Title: Water temperature dynamics and the prevalence of daytime stratification in small temperate shallow lakes

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Abstract

Small lakes are understudied compared to medium- and large-sized lakes, but have recently received increased attention due to their abundance and importance for global scale biogeochemical cycles. They have close terrestrial contact, extensive environmental variability and support high biodiversity among them. Temporal and spatial variability of water temperature, oxygen and stratification-mixing dynamics were examined during a year in nine small Danish lakes. We found that diel mean surface water temperatures were similar among lakes while the diel range decreased with increasing water depth. Vertical temperature stratification occurred on 47 % of the days during the entire year and 64 % of summer days; usually with daytime stratification and nocturnal convective mixing. The probability of daytime stratification increased with higher incident irradiance, higher air temperature and lower wind speed. During spring, daytime stratification caused differences in oxygen saturation between surface and bottom waters. These findings offer new insights on the high variability of water temperature and oxygen in time and space in small temperate shallow lakes. The variable water temperature and the regular stratification-mixing processes will have a pronounced influence on biogeochemical cycles. Also, these features are expected to affect the performance and evolutionary process of organisms associated with small lakes.

Introduction

Small lakes are numerically abundant worldwide (Downing et al. 2006; Verpoorter et al. 2014) and exhibit high environmental variability as a consequence of their shallow water column and strong influence of the terrestrial surroundings (Christensen et al. 2013; Sand-Jensen & Staehr 2007). They support a high biodiversity (Biggs et al. 2017; Williams et al. 2004) and are significant ecosystems in regional and global biogeochemical cycles (Holgerson & Raymond 2016). Nonetheless, small lakes remain understudied compared to medium- and large-sized lakes and the specific environmental characteristics and determinants are poorly known (Downing 2010). We investigated surface water temperature dynamics and the extent and frequency of stratification and mixing in nine small Danish lakes during a full year in order to improve knowledge on environmental conditions in these very common habitats.

A fundamental feature of particular interest in the ecology of small lakes is the large water temperature variability, which may involve diel vertical stratification and mixing patterns and, in turn, influence the distribution of dissolved oxygen and environmental conditions for animal life (Andersen et al. 2017b). Water temperature is a key parameter in aquatic ecology because it influences rates of chemical and biological processes, biogeochemical cycling and performance of organisms (Gillooly et al. 2001; Yvon-Durocher et al. 2012). Lake surface water temperature (LSWT) is directly influenced by solar radiation, air temperature, cloud cover, relative humidity and wind speed through the exchange of energy across the air-water interface (Woolway et al. 2015b). Small (< 1 ha), shallow (< 3 m) lakes may experience particularly rapid heating and cooling of the water column dictated by meteorological variables along with lake morphometry and optical properties of the water (Woolway et al. 2016). These characteristics likely promote high (10-15 °C) diel variability in surface water temperature (diel temperature range, DTR). Because the lakes experience the same meteorological conditions, the drivers of variation between lakes can be examined.

Stratification and mixing events are crucial physical processes in lakes with strong system-scale implications (Boehrer & Schultze 2008). During stratification, the water column is conceptionally compartmentalized with an epilimnion dominated by turbulent mixing and a hypolimnion with reduced turbulence separated by a metalimnion with a steep density gradient (Kalff 2002). Heating of the surface water stabilizes the water column, while cooling and wind shear destabilize it and promote vertical mixing (Imberger 1985). Surface water heating is influenced by light attenuation and lake morphometry (Fee et al. 1996; Gorham & Boyce 1989). In small lakes, surface waters are likely to heat rapidly owing to high turbidity (Condie & Webster 2002), high phytoplankton biomass (Losordo & Piedrahita 1991) or high cover of submerged macrophytes which cause strong light absorption (Andersen et al. 2017b; Herb & Stefan 2004). When stabilizing forces exceed destabilizing forces, the water column stratifies and allows for chemical gradients to develop with important implications for biota and biogeochemistry (Branco & Torgersen 2009; Kalff 2002).

Due to the rapid exchange of energy across the surface and the restricted volume, small lakes may undergo daytime stratification and nocturnal mixing. This phenomenon is well documented in single-lake studies (Branco & Torgersen 2009; Herb & Stefan 2004; MacIntyre 1993), but studies considering the frequency of stratification and mixing in a broad range of small lakes are lacking. Diel stratification may be common in small lakes due to terrestrial sheltering, small surface area and extensive cover of submerged macrophytes which all decrease the wind-driven mixing (Andersen et al. 2017b; Fee et al. 1996; Markfort et al. 2010). The diel stratification-mixing pattern may be a recurring feature in small shallow lakes during periods of heating in spring and summer (Andersen et al. 2017b). The consequences of stratification in small lakes depend on the duration but even short duration of stratification may result in steep changes in dissolved oxygen over short vertical distances when respiration is high in bottom waters (Ford et al. 2002). When little or no light reaches the bottom waters, photosynthesis is restricted and bottom waters may experience severe oxygen depletion due to respiration until vertical mixing is reestablished (Andersen et al. 2017a). Recurring daytime hypoxia or anoxia in bottom waters has ecological consequences for both animals and submerged macrophytes. This requires adaptations from sessile organism in order to withstand such unfavorable oxygen conditions while motile organisms may seek better conditions (Rahel & Kolar 1990; Vad et al. 2013). This situation could likely be more pronounced during late summer or autumn due to plant senescence or phytoplankton die-off. However, if sufficient light reaches the bottom waters, which is likely in shallow lakes, submerged macrophytes or other benthic primary producers may ensure good oxygen conditions (Vadeboncoeur et al. 2008).

We investigated water temperature and stratification-mixing dynamics in nine small Danish lakes during a full year. The main objectives were to investigate the temporal (diel to seasonal) and spatial (stratification-mixing) variability in water temperature in small lakes. In this study, we examined LSWT variability on a diel time scale (DTR) between nine lakes. Additionally, we quantified the frequency and extent of temperature stratification. Using meteorological and morphometric variables, we examined their influence on the probability of water column stratification. Specifically, we hypothesized that: 1) the variability in DTR between lakes is driven by morphometry which influences the absorption and distribution of heat in the surface mixed-layer, 2) the diel stratification and mixing cycle is a common feature in northern temperate small lakes and 3) the probability of stratification can be predicted from meteorological variables and lake morphometry.

