BOREAL ENVIRONMENT RESEARCH 23: 237–247
ISSN 1797-2469 (online)

Helsinki 29 August 2018

Effects of similar weather patterns on the thermal stratification, mixing regimes and hypolimnetic oxygen depletion in two boreal lakes with different water transparency

Ivan Mammarella[1,*], Galyna Gavrylenko[2], Galina Zdorovennova[2], Anne Ojala[1,3,5], Kukka-Maaria Erkkilä[1], Roman Zdorovennov[2], Oleg Stepanyuk[1,4], Nikolay Palshin[2], Arkady Terzhevik[2], Timo Vesala[1,5] & Jouni Heiskanen[1,6]

1) *Faculty of Science, Institute for Atmosphere and Earth System Research/Physics, P.O. Box 68, FI-00014 University of Helsinki, Finland (*corresponding author's e-mail: ivan.mammarella@helsinki.fi)*
2) *Northern Water Problems Institute, Karelian Research Centre, Russian Academy of Sciences, Aleksander Nevsky st. 50, RU-185030 Petrozavodsk, Russia*
3) *Faculty of Biological and Environmental Sciences, Ecosystems and Environment Research Programme, Niemenkatu 73, FI-15140 Lahti, Finland*
4) *Institution of Russian Academy of Sciences, Dorodnicyn Computing Centre of RAS, Vavilov st. 40, RU-119333 Moscow, Russia*
5) *Institute for Atmosphere and Earth System Research/Forest Sciences, P.O. Box 27, Faculty of Agriculture and Forestry, FI-00014 University of Helsinki, Finland*
6) *ICOS ERIC, Erik Palménin aukio 1, FI-00560 Helsinki, Finland*

Received 18 Aug. 2017, final version received 22 Aug. 2018, accepted 23 Aug. 2018

Mammarella I., Gavrylenko G., Zdorovennova G., Ojala A., Erkkilä K.-M., Zdorovennov R., Stepanyuk O., Palshin N., Terzhevik A., Vesala T. & Heiskanen J. 2018: Effects of similar weather patterns on the thermal stratification, mixing regimes and hypolimnetic oxygen depletion in two boreal lakes with different water transparency. *Boreal Env. Res.* 23: 237–247.

Mechanistic understanding of the impacts of changing climate on the thermal stratification and mixing dynamics of oxygen in lake ecosystems is hindered by limited evidence on how functioning of individual lakes is affected by interannual variability in meteorological conditions. We studied two boreal lakes (Kuivajärvi and Vendyurskoe) with different water clarity during three years representing a gradient of meteorological forcing. The lakes are located in the same climatic region and have a similar depth, but, because of the difference in water transparency, they responded differently to the weather fronts. Long spring overturn and relatively cold summer resulted in weak stratification and well-oxygenated water column in both lakes. However, in dark-water Kuivajärvi, the hypolimnion was unusually warm leading to high production rate of CO_2. Warm summer had the most dramatic impact on clear-water lake Vendyurskoe changing its mixing regime from typical polymixis to dimixis, leading to strong oxygen depletion and ensuing anoxia. In dimictic dark-water Kuivajärvi, hot spring resulted in early onset of stratification with ensuing low hypolimnetic temperatures and persistent oxygen depletion. These results indicate that climate warming will increase the risk of occurrence of deep water anoxia.

Editor in charge of this article: Sari Juutinen

Introduction

In northern latitudes, freshwater ecosystems are an intrinsic component of the landscape (Meehl *et al.* 2007, van Oldenborgh *et al.* 2013). In Europe there are more than 500 000 natural lakes larger than 0.01 km^2 and three out of four lakes are in Scandinavia, Finland and North West Russia (https://www.eea.europa.eu/themes/water/european-waters/lakes). Surface water temperatures in lakes are increasing throughout the globe, including the northern areas (O'Reilly *et al.* 2015, Weyhenmeyer *et al.* 2017). Besides the long-term trends, lakes are facing more regularly extreme events such as spells of strong winds, episodes of high precipitations and heat waves (Stocker *et al.* 2013, Kuha *et al.* 2016).

Climate change affects water column stratification in global lakes. In some northern lakes, effects of climate warming may be strong and eventually lead to a mixing regime shift from typical polymictic or dimictic to monomictic or meromictic (Kirillin 2010, Shatwell *et al.* 2016). However, this shift is likely controlled by intrinsic characteristics of individual lakes, such as depth, morphometry and water transparency. Understanding mechanistic relationships between mixing regimes of different lakes is needed when assessing climate change effects on the timing of emission peaks of greenhouse gases (GHG) and appearance of noxious phytoplankton blooms. Increasing air temperatures may result in an earlier and sometimes longer spring turnover periods (Weyhenmeyer *et al.* 1999, Arvola *et al.* 2010). On the other hand, there is also emerging evidence that, in some small dark-water lakes surrounded by forest and sheltered from wind effect, increasingly warm spring weather conditions may lead to strong stratification arising almost immediately after ice-cover disappearance. In this weather pattern, spring turnover does not take place and the lake becomes effectively monomictic, e.g. as found in Valkea-Kotinen, a lake in Finland (Huotari *et al.* 2009, Arvola *et al.* 2010). Disappearance of spring mixing have significant consequences for lake ecosystem functioning, e.g. for the development of phytoplankton communities, especially diatoms, and release of GHGs accumulated in winter underneath the ice cover (López-Bellido *et al.* 2009, Ojala *et al.* 2011). Rapid heating of surface water during spring may also favor strong summertime stratification and such thermal-shielding (Bartosiewicz *et al.* 2015) leads to a relatively cooler temperatures in the hypolimnion and in the sediments (Golosov *et al.* 2007, Heiskanen *et al.* 2015). As temperature regulates microbial processing, these effects can have consequences for the production of GHGs, such as carbon dioxide (CO_2) and methane (CH_4) (Schulz *et al.* 1997), and progress of oxygen depletion in the bottom waters (Golosov *et al.* 2007).

