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Ecological collapse of Lake Baikal and Lake Hovsgol ecosystems during the Last Glacial and consequences for aquatic species diversity

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Abstract

Sedimentary sections from Lake Baikal in Siberia and Lake Hovsgol in Mongolia show that during the Last Glacial Maximum (LGM), planktonic/benthic diatoms, chrysophyte cysts, sponge spicules and zooplankton remains did not accumulate in the lake sediments. The combined data suggest a drastic lowering of photosynthetic production and perhaps the collapse of the ecosystems of both lakes due to significant environmental changes during the LGM. Both lakes were almost uninhabited during the LGM. Starting from ~ 12,000 to 13,000 ¹⁴C years ago, the planktonic communities redeveloped and primary production increased in both lakes. As a result, Holocene sediments contain abundant and well-preserved planktonic/benthic diatoms, stomatocysts, sponge spicules and zooplankton remains.

The ecosystem stress in Lake Baikal during glacial time appears to be due to a decrease in nutrient loading from the watershed, lowering of surface water temperature, and very low transparency of water and ice. We believe that endemic species in Baikal survived during glacial ecological catastrophes in refugia that could have been a source of species that invaded and repopulated Baikal after intense and long glacial winters. The ecosystem stress in Lake Hovsgol during glacial time appears to be due primarily to drastic lake level falls, and changes in water chemistry. At the beginning of the Holocene, Lake Hovsgol was reoccupied again by cosmopolitan species probably from surrounding small lakes and rivers.

In addition to the LGM results, we also show that Lake Baikal planktonic diatom species diversity during the last 350 ka is closely related to solar insolation fluctuations caused by the 23 and 41 ka cycles of the Earth's precession and

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obliquity. Our results also indicate that Baikal's planktonic diatom species diversity, as measured by the Shannon–Weiner index, correlates with the oxygen isotope record that represents changes in global ice volume.

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1. Introduction

Lake Baikal (1642 m deep) and Lake Hovsgol (Khubsugul) (262 m deep) are two large and deep lakes in Central Asia that occupy valleys of the Baikalian Rift Zone. The age of Lake Baikal is about 20–30 Ma while Lake Hovsgol is 2.5–4 Ma old (Logatchev et al., 1974; Goulden et al., 2003). Present-day Lake Baikal has a unique flora and fauna with more than 1600 endemic aquatic species (Timoshkin, 1997, 1999). Lake Hovsgol is also characterized by a diverse fauna and flora (approx. 390 species) of which only about 20 benthic species are endemic (Kozhova et al., 1994). The difference in the level of endemism between lakes Baikal and Hovsgol is a significant and intriguing problem (Kozhova et al., 1994, 2000; Kozhova and Izmet'seva, 1998; Timoshkin, 1997, 1999).

According to previous studies, the mountain ranges around lakes Baikal and Hovsgol were glaciated during cold periods of the Pleistocene. Glacial valleys and moraines found below present-day water level in Lake Baikal (Lut, 1964; Logatchev et al., 1974; Bazarov, 1986; Mats, 1993) show evidence for advances of glacial tongues into the lake. It has also been well documented that the Lake Baikal basin was never completely glaciated or filled by glacial ice (BDP Members, 1997a,b, 1998, 2000).

Records of diatom distribution in Lake Baikal sediments provided data showing that diatom valves were abundant in the Holocene and absent in the Last Glacial Maximum (LGM) deposits (Bezrukova et al., 1991; Bradbury et al., 1994). These studies made it possible to conclude that major changes occurred in the Lake Baikal ecosystem during the LGM–Holocene transition (Bezrukova et al., 1991).

Lake Hovsgol is smaller and at a higher elevation (1645 m above sea level) than Lake Baikal (455 m above sea level). The glacial limit during the Late Pleistocene for the Lake Hovsgol basin was at 1550–1650 m level, just below the modern lake surface

(Belova and Kulakov, 1982). Several underwater terraces have been described in the Lake Hovsgol basin at 20–40, 50–80, 90–120 and 190 m depth, and numerous sublacustrine valleys show evidence for lake level changes and glacial advances into the lake basin during the Late Pleistocene (Zolotarev and Kulakov, 1973, 1976; Kulakov, 1981; Belova and Kulakov, 1982; Gluchovskaia et al., 1987; Kozlov et al., 1989). New seismic surveys show that Hovsgol lake levels were 200 m lower probably during the LGM (Fedotov et al., 2002), in good agreement with previous conclusions from geomorphological data (Zolotarev and Kulakov, 1976).

During glacial times, glacial meltwater streams carried fine detritus into Lake Baikal, depositing fine glacial-lacustrine clay on the bottom (Karabanov et al., 1998; Karabanov, 1999). Coarse inclusions of boulders, pebbles, gravel and silty sand lenses were deposited in glacial-lacustrine clays by icebergs as ice-rafted detritus (IRD) (Karabanov et al., 1998; Karabanov, 1999). Similar glacial-lacustrine clays with IRD have been found in Lake Hovsgol (Fedotov et al., 2000, 2001; Prokopenko et al., 2003a,b; Solotchina et al., 2003).

2. Materials and methods

For our study we use the 4.72-m-long gravity core (VER93-2 st.24GC) obtained from the topographically high Buguldeyka uplift of Lake Baikal and a 1.74-m-long gravity core (HSG-01-08) collected from basin floor of Lake Hovsgol. Water depths at the coring locations were 355 m for Baikal and 222 m for Hovsgol. Sediments of both cores are comprised of an upper unit of diatomaceous silty clay or clayey silt with high diatom content (up to 30–80% by weight) and a lower unit of silty clay barren of diatoms (Fig. 1). Core st.24GC was sampled at 1.0 cm intervals (approx. 50 years resolution). The sampling interval for core HSG-01-08 was 2.0 cm for

Lake Baikal: core VER93-2 st.24GC

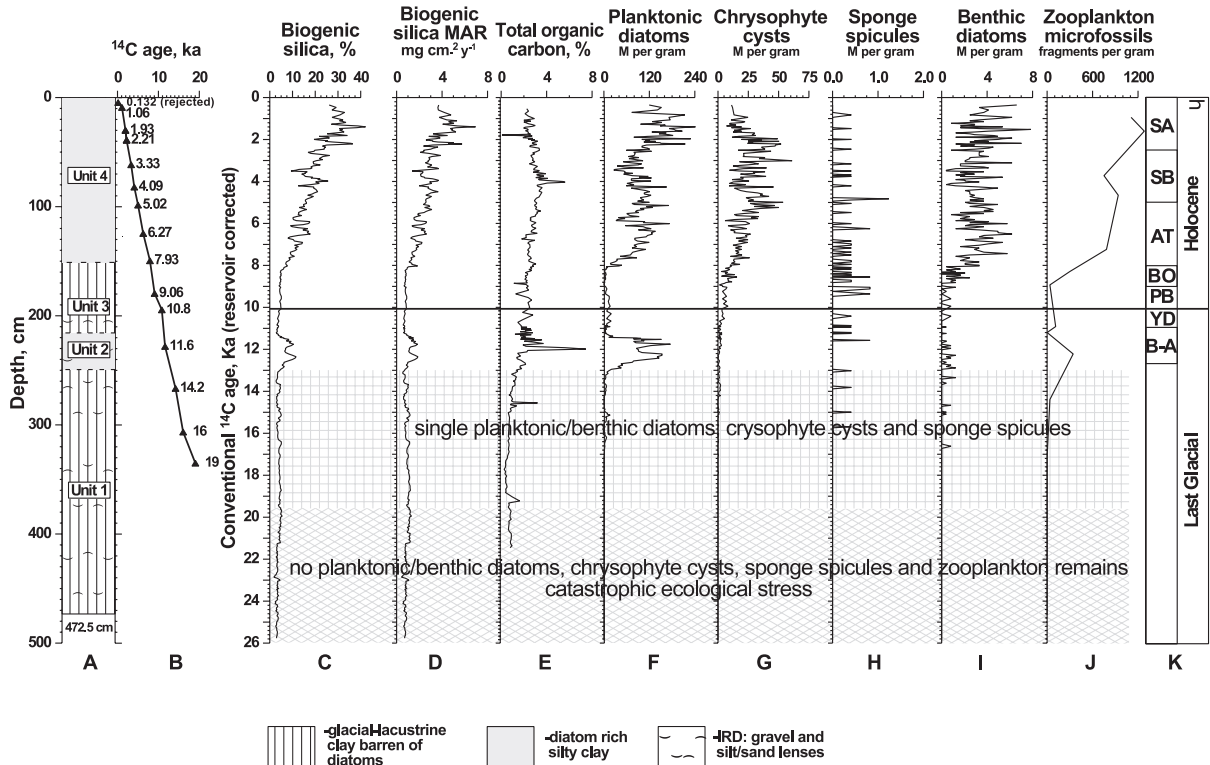


Fig. 1. Lake Baikal paleoclimate proxy records for Last Glacial Maximum–Holocene time. (A) Core VER93-2 st.24GC lithology. (B) Radiocarbon age–depth relation, reservoir corrected. (C) Biogenic silica record where low biogenic silica corresponds to glacial conditions and high biogenic silica corresponds to the warm interglacial period (Holocene). (D) Biogenic silica mass accumulation rate showing that low concentrations of biogenic silica in units 1 and 3 are not the result of dilution by clastic sediments. (E) Total organic carbon record showing that during glacial time accumulation of carbon was several times lower than during interglacial time. (F–J) Records of siliceous microfossils showing no planktonic/benthic diatoms, chrysophyte algae, sponge spicules and zooplankton remains during glacial time. (K) Blytt–Serander climatic divisions for Western Europe. This scheme is widely adapted for paleoclimatic research as a chronostratigraphic scheme and commonly used in Siberian palynological studies. SA—Subatlantic, SB—Subboreal, AT—Atlantic, BO—Boreal, PB—Preboreal, YD—Younger Dryas, B–A—Bølling–Allerød.

biogenic silica and 4.0–6.0 cm for carbonates, providing an age resolution of about 400 and 1000 years, respectively, according to sedimentation rates determined by Prokopenko et al. (2003a,b).