Methods

Study site

Data were collected in nine small lakes located close to each other (maximum distance 1.6 km) at Roennebaeksholm, Zealand, Denmark (Online resource 1, Figure S1) from October 2015 to October 2016. The lakes were numbered 1 to 9 according to increasing maximum water depth. The lowland landscape (altitude of sites ranged from 13 to 24 m) is a nutrient-rich calcareous moraine. The surroundings are mainly open grassland with scattered shrubs. Lake 3, and to a smaller degree, Lake 4, 6, 7, were partly sheltered by short trees. On the shore of Lake 6 and 7, and in shallow sections of Lake 3 and 4, the emergent species *Phragmites australis* and *Typha latifolia* were present and provided sheltering. Submerged macrophyte species of the genera: *Chara*, *Potamogeton* and *Ranunculus* were common in the lakes.

Data collection

Water levels were recorded in eight lakes (all lakes except Lake 2, which was measured manually) using the difference between atmospheric and underwater pressure (HOBO U-20-001-04, Onset Computers, Bourne, Ma, USA) at the deepest site (HOBOware). The pressure was recorded at 10 minute intervals, however, only midnight water levels were used in further analysis when waters were mixed and no interference of differences in temperature between surface and bottoms waters are possible. Data in periods between manual measurements in Lake 2 were filled by linear interpolation. Bathymetric maps were made by measuring depth at regular intervals (0.25-1.0 m) along two to four transects across each lake with concurrent estimation of surface area. The measurements were performed during periods of high water levels. Polynomial functions of different order were fitted to calculations of the area represented by each depth interval yielding a relationship between surface area and water depth. Integrating this function yields lake volume as a function of depth (Christensen et al. 2013). Mean depth (z_{mean}) was calculated as volume divided by total surface area. In July 2016, coverage of submerged macrophytes across the lake bottom and the water surface was estimated by measuring presence or absence of submerged macrophytes along similar transects and measuring intervals. Water temperatures were recorded in the lakes using two to four sensors (HOBO UA-002-64, accuracy of ±0.53 °C) located along a vertical profile from surface to bottom waters at the deepest site or at the deepest site accessible by wading (max. 1.50 m). The diel temperature range (DTR) was calculated as the difference between maximum and minimum surface water temperature.

During spring 2016, oxygen sondes (MiniDOT, PME, Vista, CA, USA) were deployed in six lakes. The oxygen sondes were mounted on steel pegs 10-30 cm below the water surface and 20-50 cm above the sediment surface. Sensors were tested for drift by placing them in water with 100 % oxygen saturation before and after deployment. Small drift in oxygen signal was assumed to have been linear over time.

A meteorological measuring station was established in the open landscape between 100 and 1200 m from the lakes (Online resource 1, Figure S1). The station recorded incident irradiance (PAR; HOBO S-LIA-M003), wind speed (HOBO S-WSET-A), atmospheric pressure (HOBO U-20-001-04), air temperature and relative humidity (HOBO U23 Pro v2) at a height of 2.5 meters above the ground. Meteorological variables, water depth, water temperature and dissolved oxygen were measured and recorded every 10 minutes.

Surface water samples were collected 6-9 times during the period and analyzed the following day for alkalinity (acid-neutralizing capacity) by acidimetric titration (Gran 1952), chlorophyll *a* by ethanol extraction (Jespersen & Christoffersen 1987) and colored dissolved organic matter (CDOM) as spectrophotometric absorption at 400 nm of a 0.07 µm (GF/F) filtrate (Sand-Jensen & Staehr 2007). Frozen water samples were later thawed and analyzed for nutrients (total-P, total-N, ortho-phosphate, nitrate and ammonium) on an auto analyzer (AA3HRAutoAnalyzer, SEAL, USA) using standard protocols (University of Copenhagen 1992).

Statistical analysis

A statistical classification model with a binary response ("stratified" or "mixed") was used to investigate the influence of lake morphometry and meteorological variables on the probability of stratification on a daily scale. The water column was considered to be stratified when the difference in water temperature between the surface and bottom sensors exceeded 1°C. For each day in each lake the water column was classified as either being stratified or mixed. This threshold was found appropriate considering sensor accuracy, and was backed up by oxygen measurements during spring, when only small temperature differences occurred, but vertical differences in oxygen concentrations were observed. Data from January 2016 were omitted from further analysis because the lakes were ice covered. During the period they became sealed from the influence of wind mixing and showed inverse vertical stratification.

We fitted generalized linear mixed models (GLMMs) to account for the spatial random effect, acknowledging that observations within a site (a lake) are likely to be more similar than observations between sites (Bolker et al. 2009). Applying mixed-effect models are therefore more appropriate compared to generalized linear models due to the error structure in the data. We fitted GLMMs with a binominal distribution (logit-link function) with "site" as a random effect using the glmer() function from the "lme4" package in R (Bates et al. 2015; R Core Team 2017). Starting with an initial model, we applied model selection in an information theoretic framework to evaluate and rank all possible models using the Akaike Information Criterion (AIC, Burnham & Anderson (2002)). To avoid selecting a model with intercorrelation between predictors (co-linearity), we calculated the variance inflation factor (VIF) and sequentially discarded the predictor with the highest VIF until the VIF among predictors was no higher than three following recommendations in Zuur et al. (2010). The initial model included data on lake area and maximum depth (z_{max}) along with diel mean air temperature, incident irradiance (PAR) and wind speed as predictor variables. Including interactions only resulted in minor improvements in model performance as judged from the classification error rate and were therefore left out. To ensure convergence during model fitting, predictor variables were scaled (subtracting the mean and dividing by the standard deviation). Scaling also made interpretation of the estimated effect sizes easier, because parameter estimates share the same unit.