Strong stratification carries higher risk of oxygen depletion, especially in lakes, which, due to higher precipitation and reduced soil frost, receive enhanced nutrient loadings from agricultural land. However, hypolimnetic anoxia is a common feature in boreal forest lakes, because lakes with high humic content and thus dark color, typical of lakes surrounded by forested catchments, leads to stronger stratification, warmer epilimnion and colder hypolimnion (Nordbo *et al.* 2011, Peltomaa *et al.* 2013, Heiskanen *et al.* 2015). On the other hand, clear water lakes, which are often polymictic, can develop towards dimixis as a result of warmer summers, and may experience time periods of hypolimnetic hypoxia and finally anoxia (Wilhelm and Adrian 2008, Efremova *et al.* 2015).

The aim of this study is to investigate how different weather conditions affect water column stratification and gas concentration patterns (especially in the hypolimnion) in two boreal lakes (Kuivajärvi and Vendyurskoe) located within the same geological and climatological region, but with differing size and water transparency. We used simultaneous high frequency water temperature and gas (O_2 and CO_2) concentration data measured in three years, characterized by different weather conditions and representing three distinct climate forcing patterns.

Material and methods

Study sites

The study lakes reside in the boreal zone approximately 500 km apart (Fig. 1). Vendyurskoe is a relatively small (7 km long, 1.5 km wide, surface area of 10.4 km^2) and shallow (mean depth of

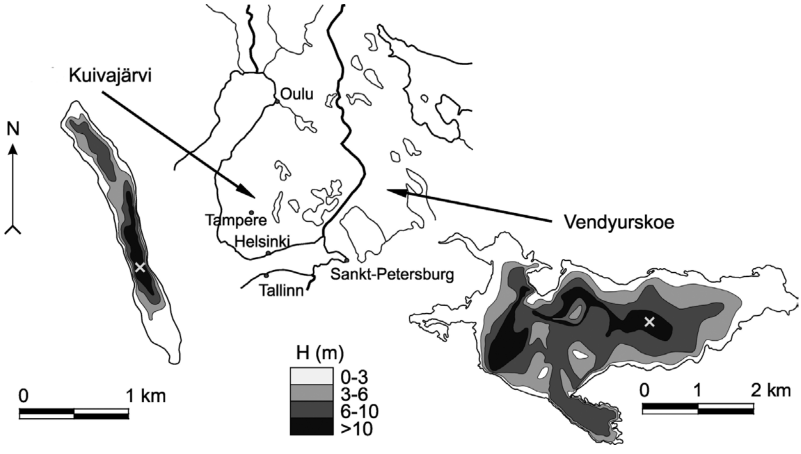

Fig. 1. Approximate locations (shown by arrows) and bathymetric maps of Vendyurskoe and Kuivajärvi. The white crosses indicate the measurement locations.

5.3 m, maximum depth 13.4 m) lake of glacial origin located in southern part of Karelia, Russia (62°10′–62°20′N, 33°10′–33°20′E, 145 m above sea level). Vendyurskoe is polymictic, i.e. repeatedly mixed during the open water period. The lake is currently mesotrophic, and Secchi disk depth is 3.0 ± 0.5 m. The dissolved organic carbon (DOC) concentration is 5–6 mg l^{-1}, the organic nitrogen concentration 400–600 µg l^{-1} and the phytoplankton growth is limited by low concentration of phosphorus (inorganic 0–5 µg l^{-1} and total 10–25 µg l^{-1}) (Filatov and Kuharev 2013).

Kuivajärvi is a small humic lake (2.6 km long, 0.4 km wide, surface area of 0.6 km^2) located in southern Finland (61°50′N, 24°17′E, 141 m above sea level) and surrounded by mixed coniferous forest. There are two distinct basins within the lake: the deeper southern part and shallow northern one. Maximum and mean depth of the lake are 13.2 m and 6.4 m, respectively (Heiskanen *et al.* 2014). Kuivajärvi is dimictic, its complete mixing takes place twice a year, i.e. in the spring after ice-off and during the autumn cooling after the destruction of the seasonal thermocline. The lake DOC concentration is 11.8–14.1 mg l^{-1}, total nitrogen concentration 370–500 µg l^{-1}, and the total phosphorus concentration 14–21 µg l^{-1} (Miettinen *et al.* 2015). The Secchi disk depth ranges from 1.2 to 1.5 m.

Data collection and analysis

Years 2010, 2013 and 2015 were chosen for the analysis since they present three different meteorological conditions and have extensive data coverage in both lakes.

In Vendyurskoe, measurements of water temperature (T_{water}) and dissolved oxygen (DO) were carried out in the central deep-water part of the lake (Fig. 1). The thermistor chain was equipped with temperature sensors TR-1060 (range –5 to +35 °C, accuracy ±0.002 °C, resolution < 0.00005 °C) and dissolved oxygen sensors DO-1050 (range 0%–150%, accuracy ±1%) (RBR Ltd., Canada). There were 9–11 sensors between 2 and 11 m with slight changes to the exact depths each year. Time interval for the readings was 1 min. Meteorological data, including wind speed, precipitation and air temperature (T_{air}), were obtained from the nearest weather station “Petrozavodsk” located at a distance of 70 km from the study site.