Siliceous microfossils (diatoms, chrysophyte cysts and sponge spicules) were quantitatively determined by counting permanent smear slides prepared according to the method described in Grachev et al. (1997). Five-milligram samples of dried sediment were weighed and suspended in 50 µl of distilled water. The suspension was centrifuged for 1 min at 12,000 rpm. After decanting the water, 100 µl of 5% sodium pyrophosphate solution were added and the

resultant suspension was held for 2 h at 50 °C. After centrifuging and decanting the solution, the sediment was rinsed by 100 µl of distilled water and centrifuged twice and finally suspended in 500 µl of water. The resultant suspension was thoroughly shaken and three identical 5 µl aliquot drops were collected by pipette and transferred onto a clean microslide and dried. After drying, a cover glass was placed over the microslide and mounted with Naphrax (*n* = 1.7).

The quantitative counting method is based on counting diatom valves along transects of smear slides by light microscope with a magnification of 1000 × in

all three aliquot drops. Depending upon diatom concentration, an average of 50 to 200 fields of view were counted. The standard error for determining the total number of valves by this method does not exceed 15% (Grachev et al., 1997). The results are given in million valves (or cysts and spicules) per gram of dry sediment.

Diatoms were examined by oil immersion light microscopy (Ergaval microscope with $100\times$ objective, NA=1.25) and by scanning electron microscopy (JEOL JSM-35C). Biogenic silica content was determined using a wet-alkaline extraction method (Mortlock and Froelich, 1989) and colorimetric determination of the blue silica molybdate complex with an average error of 2.5%. The results are given as percent of dry sediment weight. We calculate biogenic silica flux for core st.24GC using the equation $F=(V\times P\times DBD)/100$, where V is the sedimentation rate calculated between radiocarbon dates in cm per 1000 years; P is the biogenic silica proportion; and DBD is a dry bulk density of the sediments in g cm^{-2} .

For total organic carbon and nitrogen analyses, the standard sample preparation procedure included drying, grinding and leaching in a 1 M H_3PO_4 solution in an ultrasonic bath. Samples of 5–15 mg weight were analyzed on an Optima Isotopic Ratio Mass Spectrometer in line with a Carlo-Erba CHN Elemental

Analyzer. All samples were run in triplicate. The standard error for total organic carbon was 1.6%.

Zooplankton remains including unspecified cladoceran head shields, shells and claws were counted using pollen samples prepared according to a standard method with HF and HCl acids (PALE, 1993). From each sample 10 slides were counted. Raw data were transformed to numbers of fragments per gram of dry sediments. Carbonate concentration was determined by X-ray powder diffraction and IR spectroscopy in the United Institute of Geology, Geophysics and Mineralogy, Siberian Branch of Russian Academy of Sciences, Novosibirsk, according to method described in Solotchina et al. (2002).

In this article we also investigated biogenic silica, planktonic and benthic diatom, chrysophyte cyst and sponge spicule distribution data from the upper section (0–13 m) of BDP96-2 core that covered the last 350 ka (Williams et al., 1997; Prokopenko et al., 2001a,b; Khursevich et al., 2001a,b). The sampling interval for biogenic silica and microfossils analysis in that core was 2 cm, providing a time resolution ~ 500 years. The age model for this core is based on orbital tuning to the solar insolation record (Prokopenko et al., 2001a,b). To calculate the Shannon–Weiner index for this core, we used the data set of planktonic diatom species distribution for core BDP96-2 (Khursevich et al., 2001a,b). The calcula-

Table 1
Radiocarbon ages for Lake Baikal core VER93-2 st.24GC

Core depth	$\delta^{13}\text{C}$ (‰ relative to PDB)	Material	Analytical age	1 σ error	Corrected age ^a	Lab. number	Evaluation
4.5	–26.2	TOC	1720	± 55	132	OS-25976	Rejected
9	–25.8	TOC	2650	± 35	1062	OS-25977	Accepted
30	–26.5	TOC	3520	± 35	1932	OS-25978	Accepted
39	–25.3	TOC	3800	± 35	2212	OS-25979	Accepted
61.5	–27.7	TOC	4920	± 40	3332	OS-25980	Accepted
82	–28.2	TOC	5680	± 40	4092	OS-25981	Accepted
98.5	–28.5	TOC	6610	± 50	5022	OS-25982	Accepted
124.5	–28.1	TOC	7860	± 60	6272	OS-25983	Accepted
149.5	–28.2	TOC	9520	± 50	7932	OS-25984	Accepted
179.5	–29.2	TOC	10,650	± 55	9062	OS-25985	Accepted
194.5	–26	TOC	12,420	± 70	10,832	OS-25986	Accepted
228	–28.7	TOC	13,210	± 65	11,622	OS-25987	Accepted
266.5	–25.8	TOC	15,770	± 80	14,182	OS-25988	Accepted
306.5	–25	TOC	17,630	± 110	16,042	OS-25989	Accepted
335	–24.6	TOC	20,620	± 95	19,032	OS-25990	Accepted

TOC—decalcified total organic carbon. All depths in cm; all ages in years BP.

^a Age corrected using an estimated reservoir effect of 1588 years calculated from regression line.

tion of the Shannon–Weiner diversity index was based on equation $H = -\sum P_i \times \ln P_i$; where P_i is the proportion of i species relative to the total number of species; and $\ln P_i$ is the natural logarithm of this proportion with the base-10 (Sanders, 1968). This index is commonly used to measure diversity and is not sensitive to abundance.

3. Dating and age models

Terrestrial macrofossils were not present in sufficient quantities for ^{14}C dating, and biogenic carbonates are usually not preserved in Lake Baikal sediments. We therefore obtained 15 AMS ^{14}C dates on decalcified bulk sediments from core st.24GC. All radiocarbon

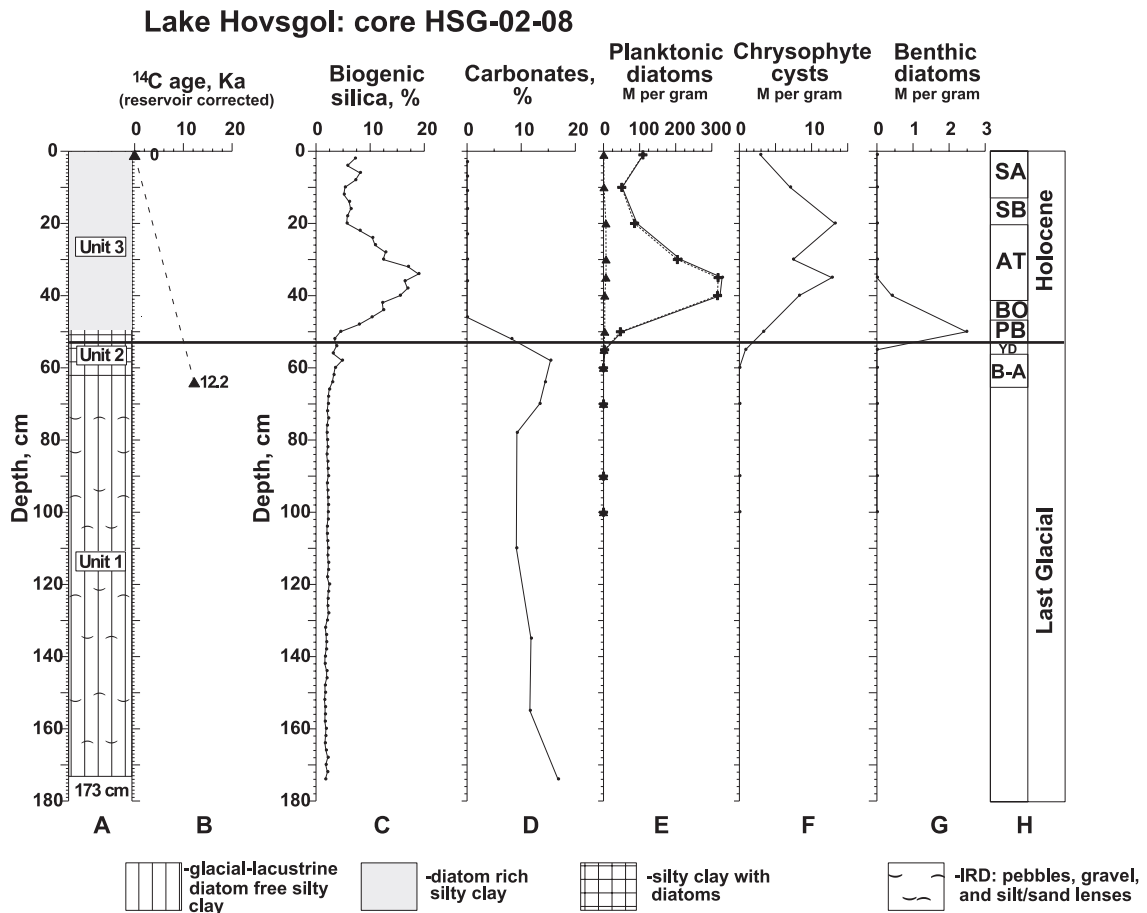


Fig. 2. Lake Hovsgol paleoclimate proxy records for Last Glacial Maximum–Holocene. Holocene sediments are diatom-rich, whereas the glacial-lacustrine clay is almost barren of diatoms. The diatom-barren clay also contains isolated pebbles, gravel grains, and silt and sand lenses that are interpreted as ice-rafted detritus (IRD). (A) Lithology of core HGS-02-08. (B) Age–depth relation based on two AMS dates, reservoir corrected (Prokopenko et al., 2003a,b). (C) The biogenic silica record where low biogenic silica corresponds to glacial conditions, and high biogenic silica correspond to the warm interglacial conditions of the Holocene. (D) Record of carbonate concentration. Glacial-lacustrine clay contains high amounts of carbonates while Holocene diatom rich sediments are carbonate free. (E–G) The records of siliceous microfossils show that during glacial time no planktonic/benthic diatoms and chrysophyte cysts accumulated in lake sediments. Planktonic diatom community includes the species *Cyclotella ocellata*, *Cyclotella bodanica*, *Cyclotella meneghinianna*, *Cyclotella krammeri*, *Aulacoseira granulata* and *Stephanodiscus* aff. *alpinus*. However, diatom valves of *C. ocellata* dominate (+) with subdominant species (▲) *S. aff. alpinus*. (H) Blytt–Serander climatic scheme for Western Europe. Position of the Holocene–LGM boundary and the boundaries of other units were calculated according to the mean sedimentation rate in this core.