Results

Meteorology and general lake characteristics

Air temperature and incident irradiance (PAR) followed typical annual courses (Figure 1). Diel mean wind speeds were generally low with an overall average of 1.5 and a maximum of 6.9 m s^{-1} (Figure 1). Maximum wind gust speed reached 16.4 m s^{-1}. Surface area of the nine small lakes ranged from 230 to 4400 m^2 and maximum water depth from 0.26 to 2.3 m (Table 1) and varied in depth, area and volume during the investigated period. From October-November 2015**,** maximum depth increased during high precipitation and low evapotranspiration (DMI 2016) and decreased during spring 2016 when evapotranspiration exceeded precipitation (Figure 2). The lakes were highly alkaline (2.9-4.4 meq L^{-1}, pH 7.8-8.2 at air equilibrium), with low to medium levels of colored dissolved organic matter (CDOM-absorbance, 3.2-8.2 m^{-1} at 400 nm) and had medium to high nitrogen and phosphorus concentrations (Table 1). Submerged macrophytes were only absent in Lake 2. After a period of ice cover in January 2016, submerged macrophytes expanded during spring covering the majority of the bottom in eight of the nine lakes by early summer (Table 1).

Surface water temperature dynamics

The observed fluctuations in lake surface water temperature (LSWT) highlight the dynamic nature of small lakes on both seasonal and diel scales (Figure 2). Mean diel LSWT in all lakes over the year was closely correlated to diel mean air temperature with coefficients of determination (R^2) ranging between 0.85 and 0.91 and water temperatures were generally higher than air temperatures (Online resource 1, Figure S2). Diel mean LSWT differed only slightly between the nine lakes; only during periods of rapid warming, did the shallower lakes warm faster than the deeper lakes (Figure 2A).

In contrast, the DTR was very variable between lakes and between days within the lake (Figure 2B). DTR was highest during summer and exceeded 10 °C on 39 occasions in six of the lakes and even 15 °C on two occasions in the shallow Lake 2 (Figure 2B). The best lake morphometric predictors of DTR were mean and maximum water depth (Figure 3) based on R^2, while lake volume and area were poor predictors. The slope of the relationship between DTR and maximum water depth was steepest during summer and decreasing through spring, autumn and winter.

Water column stratification and mixing

Differences in water temperature between surface and bottom waters revealed that the water columns in the nine lakes often were stratified (Figure 4 and 5). Temperature stratification was observed in all lakes at some points during the study period. In contrast to our expectations a priori, stratification events were not restricted to warm summer days but occurred throughout the period from March to October, although being strongest in June-July (Figure 5). On 47 % of all days in the nine lakes during the year (n = 2973), the 1 °C stratification threshold for vertical temperature differences was exceeded. Using a 2 °C threshold, the lakes were stratified on 31 % of all days. Excluding the winter months (December, January and February), these percentages were 64 and 43, respectively. The vertical temperature stratification on a given day can be divided into two types of stratification-mixing scenarios based on the diel maximum and minimum water temperature differences between surface and bottom waters (dif_{max} and dif_{min}, °C). Of the 47 % of days with stratification, 94 % were stratified during daytime and experienced nocturnal mixing ($dif_{max} \geq 1$ and $dif_{min} \leq 1$) and 6 % remained stratified during the night as well ($dif_{min} \geq 1$). On days with both stratification and mixing, the transient daytime stratification lasted on average for 9.1 hours (10.9 hours during summer).

The water temperature difference varied between lakes and season (Figure 4 and 5). During shorter periods, nocturnal mixing was insufficient to break the stratification in some of the deeper lakes, resulting in stratification lasting for several days (e.g. Lake 6 and 9, Figure 4). The shallowest and largest of the investigated lakes, Lake 1, was the only lake in which the vertical temperature differences were small (Figure 5). On days with daytime stratification and nighttime mixing dif_{max} was on average 2.9 °C, while the corresponding value for days with no mixing was 4.9 °C. The diel mean (maximum in parenthesis) vertical water temperature gradient (temperature difference divided by distance between sensors) was on average 2.9 (8.9) °C m^{-1} and 5.4 (8.5) °C m^{-1} on days with alternating stratification and mixing or only stratification, respectively.

Predictors of daytime stratification

The fitted mixed effect logistic regression models showed that the stratification response on a daily scale could be well predicted from a combination of morphometric variables (z_{max} and area) and diel mean meteorological variables (air temperature, PAR and wind speed; Table 2). Increasing surface area and wind speed had a negative effect on the probability of stratification while the effect of increasing water depth, incident irradiance and air temperature was positive, with incident irradiance having the largest effect size. Models within two AIC units of the best model (Wind + PAR + Air temperature) fitted data almost equally well but all the best models included wind speed, incident irradiance and air temperature (Figure 6) and adding maximum water depth or area had a minor influence only (Table 2). The classification error rate of the best model was 9.3 % against a null rate (proportion of observations with stratification) of 50.9 % which shows that the selected predictors markedly improved classification compared to random.

Vertical oxygen profiles

As expected, vertical heterogeneity in oxygen saturation was observed when the lakes stratified, although patterns differed between lakes (Figure 7). Diel oxygen cycles were evident in all lakes in both surface and bottom waters. These diel patterns indicated that sufficient light reached bottom waters to maintain oxygen production during stratification. Oxygen supersaturation in bottom waters was observed in Lake 3, 7 and 8. Supersaturated surface water was observed in Lake 5. A combination of these two patterns occurred in Lake 4 and 6. Oxygen saturation in bottom waters did not approach critically low levels (<50 %) during daytime stratification in spring in any of the studied lakes.

Discussion

The lakes investigated in this study were small, shallow and situated in a nutrient rich, mainly open landscape, though with scattered shrubs and small trees (Table 1; Online resource 1, Figure S1).. Lakes with similar characteristics and settings are common throughout the world, and the temperature and stratification-mixing dynamics described here are likely to represent a very large number of small lakes world-wide (Downing 2010). Our study differs from most other studies in that we investigated nine lakes simultaneously over a full year as opposed to studies of single lakes and/or shorter durations (Andersen et al. 2017b; Branco & Torgersen 2009; Laas et al. 2016). Our approach allowed for statistical empirical evaluation with focus on occurrence and drivers of stratification in small lakes, as an alternative to mechanistic physical modelling. We used a classification approach to examine water column stratification because the presence of a thermocline may have profound ecological consequences in small lakes despite the short duration. We discuss our findings and potential impacts of the variable LSWT and stratification-mixing dynamics.

