Disturbance of meromixis in saline Lake Shira (Siberia, Russia): possible reasons and ecosystem response

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Abstract

Saline Lake Shira (Southern Siberia, Russia) was meromictic through the observation period 2002-2015. During the under-ice periods of 2015 and 2016, complete mixing of the water column was recorded for the first time, and hydrogen sulphide temporarily disappeared from the water column of the lake; i.e. in those years the lake turned to holomixis. In the summer of 2015, a sharp increase in chlorophyll a, organic carbon, zooplankton, and phytoflagellates was observed in the lake, which was probably due to the release of nutrients from the monimolimnion. Purple sulfur bacteria completely disappeared from the lake after the first mixing in 2015, and did not reappear despite the restoration of meromixis in 2017. Thus, it was demonstrated that purple sulfur bacteria are sensitive to the weakening of the stratification of Lake Shira. Based on the data of the seasonal monitoring of temperature and salinity profiles over the period 2002-2017, it was presumed that the main cause of deep mixing in 2015 was the weakening of the salinity gradient due to strong wind impact and early ice retreat in the spring of 2014. In addition, it was shown that in previous years a significant contribution to the maintenance of meromixis was made by an additional influx of fresh water, which caused a rise in the lake level in the period 2002-2007. Thus, we identified a relationship between the stratification regime of the lake and the change in its level, which provides valuable information both for the forecast of water quality and for reconstruction of the Holocene climate humidity in this region of Southern Siberia from the sediment cores of Lake Shira.

Keywords: meromixis, mixolimnion, stratification, stability, mixing, food chain, purple sulfur bacteria.

Introduction

Meromictic lakes are lakes in which the deep recirculation does not include the entire water body (Boehrer and Schulze, 2008; Gulati et al., 2017). In meromictic state the nutrients accumulated in the monimolimnion with the sedimentation flow of organics are not available for the primary producers. Thus, in case of meromixis destruction, nutrients are released from the monimolimnion, resulting in outbreaks of phytoplankton bloom, i.e. in deterioration of water quality and changes in the species composition of plankton organisms (MacIntyre and Jellison, 2001). For example, the increase in phytoplankton biomass and primary production after meromixis destruction was demonstrated in Mono Lake when the lake changed its circulation regime from meromictic to holomictic (Melack et al., 2017). Similarly, in case of the meromictic Lake Iseo (Italy) it was shown that in the years when the lake was completely mixed, an increase was registered in the content of nutrients and the total amount of phytoplankton in the epilimnion, and changes were observed in the composition of zooplankton (Leoni et al., 2014). In Lake Lugano an abnormally deep mixing caused more than a tenfold increase in the biomass of phytoplankton and changed the trophic status as a result of a large nutrient input in the photic zone (Simona, 2003). Thus, prediction of lake transitions from a holomictic to meromictic state and back is a pressing issue with respect to water quality.

The weather conditions are among the main reasons for destruction of meromixis. For example in Lake Zabinskie (Poland) the alterations between monomictic, dimictic and meromictic regimes were caused by weather conditions of two consecutive winters (Bonk et al., 2015). Also in Lake Lugano two consecutive cold and windy winters destabilized the water column and led to two exceptionally strong mixing events (Holzner et al., 2009). Another reason for destruction of meromixis is change in water level. The well-known example is Mono Lake (California, USA) which turned from meromixis to holomixis after level decrease and vice versa (Melack et al., 2017).

Since the change in mixing regime gives rise to changes in the composition of the sediments, the alterations between mixing regimes can be reconstructed for the long period of a lake history (Schmidt et al., 2002). Therefore the knowledge of the causal relationship between environmental factors and stratification and its impact on the living conditions of planktonic organisms can help to solve the fundamental problem — reconstruction of paleo-climate (Wirth et al., 2013). In particular, hydraulically closed water bodies located in arid climates sensitively react by changes in water level to the changes in the balance of precipitation and evaporation in the area (Last and Ginn, 2005). In turn, the change in water level may result in change in mixing regime. Therefore reconstruction of mixing regimes of closed lakes provides valuable information on their level dynamics, consequently – about effective moisture of local climate.

Lake Shira is one of the most studied small lakes in Siberia, the information about its biota and ecosystems has been published in many sources (Degermendzhy et al., 2010; Rogozin et al., 2017). In this paper we analyze the long-term field data on the vertical structure of Lake Shira and demonstrate for the first time the documented change in the lake stratification regime from meromictic to holomictic. In the discussion several hypotheses are suggested regarding the possible causes of this phenomenon.

Materials and methods

Study site

Lake Shira (N 54.30, E 90.11) is located in Southern Siberia, in the steppe zone of the northern part of the Minusinsk valley (Republic of Khakassia, Russia), 15 km from Shira settlement. The lake has an elliptical shape of 9.35 × 5.3 km, the water surface area of 35.9 km^2, the average depth of 11.2 m, the maximum depth of 24 m (2007-2015) (Fig. 1). The lake has no outflow, the main water inflow is carried by the Son river (40%), land and atmospheric runoff (33%), and underground waters (7.5%). In addition, the lake receives domestic sewage due to water consumption of Zhemchuzhny settlement. The average salinity in the mixolimnion during the summer stratification is about 15 g l^{-1}, and in the monimolimnion — about 19 g l^{-1} (Rogozin et al., 2010a). The dominant anions are sulfate and chloride, cations are sodium and magnesium (Kalacheva et al., 2002.). The lake freezes over in late November - early December, and frees from ice in late April - early May. Ice thickness reaches about 1 m in March. The climate of the steppe zone, where the lake is located, is sharply continental and arid. The average July temperature is +18° C, -19° C in January. The ridges of Kuznetsky Alatau prevent the penetration of humid air masses to the territory, so the potential evaporation (600 mm $year^{-1}$) is much higher than the amount of rainfall (around 300 mm/year) (Parnachev and Degermendzhy, 2002). Lake Shira is an important recreational facility and has therapeutical properties. On its shore the well known resort "Lake Shira" has been working for more than 100 years (Krivosheev and Khasanov, 1990).

Physical-chemical characteristics

The physical-chemical characteristics of the water were measured seasonally from July 2002 to January 2017 (except 2006) in the central part of the lake (N

54°30'350 E 90°11'350) in the area of the maximum depth. There was no survey in 2006. The sampling dates were coordinated with the major hydrological seasons: during the autumn circulation prior to freeze-up (October), at the time of the highest ice thickness (late February- middle of March), after ice disappearance (end of May), and during the period of summer stratification (July-August). In some years, we carried out additional surveys on other dates. Thus, in 2015 and 2017, additional surveys were conducted in early January. The 50 profiles were measured in total. In the winter time, sampling was carried out through a hole in the ice. Samples were taken using a standard 0.5 liter sampler or by pumping water using a hose with a conical nozzle connected to a vacuum pump.

Before sampling, the vertical profiles of temperature, conductivity, redox potential and dissolved oxygen were measured with submersible multichannel probes Data-Sonde 4a (Hydrolab, Austin, Texas, USA) or YSI 6600 (Yellow Springs, Ohio, USA). After March 2015 the oxygen was estimated from redox-potential because oxygen sensor was broken. To estimate the concentration of hydrogen sulfide, the samples were fixed with basic zinc carbonate, and sulphide concentration was determined by iodometric method (Volkov and Zhabina, 1990). The conductivity measured in the lake at a temperature *in situ*, was converted to the conductivity at a constant temperature of 25° C (K_{25}) according to the formula recommended by the ISO (International Organization for Standardization (ISO), 1985) (Boehrer and Schulze, 2008) modified for Lake Shira (Rogozin et al., 2016).

The number of purple sulfur bacteria

The number of purple sulfur bacteria (Chromatiaceae) (PSB) was calculated on a fluorescent microscope using DAPI fluorochrome staining as previously described (Rogozin et al., 2010b). The detection limit was about 10^3 cells ml^{-1}. The amount of bacteriochlorophyll *a* in water was evaluated spectrophotometrically in acetone extracts using the previously described method (Rogozin et al., 2010b).

Chlorophyll a concentration

Chlorophyll was measured on a regular basis until 2012, after which regular monitoring was interrupted due to the end of research projects. However, in the summer 2015 a new survey was undertaken specifically to identify possible changes after the destruction of meromixis (see below). For the analysis of chlorophyll *a* concentration, water samples were collected at every 1 m by Ruttner sampler in the range of 0-18 m in the central part of the lake in late July-early August. The amount of chlorophyll *a* in the samples was determined by fluorescence method. Fluorescence was recorded using a planktofluorimeter PL-3003 (Siberian Federal University, Krasnoyarsk). The fluorescent signal was calibrated against the Chl *a* concentrations determined spectrophotometrically in acetone extracts. The values of chlorophyll *a* concentration were obtained by solving the system of algebraic linear equations as described by Gaevsky et al. (2005).

Organic carbon and zooplankton

Regular measurements of the total organic carbon content in the sestone and the biomass of the dominant zooplankton species *Arctodiaptomus salinus* (Zadereev and Tolomeev, 2007) were conducted in the period from 2007 to 2011 on the dates corresponding to the major hydrological seasons. In the summers 2015 and 2016 samplings were undertaken specifically to identify the response to the destruction of the lake meromixis.