dates become progressively older with depth (Fig. 1), indicating generally undisturbed sedimentation in the studied core. Raw ^{14}C dates were corrected for isotopic fractionation ($\delta^{13}\text{C}$) and an estimated reservoir effect of 1588 years calculated from the regression line (Table 1). This correction agrees with previous corrections suggested for Lake Baikal sediments (1500 ± 500) (Colman et al., 1996). The resulting age–depth profile indicates that sedimentation was almost continuous spanning the last ~ 26 ka. Fourteen ^{14}C dates were used to constrain the age model of the studied section. The uppermost date was excluded from the age model because according to the core description sediment mixing was suspected.

The age model for HSG-01-08 from Lake Hovsgol is based on two AMS ^{14}C dates, which were determined on decalcified bulk sediments. The raw data were corrected for a reservoir effect applying 1720 years (Prokopenko et al., 2003a,b). Age data for both cores were not calibrated to calendar ages and conventional ^{14}C ages are used for this contribution (Figs. 1 and 2). All AMS dates were determined at the Woods Hole AMS Facility according to standard procedures.

According to the age–depth relationship obtained from core st.24GC, the sedimentation rates vary between 8.5 and 42.4 cm per 1000 years with mean sedimentation rate of 20.6 cm per 1000 years. The sedimentation rate in the Lake Hovsgol core is much lower and does not exceed 5.2 cm per 1000 years during the Holocene. Although only two dates are available for this core, this sedimentation rate is consistent with other Hovsgol cores, unpublished AMS dates and correlation of magnetic susceptibility profiles (Prokopenko et al., 2003a,b).

4. Core lithology

4.1. Core VER93-2 st.24GC from Lake Baikal

The sediments of core st.24GC exhibit visible lithostratigraphic variations and four different sedimentary units. Unit 1 of core st.24GC (472.5–249 cm) covers the period from ~ 25.8 to 13.0 ka ^{14}C years and consists of bluish-gray dense silty clay with chaotically stratified sand and silt lenses and pockets (Fig. 1). Dispersed sand and silt grains are also present in the clay. Few medium-size gravel grains were

observed in unit 1. The clay is finely laminated (mm-scale). No signs of bioturbation were observed. Unit 1 is characterized by very low abundance of diatom valve, chrysophyte cyst, sponge spicule and zooplankton remains, low biogenic silica and low total organic carbon values (Fig. 1). The lower part of unit 1 from 472.5 to 350 cm is barren of siliceous microfossils.

Unit 2 spans the interval from 249 to 216 cm and is a poorly laminated, greenish-gray, soft silty clay with diatoms. Unit 2 is also comprised of chaotically stratified sand/silt lenses, dispersed sand and silt grains, and isolated gravel grains (Fig. 1). Visible signs of bioturbation were present in this section. Unit 2 is characterized by increasing microfossils and biological components (Fig. 1). According to the age model unit 2 corresponds to 13.0–11.37 ka ^{14}C years.

Unit 3 spans the depth interval from 216 to 152 cm and is characterized by weakly laminated (cm-scale) bluish-gray silty clay. Unit 3 lacks visible primary structures, but occasionally shows very indistinct bedding. Unit 3 is also comprised of chaotically stratified sand/silt lenses, dispersed sand and silt grains, and single granules, which are localized at 216–186 cm depth (Fig. 1). Diatom valves are not abundant in unit 3 and biogenic silica concentrations are very low and comparable with concentrations in unit 1. Total carbon content is higher than in unit 1 and fluctuates significantly. According to the age model unit 3 spans the time interval from 11.37 to 8.05 ka ^{14}C years.

Unit 4 spans the time interval from 8.05 ka ^{14}C years to present (152–0 cm) and is characterized by an olive-gray organic and diatom-rich silty clay (Fig. 1). Unit 4 is weakly laminated and occasionally shows indistinct bedding or banding. Obvious signs of bioturbation were also observed. Unit 4 also has dispersed sand and silt grains but with no silt/sand lenses. The sediments of unit 4 are very soft and porous with high water content. Unlike unit 3, this section has a clear trend from the base to the top characterized by the increasing abundance of all microfossils and biogenic components (Fig. 1).

4.2. Core HGS-02-08 from Lake Hovsgol

The sediments of Lake Hovsgol show very similar compositions to those of the Lake Baikal and, according to Prokopenko et al. (2003a,b), three units can be

distinguished in core HGS-02-08. Representing the LGM, unit 1 (172.5–64.5 cm) is comprised of dense olive-gray silty clay with dispersed sand and occasional gravel and pebble grains. Unit 1 of the Hovsgol core probably corresponds to unit 1 of the Lake Baikal core. Unit 2 (64.5–49 cm) is transitional. It comprises fine laminated light-gray silty clay with low numbers of diatoms and is barren of coarse components (Prokopenko et al., 2003a,b). Unit 2 in Hovsgol is probably the equivalent of units 2 and 3 from core st.24GC of Baikal. Unit 2 corresponds to the LGM–Holocene transition and probably spans the Bølling–Allerød warming and the Younger Dryas cooling. Unit 3 (49–0 cm) is Holocene in age and contains greenish-gray obviously laminated diatom rich mud (Fig. 2). Unit 3 of core HGS-02-08 therefore corresponds to unit 4 from Baikal.

5. Analytical results

In core st.24GC from the Buguldeyka uplift of Lake Baikal, we analyzed biogenic silica, total organic carbon, total nitrogen content and concentrations of planktonic and littoral benthic diatoms, chrysophyte cysts, sponge spicules, and zooplankton remains (Fig. 1). Diatoms, chrysophyte cysts, biogenic silica and carbonate concentrations (Fig. 2) were measured in core HSG-01-08 collected from the Lake Hovsgol (Prokopenko et al., 2003a,b; Solotchina et al., 2003).

The biogenic silica signal fluctuated significantly in Lake Baikal ranging from 3.5% to 42% with two intervals of low concentration in unit 1 and unit 3 (Fig. 1). Biogenic silica values increase near the core top suggesting increased diatom production during the Holocene. Diatom concentrations (Fig. 1) show considerable variation and range both within the core and between lithological units. In general, however, the concentration of diatoms tends to increase upward through the core. The diatom record begins with single diatom valves occasionally occurring in unit 1 from 3.49 to 3.16 m depth (18.8–16.8 ka ^{14}C years ago). Below this depth diatom valves are absent. Unit 2 is characterized by significant increases in diatom abundance up to 153.7 million valves per gram of dry sediment. Diatoms increase rapidly at the base of unit 2 and drastically decline at the top of the unit. Unit 3 is characterized by very low diatom frustule concentra-

tions, comparable with diatom amounts in unit 1. Unit 4 has a clear trend from the base to the top characterized by increasing diatom concentrations from 39.2 to 119.4 million valves per gram of dry sediments. The concentration of diatoms is highest in unit 4 of core st.24GC and exceeds 207 million per gram of dry sediment.

Although benthic diatom abundance is much less than planktonic diatom abundance in core st.24GC (never exceeding 8 million per gram), the down-core distribution of benthic diatoms closely follows that of planktonic diatoms excepting unit 2 where benthic diatoms are not abundant. Both benthic and planktonic diatoms are absent during the LGM and well developed during the Holocene. Most maxima/minima in the planktonic diatom record correlate with benthic diatom maxima/minima (Fig. 1) reflecting similar responses to environmental variability.

The first chrysophyte cysts in core st.24GC appear in small numbers in unit 1 coeval with the diatoms (Fig. 1). After unit 1, the chrysophyte cyst values remain very low until the middle part of unit 3 when their concentration starts to increase, reaching maximum values (61.1 million cysts per gram of dry sediment) at the top of unit 4. The record of chrysophyte cysts exhibits a different pattern from the biogenic silica and diatom abundance records. Unlike the diatoms, chrysophyte cysts are very infrequent in unit 2 and slightly more abundant in unit 3, whereas the diatom concentration decreases in this unit. As with the diatom record, the highest chrysophyte cyst concentrations are in unit 4; however, maximum chrysophyte concentrations are observed in different depth intervals (Fig. 1).

Sponge spicules in the sediments of core st.24GC are absent in the lowest part of unit 1 and appear at a depth of 2.99 m (15.7 ka ^{14}C years ago) almost at the same depth as diatom valves and chrysophyte cysts (Fig. 1). Spicules are less abundant in the sediments of unit 2 and are more frequent in units 3 and 4.

