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Benthic oxygen flux in the highly productive subarctic Lake Myvatn, Iceland: *In situ* benthic flux chamber study

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Abstract

In situ paired light and dark-stirred benthic flux chambers were used to estimate dissolved oxygen flux across the sediment–water interface in Lake Mývatn, Iceland. Three sampling stations were selected, each station reflecting a specific sedimentary environment, benthic communities, and water depth. During this study the phytoplankton density was low. Spatial and seasonal variations of bottom DO concentration and DO flux have been observed during this study. The oxygen consumption rate at all study sites had a mean of -89 (± 44) mmol m^{-2} d^{-1} while the oxygen production rate due to benthic algae had a mean of 131 (± 103) mmol m^{-2} d^{-1}. There was a strong correlation ($r = 0.91$) between oxygen consumption rate and temperature. This was presumably because of the temperature influence on rates of microbial and macrobenthic processes. The mean benthic primary production rate at all study sites was 1216 (± 957) mg C m^{-2} d^{-1} between June 2000 and February 2001. Annual gross benthic primary production was estimated from the gross mean daily benthic DO production (P) and Redfield's C:O_2 ratio of 106:138 to be 420 g C m^{-2} y^{-1} at station HO, 250 g C m^{-2} y^{-1} at B2 and 340 g C m^{-2} y^{-1} at station 95. Thus, the mean gross benthic primary production was estimated as 1151 mg C m^{-2} d^{-1} at station HO, 685 mg C m^{-2} d^{-1} at station B2, and 932 mg C m^{-2} d^{-1} at station 95.

Introduction

The flux of dissolved constituents across the sediment-water interface is important in controlling the composition of oceans and lakes (Stumm and Morgan 1996). Sediments in natural water bodies act as a sink/source for many nutrients and trace elements. The cycling of nutrients and metals is controlled to a significant extent by processes in sediments (DiToro 2001). The importance of internal loading research has grown since farming and urbanization have an increasing effect on key nutrient concentrations, and atmospheric pollutants and industry influence the concentration of trace elements (Moss 2000). Research on solute exchanges across the sediment-water interface in natural water bodies has been carried out for decades, worldwide, in oceanic environments, lakes and rivers (e.g., Boudreau and Jørgensen 2001; Jahnke et al. 2000; Song and Müller 1999; Hulth et al. 1999; Kuawabara et al. 1999).

The method of *in situ* benthic flux chambers has been used for determination of fluxes of many chemical species in a number of oceanic and freshwater environments. *In situ* benthic flux chamber incubation has been valuable in determining the benthic flux of dissolved species in aerobic organic-rich environments. Flux calculations approached by the use of benthic flux chambers have the advantage of integrating fluxes over a large surface of sediments, thus minimizing variations due to small-scale sediment heterogeneity (Tessier et al. 1994). Also, the benthic flux chambers make a large sample possible, yielding oxy-

gen concentrations at the same time as flux of nutrients and other solutes across the sediment-water interface (Hulth 1995). But relative to other flux methods, quantifying benthic flux is instrument and labour intensive (Kuawabara et al. 1999).

Flux of some solutes across the sediment-water interface is known to be redox-driven (Hamilton-Taylor and Davison 1995) and redox conditions in lakes are largely controlled by the processes of photosynthesis and bacterial decomposition of organic matter, as well as by the supply of oxygen by circulation or vertical mixing of the water (Drever 1997). Macrobenthos, through their burrowing, feeding, locomotive, respiratory and excremental activities, play an important role in mediating both physical and chemical processes near the sediment-water interface (Fisher 1982).

Lake Myvatn, in N-Iceland, has a long research history and the density changes observed in the biological community are not fully understood. The lake is shallow and highly productive, with a fine-grained sediment bottom (diatomaceous gyttja). The primary production in Lake Myvatn, as in many shallow lakes, is mostly through benthic diatoms and other littoral algae (Ólafsson 1979b; Wetzel 2001). According to mass balance calculations of dissolved P and N in Lake Myvatn and previous primary production measurements only about 20% of the P needed for the primary production is brought into the system by the groundwater inflow. The rest comes from cycling of nutrients within the lake (Jónasson 1979; Jónasson and Aðalsteinsson 1979; Ólafsson 1979b). As an attempt to quantify internal loading in Lake Myvatn *in situ* benthic flux chambers were used.

We present the results of dissolved oxygen (DO) flux measurements of *in situ* paired light/dark benthic flux chamber incubations. The results are interpreted in the context of benthic organic community, light flux and bottom water temperature. Then the dissolved oxygen flux results are used to estimate the gross annual benthic primary production (BPP) during a year of low phytoplankton density.

Study area and sampling sites

Lake Myvatn is at the flank of the active rift zone in the northeastern part of Iceland (Thorarinsson 1979) and is one of the most productive lakes in the Northern Hemisphere (Jónasson 1979). It is centred on 65°35′ N, 17°00′ W at 277 m above sea level (The

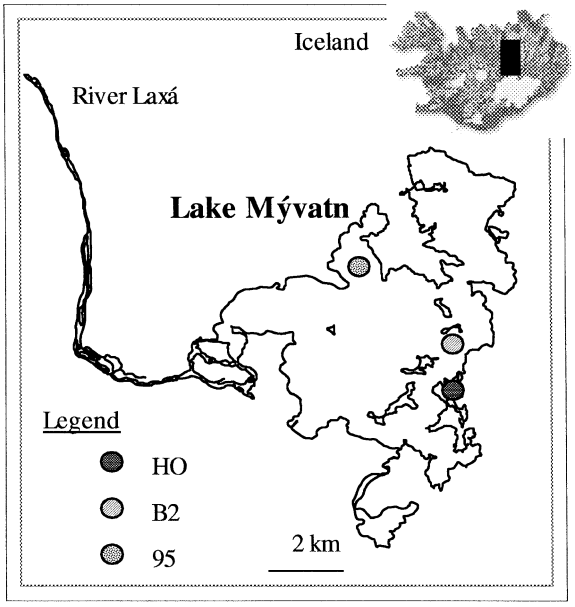

Figure 1. Lake Myvatn and the stations used for direct measurements of benthic solute flux.