In Kuivajärvi, measurements were carried out on a platform in the central deep-water part of the lake (Fig. 1). T_{water} was measured with a thermistor chain equipped with 16 Pt-100 resistance thermometers (accuracy 0.2 °C, depths 0.2, 0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0, 4.5, 5.0, 6.0, 7.0, 8.0, 10.0, and 12.0 m). Also the vertical profiling of DO concentration (mg l^{-1}, YSI ProODO, Yellow Springs Instruments, Yellow Springs, OH, USA) was carried out in 2013 and 2015 near the thermistor chain. Profiling was performed every week at 0.5 m intervals between the surface and 9 m and deeper than 9 m at 1 m intervals down to near the sediment (Miettinen *et al.* 2015). Partial pressure of CO_2 (pCO_2)

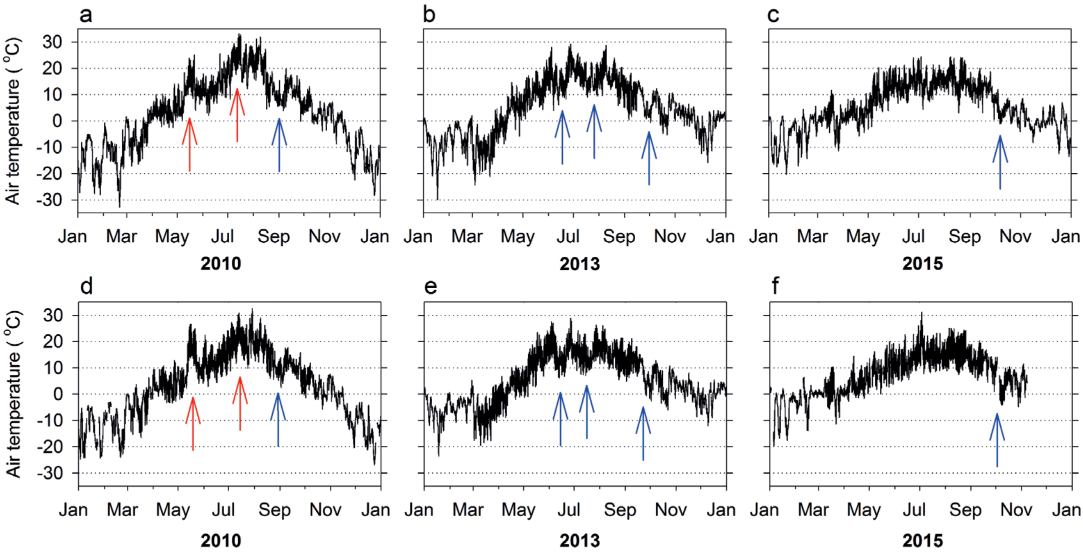

Fig. 2. Air temperatures in 2010, 2013 and 2015 at Vendyurskoe (**a**, **b**, **c**), and at Kuivajärvi (**d**, **e**, **f**). Examples of warm fronts are indicated by upward red arrows and cold fronts by blue arrows. Data are 3 hours and 30 min averages.

throughout the water column was estimated in 2010 from weekly manual samples using the head space method as described in López-Bellido *et al.* (2009). In 2013 and 2015, continuous measurements of CO_2 at 7 m depth were performed with airstream circulation system as described in Hari *et al.* (2008). Meteorological data were collected on a platform in the middle of the lake. More details related to meteorological measurements are given in Heiskanen *et al.* (2014) and Mammarella *et al.* (2015).

The combined information on water temperature and bathymetry was used in the Lake Analyzer 3.4 program (Read *et al.* 2011) to calculate the Schmidt stability (St), which describes the water column stability as resistance to mechanical mixing that is caused by the potential energy of the stratification (Idso 1973). The Pearson’s linear correlation method was used to calculate correlation coefficients between the time series (T_{air} and air pressure) measured at the two lake stations.

Results

The lakes were exposed to same major weather events in all studied years, indicated by the similar T_{air} (Fig. 2) and atmospheric pressure (not shown) time series, and by the occurrence of warm and cold fronts. The correlation coefficients between the T_{air} time series were 0.95, 0.92 and 0.89 for 2010, 2013, and 2015, respectively. Similar high correlation values were found for atmospheric pressure time series (0.91 for 2010, 0.82 for 2013 and 0.97 for 2015). Annual amount of precipitation in Vendyurskoe were 588 mm (in 2010), 545 mm (in 2013) and 551 mm (in 2015), while corresponding values in Kuivajärvi were 720 mm (in 2010), 630 mm (in 2013) and 670 mm (in 2015).

Long spring overturn and hot summer in 2010

The winter 2010 (January–March) was the coldest, T_{air} being mainly between –5 and –20 °C with an average value of –10.9 °C for Kuivajärvi area and –9.4 °C for Vendyurskoe area (Table 1). Starting on 23 March, the daily mean values of T_{air} were above 0 °C, and a long period of warming followed until mid-July, when daily mean value of T_{air} of about 30 °C was reached. July was particularly warm with average T_{air} of 22.3 °C and 20.6 °C for Vendyurskoe and Kuivajärvi areas, respectively (Table 1).

Ice-off occurred on Vendyurskoe on 1 May 2010. Due to long spring and relatively slow