The distribution of zooplankton remains in core st.24GC is generally comparable to that for diatoms. Although the resolution of this record is much lower than for diatoms, it is evident that in unit 1 zooplankton remains are absent and appear only in unit 2 in small numbers (Fig. 1). Zooplankton remains in unit 3 are low and increase in unit 4. The maxima in zooplankton remains correspond to maxima in diatom abundance in unit 4 (Fig. 1).

Concentrations of biogenic carbon are low in unit 1 (0.26–0.9%) and increase in units 2–4 (Fig. 1). The C_{org} maximum 7.45% is reached at 233 cm in unit 2, corresponding to the Bølling–Allerød warming (Fig. 1). Total nitrogen concentration is also low in unit 1 and increases in units 2–4 (not shown).

The biogenic silica record from core HGS-02-08 exhibits similar patterns to the opal records in the Lake Baikal core: the concentration is very low in unit 1 and increases up to 20% in unit 3. The presence of carbonates makes the Hovsgol sediments different from the Baikal sediments. In unit 1 carbonate concentrations are significant, varying from 9% to 12% (Fig. 2). In unit 2 carbonate concentration increases to 15.4% and then decreases to zero in unit 3 (Fig. 2). Three types of carbonates (calcite, dolomite and magnesium calcite) are recorded in the sediments of unit 1 (Solotchina et al., 2003).

6. Reconstruction of paleoenvironments

The LGM–Holocene sedimentary sections from Lake Baikal and Lake Hovsgol exhibit similar lithologies and two major components (Figs. 1 and 2). The upper diatom-rich sediments are of Holocene age and began to accumulate ~ 13 ka ^{14}C years ago in Lake Baikal and ~ 12.23 ka ^{14}C years ago in Lake Hovsgol (Figs. 1 and 2). The lower LGM sediments contain fine dense silty clay barren of diatoms (Figs. 1 and 2). The Holocene diatomaceous sediments represent warm interglacial climatic conditions with rich and diverse planktonic/benthic diatom floras, chrysophyte algae and sponges, whereas the diatom-barren clay represents cold glacial environments devoid of the major primary producers (diatoms, chrysophytes) and sponges.

Since both lakes were surrounded by numerous glaciers with tongues extending into the lakes during the LGM, we propose that fine dense clay from glacial outwash was delivered by meltwater into both lakes. This clay was dispersed by surface currents throughout the lakes and is found in all environments and at all depths, from the very shallow zone (3–5 m) to the abyssal floors of Lake Baikal. Coarse inclusions in clay such as sand, gravel, pebbles and boulders in both lakes appear to be IRD material delivered by seasonal ice and icebergs (Karabanov et al., 1998;

Karabanov, 1999; Fedotov et al., 2000, 2001; Prokopenko et al., 2003a,b). During the LGM both lakes became glacial-fed lakes with glacial-lacustrine sedimentary environments.

7. Ecological stress in Lake Baikal during the Last Glacial Maximum

The Lake Baikal sedimentary records contain important information about ecological changes that happened during the LGM. Data from core st.24GC (Fig. 1) and many different cores from different localities (Bezrukova et al., 1991; Bradbury et al., 1994; Karabanov et al., 2001; Khursevich et al., 2001a,b and our unpublished data) show that the LGM-lacustrine sediments of Lake Baikal are barren of diatom valves and chrysophyte cysts. The lack of diatom valves and chrysophyte cysts in the LGM sediments of Lake Baikal implies that diatoms and chrysophyte algae were not present in the phytoplankton of the lake during the LGM. However, not only did diatoms and chrysophyte algae disappear during the LGM but also the abundance of all phytoplanktonic primary producers became very low probably including species that do not leave preserved remains in lake sediments. This significant lowering of overall phytoplanktonic primary production of Lake Baikal during the LGM is supported by very low concentrations of total organic carbon and nitrogen in glacial-lacustrine sediments (Ishivatary et al., 1992; Karabanov et al., 2001; Prokopenko et al., 2001a,b and our unpublished data).

The observed declines in diatom valves, biogenic silica and C_{org} and N_{tot} concentrations in the LGM-lacustrine clay are not controlled by dilution of terrestrial sediments because biogenic opal flux during the Holocene was higher than during the LGM and sedimentation rates in the studied core do not increase during glacial time. A similar conclusion was made from studies of other cores collected from this area (Colman et al., 1996; BDP Members, 1997a,b, 1998, 2000). Moreover, the thickness of Holocene units of the cores collected from the elevated Buguldeyka uplift and Academician ridge usually equals or exceeds the thickness of LGM units. These observations suggest that sedimentation rates on the elevated block of the Buguldeyka ridge during the LGM were similar or lower than during the Holocene. The

biogenic silica mass accumulation rate shows that the biogenic opal flux during Holocene was several times higher than during the LGM (Fig. 1).

Significant dissolution of diatom frustules in the water column or the sediments is unlikely to be the primary control on the siliceous paleorecords and certainly dissolution is not an applicable process for zooplankton remains and C_{org} and N_{tot} concentrations, which covary with the siliceous productivity signal. From these results we can assume that the decreases in biogenic silica, diatoms and other biogenic components in LGM sediments are part of a natural process associated with a significant lowering of primary production in Baikal and not related to dilution or dissolution of diatom valves.

In our opinion, the disappearance of planktonic primary producers in the Lake Baikal happened due to a nutrient-depleted and turbid surface layer that originated from glacial meltwater. Meltwater flows, which come from the bottom of glaciers, carry high concentrations of rock flour, the product of ‘glacier grinding’. The very small grain size of glacial detritus allows it to remain suspended in the water column for a very long time. Electron microscopy of the Lake Baikal glacial clay reveals details of individual sediment particles that are mostly 1–0.1 μm in size and made up of siliclastic grains with very rough, broken or burst surfaces. According to Stoke’s law, grains of such size are able to stay in the euphotic zone for several months up to a year. This process in Lake Baikal has a close analogue with meltwater pulses in the North Atlantic, when cold nutrient-depleted meltwater form a non-productive surficial layer during the degradation of glaciers. In the case of Lake Baikal, similar layers formed during each summer of the LGM due to the relatively warm climate of South Siberia that permitted glaciers with areas of basal melt to produce large amounts of meltwater.

The high turbidity of meltwater made the transparency of lake water and seasonal ice very low. Transparency of seasonal ice is a very important factor because Lake Baikal planktonic algae have maximum productivity under ice during late winter and spring (Popovskaya, 1987; Bondarenko and Guselnikova, 1989). Present-day studies show that the thickness of snow cover on ice is a very important factor in the diatom productivity of Lake Baikal. Decreased light transmission through ice inhibits diatom production

(Granin et al., 2000). We believe that in combination, the low temperature of surface water, low nutrient loading from the watershed and very low ice transparency during the LGM suppressed the primary production of algae in the lake. Submerged macrophyte and periphyton may also have been suppressed, as suggested by the near complete absence of benthic (epilithic and epiphytic) diatoms in the lake sediments.

The suppression of total submersed photosynthetic productivity via high-turbidity water formation due to rain events in clay-rich regions is common in many ponds, streams and reservoirs (Wetzel, 2001). However, such events are temporary and lake ecosystems are able to recover quickly. In case of Lake Baikal, the disturbances were of long duration with potential catastrophic effects on ecosystem stability.

Dead organic matter or detritus has manifold implications for ecosystem stability (Wetzel, 1995, 2001). The disappearance of planktonic primary producers in the lake and changes in the detritus flux probably led to a total collapse if not destruction of the pelagic and benthic food webs including species of higher trophic levels: cladoceran zooplankton, benthic invertebrates and fishes. The absence of zooplankton remains in glacial-lacustrine clay in the LGM intervals of the two cores st.24GC (Fig. 1) and 323PC1 (Kadota, 1992) support this explanation. It seems that during the LGM the Lake Baikal pelagic zone was barren of algae and zooplankton, and, probably, it was largely abiotic.

The lack of bioturbation in the glacial-lacustrine clay of our core also supports the conclusion that a low number or absence of benthic invertebrates and fishes occurred on the lake bottom during the LGM. This observation and the absence of littoral benthic diatoms and sponge spicules in LGM sediments (Fig. 1) indicate that significant changes also occurred within the Baikal littoral and abyssal benthic communities through the LGM. This is consistent with a deficiency of biodetritus rain from productive zones of the lake and a limited amount of food for filter-feeding sponges and different types of benthic detritivores due to a collapse of the detritus food chain.

Our data show that the initiation of planktonic and littoral benthic community recovery in Lake Baikal started about 17 ka ^{14}C years ago associated with the beginning of deglaciation. However, only during the Bølling–Allerød warming (~ 13 –11 ka ^{14}C years ago) did the planktonic diatom community approach