Icelandic Geodetic Survey, 1996). Subsided basaltic lava and a lava dam form the lake basin, and lava also partially forms the bed of the River Laxá which drains Lake Myvatn and flows 55 km north to the ocean. Lake Myvatn is shallow with numerous islands and covers an area of 37.2 km^2. The smooth bottom is of fine-grained diatomaceous sediment (Ólafsson 1979a), several metres thick, and is partly covered by macrophytes in the North Basin and by *Cladophora* and *Aegagropila* sp. in the South Basin (Gardarsson and Einarsson 1991).

Three sampling stations were used (Figure 1) for direct measurements of solute flux across the sediment–water interface. Each station reflects a specific sedimentary environment, benthic community and water depth. All three stations are located in the South Basin: one station is in a bay north of Höfdi (HO), another in the Strandarbolir area (B2) in the eastern part of the South Basin, and the third one in the western part of the lake in Neslandavík Bay (95) (see Table 1 for GPS locations).

Station HO is fed by a cold spring (6.6 °C) and is at a water depth of 1.7 m. The bottom sediment in station HO is covered with *Tanytarsus gracilentus* larvae (chironomids) and benthic algae (mostly diatoms). The bay is sheltered from wind from all directions except from the west. The water at station HO is clear throughout the summer and free from ice in the winter.

Table 1. GPS locations (system WGS84) of the sampling stations used for direct measurement of solute flux across the sediment–water interface in Lake Myvatn.

Station	N	W
HO	65°34′49.74″	16°57′16.31″
B2	65°35′43.75″	16°57′15.71″
95	65°37′10.51″	17°00′49.28″

In the Strandarbolir area, as in station HO, the bottom sediment is covered with *Tanytarsus gracilentus* larvae and benthic diatoms but at 2.6 m water depth. In Neslandavík the sediment is covered by filamentous green algae, inhabited by *Chironomus islandicus* Kieffer larvae as well as diatoms. The water depth at station 95 is 2.2 m. In the summer phytoplankton and resuspended sediment sometimes affect the clarity of the water in Strandarbolir and Neslandavík and in the winter these areas are ice-covered.

Materials and methods

Principles of benthic flux chambers – Direct measurement of flux

The real value of direct benthic flux measurements is realized in areas where the pore water gradient method cannot be used because of enhanced fluxes due to factors such as bioturbation and irrigation (e.g., Aller 1980; Christensen et al. 1984; Tessier et al. 1994). With the use of benthic flux chambers analysis of changes in concentration with time is made in a known volume of water through known sediment surface area, yielding flux estimations of the solute of interest (Tessier et al. 1994). The flux of solute (J) across a sediment–water interface can be defined by the equation (Berner 1980)

$$J = \frac{\Delta M}{\Delta t\ A}$$

as changes in mass (ΔM) per unit time (Δt) per unit area (A).

In the present study each time a sample was taken from chambers used in Lake Myvatn, an equal volume of ambient water flowed into the chamber through a one-way valve. Due to this dilution a correction had to be made to obtain the correct concentration (Hulth 1995). The flux was therefore calculated by the equation

$$J = \frac{\sum \Delta M(t)}{\Delta t\ A}$$

where

$$\sum \Delta M(t) = [C(t) - C_c(t - \Delta t)]V$$

where $C(t)$ = solute concentration at time t. $C_c(t - \Delta t)$ = solute concentration in a previous sample corrected for any volume of water replaced during sampling, V = volume of water overlying the sediment in the chamber, A = surface area of sediment in the chamber, (e.g., Aller 1994; Aller et al. 1996). Thus, the benthic flux rate, normalized to the sediment surface area (mmol m^{-2} h^{-1}), was obtained by multiplying the slope of the regression line of the 'corrected concentration' time series with the measured incubated water volume divided by the sediment surface area in the flux chamber.

Methods of paired light/dark flux chambers were used in this study to be able to collect data sets for daytime fluxes at the same time as nighttime fluxes. The net flux (J_T) of solute in mmol m^{-2} d^{-1} was calculated by the equation

$$J_T = J_D L + J_N(24 - L)$$

where J_D is the measured flux in the transparent chamber (mmol m^{-2} h^{-1}), J_N is the measured flux in the dark chamber (mmol m^{-2} h^{-1}), and L represents the hours of daylight (see e.g., Moss 2000).

In the case of DO the net daily flux (J_T) can be split into two components: oxygen consumption (R) due to the respirating sediment community, organic decomposition by bacteria and chemical oxidation; and oxygen production (P) due to photosynthesising benthic algae. R is the same as the nighttime oxygen fluxes normalized to 24-h periods. P was extended to a d^{-1} basis assuming that the measured P rate applied to the period from sunrise to sunset and calculated as R subtracted from J_T. Gross BPP of each sampling day at each station was calculated from the oxygen production rate in context with Redfield's C:O_2 ratio of 106:138 represented in g C m^{-2} d^{-1}. Gross annual BPP (in g C m^{-2} y^{-1}) was then calculated from the estimation of gross mean daily BPP multiplied by 365 days.

Benthic flux chambers

Direct measurement of solute flux across the sediment-water interface in Lake Myvatn was made by using *in situ* stirred benthic flux chambers (from

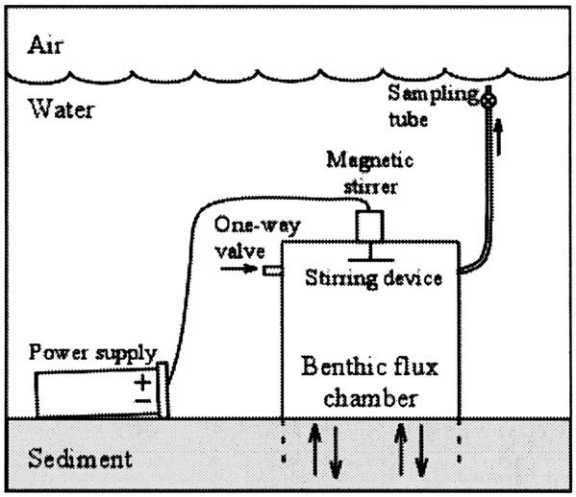

Figure 2. Benthic flux chamber and applied equipment used for direct measurement of solute flux across the sediment–water interface in Lake Myvatn.