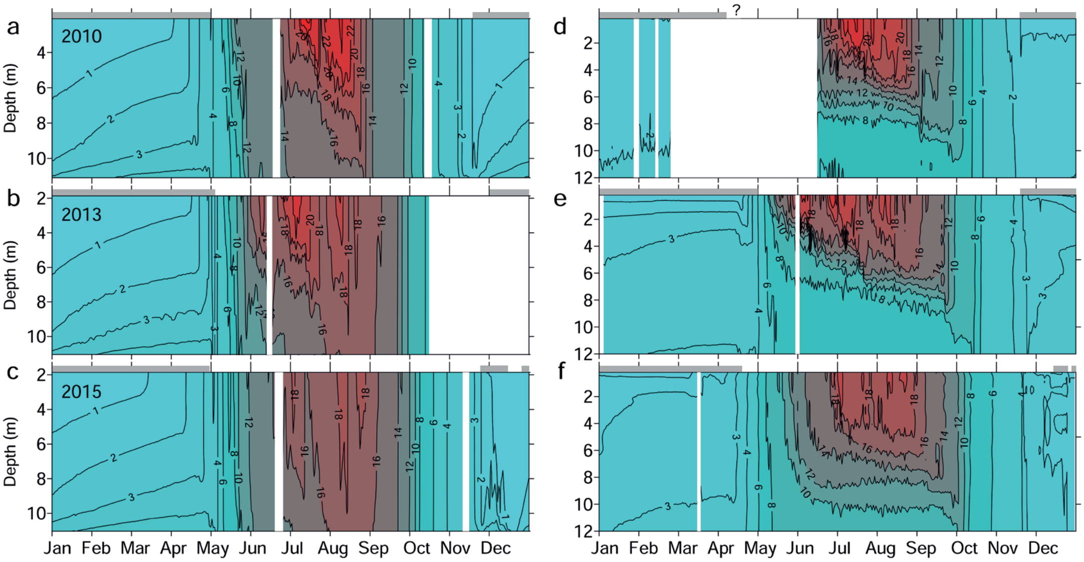

Fig. 3. Isotherms (°C) in 2010, 2013, and 2015 for Vendyurskoe (**a**, **b**, **c**), and Kuivajärvi (**d**, **e**, **f**). White areas indicate missing data and horizontal grey bars ice cover. ? = the exact date of ice off is not known.

warming, the overturn continued to mid-June (Fig. 3a). Along with the very strong warm front in mid-May, the water column started to stratify, but lake Vendyurskoe entered again into state of complete mixing after the front had passed. When the weather continued to warm again in mid-June, summer stratification commenced in Vendyurskoe. We lacked thermistor data from Kuivajärvi in spring 2010, but according to the pCO_2 data, stratification ensued in June (Fig. 4d). The particularly warm weather in July caused strong stratification in both lakes with high surface T_{water} (> 20 °C) and relatively low hypolimnetic T_{water} (roughly 15 °C in Vendyurskoe and 7 °C in Kuivajärvi). The summer values of Schmidt stability, which indicates the energy needed to mix the water column, were larger than 60 J m^{-2} in both lakes (Fig. 5). In Vendyurskoe, the strong stratification (ΔT_{water} ~ 10 °C between surface and bottom) lasted for two months, which led to hypoxia (DO < 3 mg l^{-1}) in almost half of the water column and resulted later in anoxia

Table 1. Monthly average air temperatures (°C) at Vendyurskoe and Kuivajärvi.

	Vendyurskoe			Kuivajärvi		
	2010	2013	2015	2010	2013	2015
Jan	–15.21	–8.99	–7.09	–14.16	–6.46	–4.45
Feb	–12.07	–4.96	–2.73	–10.71	–3.89	–1.91
Mar	–5.34	–10.23	0.70	–3.47	–7.16	0.38
Apr	3.84	2.73	2.22	3.53	2.14	3.42
May	11.38	11.12	10.43	10.89	12.53	8.45
Jun	13.21	17.06	14.19	13.23	16.20	12.76
Jul	22.30	16.87	14.31	20.57	15.85	15.39
Aug	16.97	16.39	15.44	15.48	15.19	16.48
Sep	10.19	9.21	11.83	9.65	10.09	11.23
Oct	3.57	4.76	3.48	3.09	4.51	4.78
Nov	–3.65	1.79	0.07	–4.51	1.45	2.74
Dec	–14.24	–2.05	–1.66	–13.22	–0.52	0.29

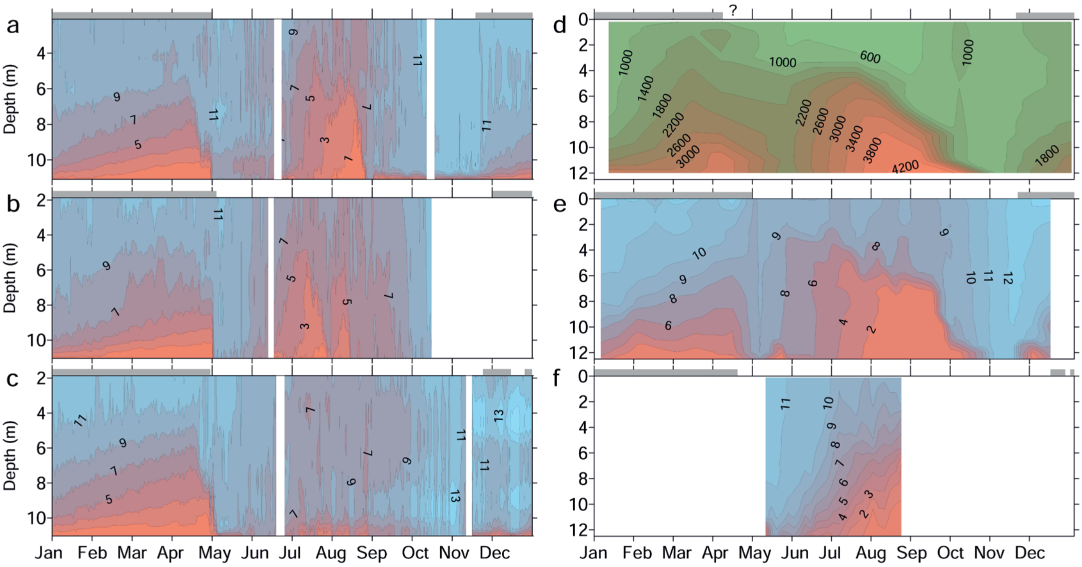

Fig. 4. Dissolved oxygen (mg l^{-1}) in Vendyurskoe in 2010 (**a**), 2013 (**b**) and 2015 (**c**), and CO_2 partial pressure (ppm) in Kuivajärvi in 2010 (**d**), as well as dissolved oxygen (mg l^{-1}) in 2013 (**e**) and 2015 (**f**). Note the different color scheme for different gases. Horizontal grey bars indicate ice cover. ? = the exact date of ice off is not known.