Lake Baikal: core BDP96-2

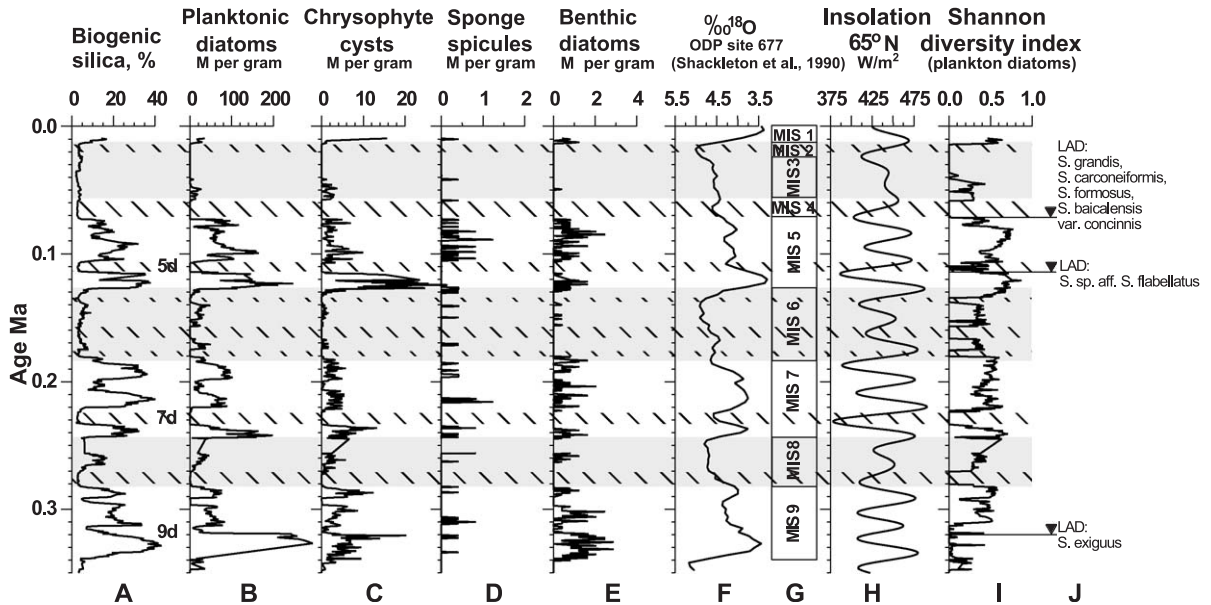


Fig. 3. Late Pleistocene paleolimnological records from core BDP96-2, Lake Baikal. The age model was based on tuning the biogenic silica record to insolation (Prokopenko et al., 2001a). Glacial periods (gray shading) and intervals of glacial catastrophes (shaded zone) in Lake Baikal, when planktonic/benthic diatoms, chrysophyte algae and sponges disappeared, correlate with the marine oxygen isotope record (F) (based on benthic foraminifera) from equatorial Pacific ODP site 677 (Shackleton et al., 1990) and the insolation record (H) (Laskar et al., 1993). (A) The biogenic silica record reflects changes in planktonic diatom productivity and represents the glacial/interglacial stratigraphy of Lake Baikal sediments (Williams et al., 1997). Low biogenic silica intervals correspond to glacials and sections with high biogenic silica concentration correspond to warm interglacial periods. (B–E) The records of siliceous microfossils (Khursevich et al., 2001a,b) show that during glacial intervals no planktonic/benthic diatoms, chrysophyte cysts and sponge spicules accumulated in lake sediments. These intervals are associated with glacial ecological catastrophes in Lake Baikal. (F–G) Marine isotope stratigraphy. MIS—marine oxygen isotope stages. 5d–9d—marine oxygen isotope substages. (I) Record of planktonic diatom diversity based on Shannon–Weiner diversity index. Low diversity of Lake Baikal planktonic diatoms corresponds to glacial periods and high global ice volume. High diversity corresponds to interglacials and low global ice volume. During glacial catastrophes, the species diversity index falls to zero indicating the absence of diatoms in Lake Baikal. Almost all diversity minima follow just after insolation minima indicating a strong correlation between planktonic algae diversity and solar insolation. (J) Last abundance data points (LAD) show that during the Late Pleistocene planktonic diatom species frequently become extinct mostly throughout glacial periods.

Holocene levels (Fig. 1). Climatic deterioration during the Younger Dryas event depressed planktonic diatoms again and the population declined almost to full glacial levels. During this time, planktonic diatoms were replaced by planktonic chrysophyte algae (Fig. 1). Diatom phytoplankton redeveloped again only 8.05 ka ^{14}C years ago at the beginning of Atlantic time. After this time, planktonic primary production increased significantly and both the planktonic and benthic communities reached present-day levels with the Baikal Holocene sediments containing abundant and well-preserved planktonic diatom valves, chrysophyte cysts, benthic diatoms, sponge spicules and

abundant zooplankton remains (Fig. 1). Our record shows that the diversity of the Holocene planktonic diatom population in the Lake Baikal was able to return to pre-glacial levels (Fig. 3).

8. Climate-driven planktonic diatom species diversity according to long paleolimnological records from Lake Baikal

Long Lake Baikal sedimentary records show that disappearance of diatoms, chrysophyte alga, sponge spicules happened during almost all glacials through-

out the Pleistocene (Khursevich et al., 2000, 2001a,b). It seems that glacial “catastrophes” in the Baikal were regular with a frequency of 23 and 41 ka (Fig. 3) (Prokopenko et al., 2001a; Khursevich et al., 2001a,b). Many diatom species disappeared from the diatom community of Lake Baikal during glacial episodes for several thousand years but re-appeared again during warm episodes only to become extinct with subsequent glaciations (Khursevich et al., 2001a,b). Our data show that 6 endemic planktonic species became extinct just during the last 350 ka (Fig. 3). However, catastrophic disturbances of the Baikal ecosystem did not happen during all glacials. During some glacials, diatoms and chrysophyte algae disappeared from Baikal only for very short intervals lasting few thousand years (see MIS 6 and MIS 8—Fig. 3). Almost all these collapses of Baikal diatom communities follow after insolation minima (Fig. 3) and are probably the result of episodes of climate deterioration in Siberia driven by orbital forcing.

The longest and probably more critical diatom free period in the Lake Baikal was during marine isotope stage (MIS) 4 or the Ermakovo Glacial in the Siberia (Fig. 3). This event lasted for about 13 ka (71–57 ka BP) and four dominant diatom species (*Stephanodiscus grandis*, *Stephanodiscus carconeiformis*, *Stephanodiscus formosus* and *Stephanodiscus baicalensis* var. *concinis*) became extinct during this glacial collapse. However, many planktonic diatom endemic species such as *Aulacoseira baicalensis*, *Aulacoseira zkvortzowii*, *Cyclotella baicalensis*, *Cyclotella minuta*, *Cyclotella ornata* and others survived and reoccupied the lake again in the Holocene.

Catastrophic disturbances of the Lake Baikal ecosystem happened not only during glacials but also during cold episodes within interglacials such as substages 5d and 7d. These short cold events correspond to deep insolation minima (Fig. 3), but in marine oxygen isotope records these substages are sometimes expressed as temperate coolings. In Siberia however, these substages exhibit all the characteristics of regional glaciations with full glacial conditions in the Lake Baikal area: glaciers in nearby mountains advanced to Lake Baikal (Karabanov et al., 1998; Kuzmin et al., 1999; Prokopenko et al., 2001a). During these substages, diatom-barren glacial-lacustrine clay accumulated on the lake bottom, the production of

planktonic/benthic diatoms and chrysophyte algae was depressed, and several diatom species became extinct (Fig. 3) (Khursevich et al., 2001a,b).

Our data suggest that these catastrophic disturbances periodically occurred in Lake Baikal throughout the Pleistocene and began with the first accumulation of glacial-lacustrine clay and first disappearance of diatoms recorded in lake sediments in the Late Pliocene at 2.5–2.8 Ma (Karabanov et al., 2000a,b). Two diatom genera (*Stephanopsis* and *Tertiarius*) became extinct in Lake Baikal after this glacial event (Karabanov et al., 2000a,b; Khursevich et al., 2000). However, after each succeeding catastrophic disturbance, the Lake Baikal diatom and benthic community recovered and the planktonic diversity recovered to similar interglacial levels (Fig. 3).

How did these climatic changes and glacial catastrophic disturbances of the Baikal ecosystem affect planktonic diatom diversity? Fig. 3 shows a clear relationship between climate change during the last 350,000 years and planktonic diatom diversity. Low diversity values correspond to heavy $\delta^{18}\text{O}$ values (large ice volume) and glacial climates. High diversity values correspond to light $\delta^{18}\text{O}$ values (smaller ice volume) and interglacial climates. Maximum diversity of the Lake Baikal planktonic community appears during warm marine oxygen isotopic substages 5a, 5c and 5e. Substage 5e (or Kazantsevo on the Siberian stratigraphic scale or Eemian on the European stratigraphic scale) was the warmest time during the Late Pleistocene in Siberia. Diatom diversity during the Holocene was slightly lower than MIS 5. Diatom diversity declined to its lowest point during glacial intervals with diversity minima corresponding to solar insolation minima related to the 23,000 years precession cycles (Fig. 3). It is probable that decreases in planktonic diatom abundance and diversity are linked to decreases in solar insolation and climate deterioration in the North Hemisphere.

The control of planktonic diatom diversity by climate cycles at relatively short time scales of several thousand years is probably an important mechanism of diatom evolution in the unstable environments of Lake Baikal. Oscillations in diversity reflect large-scale responses of the lacustrine planktonic community to climatic-driven changes that probably affect all levels of the lake's biota. Similar large-scale responses to climate fluctuations

driven by orbital forcing have been found in the North Atlantic where benthic ostracod diversity fluctuated with glacial–interglacial cycles that affect changes in environments and food availability (Cronin and Raymo, 1997). Changes in food supply to the benthic communities of Lake Baikal due to glacial–interglacial photosynthetic productivity fluctuations may have also affected benthic species diversity in Baikal. Perhaps detailed studies of benthic diatoms and sponge spicules distribution in lake sediments may provide such information.

9. Ecological stress in Lake Hovsgol during the Last Glacial Maximum

Sedimentologically and micropaleontologically, the last glacial–interglacial sediments of Lake Hovsgol are similar to those of Lake Baikal. Hovsgol's LGM clay is almost barren of diatoms (Fig. 2). In our opinion several processes may be responsible for this: the lowering of surface water temperature, the formation of a nutrient-depleted turbid surface layer, and a change in water chemistry. During the LGM, mountain glaciers fed Lake Hovsgol with meltwater rich in fine glacial detritus forming the LGM clay. We think that as in Lake Baikal, low nutrient supply from the watershed, the low temperature of surface water and the low transparency of water and ice during glacial time eliminated photosynthesis of planktonic and benthic algae in Lake Hovsgol.