KC-Denmark) of 3-mm-thick acrylic plates constructed with a rectangular shape in favour of turbulence of the stirred water. Calibration tests demonstrated that the transparent acrylic chamber transmitted about 84% of the light flux. Figure 2 illustrates schematically how the chambers were placed on the lake bottom. The two chambers were 300 × 300 mm wide and 480 mm high (exclusive motor housing). On top of each chamber there was a hole of 250 mm diameter for a stirring device. The hole was sealed by a 6-mm silicon sealing ring milled into the chamber's top and on top of the chambers there was a removable acrylic lid that held the motor housing. The stirring device was driven by a motor with a variable speed of rotation (mini-motor) in order to stimulate a current speed approximating that found in the proximity of the sediment and to get a homogenous water mass in the chambers. Neodymium magnets (12 pieces, 10 × 4 mm) transmitted power from the motor to the stirring device. A 12-volt rechargeable battery that can supply power for 3 days without being recharged drove the motors. A one-way valve was fastened to one side of each chamber for replacement water to flow in during sampling through a ca. 4-m-long plastic tubing that reached the water surface from the chambers. The equipment tolerated hydrostatic pressure down to a depth of 10 m.

A heavy weight frame technique was used to deploy the chambers from a boat. A Plexiglas frame filled with 15 kg of lead pellets was put on top of each chamber, and the chamber and the weight frame gently lowered down to the bottom. As the chamber sank a few cm into the sediment excessive water flowed through a tubing connected to the upper part of the chamber. The weight was pulled into the boat when the chamber had penetrated about 10 cm into the sediment. About 10 min after insertion the sampling tubing was closed at the upper end. The power supply was submerged along with the chambers during the experiment.

During the ice-cover period deployment was brought out through holes in the ice, each measuring an area of about 60 × 100 cm. Since the lake water was stratified, the dissolved oxygen concentration was much lower at the sediment-water interface than near the ice and extra pumping time was added to replace the surface water that filled the chambers with bottom water. First the chambers were lowered down to about 15 cm above the sediment–water interface, and then about 30 litres of water were pumped through the tubing to replace the initial oxygen rich water with bottom water of low oxygen concentration. This procedure took about half an hour and one test of oxygen concentration measurement was made during the water replacement time. The hole in the 50-cm-thick ice was left without a cover during the time of incubation.

The depth down to each of the four top corners of the chambers was measured, as well as the depth of the water column, in order to be able to calculate the volume of the incubated water. The incubated volume/sediment surface area ratio varied from 20 to 40 cm depending on penetration depth and possible slight tilting of the chambers. The chambers remained on the lake bottom during the daylight period and samples were taken from the chambers three to five times a day depending on the length of the daylight period.

Sampling and analytical methods

Samples of the ambient water were, in most cases, collected before deployment of the chambers and used as a reference for replacement water that was allowed to flow into the chambers during sampling. Long tubing with an inert plastic coated weight was lowered down to the sediment bottom. With a battery-driven peristaltic pump samples were pumped up from 10 to 15 cm above the sediment after thorough flushing of the tubing.

During the time of incubation sampling took place every 2 to 3 h for analysis of oxygen, pH, alkalinity, dissolved nutrients (orthophosphate [PO_4^{3-}], total phosphorus [TP], ammonium [NH_4^+], nitrate [NO_3^-],

nitrite [NO_2^-], total nitrogen [TN], and silica [SiO_2]), dissolved major and trace elements through ca. 4-m-long tubing (with a radius of 3 mm). The tubing was connected to a battery-driven peristaltic pump and during each sampling a total of 1 to 1.3 litres were pumped out of the chamber. The same amount of ambient water was allowed to enter the chamber in replacement through the one-way valve.

The actual sampling began after flushing of the tubing. Samples were collected in this order: oxygen, alkalinity, pH, nutrients and finally samples for major and trace element analyses. An oxygen glass bottle was flushed well with unfiltered water and the collected water preserved immediately with Winkler reagents. The pH and alkalinity bottle was also flushed well with unfiltered water and the bottle quickly sealed off after sampling. Samples for nutrients and major and trace elements were filtered through a 0.2 μm Cellulose Acetate filter with a diameter of 47 mm in a polyethylene disc filter holder. The first 10 to 40 ml of water entering the filter was used to wash the filter holder before actual sampling began. Nutrient samples were collected in acid-washed 20-ml polyethylene bottles in this order: silica, nitrate plus nitrite, total P and total N, ammonium and phosphate. The orthophosphate samples were acidified with 1.2 M HCl down to ca. pH 2, and ammonium samples were acidified with 0.12 M HCl down to ca. 4 pH. All nutrient samples, except silica samples, were put into a freezer after sampling. Samples for major and trace element studies were collected in 100-ml acid-washed polyethylene bottles and acidified with 1 ml of concentrated nitric acid (Suprapure® HNO_3).

On every sampling occasion, measurement of air and bottom water temperature (°C) at the sampling site was carried out with a Digi-Sense thermometer model no. 8525-00 as well as measurement of light flux in units μmol m^{-2} s^{-1} with a data logger (from LI-COR, model LI-1000, serial no. LDL-1169). Temperature and sometimes oxygen profiles of the lake water were measured to evaluate how well the water was mixed.

Oxygen, pH, alkalinity and some of the silica samples were analysed in the laboratory a few hours after sampling. Concentrations of dissolved oxygen were determined by standard Winkler titration (Grasshoff, 1983) and pH was determined using glass electrodes relative to pH buffers (Jeffrey et al., 1989). The endpoint of the alkalinity titration was determined by differentiation of the amount of HCl added to the sample vs. the pH, and total dissolved inorganic carbon (DIC) was calculated from the pH, temperature, alkalinity, and dissolved constituents using the PHREEQC program (Parkhaus & Appelo, 2001). The nutrient samples were analysed at the Science Institute, University of Iceland. All nutrient samples, except silica samples, were kept frozen until analysed. Determination of nutrient concentrations were performed in an auto-analyser (colorimetry) (Skoog et al., 1990; Jeffrey et al., 1989) and of dissolved silica in a spectrophotometer (Jeffrey et al., 1989).