Water temperature dynamics

High frequency measurements showed large fluctuations in LSWT on both diel and seasonal scales. Diel mean LSWT were similar among lakes, except during periods of rapid heating, and were closely related to air temperature (Online resource 1, Figure S2). In contrast, the diel temperature range (DTR) differed markedly among lakes and was negatively related to water depth with the steepest slope during summer as would be expected (hypothesis 1, Figure 3). DTR often exceeded 10 °C and reached 15 °C during summer. Differences in water temperature dynamics are expected among lakes because local factors like morphometry, light attenuation, shading and sheltering against wind exposure affect water temperature (Livingstone et al. 1999). These local factors create differences in water temperature dynamics among neighboring lakes. Lake 1 and 2 are situated 50-100 meters from Lake 9 (Online resource 1, Figure S1) but show contrasting patterns in both LSWT and stratification-mixing dynamics. Woolway et al. (2016) found that lake morphometry explained much of the variation in DTR with lake area having the strongest impact. The lower influence of surface area compared to water depth found here could be a consequence of low surface areas and sheltering of the study lakes resulting in low fetch and decreasing the role of wind. Sheltering of the water surface may be created by trees, shrubs or emergent aquatic vegetation on the shoreline or in shallow sections which was present to some extent in some of the lakes (Lake 3, 4, 6 and 7). Wind forcing on the lake surface influences the mixed layer depth and volume which in turn affect the DTR (Woolway et al. 2015a). In the small lakes investigated here, water depth is likely a better predictor of mixed layer depth which could explain the observed relationship. Other lake variables such as chlorophyll or submerged macrophyte cover may further distort the relationship during certain periods, for example during dense summer growth of phytoplankton or macrophytes.

Stratification in small lakes

Vertical temperature stratification was very common in the lakes during spring, summer and autumn. The recurring pattern was daytime stratification and nocturnal mixing. Although we expected this feature to be common based on other investigations (hypothesis 2, Andersen et al. (2017b); Branco & Torgersen (2009)), we were surprised to realize how prominent it actually was between early spring and late autumn, prompting questions regarding the implications of daytime stratification for adaptation and behavior of organisms.

Temperature stratification in small lakes is common for a number of reasons. Stands of submerged macrophytes are known to be able to induce steep thermal gradients (Dale & Gillespie 1977), and promote stratification by generating intensive light absorption in the upper canopy as well as dampening turbulent mixing of the water column (Andersen et al. 2017b; Herb & Stefan 2004). The role of submerged macrophytes is likely to be strong in small lakes, because of the larger proportion of the lake volume they can occupy (i.e. up to 100%) compared to medium- and large-sized lakes. This is likely one of the reasons why incident irradiance was a good predictor of stratification as well as having the largest effect size (Table 2). The role of wind as the primary driver of turbulence in the surface mixed-layer is reduced in small lakes owing to small surface area (short fetch) and terrestrial sheltering around the lakes (Gorham & Boyce 1989; Woolway et al. 2015a). One consequence of reduced surface wind shear is a shallow surface mixed-layer which is rapidly heated during the day and rapidly cooled during the night, thus, facilitating diel stratification and mixing.

Turbulence in the surface mixed-layer is generated by wind and convection induced by heat loss from surface waters (Imberger 1985). Convection is likely responsible for the recurring nighttime mixing, which is not strongly impeded by the presence of submerged macrophytes because of the directional flow generated by convection (Andersen et al. 2017b; Herb & Stefan 2005). In the shallow lakes ($z_{max} < 1$ m) convection ensured that vertical temperature stratification established during the day was reset every night even at low wind speeds. In the deeper Lake 6 and 9 ($z_{max} > 1$ m), the convective mixing at night was often insufficient to completely mix the water column unless assisted by high wind speeds. Convective mixing is enhanced by a high diel temperature range which results in much higher surface water than air temperatures at sunset and, thus, rapid nocturnal cooling of surface waters. The reduced influence of wind-induced mixing in small lakes is also supported by Read et al. (2012), who showed an increasing contribution of convection to surface mixed-layer turbulence with decreasing lake area. If convection is also important for gas exchange across the water-air interface, the role of small lakes in global estimates of CO_2 and CH_4 emissions from inland waters may have been underestimated because this phenomenon has been ignored so far in models of gas fluxes across water surfaces (Holgerson & Raymond 2016; Holgerson et al. 2016).

Thermal stratification in the nine shallow lakes during the year could be well predicted from few easily measured meteorological variables (hypothesis 3), while the inclusion of morphometric variables had minor impact. The strong influence of meteorological variables on temperature stratification in small lakes should be considered in future monitoring and sampling, especially on days with mean diel air temperatures exceeding 8-9 °C and incoming mean irradiance exceeding about 200-250 µmol m^{-2} s^{-1} (PAR) during which the probability of stratification is very high (Figure 6).

Oxygen in small lakes

Large differences in oxygen saturation over short vertical distances were observed during spring periods of temperature stratification in six of the investigated lakes. Unfortunately, additional oxygen measurements from the remaining lakes which include the most nutrient rich lakes (Lake 2 and 9, Table 1) could not be obtained due to limited equipment. In the lakes where oxygen was measured, no incidences of hypoxia or anoxia developed in the bottom waters during daytime stratification as could be expected. This finding was in contrast to previous studies on small, shallow lakes dominated by charophytes in which the formation of a strong thermocline was followed by oxygen supersaturation in surface waters and anoxia in the shaded bottom waters (Andersen et al. 2017a; Martinsen et al. 2017). Similar patterns have been observed in turbid lakes (Laas et al. 2016). Bottom anoxia is likely a result of the interplay between stratification and steep light attenuation through the water column. In this situation the majority of photosynthesis takes place above the thermocline while respiration dominates below the thermocline. In larger lakes, the light attenuation by phytoplankton and humic substances is typically lower, but greater depths still results in a thermocline located in darkness (Fee et al. 1996). Only when the light attenuation coefficient is low, sufficient light may reach the bottom and cause oxygen supersaturation in the hypolimnion (Lake 7, Figure 6) or metalimnion as in the case of larger lakes (Giling et al. 2017).