Water sampling was carried out in 2007-2009 from the surface to the redox zone at an interval of 1-2 meters (depending on the weather conditions), from the redox-zone to the bottom at an interval of 2-3 meters (depending on the weather conditions) using a submersible 6-liter sampler; in 2010-2011 and 2015 with a vacuum pump and a submersible hose with a funnel at the end (diameter 10 cm) in a volume of 5 liters from the surface to the bottom at intervals similar to the ones made with a sampler in previous years.

To determine the biomass of *A.salinus* (hereinafter "zooplankton"), 5 liters of water taken from the relevant depth were filtered through a plankton net with a mesh size of 75 microns, then the collected zooplankton was fixed with 70% alcohol with the addition of 5% glycerol in a volume of 10 ml. Next, a light binocular microscope with magnification x32 was used to count the nauplii, copepodid stages C1 to C3 (0.50-0.75 mm) and C4-C5 (0.80-1.00 mm) of males and females of *A.salinus* in the sample. The raw biomass of zooplankton in the sample was calculated according to the formulas connecting the linear body size and weight of the animals (Vinberg, 1979).

For the analysis of organic carbon in the sestone, the water previously filtered through a plankton net with mesh diameter 75 microns was filtered through a glass fiber filter GF/F (Whatman). The glass fiber filters were precalcinated at 400° C for 4 hours. After filtration, the filters were dried and stored in a dark, dry place prior to the analysis. The carbon content was measured by the elemental analyzer Flash EA 1112 NC Soil / MAS 200 (ThermoQuest, Italy) using the method described by Gladyshev et al. (2007). As in the water of the saline Lake Shira there is a high content of inorganic carbon compounds, the analysis revealed up to 20% of inorganic carbon on the filter. With this in mind, to determine the organic carbon content, the data obtained by the elemental analyzer, were multiplied by a correction factor of 0.8.

Phytoflagellates

To investigate phytoflagellates in the water column, we collected samples in the central part of the lake with a water pump sampler in different depth layers at 1 m intervals from the surface down to the chemocline zone. The organisms were counted in samples fixed with Kuzmin's solution (Kuzmin, 1975) (1% end concentration). Fixation was carried out during sampling with a minimum time delay. The samples were concentrated by using the settling method. Fixed phytoflagellates were counted in a Fuchs-Rosenthal chamber under an MBI-11 light microscope (Russia) and an Axioskop 40 fluorescence microscope (CarlZeiss); 10 pseudo-replicates were used.

Meteodata

In the study we used the daily averaged temperature and wind speed data for the meteorological station "Shira" located at 15 km from the lake. The dates of ice formation and ice melt, and water levels were obtained at the gauging station in Zhemchuzhny settlement located directly at Lake Shira. All the data were provided by Middle Siberian Department of Russian Hydro-Meteorological Service (Krasnoyarsk, Russian Federation).

Calculations

Estimation of the integral amounts of cells, pigments and hydrogen sulfide in the water column was carried out by numerical integration of the vertical distributions using the method of trapezoids.

In order to assess the evolution of the density stratification of the water column, we computed the Schmidt stability (Idso, 1973) for each CTD profile (Fig. 3B). Schmidt stability is the difference in potential energy between the stratified lake and the hypothetically mixed lake. A Schmidt stability value of zero means that the water column is not stratified and hence homogeneous, allowing vertical mixing to be triggered by a minimal input of turbulent kinetic energy. Schmidt stability is computed as follows:

$$S = \frac{g}{A_0}\int_0^{z_m} (z - z_{g,z})(\rho(z) - \rho_{bar})\,A(z)dz \qquad (1)$$

where g is the acceleration of gravity (9.81 m s^{-2}), A_0 is the surface area of Lake Shira (39.5 km^2), z_m is the maximum depth of the lake (24 m), $z_{g,z}$ is the depth of the center of volume in interval 0-z, ρ_{bar} is the hypothetical density of the homogeneous lake after mixing, ρ(z) is the observed density at depth z, and A(z) is the isobath area at depth z.

In order to estimate the contribution of salinity stratification (hereinafter referred as ST) into total Schmidt stability, for each CTD profile we calculated the density at the constant temperatures +3 °C and +25 °C according to formula (2). The difference between ST calculated for two temperatures was negligible so we show the only values for +3 °C on the figures. Ice was excluded from the calculations of Schmidt stability (see Results).

Density was calculated using

$$\rho\ (T,\ K_{25}) = 1.0034 + 5.5\times10^{-5}\ T - 6.3\ \times10^{-6}\ T^{2} + 4.7\times10^{-4}\ K_{25} + 8.9\times10^{-6}\ K_{25}^{\ 2} - 9\times10^{-7}\ T\, K_{25} - 0.0184(1/K_{25}) + 8\times10^{-8}\ K_{25}^{\ 3} \qquad (2)$$

The formula (2) was derived from the equation proposed by Melack and Jellison (1998), with coefficients modified for Lake Shira on the basis of laboratory measurements of lake water density. According to these data the temperature of maximal density of Lake Shira is about +3 °C (data not shown).

Conductivity readings $C(T)$ at in situ temperatures were standardized to specific conductance at 25°C (K_{25}) using the UNESCO formula (Fofonoff, 1985) with coefficient slightly modified for Lake Shira water:

$$K_{25} = C(T)/(1+0.0204(T-25^{\circ}\mathrm{C})) \qquad (3)$$

where T is the in-situ temperature in degrees Centigrade. The salinity (g l^{-1}), was calculated from K_{25} using:

$$S = 1.117K_{25}\ - 7.9716 \qquad (4)$$

The relationships (3) and (4) for conductivity and salinity were derived with Lake Shira water (unpublished data). Conductivity sensors were calibrated against 0.2 M KCl (Hydrolab, YSI) before each survey.

Kinetic energy from wind action was estimated from the daily averaged wind speeds according to Imboden and Wüest (1995) using averaged value of coefficient $\eta = 2.5\times 10^{-5}$ kg m^{-3}.

SURFER 8 (Golden Software) was used for contour plots of temperature, electrical conductivity and oxygen.

Results

Long-term stratification dynamics of Lake Shira

The overall picture of the long-term dynamics of the vertical distribution of temperature and conductivity (K_{25}) is shown on Fig. 2. The main cause of the difference in salinity in the upper layers of Lake Shira is the freezing-thawing of ice. In spring due to melted ice (ice salinity is about 2.6 g l^{-1}) a freshened surface layer appears that shields the underlying layers from wind mixing and provides for the presence of the warm and relatively freshened epilimnion during summer (Fig. 2, 3).

In 2007 the pattern of summer stratification was different from common scheme described above. In spring the windy weather caused the anomalously deep mixing such that the surface layer was completely mixed with hypolimnetic waters. That is why in summer 2007 the only thermal stratification was formed in mixolimnion, whereas the salinity in mixolimnion was uniform (Fig.3). In addition, snowless winter 2006-2007 caused the absence of spring flooding (Fig. 6) and consequently the stability of mixolimnion to wind stress in spring was the lowest.

Epilimnion destruction begins in autumn due to convection as a result of lake cooling and then continues in winter due to freezing of ice. When water freezes, salt is excluded into the solution; as a result, the upper water layers become heavier and go down, i.e. thermohaline convection occurs, which leads to a further mixing of the water column (Genova et al., 2010). The minimum heat content and consequently minimum temperature stratification is reached at the middle of March as it can be deduced from regular measurements of ice thickness (data by Hydro-Meteorological Service) and mathematical modeling (Genova et al., 2010).

Therefore, by March, when the ice thickness reaches its maximum (about 1 m), the water column is mixed to a maximum depth (Genova et al., 2010; Rogozin et al., 2010a). In this depth range the salinity and temperature profiles are uniform, and this mixed layer is the mixolimnion of the lake. The lower boundary of the mixolimnion always coincided with the boundary of the hydrogen sulphide zone (redox zone) in winter (Fig. 2). Deeper layers are monimolimnion, i.e. an unstirred zone, where hydrogen sulfide is accumulated. In general, the seasonal dynamics of vertical CTD profiles in Lake Shira was previously described for 2002-2009 by Rogozin et al. (2010a; 2016).

The Schmidt stability in Lake Shira shows an annual cycle with the lowest values occurring in winter, when vertical density gradients are lowest because of seasonal cooling at the surface. In order to demonstrate the evolution of meromixis we also consider the density stratification according to salinity gradient only (Boehrer et al., 2014), hereinafter referred as ST (Fig.4).

Actually the ice formation shifts salinity gradients into the ice hence there are salinity gradients and stability throughout most years, if ice is considered part of the water body. Thus, the salinity stratification is present during ice period and actually enhanced through the ice cover. However, in order to demonstrate the mixing behavior of the water column during ice periods we excluded the ice from stability calculations on Fig.4.