Collection and treatment of sediment cores

Before the chambers were retrieved, 3 sediment cores with a 5-cm inner diameter were taken with a Kajak corer (a product of KC-Denmark) and the topmost 5 cm of the sediment put in a plastic container. The sediment samples were rinsed in a 125-μm filter and what was left in the filter put on a tray with some extra water. The chironomid larvae were counted and identified and *Cladophora* were dried at 40 °C.

Results

Research of benthic flux was carried out during three seasons at three sampling stations in the South Basin of Lake Myvatn (Figure 1). The results presented here refer to the lake bottom DO concentration and the benthic DO flux. As temperature, light flux and benthic community affect the DO concentration these data are also interpreted here.

DO conditions

Results of DO changes in incubated water for the four *in situ* benthic flux chamber deployments from the three stations are displayed in Figure 3. In all stations oxygen concentration increased in the transparent chamber, but was reduced in the dark chamber, representing oxygen production due to photosynthesis in the transparent chamber from June to October. Because of heavy wind and ice melting in station HO and DO stratification in station 95 the February sampling had some difficulties and thus gives misleading information. Further, the DO changes in the dark chamber in station HO on the 24th of July, imply a deployment failure.

Station HO has a rather stable oxygen supply from cold springs. The bottom DO concentration did reach 83% of oxygen saturation in June and did not exceed that value in later samplings at this station. The lowest oxygen saturation was 71%. The DO at B2, on the

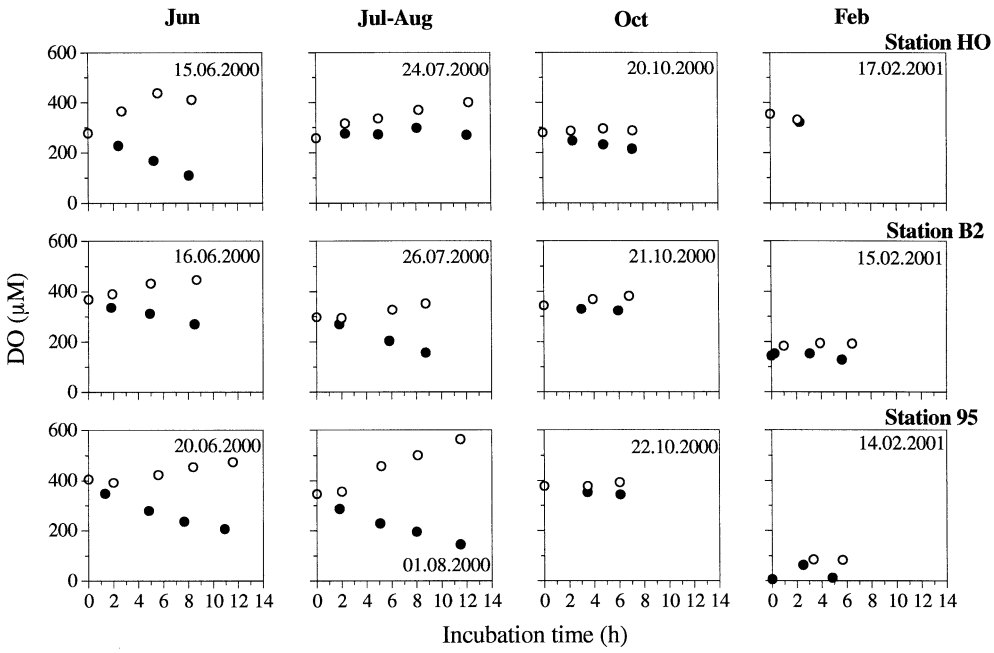

Figure 3. Dissolved oxygen (DO) concentration changes over time period of benthic flux chamber incubation in three sampling stations in Lake Myvatn in 2000–2001. The initial DO concentration (at time 0) on each of the graphs is the reference sample collected from the bottom water prior to chamber incubation. Open circles represent DO concentrations in the transparent chamber and the filled circles DO concentrations in the dark chamber.

other hand, reached 100% oxygen saturation during June and declined until autumn. In February, under 40-cm-thick ice cover, the oxygen saturation of the bottom water at B2 was 35%. The oxygen concentration at station 95 reached 114% of oxygen saturation in June but, as happened at the two other stations, the bottom oxygen saturation decreased from mid-June to the beginning of August. In February, under 50-cm-thick ice cover the bottom oxygen concentration was 0 to 10% depending on the time of sampling and there was a faint smell of H_2S during one sampling at station 95.

Benthic DO flux

The benthic DO flux at the sampling stations during three seasons in 2000 to 2001 is shown in Figure 4. The dissolved oxygen consumption rate of all study sites had a mean of -89 (± 44) mmol m^{-2} d^{-1} while the oxygen production rate due to benthic algae had a mean of 131 (± 103) mmol m^{-2} d^{-1}. Oxygen was produced at a high rate during sampling in June and July but there was a net flux of DO to the sediment during autumn. Not surprisingly, the calculated P rate in the summer seems to be related to depth of the water column as the highest P rate was observed at station HO, that is the shallowest station, and the lowest at the deepest station, B2.

Benthic primary production

The data presented for the benthic oxygen production (P) in Figure 4 are limited but make it possible to calculate the daily gross benthic primary production, as shown in Figure 5, leading to a consideration of the gross BPP in Lake Myvatn for the whole year. If the gross daily BPP is presumed to reach maximum values, as shown in Figure 5 for June and July, and be lowest during the darkest period of the year from December to January, the gross annual BPP can be estimated. In this study the annual gross benthic primary production was estimated from the gross mean daily benthic DO production (P) and Redfield's $C:O_2$ ratio of 106:138 as 420 g C m^{-2} y^{-1} at station HO, 250 g C m^{-2} y^{-1} at station B2, and 340 g C m^{-2} y^{-1} at station 95. Thus, the gross mean benthic primary production was estimated as 1151 mg C m^{-2} d^{-1} at station HO, 685 mg C m^{-2} d^{-1} at station B2, and 932 mg C m^{-2} d^{-1} at station 95. The mean daily benthic primary production rate at all study sites was 1216 (± 957) mg C m^{-2} d^{-1} between June 2000 and February 2001.