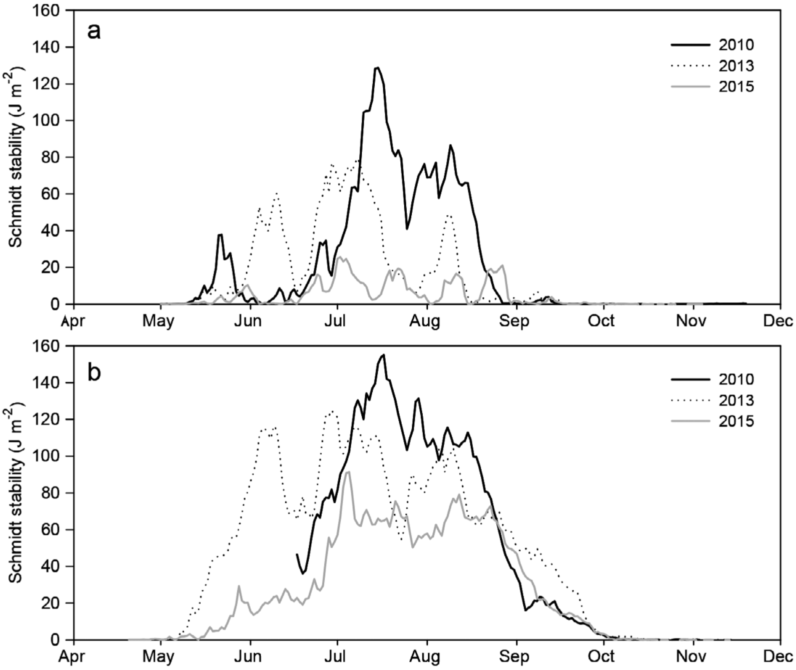

Fig. 5. Schmidt stabilities in (**a**) Vendyurskoe and (**b**) Kuivajärvi in 2010 (solid black line), 2013 (dotted line), and 2015 (solid grey line).

(defined here as DO < 1 mg l^{-1}, according to Nurnberg (1995)) from 8 m depth to the bottom (Fig. 4a). In Kuivajärvi, CO_2 started to accumulate in the hypolimnion after the onset of stratification. As the thermocline deepened, the volume of CO_2 rich water decreased, but at the same time the production of CO_2 continued so that pCO_2 exceeded 4000 ppm.

Autumn cooling started quickly with a strong cold front at the beginning of September. The stratification in Vendyurskoe lake was rapidly destroyed in just over a week, and the overturn lasted for 2.5 months until the lake froze over already in mid-November. The large T_{water} difference of 15 °C between the hypolimnion and the surface in Kuivajärvi from mid-June to early August switched to long and gradual destratification of almost two months. The autumn overturn lasted roughly 5 weeks, from the first week of October untill mid-November, when ice-on ensued.

Short spring overturn and relatively cold summer in 2013

Winter 2013 (January–March) was milder, T_{air} being higher than –10 °C most of the time with an average value of –5.8 °C for Kuivajärvi and –8.1 °C for Vendyurskoe. In April, the average value of T_{air} was lower than in 2010 (Table 1). Ice-off occurred on 3 May 2013 at Vendyurskoe and on 1 May 2013 at Kuivajärvi. Short and intense period of warming in May resulted in very short spring overturns, less than 2 weeks in Vendyurskoe and 1 week in Kuivajärvi (Fig. 3), and the lakes started to stratify earlier than in 2010. This led to the development of summer hypoxia and anoxia earlier than in 2010. However, concomitantly with lower T_{air} in July, the water column in both lakes was more weakly stratified than in 2010, as seen by the difference in Schmidt stability values between the two years (Fig. 5). Cold fronts during summer resulted in deep water column mixing in Vendyurskoe, causing near or full overturns in mid-June and late July (Fig. 3b), and Schmidt stability values were less than 25 J m^{-2} during these events (Fig. 5a). However, because of darker water and smaller size, only moderate mixed layer deepening was observed during these fronts in Kuivajärvi (Fig. 3e) and at least 60 J m^{-2} would have been needed for full mixing of the water column (Fig. 5b). Hypoxia in the hypolimnion started to develop roughly in mid-July and it extended to 7 m in early August in Kuivajärvi (Fig. 4e), whereas in Vendyurskoe, the late July overturn increased the water column oxygen concentration and therefore hypoxia and anoxia was not as severe as in 2010. The moderate and long autumn cooling led to longer open-water period, and Kuivajärvi froze in mid-November and Vendyurskoe almost two weeks later.

Long spring overturn and relatively cold summer in 2015

The year 2015 in Kuivajärvi was very different from the previous ones. Early ice-off (22 April) and long period of cold weather (average T_{air} was 4.7 °C on the last decade of April, and 7.5 °C on first and second decade of May) caused long overturn (25 days) and gradual heating of the water column (Fig. 3f). Therefore, when the stratification finally began, bottom T_{water} was 9 °C, i.e. about 3 °C higher than in 2010 (6 °C) and 2013 (6.5 °C). Cold summer resulted in weak stratification (Fig. 5) and low T_{water} in the mixed layer (3.5 m), ranging between 15 and 22 °C with an average value of 18.5 °C over the summer. The late onset of stratification resulted in low hypolimnetic pCO_2 even in late June (Fig. 6). However, concomitantly with higher hypolimnetic T_{water}, pCO_2 increased ~50% faster in 2015 than in 2013 (600 ppm per week versus 400 ppm per week in 2013). As a result, pCO_2 was roughly the same (5000 ppm) in both years by the beginning of August, even though in the more typical spring of 2013, pCO_2 started to increase much earlier, already at the beginning of May (Fig. 6). Due to long and slow cooling in autumn 2015, the overturn commenced at the beginning of October. However, T_{water} was much higher than in previous years (water column T was 11 °C, whereas in 2010 and 2013 it was ~7 °C), and as the thermic winter began in mid-November, Kuivajärvi was still too warm for the ice formation, surface T_{water} was about 4 °C. Therefore ice-on was postponed until mid-December. In Vendyurskoe, the long cold spring resulted in late onset of stratification, similarly to 2010 (Fig. 3c). However, due to cold summer, stratification was only temporary. Frequent overturns kept the whole water column well aerated throughout the summer (Fig. 4c). The mild autumn resulted in ice-on at the end of November.