The densities of macrophytes in the lakes studied here were much lower than in the charophyte lakes studied before (Andersen et al. 2017b; Martinsen et al. 2017). Light attenuation with depth was much lower and light could support photosynthesis throughout most of the water column. Presence of benthic plants and macroalgae therefore resulted in oxygen supersaturation in the hypolimnion of some lakes in direct contrast to the hypoxia or anoxia in the hypolimnion observed by Ford et al. (2002) and Andersen et al. (2017a). Those contrasting results document the diversity of environmental niches found among small, shallow lakes. This study also highlights that factors such as internal and external shading, sheltering, nutrient levels, water turbidity and macrophyte growth may create vastly different conditions in lakes that otherwise appear very similar.

Implications for the biota

Focus on temperature stratification and oxygen distribution is highly relevant due to strong effects on the distribution and performance of organisms as demonstrated in previous work on small lakes (Vad et al. 2013). Water temperature has profound impact on insects as it influences their rate of development and time of emergence (Macan & Maudsley 1966). Motile animals have the opportunity to select suitable temperatures for their performance and development by moving a relatively short vertical distance in small lakes (Martin 1972), similar to the ability of mosquito larvae to track the highest temperatures in shallow waters during the day and in deeper locations at night (Iversen 1971).

Motile organisms can escape hypoxia in the bottom waters by simply moving to oxygenated surface waters, although this may expose them to predation (Rahel & Kolar 1990). Sessile animals and submerged rooted macrophytes, on the other hand, have to withstand unfavorable oxygen conditions (Vilas et al. 2017). In situations where hypoxia is a recurring phenomenon, organisms need to possess special adaptations to inhabit these small lakes (Kragh et al. 2017), whereas lakes with deep oxygen maxima may prove ideal habitats for organisms unable to cope with hypoxia. Lakes with contrasting oxygen conditions may be found within a relative short distance as demonstrated in this study. Small shallow lakes can, therefore, be expected to support very different species composition and favor different adaptations of organisms capable of surviving across a wide range of temperature and oxygen regimes.

As a consequence, small lakes with their vastly different niches can be important for local and regional biodiversity and evolutionary processes (Scheffer et al. 2006; Williams et al. 2004). The diverse temperature and oxygen patterns, coupled with the ongoing climate changes, may create local conditions suitable for studying changing selection patterns which may develop much more rapidly than in larger lakes. Small, shallow lakes may, thus, play the role of climate ‘canaries’.

During daytime stratification, oxygen saturation in bottom waters mainly depends on the rates and balances of photosynthesis and respiration, as well as the volume of the hypolimnion. Small lakes are particularly susceptible to hypolimnetic anoxia due to high oxygen consumption in the sediments and small hypolimnetic water volumes, as observed in studies of small forest lakes (Holgerson 2015; Sand-Jensen & Staehr 2007) and small charophyte lakes (Andersen et al. 2017a). The high oxygen saturation in the bottom waters observed here requires higher photosynthesis relative to respiration and, therefore, the presence of phototrophs in the bottom waters and sufficient irradiance reaching them. Our small lakes received sufficient light in bottoms waters in May to generate increasing oxygen saturation by photosynthesis during the day. In Lake 7 with clear waters and charophytes covering the lake bottom, bottom waters were always oxygen supersaturated similar to conditions in large clear-water lakes (Kalff 2002). Estimates of ecosystem metabolism also showed that the nine lakes were mainly autotrophic during May and this situation reduces the risk of incidences of oxygen depletion (data not shown). During macrophyte senescence in late summer with respiration exceeding photosynthesis, however, we may expect oxygen depletion in bottom waters.

Conclusions

High-frequency measurements of water temperature in nine small lakes during one year revealed high variability in both time and space on a daily scale. Surprisingly, the lakes very often underwent daytime stratification followed by nighttime mixing with potential consequences for the distribution of oxygen. The response to stratification was very different among adjacent lakes, but vertical gradients build up during daytime were usually reset by convective mixing during nighttime. The probability of daytime stratification was strongly influenced by meteorological variables while lake morphometry had a minor influence across the selected range of small lakes. Our data suggests that short term stratification-mixing events are very common in small lakes with implications for organisms and biogeochemical cycles. Future studies on oxygen dynamics in small lakes require particular attention on the role of submerged macrophytes because they affect oxygen production and consumption by their metabolism and strongly influence the physical structure and light attenuation in the water column.

References

Andersen, M. R., T. Kragh & K. Sand-Jensen, 2017a. Extreme diel oxygen and carbon cycles in shallow vegetated lakes. Proceeding of the Royal Society B 284: doi:10.1098/rspb.2017.1427.

Andersen, M. R., K. Sand-Jensen, R. Iestyn Woolway & I. D. Jones, 2017b. Profound daily vertical stratification and mixing in a small, shallow, wind-exposed lake with submerged macrophytes. Aquatic Sciences 79: 395-406 doi:10.1007/s00027-016-0505-0.

Bates, D., M. Mächler, B. Bolker & S. Walker, 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67: doi:10.18637/jss.v067.i01.

Biggs, J., S. von Fumetti & M. Kelly-Quinn, 2017. The importance of small waterbodies for biodiversity and ecosystem services: implications for policy makers. Hydrobiologia 793: 3-39 doi:10.1007/s10750-016-3007-0.

Boehrer, B. & M. Schultze, 2008. Stratification of lakes. Reviews of Geophysics 46: doi:10.1029/2006RG000210.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens & J.-S. S. White, 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24: 127-135 doi:10.1016/j.tree.2008.10.008.

Branco, B. F. & T. Torgersen, 2009. Predicting the onset of thermal stratification in shallow inland waterbodies. Aquatic Sciences 71: 65-79 doi:10.1007/s00027-009-8063-3.

Burnham, K. P. & D. R. Anderson, 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, New York.