There is also evidence that the Lake Hovsgol water level was very low during the LGM (Sondoma and Losev, 1976; Kozlov et al., 1989; Prokopenko et al., 2003a,b). Seismic acoustic data show that the lake level was 200 m lower leaving Hovsgol with maximum water depths of only about 50–60 m (Fedotov et al., 2002). This lowering happened due to enhanced evaporation linked to increased aridity in inner Asia during the LGM (Velichko, 1984). Falling lake levels and decreasing water volume produced drastic changes in water chemistry that led to the accumulation of carbonates (calcite, dolomite and magnesium calcite) during LGM (Fig. 2). Together with low surface water temperature and transparency, these changes are believed to have led to the suppression of primary production in Lake Hovsgol, perhaps affecting other parts of the ecosystem as well.

According to glaciological and geomorphologic studies, the thickness of glaciers in the Hovsgol region exceeded 500 m (Grosswald and Kuhle, 1994). Glaciers surrounding Hovsgol excavated u-shape glacial valleys about 200–300 m deep (Sondoma and Losev, 1976; Gluchovskaia et al., 1987; Grosswald and Kuhle, 1994) indicating that the thickness of glacier tongues in the Hovsgol depression was close to or exceeded the lake depth. Several terminal moraines are described close to the present-day lake shore (Zolotarev and Kulakov, 1973, 1976; Kulakov, 1981; Gluchovskaia et al., 1987) suggesting that many glaciers came to Lake Hovsgol's shore and terminated in the lake during the LGM. The presence of IRD (sand lenses, gravel and pebbles) in glacial-lacustrine sediments supports this inference (Fedotov et al., 2000, 2001; Prokopenko et al., 2003a,b). The snow line during the LGM was at most 200 m above the lake level (1450 m according to Grosswald and Kuhle, 1994) or even below it (Belova and Kulakov, 1982) and indicates that glacier ice did not melt on the shores of the lake, but instead filled the lake with icebergs and probably seasonal ice that did not completely melt during the summer. All these conditions provided the background for an ecological catastrophe in Lake Hovsgol that may have been more intense than Baikal's due to the smaller size of Hovsgol's ecosystem, its shallower waters and stronger glacial conditions due to the lake's higher elevation.

The beginning of lake level rise occurred only with the Bølling–Allerød warming around 12 ¹⁴C ka (Prokopenko et al., 2003a,b). During this time diatoms first appeared in the lake (Fig. 2). At about 8.5 ¹⁴C ka, lake level almost reached present-day elevations and stabilized (Solotchina et al., 2003). At this time, water chemistry became similar to present-day, carbonates stopped accumulating, diatom algae repopulated the lake, and the lake's ecosystem recovered from stress related to glaciation. Our fossil record from Lake Hovsgol shows that 6–10 non-endemic planktonic diatom species were present in the recovered lake community with a strong dominance of one species, *Cyclotella ocellata* (Fig. 2), which is common in alpine and cold water lakes. The diversity of the Lake Hovsgol diatom planktonic population during Holocene was very low in comparison with diatom diversity in Lake Baikal.

10. Discussion

Lake Baikal lacustrine environments were unstable during the Late Pleistocene and glacial conditions replaced interglacials almost every 23–41 ka (Fig. 3). These changes produced catastrophic disturbances in the lake's ecosystem. We propose that similar changes happened with the Lake Hovsgol ecosystem. During each disturbance, planktonic diatom diversity decline sharply, returning to high levels in the subsequent interglacial (Fig. 3). Our diatom diversity data do not support the stability–time concept and better fit the theory of spatial heterogeneity in which complex and diverse flora and fauna develop in more heterogeneous and complex environments.

The long and frequent catastrophic disturbances of the Baikal and Hovsgol ecosystems appear to have affected the numbers of endemic species in both lakes. However, the variety of plants and animals and the high level of Baikal's endemism suggest that glacial catastrophes probably did not affect species diversity in Lake Baikal. The data show that after each glacial catastrophe the diversity of planktonic diatoms reached levels almost equal to the previous interglacial levels.

The presence of numerous and highly specialized endemic families in Lake Baikal probably provides evidence of their long evolutionary history. How is this possible after numerous and fairly periodic catastrophic disturbances? Did all of these endemic species survive during glacial disasters or did they evolve after the Last Glacial?

Recent data from Lake Victoria suggest the possibility of very rapid speciation of cichlid fish (Johnson et al., 1996). More than 300 endemic species of cichlid fish evolved in the lake just during last 12,000 years after several thousand years of desiccation. According to the authors, this rapid evolution and rich diversity of Lake Victoria cichlids are associated with lacustrine instability produced by climatic fluctuation (Johnson et al., 1996). Is it possible that Lake Baikal endemic species also developed during the Holocene?

New molecular-biological and stratigraphic data suggest that many of Lake Baikal species originated in the Early Pleistocene, Pliocene or even Miocene (Ogarkov et al., 1997; Zubakov et al., 1997; Sherbakov et al., 1998; Kamal'tynov, 1999; Khursevich et al.,

2000, 2001a,b). These data do not support the idea of rapid evolution of Baikal endemics, and we must find a different mechanism to explain the high level of Baikal endemism. Diatom records show that although many endemic diatom species disappeared from the open, deep part of Lake Baikal during glacial periods (Khursevich et al., 2001a,b), these species probably survived during glacials by occupying refugia within Lake Baikal (Kamal'tynov, 1999; Karabanov et al., 2000c, 2001). Potential refugia are relatively shallow areas such as lagoons, big straits and gulfs such as the Maloe More, Chuvurkuy Bay, and the slopes of Selenga River delta. In these areas, water may have been warmer and nutrients more available due to riverine discharge and recirculation from the shallow bottom. A few available diatom records from these areas support the idea about refugia. Data from core st.287k2 (Bradbury et al., 1994) and core st.3PC (our unpublished data) from Moloe More strait show that during the LGM planktonic diatoms accumulated in the sediments. The distribution of diatoms in glacial sediments of these cores demonstrates that planktonic diatoms did not disappear from the water of Maloe More strait and were present in small numbers during glacial intervals. In our opinion, the Lake Baikal biota became displaced from the open and deep part of lake to marginal areas that were able to provide the resource requirements and physical–chemical conditions necessary for diatom survival. These refugia could have been a source of species that invaded and repopulated the open areas of Lake Baikal after intense glacial catastrophic disturbance.

Similar replacements are recorded in the North Atlantic with ostracods during Pliocene glacial periods. During each glacial, benthic ostracods shifted from the abyssal zone to bathyal zone of the ocean margins where environmental conditions and food resources became more favorable (Cronin and Raymo, 1997). After the glacials, ostracods again repopulated the abyssal zone.

The Lake Hovsgol ecosystem behaved differently. The smaller size and shallower depth of Lake Hovsgol and stronger glacial conditions during the LGM probably did not provide suitable refugia for most groups of plants and animals. From this, we hypothesize that the intensity of the glacial stress in the Lake Hovsgol led directly to the lower level of endemism there in relation to Lake Baikal. We further hypothe-

size that Hovsgol's ecosystem is therefore very young, perhaps no older than the termination of the last glaciation, approximately 10,000 years ago, as indicated by the beginning of biogenic silica and diatom accumulation in the lake sediments (Fig. 2). In this scenario, changes in water chemistry, low temperature and transparency of water and ice, and the accumulation of ice and icebergs in the lake during the LGM completely depressed Hovsgol's ecosystem. During the glacial–interglacial transition, when ice melted, and lake levels rose, species from surrounding areas invaded the lake and reestablished the ecosystem of the lake where probably some new endemic forms evolved. The limited numbers of endemic species in Lake Hovsgol supports this speculation. These endemic species may have either survived in small glacial lakes or hot springs or invaded Hovsgol from surrounding small lakes. Most elements of the fauna and flora of Lake Hovsgol are not endemic and are common in the region. The history of Hovsgol's ecosystem evolution is common for many large lakes of the Northern Hemisphere from areas that were glaciated during the LGM.

At the present time, longer sedimentary records are not available from Lake Hovsgol but both lakes occur in one mountain system and the Quaternary geology of their basins is comparable. In view of this, we think that ecological catastrophes occurred in the Lake Hovsgol throughout the Pleistocene similar to those of Lake Baikal. Moreover, new seismic reflection data show that during the Middle Pleistocene Lake Hovsgol became completely desiccated (Pouls et al., 2003). These data provide additional support for our hypothesis concerning the complete destruction of the lake's ecosystem during glacials and about the role of glacial catastrophes in producing the low level of endemism in Lake Hovsgol.

11. Conclusions

Climatic and environmental instability resulted in ecological catastrophes in lakes Baikal and Hovsgol that became one mechanism that drove species evolution in these systems. Cores from lakes Baikal and Hovsgol reveal two different cases of lacustrine ecosystem response to environmental changes and catastrophic ecological disturbances. After the collapse of

Hovsgol's ecosystem, a new ecosystem became established during the Holocene with limited numbers of species and low level of endemism. Lake Baikal contains a more ancient and diverse population of endemic aquatic species that survived in refugia during long and periodically repeated glacial catastrophes. Probably the significant diversity of Lake Baikal's ecosystem and high level of endemism are the result of evolution in unstable environments.