On the basis of seasonal dynamics described above we propose to consider the thickness of winter mixolimnion as a quantitative characteristic of annual meromixis degree. The thickness of mixolimnion is determined by the upper uniform interval of temperature and salinity (Fig. 3). Up until 2014 the lake was meromictic, which is confirmed by the presence of hydrogen sulfide deep in the water column on all the dates of surveys (Fig. 2, 3). The thickness of winter mixolimnion was different in different years (Fig. 2, 3, Table 1). Relatively shallow mixolimnions were observed in 2004, 2005, 2007, 2011 and 2012. In the period of 2004 - 2008 the difference in salinity between mixolimnion and monimolimnion was much more pronounced than in other winters (Fig.3) probably because of freshwater inflows (see Discussion). Deeper mixolimnions were observed in 2003, 2008, 2009, 2010, 2013 and 2014, when salinity and conductivity profiles became almost uniform (Fig. 2, 3). However, the profiles of temperature and sulphide indicated incomplete mixing in these winters (Fig.3). Schmidt stability and ST in these years were also very low, so it is not visible in Fig. 4.

In contrast, in winters 2015 and 2016 the temperature profiles were uniform much deeper with only slight increase near the bottom (Fig. 3). Therefore, in winters 2015 and 2016 the unusually deep mixing took place which can be considered as turn from meromixis to holomixis. Correspondingly, in the winter of 2015 an unusually deep position of the redox-zone was registered: 21 and 22 m (January and March, respectively) (Fig. 2, Table 1). In May 2015, the complete absence of hydrogen sulfide from water column was registered for the first time (Fig. 2). However, a freshened epilimnion was observed, like in all the previous years (Fig. 3). Consequently, the mixing of the lake leading to the disappearance of hydrogen sulfide occurred before ice melting, i.e., in the period from mid-March to May 2015. In the winter 2016 the position of mixolimnion was also as deep as 23 m and concentration of sulfide in May was negligible.

To the contrast, in March 2017 the mixed layer was as shallow as 16 m (Fig. 3) so the lake was meromictic again in 2017 (compare January profiles of 2015 and 2017 on Fig.3).

Purple sulfur bacteria and hydrogen sulfide

The microscopic counting data and the availability of Bacteriochlorophyll *a* in the absorption spectra of water indicate that purple sulfur bacteria were present in the redox zone and monimolimnion in all seasons until the spring of 2015 (Fig. 5a, b). The long-term dynamics of purple sulfur bacteria was characterized by a decline and increase (Fig. 5a, b) and was described and analyzed earlier up to 2013 (Rogozin et al., 2016). The typical number of PSB in the redox zone and monimolimnion throughout all the years was 10^5-10^6 cells ml^{-1} (Rogozin et al., 2016). However, in January 2015 the number of PSB was extremely low (Fig. 5a), and in March, PSB were not detected whereas the concentration of hydrogen sulfide near the bottom remained at 13 and 24 mg l^{-1}, i.e. at normal values, indicating incomplete mixing.

In May 2015, for the first time in the entire period of our study (i.e. since 2002), hydrogen sulphide was not detected (Fig. 5). Accordingly, PSB were not found, too (Fig. 5). In June 2015 hydrogen sulphide reappeared, but the redox zone was at a depth of over 20 meters (Tolomeev, personal communication), and in August the redox zone rose to a depth of 17-18 m (Fig. 2), and total amount of hydrogen sulphide was the lowest of all previously registered (Fig. 5). By late October, the hydrogen sulfide concentration increased (Fig. 5), and the redox zone rose to 16-17 m (Fig. 2). Thus, after the complete winter mixing an anaerobic sulphide hypolimnion formed again in summer and autumn 2015 in Lake Shira. Nevertheless, the number of PSB remained below the detection limit (Fig. 5). In 2016 the sulphide dynamics was similar to 2015: in March the redox-zone was registered at a depth of 23 m, then in May the sulhide was detected deeper than 21 m but in very low concentration (Fig. 5). In July 2016 the redox-zone was registered at the depth of 17 m, and by October it rose to 13 m (Fig.2). However, PSB were not found also as in 2015 (Fig. 5). In early March 2017 we registered sulphide at 16 m in correspondence with depth of mixing on Fig.3, but the PSB were not detected.

Organic carbon, copepods, phytoflagellates and chlorophyll

The total amount of organic carbon in the particle size fraction of 0.2 - 80 micrometers (seston) in the photic zone (roughly, 0-12 m) can be considered as an indicator of the lake ecosystem productivity. It can be seen that this value increased considerably in the early summer of 2015 in comparison with previous years, but decreased again in 2016 (Fig. 5d).

The biomass of copepods *Arctodiaptomus salinus* (Copepoda), which are the dominant species of zooplankton in Lake Shira (Degermendzhy et al., 2010), was also significantly higher in 2015 and 2016 than in previous years (Fig. 5e). However, in May 2015, copepods were present in the entire water column, i.e., down to a depth of 24 m, and then were registered down to a depth of 22 m in summer. In previous years copepods were absent from the monimolimnion and thus were not observed deeper than the redox zone (Zadereev and Tolomeev, 2007). However, unlike 2015, in the early summer of 2016 the copepods were absent deeper than 20 m because of sulhide presence.

The number of phytoflagellates *Cryptomonas* spp. showed sharp peaks in Mays 2015 and 2016 and was an order of magnitude higher than the values measured before (Fig. 5f). Moreover, in May 2016 the number of *Cryptomonas* spp. exceeded the value of 2015 by a factor of three (Fig. 5f).

Since then, during the period of open water, the number was also higher than in previous years; however, the population dynamics in the summer-autumn season was typical of the previous years (Prokopkin et al., 2014).

The amount of Chlorophyll *a* measured in July and August in the depth interval 0-18 m demonstrated a dramatic increase since 2009. The maximum values were recorded in 2010 and 2015 (Fig. 6). The increase in chlorophyll *a* mass generally coincides with the occurrence of deeper mixing (Fig. 6). Thus, the deep winter mixing in 2010 could cause the observed chlorophyll increase, in the same way as in 2015. However, in 2016 the chlorophyll *a* was considerably lower than in 2015 (Fig.6). There is a positive correlation between the integral amount of chlorophyll *a* in summer and the depth of previous winter mixolimnion ($r = 0.52$, n=10).

Discussion

Consequences of meromixis disturbance

As was shown by Zadereev et al. (2014), there is an excess of nutrients (nitrogen and phosphorus) in the monimolimnion of Lake Shira in all seasons, whereas in the mixolimnion their deficiency is observed, therefore the lake phytoplankton is limited by nutrients. Therefore, a significant increase in the concentration of chlorophyll, organics and plankton in the summer of 2015 can be explained by the release of nutrients from the monimolimnion. It should be noted that after 2008 the amount of chlorophyll in the lake increased (Fig. 6), which can also be explained by the additional supply of nutrients from the deep layers with an increase in the depth of winter mixing. Similarly, in Mono Lake the depth of mixing in winter was a dominant factor in controlling nutrient supply to the upper water column and annual productivity (Melack et al., 2017).

Despite the fact that after the deep mixing of 2015 and 2016, hydrogen sulfide reappeared in the photic zone (Fig. 2), the PSB population did not recover after 2015. This is probably due to the very low growth rate of PSB as a result of the small amount of light and low temperature in the redox zone of the lake (Rogozin et al., 2009, 2016). Thus, our observations indicate that the PSB biomass in Lake Shira is sensitive to the weakening of stratification. Therefore, the absence of PSB traces in the bottom sediment layers (carotenoids, DNA) can indicate periods of holomixis or weak meromixis (Zykov et al., 2012; Rogozin et al., under preparation), which is valuable information for paleo-limnological reconstruction.

Reasons for meromixis disturbance

It should be noted that in most of the winters the lake was on the verge of complete mixing. Namely, in winters of 2003, 2009, 2010, 2013 and 2014 the stability of the lake was close to zero (Fig.4), and the salinity profiles, respectively, were almost uniform (Fig.3). However, there were no complete mixing, perhaps because of temperature stratification (Fig. 3) and lack of enough mechanical energy to fully mix.

Seasonal and interannual variations of the chemocline depth are typical for meromictic lakes (for example von Rohden et al., 2009). In a freezing salt lake, the depth of mixing depends on the distribution of salinity formed by autumn, and on the depth of thermohaline convection in the process of ice formation. The autumn salinity profile, in its turn, is determined by the initial spring profile and the effect of the wind during the entire open period (most in spring and autumn, when the temperature stratification is minimal). The spring profile of salinity is affected by the ice thickness during the previous winter: the thicker was the ice, the stronger will the salinity gradient be after its melting. Moreover, the additional inflow of water to the surface also increases the salinity gradient, increasing the stability of stratification. All the above factors are summarized in Fig. 7.

In 2014, the lake had the weakest spring and summer salinity stratification for the entire observation period, as seen in Fig. 3.

Accordingly, the ST value in the spring of 2014 was also the lowest in comparison with all the previous years (Fig. 8). Unfortunately, we did not measure the autumn CTD profile in 2014, but since there is a significant correlation between autumn and spring ST (Fig. 8a) we can estimate the autumn ST by linear regression. The estimated autumn ST for 2014 is the lowest of all (Fig. 8a), which probably was the reason that caused deep mixing in the winter of 2015. In the autumn of 2015, the stability was also low, which led to deep mixing in March 2016. However, in the autumn of 2016, the stability considerably increased (Fig. 4), as a result of which in March 2017 the mixing was incomplete, i.e. the lake returned to the meromixis.