Christensen, J., K. Sand-Jensen & P. A. Staehr, 2013. Fluctuating water levels control water chemistry and metabolism of a charophyte-dominated pond. Freshwater Biology 58: 1353-1365 doi:10.1111/fwb.12132.

Condie, S. A. & I. T. Webster, 2002. Stratification and Circulation in a Shallow Turbid Waterbody. Environmental Fluid Mechanics 2: 177-196 doi:10.1023/a:1019898931829.

Dale, H. M. & T. J. Gillespie, 1977. Influence of submersed aquatic plants on temperature-gradients in shallow-water bodies. Canadian Journal of Botany 55: 2216-2225 doi:10.1139/b77-251.

DMI, 2016. Danish Meterological Institute. http://www.dmi.dk/vejr/arkiver/vejrarkiv/ Accessed June 2016.

Downing, J., Y. Prairie, J. Cole, C. Duarte, L. Tranvik, R. Striegl, W. McDowell, P. Kortelainen, N. Caraco & J. Melack, 2006. The global abundance and size distribution of lakes, ponds, and impoundments. Limnology and Oceanography 51: 2388-2397 doi:10.4319/lo.2006.51.5.2388.

Downing, J. A., 2010. Emerging global role of small lakes and ponds: little things mean a lot. Limnetica 29: 9-24.

Fee, E., R. Hecky, S. Kasian & D. Cruikshank, 1996. Effects of lake size, water clarity, and climatic variability on mixing depths in Canadian Shield lakes. Limnology and Oceanography 41: 912-920 doi:10.4319/lo.1996.41.5.0912.

Ford, P. W., P. I. Boon & K. Lee, 2002. Methane and oxygen dynamics in a shallow floodplain lake: the significance of periodic stratification. Hydrobiologia 485: 97-110 doi:10.1023/a:1021379532665.

Giling, D. P., P. A. Staehr, H. P. Grossart, M. R. Andersen, B. Boehrer, C. Escot, F. Evrendilek, L. Gómez-Gener, M. Honti, I. D. Jones, N. Karakaya, A. Laas, E. Moreno-Ostos, K. Rinke, U. Scharfenberger, S. R. Schmidt, M. Weber, R. I. Woolway, J. A. Zwart & B. Obrador, 2017. Delving deeper: Metabolic processes in the metalimnion of stratified lakes. Limnology and Oceanographyn/a-n/a doi:10.1002/lno.10504.

Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage & E. L. Charnov, 2001. Effects of size and temperature on metabolic rate. science 293: 2248-2251 doi:10.1126/science.1061967.

Gorham, E. & F. M. Boyce, 1989. Influence of lake surface-area and depth upon thermal stratification and the depth of the summer thermocline. Journal of Great Lakes Research 15: 233-245 doi:10.1016/s0380-1330(89)71479-9.

Gran, G., 1952. Determination of the equivalence point in potentiometric titrations. Part II. Analyst 77: 661-671 doi:10.1039/an9527700661.

Herb, W. R. & H. G. Stefan, 2004. Temperature stratification and mixing dynamics in a shallow lake with submersed macrophytes. Lake and Reservoir Management 20: 296-308 doi:10.1080/07438140409354159.

Herb, W. R. & H. G. Stefan, 2005. Dynamics of vertical mixing in a shallow lake with submersed macrophytes. Water Resources Research 41: doi:10.1029/2003wr002613.

Holgerson, M. A., 2015. Drivers of carbon dioxide and methane supersaturation in small, temporary ponds. Biogeochemistry 124: 305-318 doi:10.1007/s10533-015-0099-y.

Holgerson, M. A. & P. A. Raymond, 2016. Large contribution to inland water CO2 and CH4 emissions from very small ponds. Nature Geoscience 9: 222-226 doi:10.1038/ngeo2654.

Holgerson, M. A., C. J. Zappa & P. A. Raymond, 2016. Substantial overnight reaeration by convective cooling discovered in pond ecosystems. Geophysical Research Letters 43: 8044-8051 doi:10.1002/2016gl070206.

Imberger, J., 1985. The diurnal mixed layer. Limnology and Oceanography 30: 737-770 doi:10.4319/lo.1985.30.4.0737.

Iversen, T. M., 1971. The ecology of a mosquito population (Aedes communis) in a temporary pool in a Danish beech wood. Archiv für Hydrobiologie 69: 309-332.

Jespersen, A.-M. & K. Christoffersen, 1987. Measurements of chlorophyll—a from phytoplankton using ethanol as extraction solvent. Archiv für Hydrobiologie 109: 445-454.

Kalff, J., 2002. Limnology: inland water ecosystems. Prentice Hall, New Jersey.

Kragh, T., M. R. Andersen & K. Sand-Jensen, 2017. Profound afternoon depression of ecosystem production and nighttime decline of respiration in a macrophyte-rich, shallow lake. Oecologia 185: 157-170 doi:10.1007/s00442-017-3931-3.

Livingstone, D. M., A. F. Lotter & I. R. Walker, 1999. The decrease in summer surface water temperature with altitude in Swiss Alpine lakes: a comparison with air temperature lapse rates. Arctic, Antarctic, and Alpine Research 31: 341-352 doi:10.2307/1552583.

Losordo, T. M. & R. H. Piedrahita, 1991. Modelling temperature variation and thermal stratification in shallow aquaculture ponds. Ecological Modelling 54: 189-226 doi:10.1016/0304-3800(91)90076-d.

Laas, A., F. Cremona, P. Meinson, E.-I. Rõõm, T. Nõges & P. Nõges, 2016. Summer depth distribution profiles of dissolved CO 2 and O 2 in shallow temperate lakes reveal trophic state and lake type specific differences. Science of the Total Environment 566: 63-75 doi:10.1016/j.scitotenv.2016.05.038.

Macan, T. T. & R. Maudsley, 1966. The temperature of a moorland fishpond. Hydrobiologia 27: 1-22 doi:10.1007/bf00161483.

MacIntyre, S., 1993. Vertical mixing in a shallow, eutrophic lake: Possible consequences for the light climate of phytoplankton. Limnology and Oceanography 38: 798-817 doi:10.4319/lo.1993.38.4.0798.