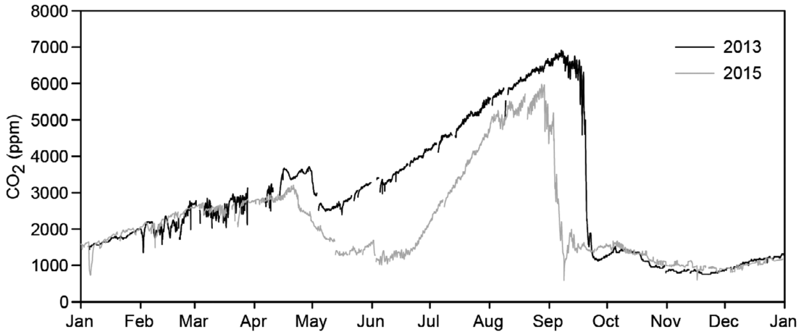

Fig. 6. Dissolved CO_2 partial pressure (ppm) at a depth of 7 m at Kuivajärvi during years 2013 (black), and 2015 (grey).

Discussion

The impacts of nearly all synoptic scale and longer weather events were seen in both lakes, even though they are ~500 km apart. This indicates that the regional climate dictates the general stratification behaviour and related impacts on lake ecosystems. Arvola *et al.* (2010) and O'Reilly *et al.* (2015) reported high spatial heterogeneity in lakes' responses to climate forcing, even in the same region. This was also observed in our case studies characterized by three meteorologically different years.

The responses of the two lakes to the seasonal climate forcing were very different and clearly related to the difference in water transparency, which affects thermal stratification and mixing of dissolved gases and nutrients. The clear-water and larger lake Vendyurskoe changed mixing regime from typical polymixis to dimixis in 2010 (characterized by long spring overturn and hot summer), which suggests that this kind of lakes may become dimictic on more regular basis due to climate change (Kirillin 2010). Long cool spring resulted in late onset of stratification and thus shorter time for the development of hypoxia and anoxia. Hot summer caused strong stratification so that no oxygen replenishment occurred to the hypolimnion. During cooler summers, the stratification was occasionally destroyed and the whole water column was oxidized. Similar findings were reported by Kuha *et al.* (2016) for two weakly stratified clear water lakes in Finland (Pyhäjärvi and Yli-Kitka). According to our results, the worst oxygen conditions in clear-water lakes would result from long spring overturn and warm summer. In Müggelsee, a lake in Germany, hot summers have resulted in fewer mixing events, but sometimes nutrient pulses from the hypolimnion to epilimnion were observed after these events, which were then followed by phytoplankton blooms (Wilhelm and Adrian 2008). On the other hand, heat wave itself has been associated with algal blooms (Bartosiewicz *et al.* 2016). Scheffer *et al.* (2001) studied how lake warming is related to plankton dynamics. They found that, with increasing temperature, zooplankton grazing on phytoplankton increased, which leads to the so-called clear-water phase affecting the whole lake ecosystem.

In the darker water lake (Kuivajärvi), long and slow spring warming resulted in warmer hypolimnion (years 2010 and 2015) and thus weaker stratification than in the case of hot spring and colder hypolimnion (year 2013). Stratification was weakest in cool summers 2013 and 2015. Weak thermocline and deep mixed layer allowed rapid overturn with decreasing temperature in autumn, yet the water temperature remained high possibly delaying the ice formation.

In 2015, the warmer hypolimnetic temperature probably caused higher microbial production of CO_2 below thermocline. However, because the overall duration of stratification was almost two months shorter than in year with hot spring, but cool summer, the CO_2 concentration was nearly the same just before autumn overturn (Fig. 6). It is uncertain how the stratification and O_2 dynamics, such as the length and extent of O_2 depletion, affect CH_4 dynamics. It is reasonable to assume that longer duration of O_2 depletion leads to high CH_4 concentrations (hot spring), but even greater might be the effect of elevated hypolimnion temperature and related higher production rates (cold spring). For example, Bartosiewicz *et al.* (2016) observed lower ebullition and overall GHG emissions (sum of GHGs weighted with their global warming potentials) during hotter than average years.

These results indicate that the weather during spring influences the biogeochemistry of a lake during summer, such as the carbon processing in the hypolimnion, but also during autumn as even the length of the open-water period can be altered. Similar results were related to changes in water clarity, as shown in a modeling study by Heiskanen *et al.* (2015). Clear water leads to higher T_{water} in the autumn and probably postpones the onset of ice cover. Dark water, on the other hand, enables earlier and stronger stratification and thus earlier ice cover, because of colder water temperatures during autumn overturn, similarly to our results here with warm spring and summer. Therefore, both warming climate and brownification of lakes can lead to similar changes in the stratification dynamics of boreal lakes.

