potential weakness in our methodology. Nevertheless, all other taxa are represented, and although differential dissolution means we cannot provide absolute quantitative estimates of how diatom assemblages will change in the future, our qualitative interpretations remain robust.

In this study, we have demonstrated that spatial differences in limnological characteristics linked to prevailing climate have a significant impact on the distribution of both endemic and cosmopolitan diatoms in Lake Baikal. We have modelled these relationships using multivariate techniques. We have then used these models to predict impacts of future climate change on diatoms in this globally significant ecosystem. Our analyses indicate that the responses to future climate change are complex, both in terms of impacts on individual species, but also on basin-wide differences between the main regions of the lake. Overall, we predict that by 2100, a decline in ice duration, decreased snow cover on the lake, increased fluvial input and increased stratification of the upper waters during summer months will result in an increase in endemic and cosmopolitan diatoms which at present dominate shallow-water, offshore regions. However, these increases will occur at the expense of slow-growing, cold-water pelagic endemics. Ongoing monitoring of phytoplankton communities across the lake will provide strong evidence to test our predictions from surface sediment diatom assemblages and quantitative data on population change. If our predictions are correct, such programmes will act as vital early warning indicators of ecological change in Lake Baikal, and their continuation needs to be supported by the international scientific community.
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