Markfort, C. D., A. L. Perez, J. W. Thill, D. A. Jaster, F. Porté-Agel & H. G. Stefan, 2010. Wind sheltering of a lake by a tree canopy or bluff topography. Water Resources Research 46: doi:10.1029/2009wr007759.

Martin, N. A., 1972. Temperature fluctuations within English lowland ponds. Hydrobiologia 40: 455-470 doi:10.1007/bf00019980.

Martinsen, K. T., M. R. Andersen, T. Kragh & K. Sand-Jensen, 2017. High rates and close diel coupling of primary production and ecosystem respiration in small, oligotrophic lakes. Aquatic Sciences 79: 995-1007 doi:10.1007/s00027-017-0550-3.

R Core Team, 2017. R: A language and environment for statistical computing. Vienna, R Foundation for Statistical Computing.

Rahel, F. J. & C. S. Kolar, 1990. Trade-Offs in the Response of Mayflies to Low Oxygen and Fish Predation. Oecologia 84: 39-44 doi:10.1007/bf00665592.

Read, J. S., D. P. Hamilton, A. R. Desai, K. C. Rose, S. MacIntyre, J. D. Lenters, R. L. Smyth, P. C. Hanson, J. J. Cole & P. A. Staehr, 2012. Lake-size dependency of wind shear and convection as controls on gas exchange. Geophysical Research Letters 39: doi:10.1029/2012gl051886.

Sand-Jensen, K. & P. A. Staehr, 2007. Scaling of pelagic metabolism to size, trophy and forest cover in small Danish lakes. Ecosystems 10: 128-142 doi:10.1007/s10021-006-9001-z.

Scheffer, M., G. J. van Geest, K. Zimmer, E. Jeppesen, M. Søndergaard, M. G. Butler, M. A. Hanson, S. Declerck, L. de Meester & L. Persson, 2006. Small Habitat Size and Isolation Can Promote Species Richness: Second-Order Effects on Biodiversity in Shallow Lakes and Ponds. Oikos 112: 227-231 doi:10.1111/j.0030-1299.2006.14145.x.

University of Copenhagen, 1992. Limnological methods (in danish). Akademisk Forlag.

Vad, C. F., Z. Horváth, K. T. Kiss, B. Tóth, A. L. Péntek & É. Ács, 2013. Vertical distribution of zooplankton in a shallow peatland pond: the limiting role of dissolved oxygen. Annales de Limnologie - International Journal of Limnology 49: 275-285 doi:10.1051/limn/2013060.

Vadeboncoeur, Y., G. Peterson, M. J. Vander Zanden & J. Kalff, 2008. Benthic algal production across lake size gradients: interactions among morphometry, nutrients, and light. Ecology 89: 2542-2552.

Verpoorter, C., T. Kutser, D. A. Seekell & L. J. Tranvik, 2014. A global inventory of lakes based on high-resolution satellite imagery. Geophysical Research Letters 41: 6396-6402 doi:10.1002/2014gl060641.

Vilas, M. P., C. L. Marti, M. P. Adams, C. E. Oldham & M. R. Hipsey, 2017. Invasive macrophytes control the spatial and temporal patterns of temperature and dissolved oxygen in a shallow lake: A proposed feedback mechanism of macrophyte loss. Frontiers in plant science 8: doi:10.3389/fpls.2017.02097.

Williams, P., M. Whitfield, J. Biggs, S. Bray, G. Fox, P. Nicolet & D. Sear, 2004. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. Biological Conservation 115: 329-341 doi:10.1016/s0006-3207(03)00153-8.

Woolway, R., I. Jones, H. Feuchtmayr & S. Maberly, 2015a. A comparison of the diel variability in epilimnetic temperature for five lakes in the English Lake District. Inland waters 5: 139-154 doi:10.5268/iw-5.2.748.

Woolway, R. I., I. D. Jones, D. P. Hamilton, S. C. Maberly, K. Muraoka, J. S. Read, R. L. Smyth & L. A. Winslow, 2015b. Automated calculation of surface energy fluxes with high-frequency lake buoy data. Environmental Modelling & Software 70: 191-198 doi:10.1016/j.envsoft.2015.04.013.

Woolway, R. I., I. D. Jones, S. C. Maberly, J. R. French, D. M. Livingstone, D. T. Monteith, G. L. Simpson, S. J. Thackeray, M. R. Andersen, R. W. Battarbee, C. L. DeGasperi, C. D. Evans, E. de Eyto, H. Feuchtmayr, D. P. Hamilton, M. Kernan, J. Krokowski, A. Rimmer, K. C. Rose, J. A. Rusak, D. B. Ryves, D. R. Scott, E. M. Shilland, R. L. Smyth, P. A. Staehr, R. Thomas, S. Waldron & G. A. Weyhenmeyer, 2016. Diel Surface Temperature Range Scales with Lake Size. PloS one 11: e0152466 doi:10.1371/journal.pone.0152466.

Yvon-Durocher, G., J. M. Caffrey, A. Cescatti, M. Dossena, P. del Giorgio, J. M. Gasol, J. M. Montoya, J. Pumpanen, P. A. Staehr & M. Trimmer, 2012. Reconciling the temperature dependence of respiration across timescales and ecosystem types. Nature 487: 472-476 doi:10.1038/nature11205.

Zuur, A. F., E. N. Ieno & C. S. Elphick, 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1: 3-14 doi:10.1111/j.2041-210X.2009.00001.x.