Although not maximum, the ice in March 2015 was rather thick (0.92 m, Table 1), which, perhaps, further contributed to deep mixing. However, the ice in March 2016 was quite thin (0.77 m, Table 1), which was probably the reason why the mixing in 2016 was less pronounced than in 2015 (in May 2016 the traces of hydrogen sulfide were still found deeper than 21 m). In general, the depth of mixolimnion in Lake Shira is weakly positively correlated with the ice thickness of (r = 0.14, Table 2), and negatively with the ice thickness in the previous winter (r = - 0.25, Table 2), which confirms the validity of the scheme in Fig. 7.

Thus, the point of the greatest interest is the weakening of the lake stratification in the spring of 2014. The spring ST significantly negatively correlated with the wind energy in the spring period (r = - 0.85, n = 10, P< 0.01, Fig. 8b). Accordingly, the depth of the winter mixing significantly positively correlated with the wind energy in the previous spring period (r = 0.63, p < 0.01, Table 2), while the autumn winds were less important (r = 0.29, Table 2). Therefore, we conclude that spring winds influenced the lake stratification to the great extent. It should be noted that in the spring of 2014 the wind energy was the greatest (Table 1); therefore, it can be assumed that the reason for the weakening of stratification in 2014 was the strong wind impact in spring, probably caused by the early ice melt.

It could be expected that anomalously large amount of wind energy in the autumn of 2013, in combination with abnormally late freeze-up (Table 1), should have led to strong mixing. However, in 2013 both spring and autumn salinity stratifications were noticeably stronger than in 2014 (Fig. 3, 8) that is probably why in the winter of 2014 there was no complete mixing.

Influence of additional inflow on stratification

During the period 2002-2007, the water level in Lake Shira considerably increased due to an additional influx of fresh water to the surface (Fig. 3). This obviously increased the salinity gradient, as seen in Fig. 3, and increased the stability of the water column to mixing. A significant positive correlation between the depth of winter mixing and the annual increase in the level (r = -0.71, P <0.01, n = 13, Table 2) supports this assumption.

We roughly estimated the quantitative contribution of additional freshwater inflow to the increase in the lake stratification stability on the basis of the following considerations. Since the rise in the level occurred mainly in spring and early summer, it can be assumed that the entire additional volume of fresh water entered the epilimnion only. Let this volume be $\Delta V = \Delta h*A$, where A is the surface area of the lake, and Δh is the level rise as compared to the previous winter. The depth of the epilimnion is determined by the upper uniform section on the measured summer salinity profile. Let the volume of the epilimnion in a given year be V, and its salinity S. Without an additional influx, the volume of epilimnion would be $V' = V - \Delta V$, and the salinity $S' = S*V/(V - \Delta V)$, respectively. Then the profile would differ from the measured one, as shown in Fig. 9. The difference between the ST values calculated for the measured and hypothetical profiles (ΔST) reflects the contribution of additional freshwater inflow to the increase in the lake stability in a given year. The values of ΔST were 554, 354 and 144 J m^{-2} for 2003, 2004 and 2005, respectively (Fig.9), and comparable in magnitude to the lake stability in the winter periods of 2004-2008 (Fig.4). Despite the fact that the 2006 summer profile is not available, it can be deduced from the level increase of 25 cm (Fig. 6) that the value of ΔST for 2006 lies most probably between the values of 2003 and 2004.

Thus, it is obvious that without additional fresh water inflow, the kinetic energy from the wind stress could have spread deeper during the autumn mixing of 2003-2006, and, thus, would lead in deeper winter mixing. It can be concluded that the additional inflow made a significant contribution to the maintenance of the lake meromixis during the period of the lake level rise in 2002-2007. Similar approach was used by Boehrer et al. (2014) to quantify the capping effect of freshwater introduction into meromictic saline mining lakes in Germany.

It should, however, be noted that during that period the spring winds were noticeably weaker (Table 1), which could also contribute to stability. Indeed, the rise in the level is significantly negatively correlated with the amount of wind energy in spring (r=-0.77, P <0.01, Table 2), so we can not reliably separate the effect of the level rise from the weakening of the wind effect on the mixing of the lake.

History of Lake Shira meromixis

The analysis of the documented dynamics of Lake Shira level for last ca. 100 years in conjunction with the analysis of the sediments composition confirms the causal relationship between origin of meromixis and lake level increase. The main biomarkers of a meromictic state are the pigments of phototrophic sulfur bacteria (Zykov et al., 2012). Their presence indicates the presence of hydrogen sulfide in the photic zone of the lake (Overmann et al., 1993). In the work by Zykov et al. (2012) it was shown that in the sediments corresponding to the period when the level of Lake Shira was minimal (7 m below the present), there was no okenone (the specific carotenoid of purple sulfur bacteria), indicating that the lake was holomictic from the 1910-s to the 1920-s. The emergence of okenone in sediments coincides with the rise of water level in the 1930-40-s, which indicates the setting of meromixis at that time (Zykov et al., 2012; Kalugin et al., 2013). In more ancient layers of the lake analyzed up to the age of about 4.5 thousand years BP, the okenone content shows sharp fluctuations, including a complete absence in some layers (Rogozin, in preparation). Thus, we can conclude that meromixis in the lake was a temporary phenomenon, which was likely to occur and increase during the rise of the lake, and to weaken or completely disappear in times of a constant level or decrease.

Thus, our results suggest that meromixis in Lake Shira pertains to ectogenic type according to the standard classification by Hutchinson (1957). Also this meromixis can be termed as a Type Ia ectogenesis (Walker and Likens, 1975), i.e. it is caused by the inflow of fresh water on the surface of the salt lake. Such mechanism is typical for closed saline lakes in Canada, where it was shown that the excessive inflow of fresh water, resulting in an increase in the lake level, leads to meromixis (Hammer, 1994). In addition, our results proved that the annual processes of formation and melting of the ice cover also support the meromixis.

No systematic all-season observations of the nature of the lake stratification were carried out until 2002, so the mixing regime of the lake in earlier periods is not known. The presence of purple sulfur bacteria in the water column of the lake was first reported by Popova (1946). Thus, at the time the lake was probably meromictic. For the first time the meromictic nature of the lake was pointed at by Zotina et al. (1999), who also comprehensively described the seasonal dynamics of the vertical distribution of salinity and temperature for 1997-1998, which was similar to that identified by us for the period 2001-2014. Then Kopylov et al. (2002) showed that in the summer of 1999 purple sulfur bacteria of the genus *Thiocapsa* formed the abundance peak of about 10^6 cells ml^{-1} at a depth of 13 m in the redox zone, therefore, at the time the lake was meromictic, too.

Conclusions

In 2015 and 2016, the stratification of Lake Shira changed from meromictic to holomictic. This phenomenon was documented for the first time. The mixing took place in the late under-ice period, i.e. after the middle of March 2015 and 2016. We assume that the most influential factor contributing to the winter mixing in 2015 was strong wind action due to early ice melt in the spring of 2014. The reasons of deep mixing of 2016 are not so evident but the mixing was probably less dramatic than in 2015 as it can be deduced from the presence of trace concentrations of sulphide in near-bottom layers. In March 2017 the mixing was not deep and the lake was meromictic again. Thus, we have shown that currently the mixing regime of Lake Shira can vary considerably, and is sensitive to external factors.

We do not claim complete coverage of all the reasons, but, judging by the data available to us, the lake mixing is largely determined by spring density profiles. In turn, the wind stress in spring was an important factor influencing the stability of initial profiles at the beginning of open-water period, and consequently – the resistance of autumnal profiles to mixing.

It was shown that in the period from 2002 to 2007 an increased inflow of fresh water caused the lake level rise, increasing the stability of the water column and consequently decreasing the depth of the autumn mixing. Also the wind stress was much lower in that period. Therefore a combination of freshwater inflows with relatively weak wind action supported the stable meromixis of the lake. In the period from 2007 to 2015 the water level did not increase, reducing the stability of the water column and making the lake mixolimnion more sensitive to the wind stress which also increased. Therefore we cannot separate the effect of level increase from effect of wind increase on the lake stratification for the period of the study.

The significant increase in the amount of organic carbon, chlorophyll a, biomass of copepods *Arctodiaptomus salinus* and number of phytoflagellates observed in the water column in the early summer of 2015 was probably due to the release of nutrients into the photic zone during the mixing of monimolimnion. The disappearance of purple sulfur bacteria from monimolimnion was a consequence of meromixis breakdown.

Our results provide valuable information about the dynamics of the ecosystem of Lake Shira, and hopefully they would help us to predict the state of the lake under different weather scenarios and anthropogenic impacts. That is especially important in terms of possible global warming. In addition, the established causal relationship between meromixis stability and the level increase can be used for the reconstruction of paleo-climate humidity based on the indicators of anoxia in bottom sediments.

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Table 1. Selected meteorological variables and parameters of Lake Shira over the years 2002-2017. **h** –mixolimnion thickness in March, **Ice** – ice thickness in March, $\mathbf{W_{spr}}$ – total wind energy over the period from the date of ice melt to May 25, $\mathbf{W_{aut}}$ – total wind energy over the period from the date of transition of the air temperature below +3°C (dates not shown) to the date of ice formation. **ΔL** – difference in water level in March as compared with the March of the previous year.