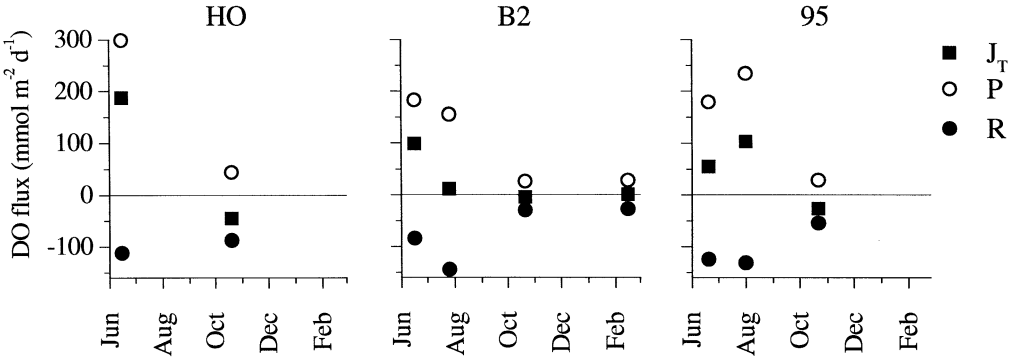

Figure 4. Dissolved oxygen (DO) flux across the sediment–water interface in Lake Myvatn from 2000 to 2001. Direct measurements of net DO flux (JT), calculated oxygen production (P) due to photosynthetic activity of benthic algae, and R, oxygen consumption of the sediment (sediment oxygen demand), zoobenthos, and bacteria.

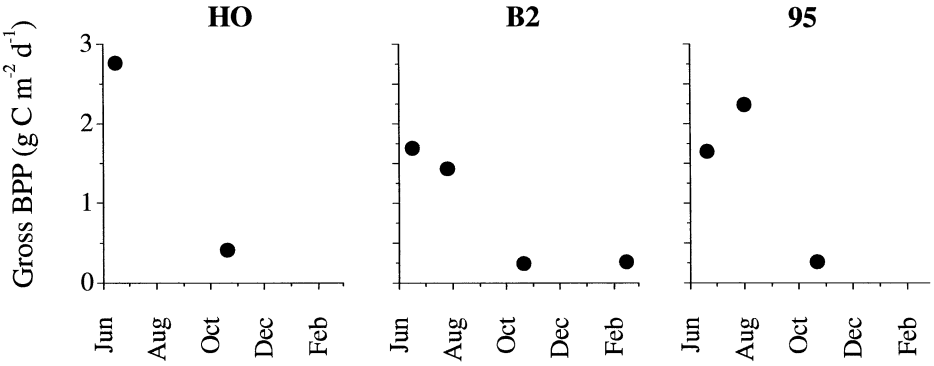

Figure 5. Gross benthic primary production (BPP) in 2000 to 2001 in Lake Myvatn.

Temperature and mixing of bulk water

During the summer temperature profiles were measured in the lake to evaluate whether the water was completely mixed or stratified. In most cases the lake water was well mixed from the water surface to the bottom. Stratification of the lake in the summer was sometimes observed early in the morning after calm weather conditions the night before, but commonly the water mass became completely mixed during the daytime because of wave action due to increasing wind.

Bottom temperature was relatively constant during each sampling day but showed seasonal variations (Figure 6). The seasonal temperature changes observed at stations B2 and 95 followed a similar trend where the highest bottom temperature was measured around 15 °C in July but was lower in October just before freeze-up. Due to bottom surface heat flux the bottom temperature rose at stations B2 and 95 during ice cover. The measured temperature at HO was almost the same on the sampling days in June and July but never reached more than 11 °C. The lowest bottom temperature was observed at HO due to ice melting during a thawing period and heavy wind in February.

DO and temperature profiles were measured during ice cover in February at stations B2 and 95 (Figure 7). At B2 there was a slight reduction in oxygen down to 2 m depth, whereas the oxygen decreased rapidly to the bottom (Figure 7A). The temperature profile mirrored the oxygen concentration with a maximum temperature of 4 °C at the lake bottom. At station 95 the temperature increased constantly with depth from below the ice cover down to the bottom but the oxygen concentration profile showed a different trend (Figure 7B). The oxygen increased in the first 50 cm below the ice, reached a maximum of about 40% DO saturation at 1 m depth, and then declined with depth down to the bottom where the DO saturation was about 10%. It is worth mentioning that this sampling at station 95 took place in the afternoon. Sampling of bottom water in the morning the day before at the same station implied anoxic conditions near the sediment–water interface, as seen in Figure 3 (February 14, 2001).

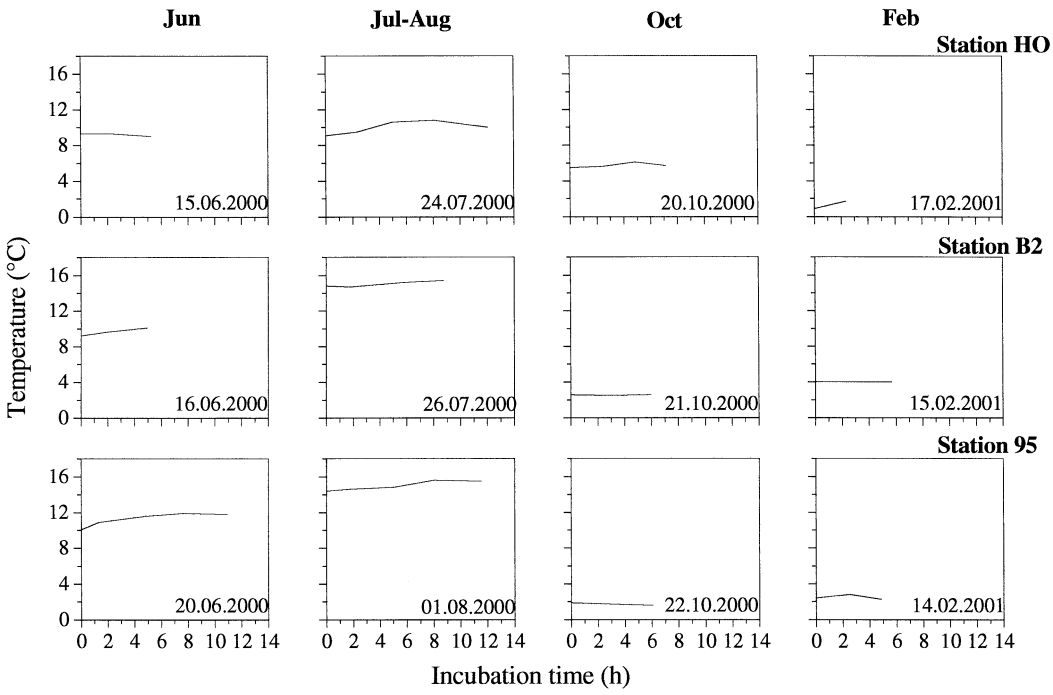

Figure 6. Bottom water temperature at the time of sampling during incubation in Lake Myvatn.