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References

- Bazarov, D.-D.B., 1986. Pribaikalie and Western Zabaikalie in Cenozoic Nauka Press, Novosibirsk. 179 pp. [in Russian].
- BDP-Members, D.-D.B., 1997a. Continuous paleoclimate record of last 5 MA from Lake Baikal, Siberia. EOS American Geophysical Union. Transactions 78, 597–604.
- BDP-Members, 1997b. Preliminary results of the first scientific drilling on Lake Baikal, Buguldeyka site, southeastern Siberia. Quaternary International 37, 3–17.
- BDP-Members, 1998. A continuous record of climate changes for the last five million years from the bottom sediment of Lake Baikal. Russian Geology and Geophysics 39 (2), 135–154 (in Russian).
- BDP Members (The Baikal Drilling Project Group), 2000. The Late Cenozoic paleoclimate record from Lake Baikal (results of 600

- m deep drilling core investigations). *Russian Geology and Geophysics* 41 (1), 3–32 (in Russian).
- Belova, V.A., Kulakov, V.S., 1982. The history of evolution of Lake Khubsugul basin. Late Cenozoic History of Lakes of USSR. Nauka Press, Novosibirsk, pp. 80–88 (in Russian).
- Bezrukova, E.V., Bogdanov, Y.A., Williams, D.F., Granina, L.Z., Grachev, M.A., Ignatova, N.V., Karabanov, E.B., Kuptzov, V.M., Kurylev, A.B., Letunova, P.P., Likhoshway, E.V., Chernyaeva, G.P., Shimaraeva, M.K., Yakushin, A.O., 1991. Deep changes of North Baikal ecosystem in Holocene. *Doklady Akademii Nauk SSSR* 321, 1032–1037 (in Russian).
- Bondarenko, N.A., Gusel'nikova, N.E., 1989. Production of phytoplankton of Southern Baikal. *Izvestia Cibirskogo Otdelenia AN USSR. Biological Sciences* 1, 77–81 (in Russian).
- Bradbury, J.P., Bezrukova, E.V., Chernyaeva, G., Colman, S.M., Khursevich, G., King, J., Likhoshway, Y., 1994. A synthesis of post-glacial diatom records from Lake Baikal. *Journal of Paleolimnology* 10, 231–251.
- Colman, S.M., Jones, G.A., Rubin, M., King, J.W., Peck, J.A., Orem, W.H., 1996. AMS radiocarbon analyses from Lake Baikal, Siberia: challenges of dating sediments from a large, oligotrophic lake. *Quaternary Science Review* 15, 669–684.
- Cronin, T.M., Raymo, M.E., 1997. Orbital forcing of deep-sea benthic species diversity. *Nature* 385, 624–627.
- Fedotov, A.P., Bezrukova, E.V., Chebykin, E.P., Khlystov, O.M., Krapivina, S.M., Levina, O.V., Mazepova, G.P., Mizandrontsev, I.B., Semenov, A.R., Vorobyova, S.S., Zheleznyakova, T.O., Grachev, M.A., 2000. Potential value of bottom sediments of Lake Khuvsgul (Mongolia) for paleoclimate reconstructions. *Berliner Geowissenschaftliche Abhandlungen* A205, 107–112.
- Fedotov, A.P., Bezrukova, E.V., Vorobeva, C.C., et al., 2001. The sediments of Lake Hubsugul (Mongolia) as an archive of paleoclimate of Holocene and Late Pleistocene. *Russian Geology and Geophysics* 42 (1–2), 135–142 (in Russian).
- Fedotov, A.P., De Batist, M., Shapron, E., De Reiker, K., Paule, T., Grachev, M.A., 2002. Seismic survey of sediments of Lake Hovsgol. *Doklady of the Russian Academy of Sciences* 382 (2), 261–263 (in Russian).
- Gluchovskaia, N.B., Devatkin, E.B., Kleiner, U.M., Konopleva, B.I., Korzhuev, S.S., Korina, N.A., Kurushin, R.A., Levitov, M.E., Murzaeva, V.E., Nikolaeva, T.V., Surnev, I.P., Timofeev, D.A., Hilko, S.D., Shuvalov, V.F., 1987. Geomorphological map of People Republic of Mongolia. Florensov N.A., Korzhuev, S.S. (Eds.), GUGK Press, Moscow.
- Goulden, C.E., Tumurtogoo, O., Karabanov, E., 2004. The geological history and geography of Lake Hovsgol, Mongolia. In: Goilden, G.E., Sitnikova, T., Gelhaus, T., Boldgiv, B. (Eds.), *The Geology, Biodiversity and Ecology of Lake Hovsgol (Mongolia)*. Kluwer Academic Publishing, Netherlands in press.
- Grachev, M.A., Likhoshwai, E.V., Vorobyova, S.S., Khlystov, O.M., Bezrukova, E.V., Veinberg, E.V., Goldberg, E.L., Granina, L.Z., Kornakova, E.G., Lazo, F.I., Levina, O.V., Letunova, P.P., Otinov, P.V., Pirog, V.V., Fedotov, A.P., Iaskevich, S.A., Bobrov, V.A., Sukhorukov, F.V., Rezchikov, V.I., Fedorin, M.A., Zolotarev, K.V., Kravchinsky, V.A., 1997. Signals of the paleoclimates of upper Pleistocene in the sediments of Lake Baikal. *Russian Geology and Geophysics* 38 (5), 957–980.
- Granin, N.G., Jewson, D.H., Gnatovsky, R.Yu., Levin, L.A., Zhdanov, L.A., Gorbunova, L.A., Tshehanovsky, V.V., Doroschenko, L.M., Mogilev, N.Yu., 2000. Turbulent mixing under ice and the growth of diatoms in Lake Baikal. *Verhandlungen International Verein Limnology* 27, 2812–2814.
- Grosswald, M.G., Kuhle, M., 1994. Impact of glaciations on Lake Baikal. *International Project on Paleolimnology and Late Cenozoic Climate. IPPCCE Newsletter*, vol. 8. Universitätsverlag Wagner, Innsbruck, pp. 48–60.
- Ishivatary, R., Uzaki, M., Yamada, K., Ogura, K., 1992. Organic matter records of environmental changes in Lake Baikal sediments: 1. Carbon isotopes, organic carbon and nitrogen. *International Project on Paleolimnology and Late Cenozoic Climate. IPPCCE Newsletter*, vol. 6. Universitätsverlag Wagner, Innsbruck, pp. 80–88.
- Johnson, T.C., Scholz, C.A., Talbot, M.R., Kelts, K., Ricketts, R.D., Ngobi, G., Beuning, K., Ssemmanda, I., McGill, J.W., 1996. Late Pleistocene desiccation of Lake Victoria and rapid evolution of cichlid fishes. *Nature* 273, 1091–1093.
- Kadota, S., 1992. Animal microfossils found in 323-PC1 core of Lake Baikal. *International Project on Paleolimnology and Late Cenozoic Climate. IPPCCE Newsletter*, vol. 6. Universitätsverlag Wagner, Innsbruck, pp. 98–103.
- Kamaltynov, R.M., 1999. On the evolution of Lake Baikal amphipods. *Crustaceana* 72 (8), 921–931.
- Karabanov, E.B., 1999. Geological structure of Lake Baikal sedimentary strata and reconstruction of climatic changes of Central Asia during Late Cenozoic. Dr. Sc thesis. Published by Institute of Lithosphere of Academy of Sciences of Russia, Moscow. 1999, 72 pp. (in Russian).
- Karabanov, E.B., Prokopenko, A.A., Williams, D.F., Colman, S.M., 1998. Evidence from Lake Baikal for Siberian glaciation during oxygen-isotope substage 5d. *Quaternary Research* 50, 46–55.
- Karabanov, E.B., Kuzmin, M.I., Prokopenko, A.A., Williams, D.F., Khursevich, G.K., Bezrukova, E.V., Kerber, E.V., Gvozdkov, A.N., Geletiy, V.F., Weil, D., Schwab, M., 2000a. Glaciations of central Asia in the late Cenozoic according to the sedimentary record from Lake Baikal. In: Minoura, K. (Ed.), *Lake Baikal: A Mirror in Time and Space for Understanding Global Change Processes*. Elsevier, Amsterdam, pp. 71–84.
- Karabanov, E., Kuzmin, M.I., Williams, D.F., Khursevich, G.K., Bezrukova, E.V., Kerber, E.V., Gvozdkov, A.N., Gelety, V.F., Weil, D., Schwab, M., 2000b. The global cooling of central Asia according to Lake Baikal sedimentary record. *Doklady of Academy of Sciences of Russia* 370 (1), 61–66 (in Russian).
- Karabanov, E.B., Sideleva, V.G., Williams, D.F., Khursevich, G.K., Kuzmin, M.I., Prokopenko, A.A., Afonina, T.E., Gvozdkov, A.N., Gelety, V.F., 2000c. Glacial ecological stresses as an evolutionary mechanism of Lake Baikal species. The Third Vereshagin Baikal conference. August, 22–27, 2000. *Limnological Institute Press, Irkutsk*, pp. 104–105. Abstracts.
- Karabanov, E.B., Williams, D.F., Sideleva, V.G., Prokopenko, A.A., Khursevich, G.K., Kuzmin, M.I., Gvozdkov, A.N., Soshina, N.M., Afonina, T.E., 2001. Glacial ecological catastrophes of Lake Baikal (Siberia) and Lake Hovsgol (Mongolia) during the Pleistocene and Late Pliocene. In: Jacoby, G.J., Pederson, N. (Eds.), *Proceedings of the Conference on Mongolian Paleocli-*