Conclusions

Our study shows that the stratification response of lakes to climate change may be different depending on their size and water transparency. Compared to the long-term stratification patterns in these two lakes, the most drastic changes were observed in the larger and clearer polymictic lake Vendyurskoe, where hot summer caused a change in the mixing regime from typical polymixis to dimixis, and supported the development of hypoxia and later anoxia, and probably an increase of GHG production. In dimictic Kuivajärvi, hot spring facilitates the rapid transition of the lake to stratification with low hypolimnion temperature. The microbial activity then remains low, which limits the production of GHGs. Cold spring increases the duration of the spring homothermy, so stratification starts with high hypolimnion temperature, which leads to activation of microbial community and increased GHG production. Since the hypolimnion temperature is higher, the destruction of the seasonal thermocline occurs earlier, but the autumn homothermy is longer and the lake freezing can be delayed. Thus, the length of the open-water period depends greatly on spring conditions. Thereby, the effect of the relatively cold spring on the GHG dynamics is twofold: on the one hand, the high temperature of the hypolimnion contributes to an increase in GHG production, and on the other hand, the period of the possible accumulation of GHGs is shortened because the period of summer stratification is reduced. These results indicate potential changes in carbon processing and dynamics in different climatic conditions, and therefore further studies are needed to explore how different climate forcing scenarios affect also the biological responses of lakes of different sizes and water clarities in the boreal region.

Acknowledgements: The authors gratefully acknowledge the EU projects GHG-LAKE (612642) and RINGO (730944), Academy of Finland projects (National Centre of Excellence (272041), ICOS (281255), CarLAC (281196) and Academy professor projects 284701 and 1281255) and the Russian Fund of Basic Research (RFBR) projects 14-05-91761 and 14-05-00787. J.H. thanks Nessling Foundation for its support.

References

Arvola L., George G., Livingstone D.M., Järvinen M., Blenckner T., Dokulil M.T., Jennings E., Aonghusa C.N., Nõges P., Nõges T. & Weyhenmeyer G. 2010. The impact of the changing climate on the thermal characteristics of lakes. In: Glen G. (ed.), *The impact of climate change on European lakes*, Springer Aquatic Ecology Series, pp. 85–102.

Bartosiewicz M., Laurion I. & MacIntyre S. 2015. Greenhouse gas emission and storage in a small shallow lake. *Hydrobiologia* 757: 101–115.

Bartosiewicz M., Laurion I., Clayer F. & Maranger R. 2016. Heat-wave effects on oxygen, nutrients, and phytoplankton can alter global warming potential of gases emitted from a small shallow lake. *Environ. Sci. Technol.* 50: 6267–6275.

Efremova T.V., Pal'shin N.I., Zdorovennova G.E. & Terzhevik A.Y. 2015. The effects of extremely hot summer 2010 on water temperature and oxygen distribution in Karelian lakes. *Russian Meteorology and Hydrology* 40: 612–618.

Filatov N.N. & Kuharev V.I. [Филатов Н.Н. & Кухарев В.И.] (eds.) 2013. [*Karelian lakes*]. Karelian Research Centre of Russian Academy of Science, Petrozavodsk. [In Russian].

Golosov S., Maher O.A., Schipunova E., Terzhevik A., Zdorovennova G. & Kirillin G. 2007. Physical background of the development of oxygen depletion in ice-covered lakes. *Oecologia* 151: 331–340.

Hari P., Pumpanen J., Huotari J., Kolari P., Grace J., Vesala

T. & Ojala A. 2008. High-frequency measurements of productivity of planktonic algae using rugged nondispersive infrared carbon dioxide probes. *Limnology and Oceanography: Methods* 6: 347–354.

Heiskanen J.J., Mammarella I., Haapanala S., Pumpanen J., Vesala T., Macintyre S. & Ojala A. 2014. Effects of cooling and internal wave motions on gas transfer coefficients in a boreal lake. *Tellus* 66B: 22827, doi:10.3402/tellusb.v66.22827.

Heiskanen J.J., Mammarella I., Ojala A., Stepanenko V., Erkkilä K.-M., Miettinen H., Sandström H., Eugster W., Leppäranta M., Järvinen H., Vesala T. & Nordbo A. 2015. Effects of water clarity on lake stratification and lake–atmosphere heat exchange. *Journal of Geophysical Research, Atmospheres* 120: 7412–7428.

Huotari J., Ojala A., Peltomaa E., Pumpanen J., Hari P. & Vesala T. 2009. Temporal variations in surface water CO_2 concentration in a boreal humic lake based on high-frequency measurements. *Boreal Environment Research* 14: 48–60.

Idso S.B. 1973. On the concept of lake stability. *Limnology and Oceanography* 18: 681–683.

Kirillin G. 2010. Modeling the impact of global warming on water temperature and seasonal mixing regimes in small temperate lakes. *Boreal Environment Research* 15: 279–293.

Kuha J., Arvola L., Hanson P.C., Huotari J., Huttula T., Juntunen J., Järvinen M., Kallio K., Ketola M., Kuoppamäki K., Lepistö A., Lohila A., Paavola R., Vuorenmaa J., Winslow L. & Karjalainen J. 2016. Response of boreal lakes to episodic weather-induced events. *Inland waters* 6: 523–534.

López-Bellido J., Tulonen T., Kankaala P. & Ojala A. 2009. CO_2 and CH_4 fluxes during spring and autumn mixing periods in a boreal lake (Pääjärvi, southern Finland). *Journal of Geophysical Research, Biogeosciences* 114: G04007, doi:10.1029/2009JG000923.

Mammarella I., Nordbo A., Rannik Ü., Haapanala S., Levula J., Laakso H., Ojala A., Peltola O., Heiskanen J., Pumpanen J. & Vesala T. 2015. Carbon dioxide and energy fluxes over a small boreal lake in southern Finland. *Journal of Geophysical Research, Biogeosciences* 120: 1296–1314.

Meehl G.A., Stocker T.F., Collins W.D., Friedlingstein P., Gaye A.T., Gregory J.M., Kitoh A., Knutti R., Murphy J.M., Noda A., Raper S.C.B., Watterson I.G., Weaver A.J. & Zhao Z.C. 2007. Global climate projections. In: Solomon S.D. (ed.), *Climate change 2007: the physical science basis*, Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 749–845.