Light flux

Light flux was measured in July and October and the measurements ranged from 25 to 75% of surface irradiance depending on the depth of the water column, phytoplankton density and resuspended sediment particles (Figure 8). Unfortunately the light-flux data logger failed during the sampling in February but little or no light is thought to reach down to the lake bottom at the time of ice cover during the darkest period of the winter (in December and January). During sampling in July, the sky was clear (bright) or partly clouded, while in October there was total cloud cover. At the time of sampling at stations HO and B2 it even snowed a bit.

Phytoplankton density in the summer of 2000 was much less than in 1999. The *Anabaena* bloom was not intensive and during sampling at the three stations the bottom could almost always be seen from the surface of the lake. The highest phytoplankton density was observed on the 1st of August, at station 95, and could account for about 10 to 15% of the gross DO production in the transparent chamber.

Sediment community

During the study spatial and seasonal variations of the chironomid larval density (no. m^{-2}) and the *Cladophora* sp. dry weight at the bottom of Lake Myvatn were observed (Table 2). Although the observed larval density was always higher at station HO than at B2 it showed a similar trend over time. That is, after the fly emergence period in June the larvae had a lower density than in July just before the flying season of the second summer generation of *Tanytarsus gracilentus*. Then again in October a dense carpet of larvae covered the bottom, though with a bit lower density than observed just before the second emergence period of *Tanytarsus* (Table 2). The larvae were most active during the summertime but their activity was greatly reduced in late October, and in February they were totally inactive. As to the *Cladophora* colonies and the inhabited larvae (mostly *Chironomus islandicus*) at station 95, the *Cladophora* colonies declined between observations in mid-June and early August, but the densest *Cladophora* mat was found in October when it was even denser than in June. Most of the *Chironomus* larvae had emerged before the benthic flux chambers were used in June. In August the population had grown. The population of *Chironomus* reached a maximum of about 35,000 in October although the

Table 2. Numbers of chironomid larvae and *Cladophora* colonies on the bottom of Lake Myvatn at the time of benthic flux measurements in Lake Myvatn from June to October 2000.

Station	HO		B2		95	
Date m/d/y	*Tanytarsus* density (no. m^{-2})	Total larval density (no. m^{-2})	*Tanytarsus* density (no. m^{-2})	Total larval density (no. m^{-2})	Total larval density (no. m^{-2})	*Cladophora* dry weight (g m^{-2})
6-15-00	91914	96864	19306	22359	1980	281
7-24-00	315594	578589	–	551485	–	–
8-2-00	–	–	–	421040	5445	66.8
10-20-00	513619	532178	437294	466172	35148	346.5

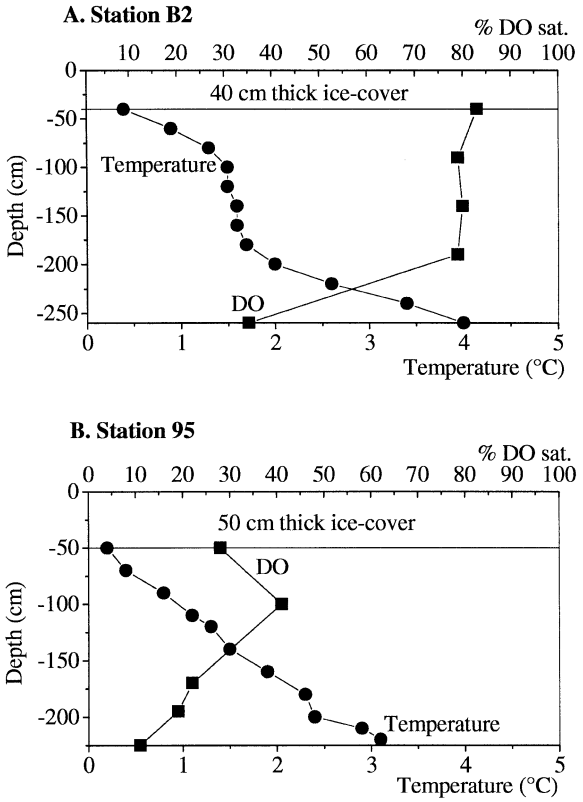

Figure 7. Dissolved oxygen (DO) and temperature profiles under ice cover at stations B2 (A) and 95 (B) in the afternoon of 15 February 2001.

total larval density was an order of magnitude lower than at stations HO and B2. As to the sediment community in February, the sediment samples have not yet been studied and are therefore not presented here. Research on the major components (such as alive and dead algae, algal fragments, detritus, and mineral fragments), apart from larvae, found at the sediment surface at station B2 showed that the diatoms were 60% of it during the spring in 2000 and the diatom proportion decreased gradually during the summer to 30% in October (Ingvason 2002; Ingvason et al. 2002).

Discussion

Seasonal and spatial DO conditions

Lake Myvatn has a complex basin morphometry and large horizontal variations in oxygen content can be expected (Wetzel 1983). When a lake consists of many bays, as Lake Myvatn does, the oxygen concentrations are very different in the different areas and each embayment may operate essentially as an individual lake. Oxygen uptake is likely partitioned into two major reactions, oxidation of organic carbon and oxidation of reduced metals while oxygen is produced as a consequence of photosynthesis and oxygen can diffuse through the air–water interface.