- matology and Environmental Research. Lamont-Doherty Earth Observatory, Palisades, NY, pp. 21–32.
- Khursevich, G.K., Karabanov, E.B., Williams, D.F., Kuzmin, M.I., Prokopenko, A.A., 2000. Evolution of fresh water centric diatoms within the Baikal rift zone during the late Cenozoic. In: Minoura, K. (Ed.), *Lake Baikal: A Mirror in Time and Space for Understanding Global Change Processes*. Elsevier, Amsterdam, pp. 146–154.
- Khursevich, G.K., Karabanov, E.B., Prokopenko, A.A., Williams, D.F., Kuzmin, M.I., Fedenya, S.A., Gvozdkov, A.N., Kerber, E.V., 2001a. Detailed diatom biostratigraphy of Baikal sediment during the Brunhes Chron and climatic factors of species formation. *Russian Geology and Geophysics* 42 (1–2), 108–129 (in Russian).
- Khursevich, G.K., Karabanov, E.B., Prokopenko, A.A., Williams, D.F., Kuzmin, M.I., Fedenya, S.A., Gvozdkov, A.N., Kerber, E.V., 2001b. Insolation regime in Siberia as a major factor controlling diatom production in Lake Baikal during the past 800,000 years. *Quaternary International* 80–81, 47–58.
- Kozhova, O.M., Izmet'eva, L.R. (Eds.), 1998. *Lake Baikal, Evolution and Biodiversity*. Backhuys, Leiden 447 pp.
- Kozhova, O.M., Izmet'eva, L.R., Erbaeva, E.A., 1994. A review of the hydrobiology of Lake Khusugul (Mongolia). *Hydrobiologia* 291, 11–19.
- Kozhova, O.M., Erbaeva, E.A., Safronov, G.P., 2000. The benthic Invertebrates of Lake Khubsugul, Mongolia. In: Rossiter, A., Kawanabe, H. (Eds.), *Ancient Lakes: Biodiversity, Ecology and Evolution*. Advances in Ecological Research, vol. 31. Academic Press, San Diego, pp. 97–124.
- Kozlov, U.P., Vorobei, V.V., Batsuur, D. (Eds.), 1989. *Atlas of Lake Hovsgol*. GUGK Press, Moscow, p. 118 (in Russian).
- Kulakov, V.S., 1981. Ancient and modern glaciation of North Mongolia (Lake Khubsugul region). *Environments and Resources of Lake Khubsugul Region of Mongolia*. Irkutsk State University, Irkutsk, pp. 10–19 (in Russian).
- Kuzmin, M.I., Karabanov, E.B., Prokopenko, A.A., Williams, D.F., Gvozdkov, A.N., Geletiy, V.F., 1999. Climatic events in Siberia during upper brunhes according to the Lake Baikal sedimentary record. *Berliner Geowissenschaftliche Abhandlungen*, Berlin E30, 315–323.
- Laskar, J., Joutel, F., Boudin, F., 1993. Orbital, precessional and insolation quantities for the Earth from –20 Myr to +10 Myr. *Astronomy and Astrophysics* 270, 522–533.
- Logatchev, N.A., Antoshenko-Olenev, I.V., Bazarov, D.-D.B., 1974. In: Florensov, N.A. (Ed.), *The Uplands of the West Baikal and Trans-Baikal Regions*. Nauka Press, Moscow. 360 pp. (in Russian).
- Lut, B.F., 1964. Geomorphology of Lake Baikal bottom. *Geomorphology of Lake Baikal Bottom and its Shores*. Nauka Press, Novosibirsk, pp. 5–123 (in Russian).
- Mats, V.D., 1993. The structure and development of the Baikal rift depression. *Earth Science Reviews* 34, 81–118.
- Mortlock, R.A., Froelich, P.N., 1989. A simple method for the rapid determination of biogenic opal in pelagic marine sediments. *Deep-Sea Research* 36 (9), 1415–1426.
- Ogarkov, O.B., Kamal'tynov, R.M., Belikov, S.I., Sherbakov, D.Yu., 1997. Phylogenetic relatedness of the Baikal Lake endemic amphipods (Crustacea, Amphipoda) deduced from partial nucleotide sequences of the cytochrome oxidase subunit III genes. *Molecular Biology* 31 (1), 24–29.
- PALE, 1993. *Research Protocols for PALE*. Paleoclimates of Arctic Lakes and Estuaries. PALE Steering Committee, PAGES Workshop Report, Series 94-1, Bern, 49–53.
- Popovskaya, G.I., 1987. The phytoplankton of deepest lake of world. *Proceeding of Zoological Institute of Academy of Sciences of USSR*, vol. 172. Academy of Science Press, Leningrad, pp. 107–116 (in Russian).
- Pouls, T., De Batist, M., Fedotov, A., Grachev, M., 2003. Seismic-stratigraphic indication for multiple desiccation events in Lake Khubsugul, Mongolia. *Third International Limnogeology Congress*. Abstract volume. Tucson, Arizona 29 March–2 April, 2003. University of Arizona, Tucson, p. 218.
- Prokopenko, A.A., Karabanov, E.B., Williams, D.F., Kuzmine, M.I., Shackleton, N.J., Crowhurst, S.J., Peck, J.A., Gvozdkov, A.N., King, J.W., 2001a. Biogenic silica record of the Lake Baikal response to climatic forcing during the Brunhes. *Quaternary Research* 55, 123–132.
- Prokopenko, A.A., Karabanov, E.B., Williams, D.F., Kuzmin, M.I., Khursevich, G.K., Gvozdkov, A.N., 2001b. The detailed record of climatic events during the past 75,000 yrs BP from the Lake Baikal drilling core BDP93-2. *Quaternary International* 80–81, 59–68.
- Prokopenko, A.A., Kuzmin, M.I., Kalmuchkov, G.V., Geletiy, V.F., Williams, D.F., Solotchin, P.A., Gvozdkov, A.N., 2003a. Glacial–interglacial changes in the sedimentary record of Lake Hovsgol, Mongolia: the initial results of the summer 2001 cruise. *Third International Limnogeology Congress*. Abstract volume. Tucson, Arizona 29 March–2 April, 2003. University of Arizona, Tucson, p. 222.
- Prokopenko, A.A., Kuzmin, M.I., Kalmuchkov, G.V., Geletiy, V.F., Gvozdkov, A.N., Solotchin, P.A., 2003b. Changes in the composition of bottom sediments of Lake Hovsgol as an indication of climatic change in the Baikal region 5–14 Ka BP. *Doklady Akademii Nauk, Proceedings of Academy of Sciences of Russia* 390 (1), 109–112 (in Russian).
- Sanders, H.L., 1968. Marine benthic diversity: a comparative study. *The American Naturalist* 102 (925), 243–282.
- Shackleton, N.J., Berger, A., Peltier, W.R., 1990. An alternative astronomical calibration of the lower Pleistocene timescale based on ODP site 677. *Transition of Royal Society, Edinburgh*. *Earth Sciences* 81, 251–261.
- Sherbakov, D.Yu., Kamal'tynov, R.M., Ogarkov, O.B., Verheyen, E., 1998. Patterns of evolutionary change in Baikalian gamma-riids inferred from DNA sequences (Crustacea Amphipoda). *Molecular Phylogenetics and Evolution* 10 (2), 160–167.
- Solotchina, E.P., Prokopenko, A.A., Vasilevsky, A.N., Gavshin, V.M., Kuzmin, M.I., Williams, D.F., 2002. Simulation of XRD patterns as an optional technique for studying glacial and interglacial clay mineral associations in bottom sediments of Lake Baikal. *Clay Minerals* 37, 105–119.
- Solotchina, E.P., Kuzmin, M.I., Stolpovskaya, V.N., Karabanov, E.B., Prokopenko, A.A., Tkachenko, L.L., 2003. Mineralogical and crystallochemical indicators of environmental and climatic changes in Holocene–Pleistocene sediments of Lake Hovsgol

- (Mongolia). *Doklady of the Academy of Sciences of Russia* 391 (N4), 527–531 (in Russian).
- Sondoma, N., Losev, N.F., 1976. *Natural Conditions and Reassures of Pre-Hubsugulya in Mongolia* Nedra Press, Moscow. 355 pp. (in Russian).
- Timoshkin, O.A., 1997. Biodiversity of Baikal fauna: state-of-the-art (Preliminary analysis). In: Wada, E., Timoshkin, O., Fujita, N., Tanida, K. (Eds.), *New Scope on the Boreal Ecosystems in East Siberia*. Proc. Intern. Symp., Kyoto, Nov. 23–25 1994 (DIWPA Ser. No.2). Russian Academy of Sciences, Siberian Branch, Novosibirsk, pp. 35–76.
- Timoshkin, O.A., 1999. Biology of Lake Baikal: “White Spots” and progress in research. *Berliner Geowissenschaftliche Abhandlungen* E30, 333–348.
- Velichko, A.A., 1984. Pleistocene spatial paleoclimatic reconstruction. In: Velichko, A.A., Wright, H.E., Barnosky, C.W. (Eds.), *Late Quaternary Environments of the Soviet Union*. University of Minnesota Press, Minneapolis, pp. 261–286.
- Wetzel, R.G., 1995. Death, detritus, and energy flow in aquatic ecosystems. *Freshwater Biology* 33, 83–89.
- Wetzel, R.G., 2001. *Limnology: Lake and River Ecosystems*, Third edition. Academic Press, San Diego. 1006 pp.
- Williams, D.F., Peck, J., Karabanov, E.B., et al., 1997. Lake Baikal record of continental climate response to orbital insolation during the past 5 million years. *Science* 278, 1114–1117.
- Zolotarev, A.G., Kulakov, V.S., 1973. The scheme of morphostructure of Lake Hovsgol basin. *Environments and Resources of Lake Hovsgol Region*, vol. 2. Irkutsk State University, Irkutsk, pp. 10–19 (in Russian).
- Zolotarev, A.G., Kulakov, V.S., 1976. Neotectonics and morphostructures. *Environments and Resources of Lake Hovsgol Region of Mongolia*. Nedra Press, Moscow, pp. 85–87 (in Russian).
- Zubakov, D.Y., Sherbakov, D.Y., Sitnikova, T.Y., 1997. Phylogeny of the endemic Baicaliidae mollusks inferred from partial nucleotide sequences of the CO1 mitochondrial gene. *Molecular Biology* 31, 935–939.