Year	h, m	Date of ice melt	Date of ice formation	Ice, m	W_{spr} J m^{-2}	W_{aut} J m^{-2}	ΔL, m
2002	-	01.05	29.11	-	1958	4160	0.12
2003	16.15	11.05	13.11	1.00	920	2745	0.11
2004	9.52	04.05	11.11	1.00	868	1109	0.42
2005	11.12	26.04	19.11	0.63	2280	2346	0.23
2006	-	14.05	23.11	0.88*	1448	3748	0.11
2007	12.6	27.04	28.11	0.77	5910	2491	0.25
2008	15.51	14.04	01.12	0.85	4447	4780	-0.13
2009	15.72	03.05	09.11	1.02	5458	2888	-0.10
2010	17.60	07.05	24.11	1.30	2007	3284	0.08
2011	12.95	25.04	18.11	1.01	3709	210	0.03
2012	11.89	24.04	24.11	0.50	5178	2525	0.06
2013	15.42	08.05	08.12	1.01	3575	13582	0.03
2014	16.5	18.04	20.11	0.88	6685	3512	0.05
2015	22	25.04	17.11	0.92	3616	4311	-0.07
2016	23	-**	-**	0.77	-**	-**	-0.09

*- data of Hydrometeorological Service

** - data of 2016 were not available in early 2017

Table 2. Coefficients of pair correlations between selected parameters from Tab.1 The marked values are significant at $p < 0.01$ ($n = 13$).

Variable	h	W_{spr}	W_{aut}	Ice	Ice_{pr}
W_{spr}	**0.63***	1			
W_{aut}	0.29*	0.04	1		
Ice	0.14	0.27	0.18	1	
Ice_{pr}	-0.25	-0.29	0.07	-0.09	1
ΔL	**-0.71**	**-0.77**	-0.14	-0.05	0.17

* Calculated for $W_{spr,\ aut}$ of previous calendar year.

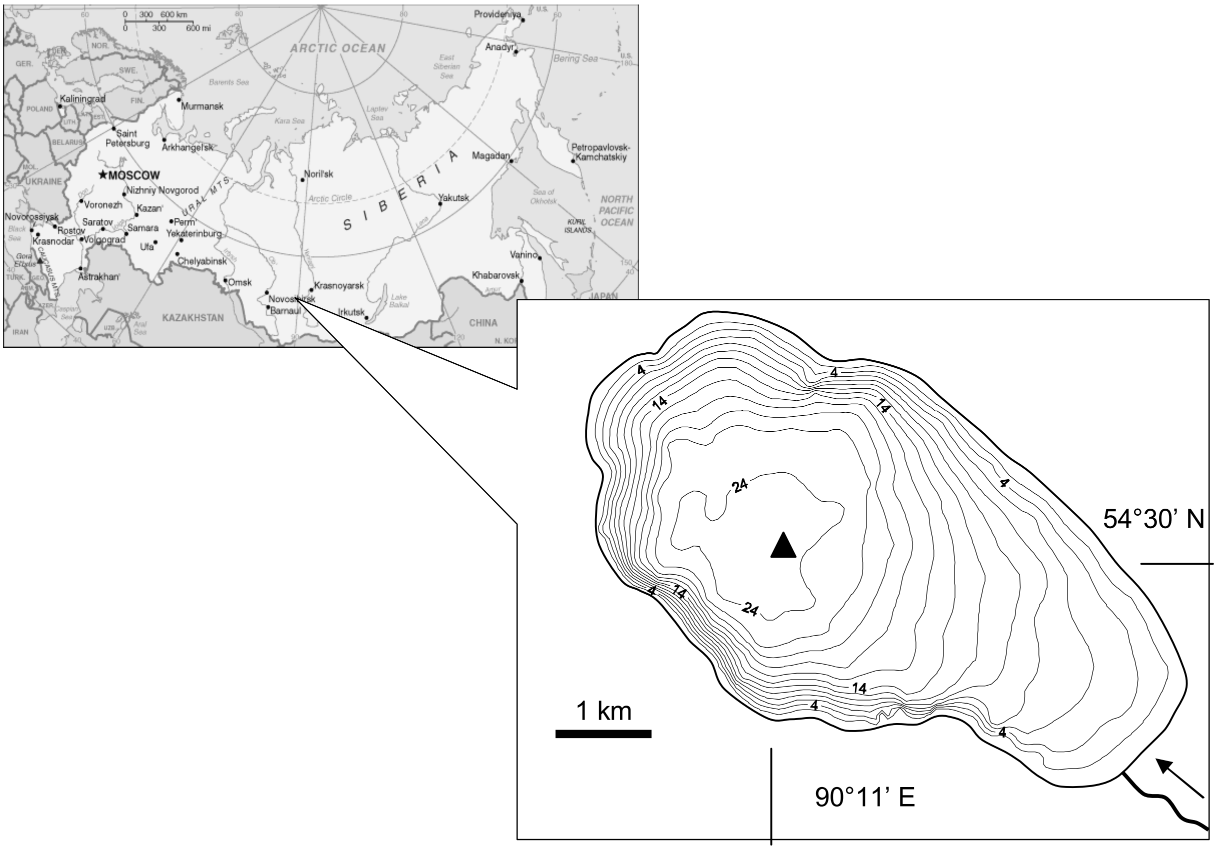
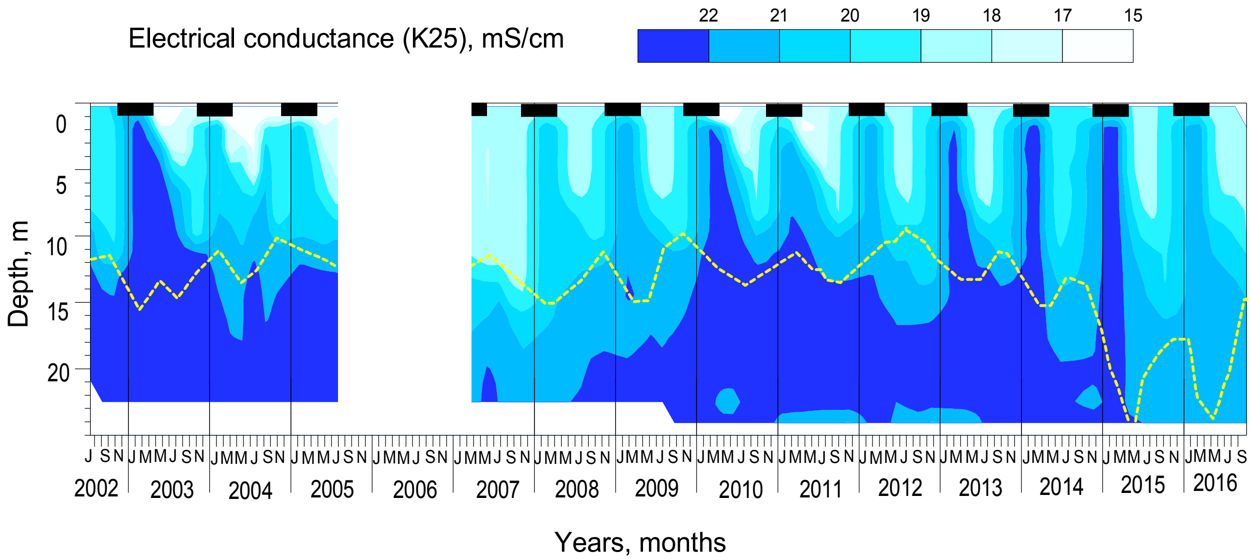
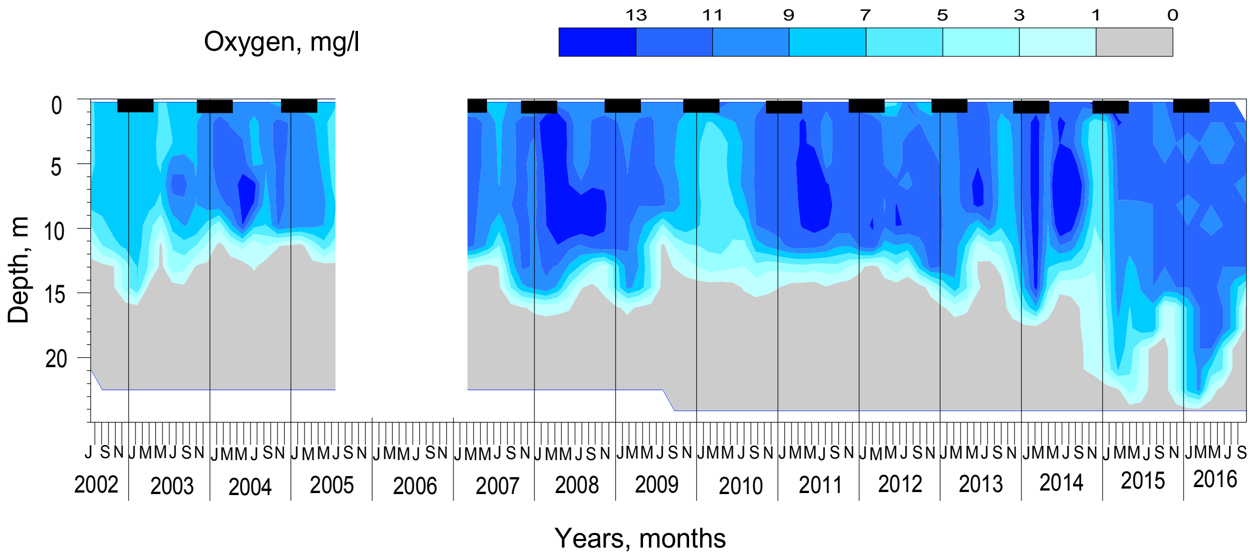


Fig. 1. Location of the study area, bathymetry map and sampling station (▲) of Lake Shira.