At station HO there was rather stable oxygen supply from cold springs. The springs in the embayment had a mean temperature of 6.6 °C and the October dissolved oxygen concentration in 2 springs located north and south of the bay imply the oxygen concentration there to be between 240 and 250 μM (Arnórsson et al. 1999), which means 60 to 65% oxygen saturation (elevation at sea level). The oxygen concentration in near bottom water at station HO reached oxygen saturation from 71 to 83%, highest in June 2000. The fact that the water did not reach 100% oxygen saturation or more is consistent with a low retention time of the water and the fact that the water is constantly being renewed by the springs in the bay. Furthermore, the bay is sheltered from wind blowing from most directions, leading to less flux of oxygen between the air–water

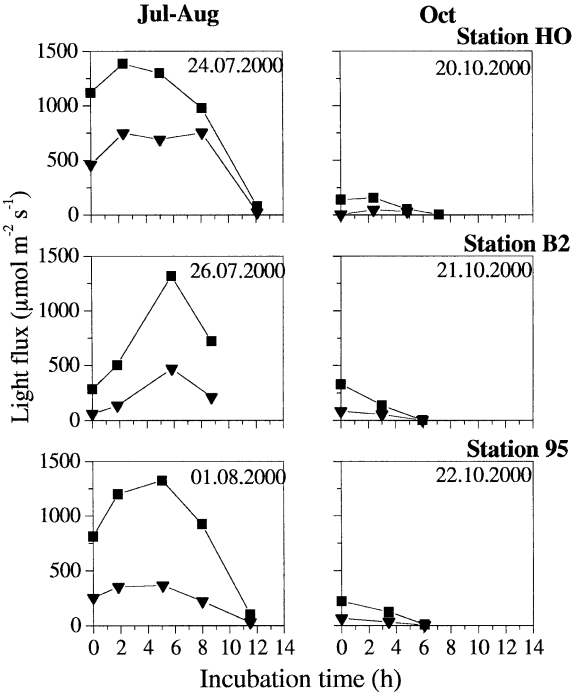

Figure 8. Light flux measured during flux chamber incubation in Lake Myvatn. Solid squares refer to light flux above the water surface and solid triangles to light flux on the lake bottom.

interface than in open areas of the lake. The sediment community is another factor affecting the bottom DO concentration that varies with seasons.

Seasonal variations of oxygen conditions at the bottom of station B2 were also consistent with the temperature, sediment community and its activity. Due to the higher density of midge larvae and the higher temperature the oxygen consumption was much higher during July than in June (Figure 4 and Table 2). The oxygen conditions at the station were also dependent on sheltering of ice cover and currents of cold water under the ice (Figure 7).

As stated earlier, the benthic community at station 95 was totally different from that observed at stations B2 and HO. It can be stated that, of the three sampling stations used in this study, station 95 had the most seasonal variations in water chemistry, from being highly oxygenated in the summer to anoxic conditions in the winter during ice cover. As to solute flux, the most seasonal changes were observed at Neslandavík where the water changed from aerobic to anaerobic conditions. The flux result of other solutes than dissolved oxygen will be considered in a following paper on solute flux across the sediment–water interface in Lake Myvatn.

During ice-cover periods in Lake Myvatn DO varies even more spatially than it does during ice-free periods (Figure 7). The depth profile of DO concentration and temperature in the water of Strandarbolir in February indicated vertical mixing of the water. This was due to currents of water emerging from the spring-fed areas, which are permanently ice-free (Ólafsson 1991 (Figures 3–10)). When the spring water sinks under the ice the water temperature is almost 0 °C and its density is less than that of the water at the bottom of deeper areas of the South Basin. Thus, cooler less dense water flows near the ice above denser warmer water at the bottom of station B2.

At station 95 in Neslandavík the temperature profiles told a story of stagnant water where constant surface heat flux from the sediment affected the behaviour of temperature with depth in the water, though, the ice cover led to some cooling of the water in the topmost centimetres (Figure 7). The oxygen concentration profile at station 95 indicated phytoplankton photosynthesis at 1 m depth. Further, the rising of oxygen concentration in the transparent chamber during ice-cover at stations B2 and 95 in February (Figure 3) was an indicator of photosynthetic activity at the bottom of the lake. Although photosynthesis by algae was strongly suppressed by snow cover on the ice, the result of patchy accumulation of snow on the surface of windswept ice can lead to photosynthesis and oxygen production below the ice (Wetzel 1983). This could have been the case with the observed oxygen accumulation below the ice cover at station 95 in February. When sampling was carried out in the morning the water was nearly anoxic but higher oxygen concentrations were observed in the afternoon, implying benthic photosynthesis taking place during the daytime. Research carried out in January through March in 1974, implied that benthic photosynthesis took place in February (Ólafsson 1979b). Furthermore, anoxic conditions at the sediment-water interface of station 95 could have enhanced fluxes of nutrients, e.g., phosphorus and ammonium, and metals such as iron (Song and Müller 1999), leading to a higher concentration of these nutrients and iron in the water column supporting primary production of phytoplankton below the ice. Even though the bottom water was anoxic in some areas of the lake in January in 1974 (Ólafsson 1979b) benthic photosynthesis could have been taking place under the ice cover. Although benthic photosynthesis took place, the net DO flux could be negative during December and January, but in February the net DO flux became positive, leading

to DO accumulation near the sediment-water interface. Then it was a matter of the decomposition rate and light intensity when the net DO flux became positive, leading to oxygen accumulation in the water near the sediment–water interface. The transfer of oxygen into sediments below the sediment–water interface is often found to be enhanced by pore water pumping caused by macroinvertebrates, or tidal or wave action. In their absence, oxygen penetrates into sediments only by molecular diffusion (e.g., Santschi et al. 1990). In Lake Myvatn oxygen is thought to penetrate a few cm into the sediment and aerobic conditions can be reached at 5 cm depth during active periods of chironomid larvae (Hunding 1979). A redox potential profile of the sediment at the Gardsvogur Beach in August 1973 indicated a high oxygen supply to the sediment due to the sediment community as the uppermost 5 cm were oxygenised. At the same time at Skútustadir and Neslandavík, where *Cladophora* colonies covered the sediment, the redox potential declined from the top of the *Cladophora* cover towards the mud surface below (Hunding 1979). Further evidence of a low redox potential below *Cladophora* colonies in the summertime was found in July 1998, when a sulfur smell and black colour were observed below *Cladophora* colonies in a sediment core taken in Álftavogur in the south part of Lake Myvatn (Gíslason et al. 2004).