Miettinen H., Pumpanen J., Heiskanen J.J., Aaltonen H., Mammarella I., Ojala A., Levula J. & Rantakari M. 2015. Towards a more comprehensive understanding of lacustrine greenhouse gas dynamics — two-year measurements of concentrations and fluxes of CO_2, CH_4 and N_2O in a typical boreal lake surrounded by managed forests. *Boreal Environment Research* 20: 75–89.

Nordbo A., Launiainen S., Mammarella I., Lepparanta M., Huotari J., Ojala A. & Vesala T. 2011. Long-term energy flux measurements and energy balance over a small boreal lake using eddy covariance technique. *Journal of Geophysical Research, Atmospheres* 116, doi:10.1029/2010JD014542.

Nurnberg G.K. 1995. Quantifying anoxia in lakes. *Limnology and Oceanography* 40: 1100–1111.

O'Reilly C.M., Sharma S., Gray D.K., Hampton S.E., Read J.S., Rowley R.J., Schneider P., Lenters J.D., McIntyre P.B., Kraemer B.M., Weyhenmeyer G.A., Straile D., Dong B., Adrian R., Allan M.G., Anneville O., Arvola L., Austin J., Bailey J.L., Baron J.S., Brookes J.D., de Eyto E., Dokulil M.T., Hamilton D.P., Havens K., Hetherington A.L., Higgins S.N., Hook S., Izmest'eva L.R., Joehnk K.D., Kangur K., Kasprzak P., Kumagai M., Kuusisto E., Leshkevich G., Livingstone D.M., MacIntyre S., May L., Melack J.M., Mueller-Navarra D.C., Naumenko M., Noges P., Noges T., North R.P., Plisnier P.-D., Rigosi A., Rimmer A., Rogora M., Rudstam L.G., Rusak J.A., Salmaso N., Samal N.R., Schindler D.E., Schladow S.G., Schmid M., Schmidt S.R., Silow E., Soylu M.E., Teubner K., Verburg P., Voutilainen A., Watkinson A., Williamson C.E. & Zhang G. 2015. Rapid and highly variable warming of lake surface waters around the globe. *Geophysical Research Letters* 42: 10773–10781.

Ojala A., Bellido J.L., Tulonen T., Kankaala P. & Huotari J. 2011. Carbon gas fluxes from a brown-water and a clear-water lake in the boreal zone during a summer with extreme rain events. *Limnology and Oceanography* 56: 61–76.

Peltomaa E., Zingel P. & Ojala A. 2013. Weak response of the microbial food web of a boreal humic lake to hypolimnetic anoxia. *Aquatic Microbial Ecology* 68: 91–105.

Read J.S., Hamilton D.P., Jones I.D., Muraoka K., Winslow L.A., Kroiss R., Wu C.H. & Gaiser E. 2011. Derivation of lake mixing and stratification indices from high-resolution lake buoy data. *Environmental Modelling & Software* 26: 1325–1336.

Scheffer M., Straile D., van Nes E.H. & Hosper H. 2001. Climatic warming causes regime shifts in lake food webs. *Limnology and Oceanography* 46: 1780–1783.

Schulz S., Matsuyama H. & Conrad R. 1997. Temperature dependence of methane production from different precursors in a profundal sediment (Lake Constance). *FEMS Microbiology Ecology* 22: 207–213.

Shatwell T., Adrian R. & Kirillin G. 2016. Planktonic events may cause polymictic-dimictic regime shifts in temperate lakes. *Scientific Reports* 6: 24361, doi:10.1038/srep24361.

Stocker T.F., Qin D., Plattner G.-K., Alexander L.V., Allen S.K., Bindoff N.L., Breon F.-M., Church J.A., Cubash U., Emori S., Forster P., Friedlingstein P., Gillett N., Gregory J.M., Hartmann D.L., Jansen E., Kirtman B., Knutti R., Krishna Kumar K., Lemke P., Marotzke J., Masson-Delmotte V., Meehl G.A., Mokhov I.I., Piao S.L., Ramaswamy V., Randall D., Rhein M., Rojas M., Sabine C., Shindell D., Talley L.D., Vaughan D.G. & Xie S.-P. 2013. Technical Summary. In: Stocker T.F., Qin D., Plattner G.-K., Tignor M., Allen S.K., Boschung J., Nauels A., Xia Y., Bex V. & Midgley P.M. (eds.), *Climate change 2013: the physical science basis*, Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 35–115.

van Oldenborgh G.J., Collins M., Arblaster J., Hesselbjerg Christensen J., Marotzke J., Power S.B., Rummukainen M. & Zhou T. 2013. Annex I: Atlas of global and regional climate projections. In: Stocker T.F. (ed.), *Climate change 2013: the physical science basis*, Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 1311–1394.

Weyhenmeyer G.A., Blenckner T. & Pettersson K. 1999. Changes of the plankton spring outburst related to the North Atlantic Oscillation. *Limnology and Oceanography* 44: 1788–1792.

Weyhenmeyer G.A., Mackay M., Stockwell J.D., Thiery W., Grossart H.P., Augusto-Silva P.B., Baulch H.M., de Eyto E., Hejzlar J., Kangur K., Kirillin G., Pierson D.C., Rusak J.A., Sadro S. & Woolway R.I. 2017. Citizen science shows systematic changes in the temperature difference between air and inland waters with global warming. *Scientific Reports* 7, doi:10.1038/srep43890.

Wilhelm S. & Adrian R. 2008. Impact of summer warming on the thermal characteristics of a polymictic lake and consequences for oxygen, nutrients and phytoplankton. *Freshwater Biology* 53: 226–237.