Electrical conductance (K25), mS/cm
22 21 20 19 18 17 15
Depth, m
0 5 10 15 20
2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016
Years, months


Oxygen, mg/l
13 11 9 7 5 3 1 0
Depth, m
0 5 10 15 20
2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016
Years, months

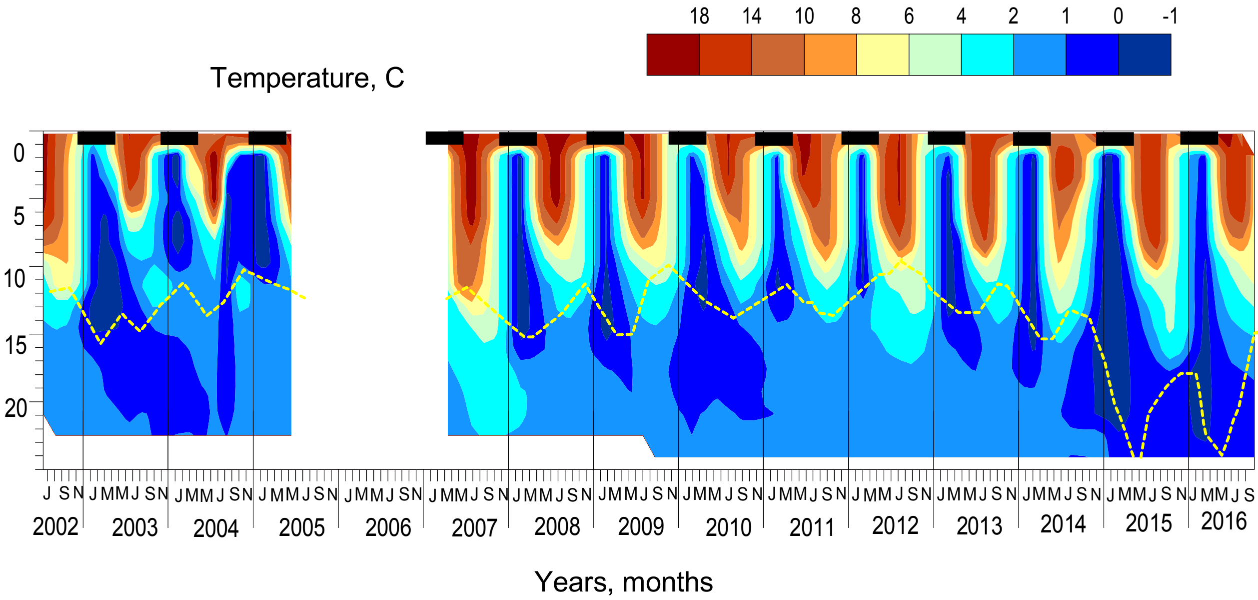

Temperature, C
18 14 10 8 6 4 2 1 0 -1
0 5 10 15 20
2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016
Years, months

Fig.2 Contour plots of electrical conductivity adjusted to 25° C (K_{25}), oxygen and temperature of Lake Shira versus time and depth through the years 2002-2016. The dashed line denotes the oxic-anoxic interface.

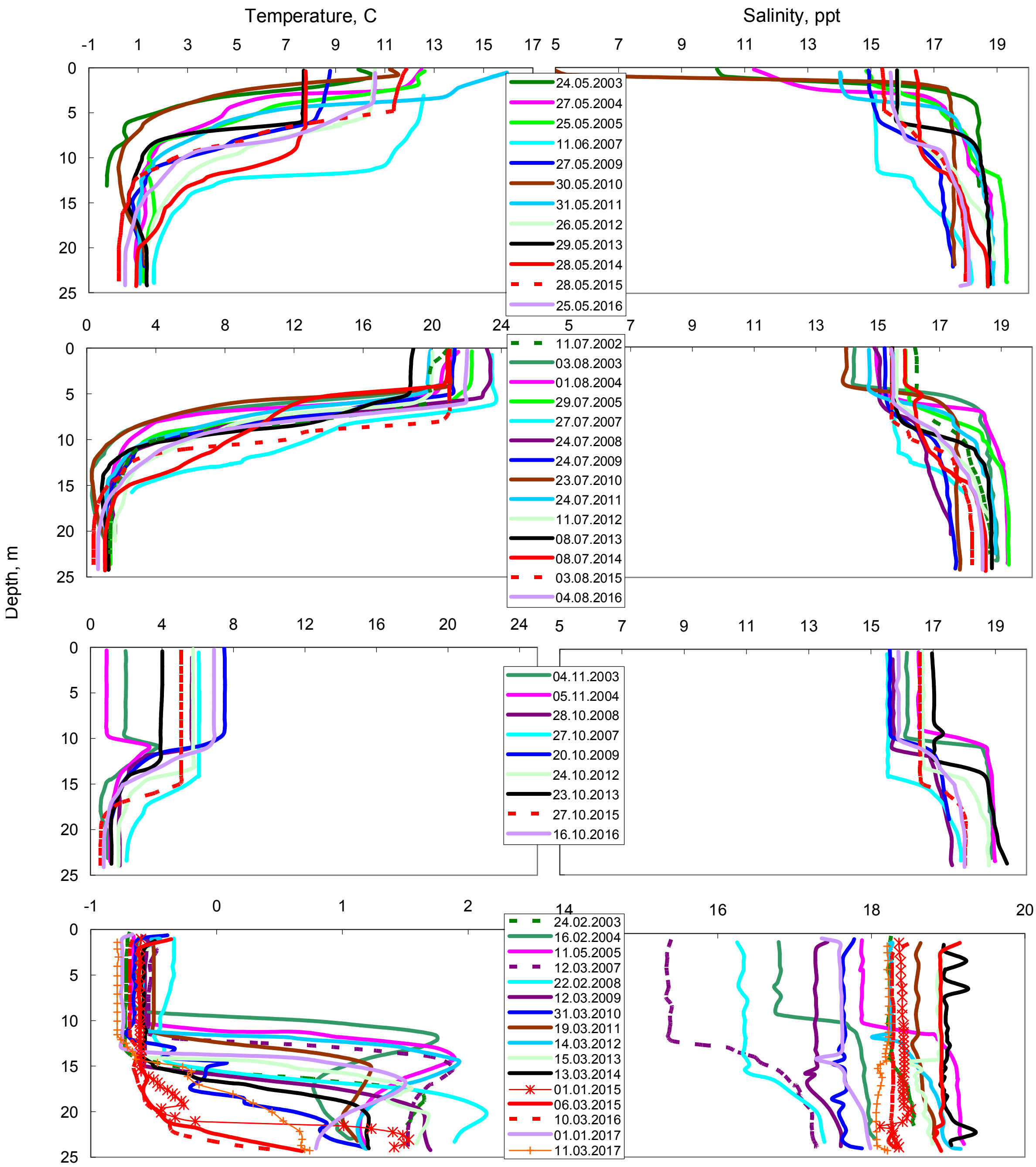


Fig. 3 Depth profiles of temperature (left panels) and salinity (right panels) at the center of Lake Shira over the years 2002 - 2017.

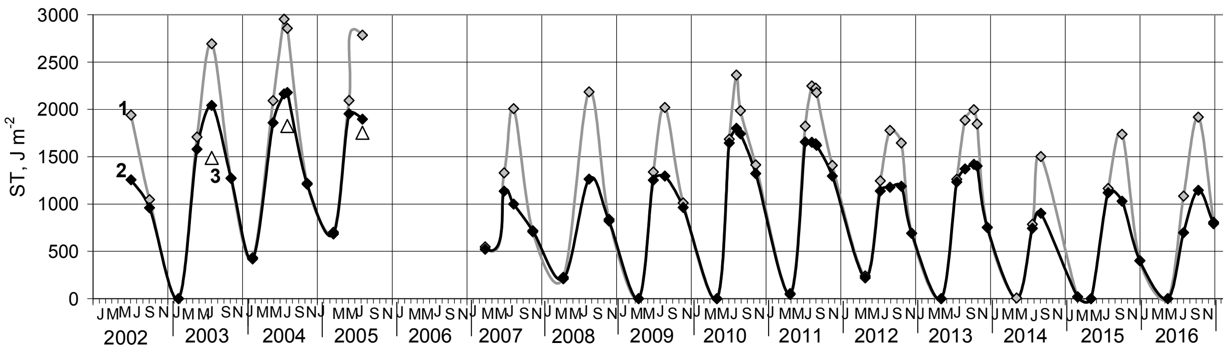


Fig. 4 Potential energy of stratification of Lake Shira through the years 2002-2016 (the ice was excluded from stability calculations): **1** – Schmidt stability, **2** – Schmidt stability at constant temperature (ST), **3** – ST estimated for the hypothetical case if there were no additional inflows of fresh water (see also Fig 9).