Although animal activity can contribute significantly to mixing at the sediment surface, wind-induced turbulence may explain most of the differences of resuspension and oxygenation of the sediment surface between lakes (Tessier et al. 1994).

Benthic primary production

In the South Basin of Lake Myvatn, colonies of *Cladophora*, with attached diatoms, cover a large area of the sediment bottom and further benthic algal production is high along the shores. *Cladophora* sp. forms important phytobenthos with an average density of 50 g m^{-2} ash-free dry weight (Hunding, 1979). Very conservative calculations of the production of *Cladophora* sp. account for twice the ash-free dry weight or 100 g m^{-2} y^{-1} (e.g., Jónasson 1979). As estimated from silica output through the outlet in 1973–1974 the net annual benthic diatom production is 220 g C m^{-2} y^{-1} (Ólafsson 1979b). Further, analysis of the sedimentation rate gave similar results for net benthic diatom production (Ólafsson 1979b). In this paper the gross BPP is presented at three stations in the South Basin and were on all occasions higher than the calculated net benthic diatom production. The gross BPP at station B2 was 250 g C m^{-2} y^{-1} where the benthic community mostly consisted of midge larvae and diatoms. But at station 95 where *Cladophora* colonies with attached diatoms covered the sediment, the gross BPP was higher. Station HO had the highest calculated gross BPP of the three stations, most likely because it is shallow, is close to the nutrient inflow from the springs and is free from ice cover in the winter.

One can estimate that the benthic diatom production is higher in years when *Anabaena* blooms fail. This was the case in the summer of 2000 when *Anabaena* density was low, much lower than observed in 1999 (when the water was green due to *Anabaena* blooms). Commonly the biomass of *Anabaena flos-aquae* reaches a maximum in late July or the beginning of August (Jónasson and Adalsteinsson 1979), that is, at the time of the second sampling trip to Lake Myvatn in 2000. The only instant when a Secchi disc was not seen at the bottom of the stations when sampling, was at station 95 on the 1st of August. But even then the *Anabaena* biomass was low and the water was not with an intense green colour.

Oxygen measurement under the ice during winter and spring in 1974, together with the silica budget, indicated a high production of diatoms at that time (Ólafsson 1979b). Rising of DO concentrations over the daylight period in mid-February 2001, as well as DO concentration changes in benthic flux chambers, also imply that benthic algal production occurs during ice cover. The P rate at B2 implied that it is dependent on the length of the day, in other words, follows a seasonal pattern. But it should be borne in mind that no measurements were made in late August or in September when, generally, phytoplankton density is low. The seasonal shifts in the daylight period did not affect the P rate at station 95 in the summer as it did at Station B2, because the mid-June P results were lower than those in the beginning of August.

DO consumption

The oxygen consumption rate in Lake Myvatn, except for July at B2, was within typical oxygen consumption rates in sediments that range from 0.1 to 140 mmol m^{-2} d^{-1} for freshwater and marine environments (e.g., Santschi et al. 1990). Oxygen consumption in Lake Myvatn was related to temperature (Figure 9) and the highest consumption rates in Lake Myvatn were consistent with a high abundance

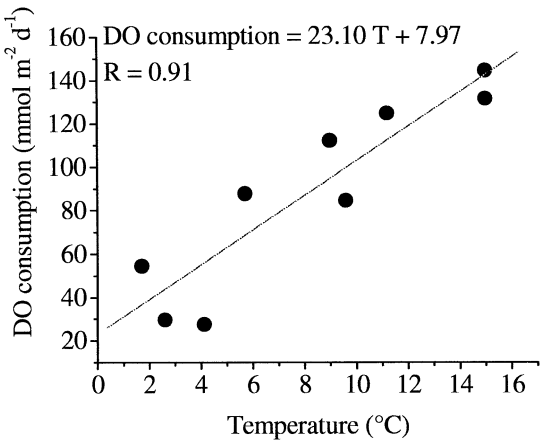

Figure 9. Dissolved oxygen (DO) consumption rate in relation to bottom temperature in Lake Myvatn from June 2000 to February 2001.

and activity of midge larvae on the sediment bottom (Figure 4 and Table 2).

If the oxygen supply from the water column and benthic algal community in shallow lakes is insufficient to counterbalance the microbial and macrobenthic uptake, the sediment surface becomes anoxic (Scheffer 1998), as was observed in Lake Myvatn during ice cover. Anoxic conditions at the lake bottom may persist during the summer. When the bottom respiration rate in Lake Myvatn is high and dense phytoplankton colonies (commonly during *Anabaena* blooms in late July to beginning of August) affect the light flux to the lake bottom, during calm periods in the summer, bottom oxygen concentrations can be highly reduced in some areas and may lead to a very low oxygen content near the sediment–water interface. This could then lead to enhancement of nutrient flux from the sediment into the water column in favour of further phytoplankton growth. Thus, light penetration to the bottom in favour of benthic photosynthesis is an important factor for respirating macrobenthos.

Conclusion

The benthic flux chamber methods can be applied to determine DO fluxes at the sediment–water interface in Lake Myvatn. Though the deployment technique used in this study is more convenient during seasons of well-mixed oxygenised bulk water, the study has shown interesting results during other seasons of not well-mixed water. Paired benthic flux chamber methods have made it possible to divide the in situ net benthic DO flux into two components, one of which refers to benthic oxygen consumption and the other to benthic oxygen production in the lake. Furthermore, the oxygen production was calculated by means of gross benthic primary production, which is important to quantify in a highly productive shallow lake system, such as Lake Myvatn, in order to understand the nutrient budget of the lake.

This study has shown the oxygen conditions in Lake Myvatn to vary both by season and area. As observed during the summer, the lowest oxygen saturations were consistently found at the station placed in a spring-fed embayment. There the oxygen diffused into the lake through the air–water boundary. The highest oxygen saturations were found at the stations farthest from the spring-fed areas, where the oxygen tended to diffuse from the lake into the air. The spatial differences of the bottom DO saturations may have been due to differences in sediment community as well as depth of the water column and temperature. Among these, vertical and horizontal differences in DO in mid-winter are also a consequence of ice cover and water currents under the ice.

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