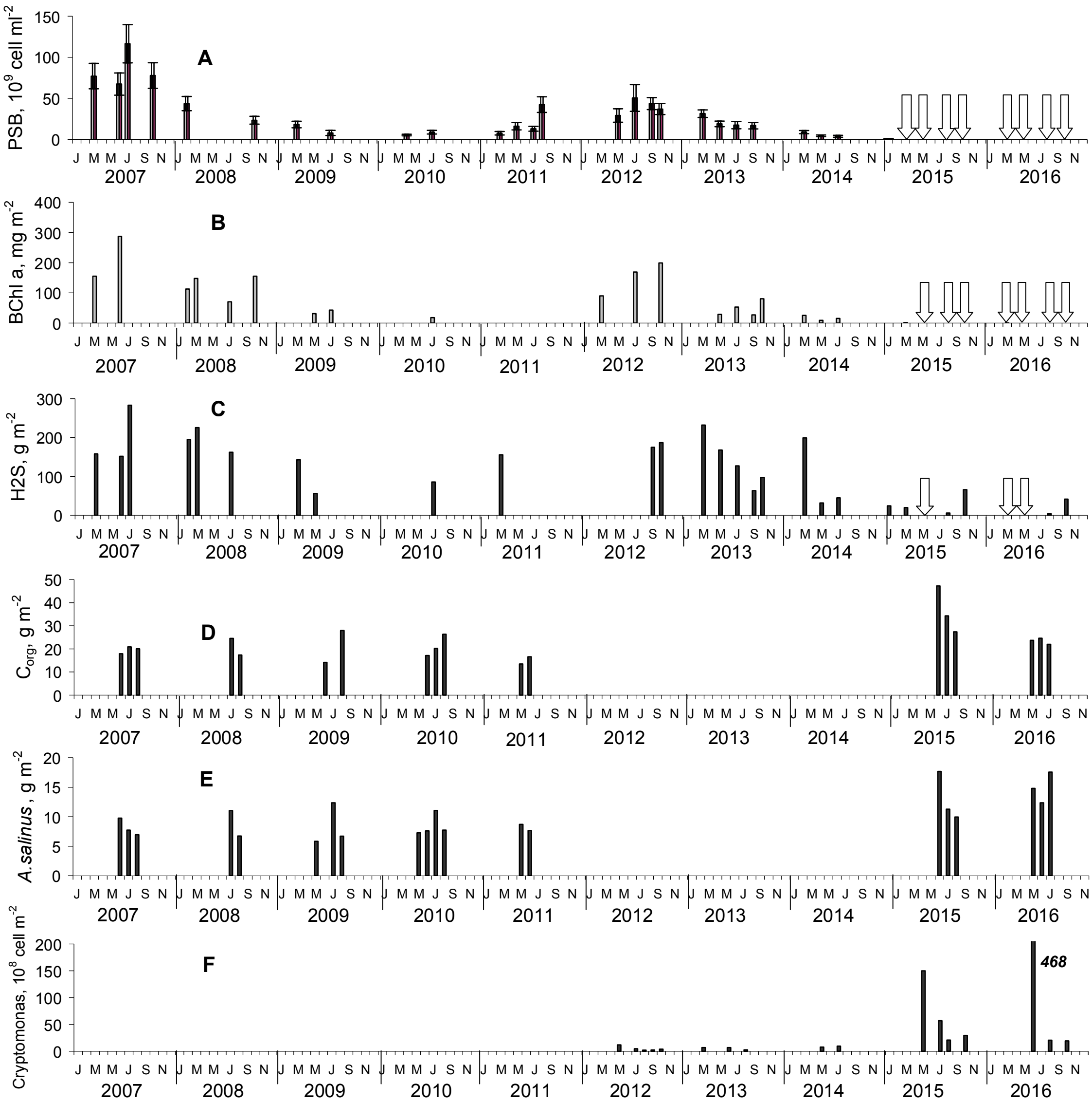


Fig. 5 Temporal variation of selected biological components and hydrogen sulfide in the water column at the center of Lake Shira over the years 2007-2016 (data for 2002 - 2013 from Rogozin et al, 2016): **A** - number of PSB cells; B - amount of Bacteriochlorophyll *a*; C - amount of hydrogen sulfide; D - amount of organic carbon in seston; E – biomass of copepods *Arctodiaptomus salinus*; F - number of *Cryptomonas spp*. In June 2016, *Cryptomonas* exceeded the range of the scale, so it is shown by the number. Arrows in diagrams A, B, C show the dates when the characteristics were below the detection limit (2015, 2016). Gaps mean no data.

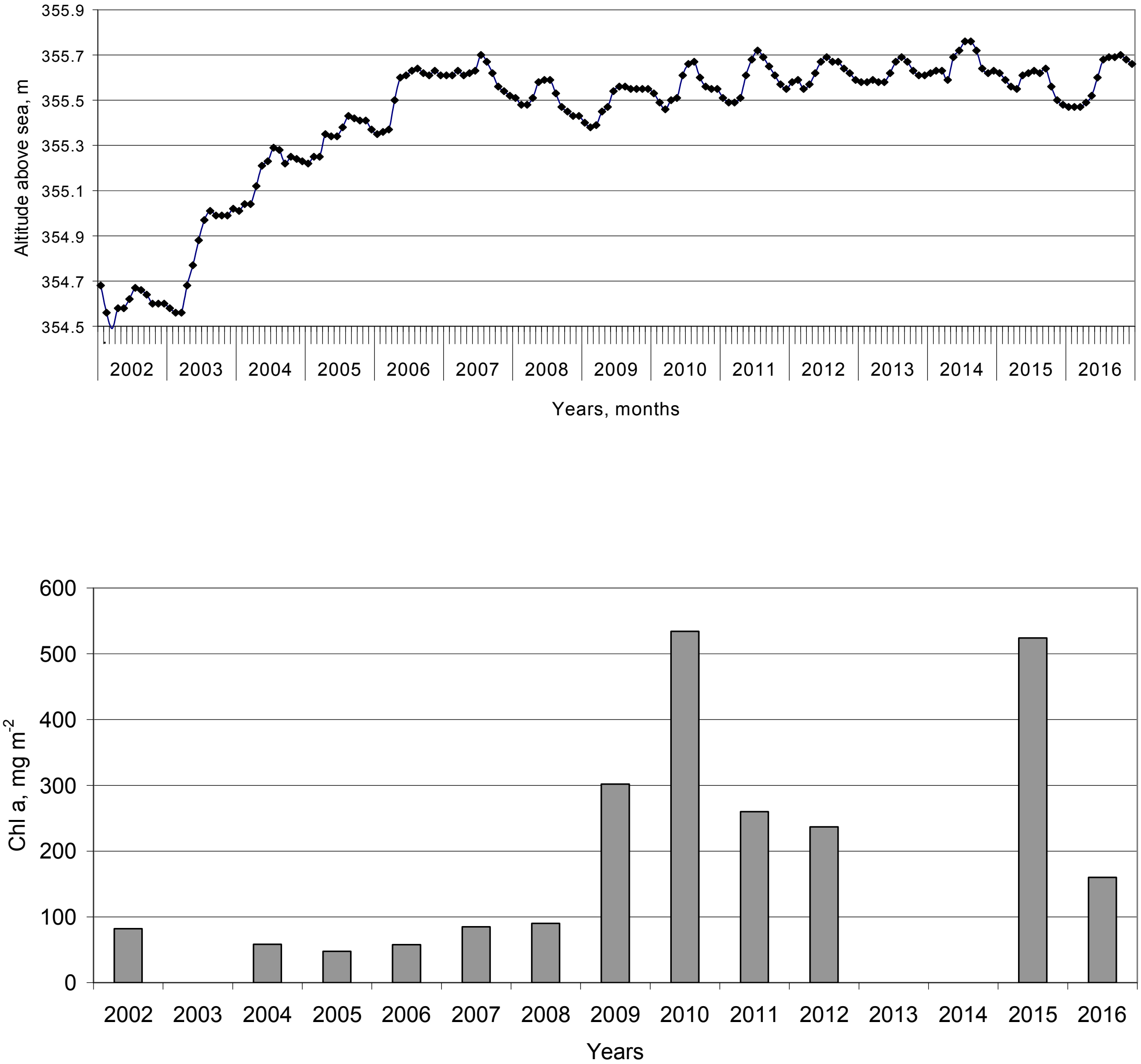


Fig.6 Water surface elevation of Lake Shira (above) and the total amount of Chlorophyll *a* in the depth range of 0-18 m in July and August (below) through the years 2002-2016. Gaps mean no data.

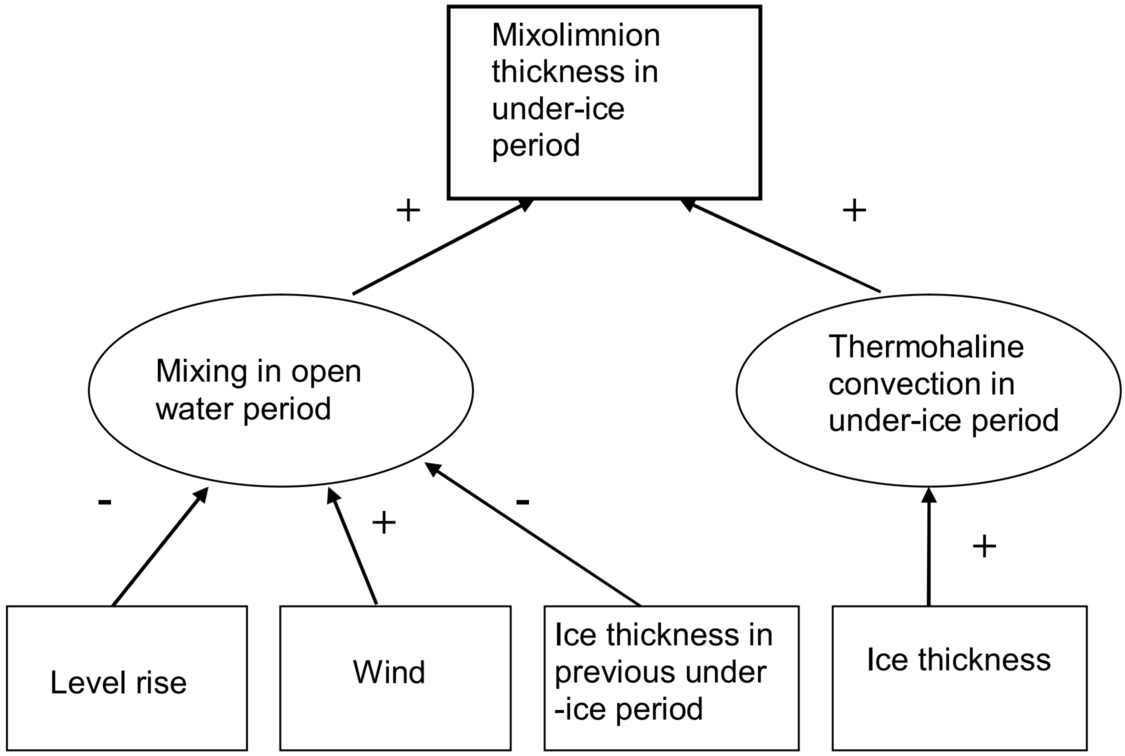


Fig.7 Schematic diagram of the main factors and processes affecting the thickness of winter mixolimnion in Lake Shira. Ellipses designate processes, rectangles - factors. See explanations in the text.

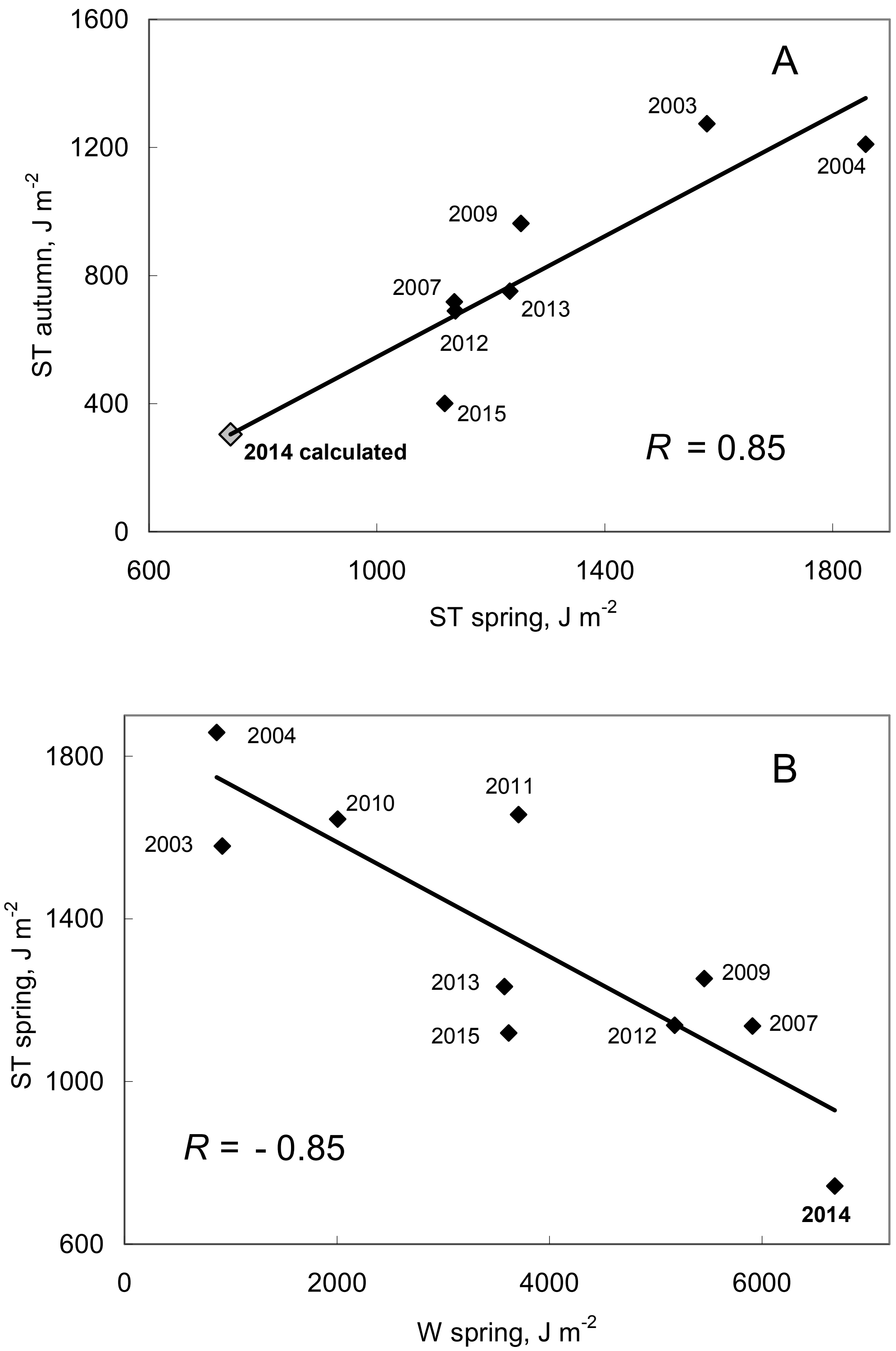


Fig. 8 **A**: autumn stability of salinity stratification (ST) versus spring one. Value for autumn 2014 was calculated by linear regression based on data 2003-2015. Values of 2010 and 2011 were excluded from analysis because the autumn profiles

were measured too early at these years. **B**: stability of salinity stratification (ST) versus wind energy in the spring.

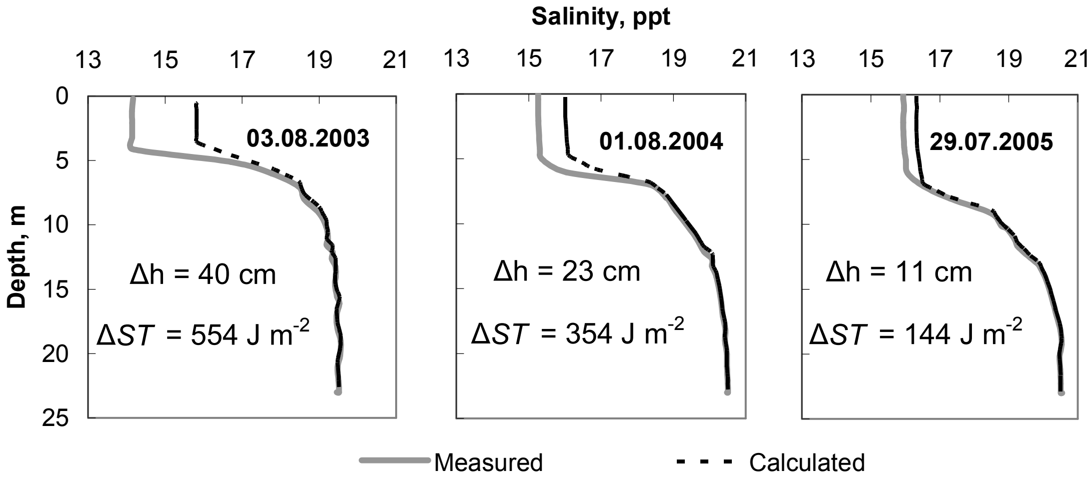


Fig.9 Depth profiles of salinity measured in summers of 2003-2005 (solid lines) and calculated (dashed lines) for the hypothetical case if there were no additional inflows of fresh water (see also Fig 4). Δh - the increase in water surface level from winter to summer (see Fig. 6), ΔST – differences between ST of measured and hypothetical profiles (see explanation in text).