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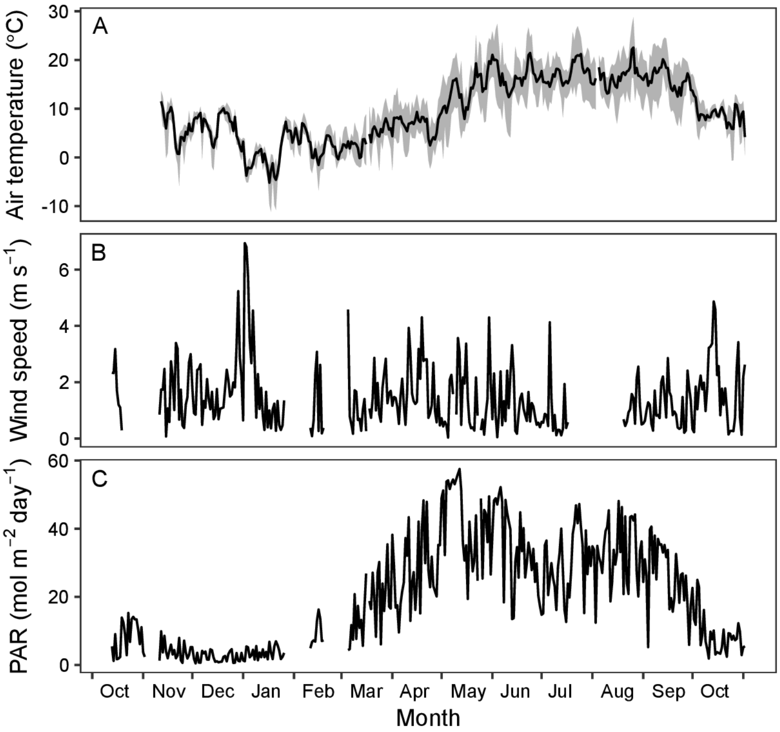

Fig. 1 Meteorological variables measured at the study site from October 2015 to October 2016. A: diel mean air temperature (solid line) with diel maximum and minimum range in grey, B: diel mean wind speed, and C: diel photosynthetic active radiation (PAR)

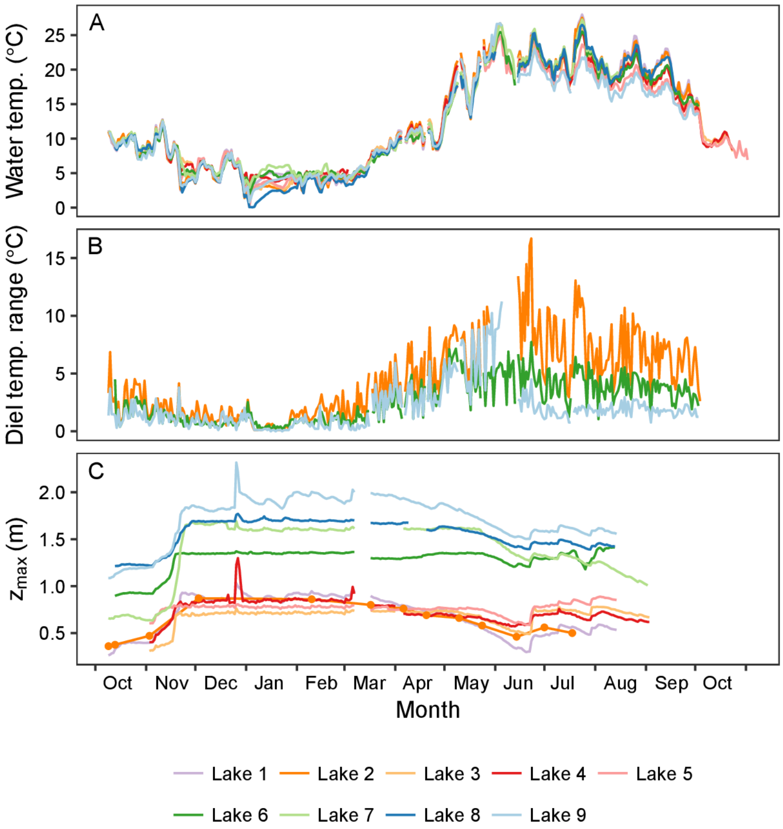

Fig. 2 Water temperature conditions and water depth in nine lakes from October 2015 to October 2016. A: mean diel surface temperature, B: diel temperature range, and C: diel maximum depth (z_{max}). For clarity, diel temperature ranges are shown for three lakes (Lake 2, 6 and 9) that represent high, intermediate and low diel variability, respectively

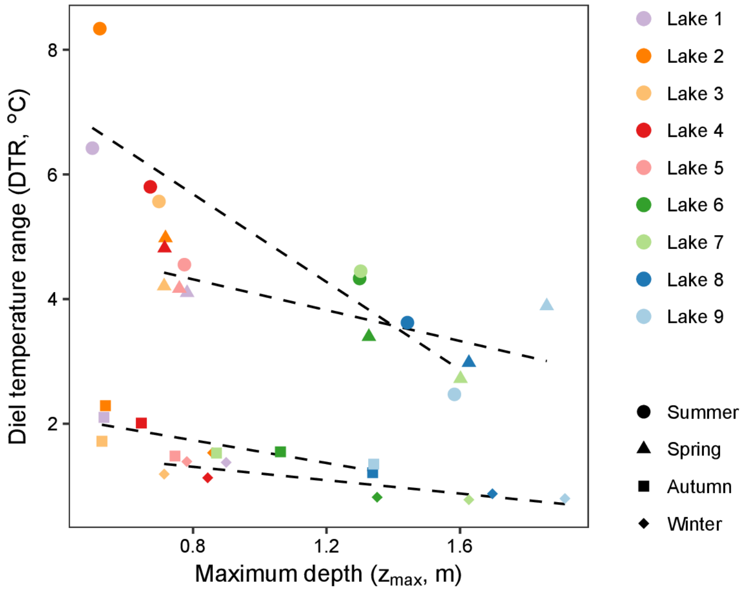

Fig. 3 Relationship between mean diel surface temperature range (DTR, °C) and maximum depth (z_{max}, m) for each season with points colored by lakes and season by shape. Linear regressions (solid line) are fitted (intercept [95% confidence interval], slope [95% confidence interval] and p-value): summer (8.5 [6.7,10.3], -3.5 [-5.3,-1.8], p = 0.002), spring (5.3 [4.2,6.4], -1.2 [-2.1,-0.3], p = 0.016), autumn (2.5 [2.0,3.0], -0.9 [-1.5,-0.4], p = 0.006) and winter (1.7 [1.4,2.1], -0.5 [-0.8,-0.2], p = 0.005)

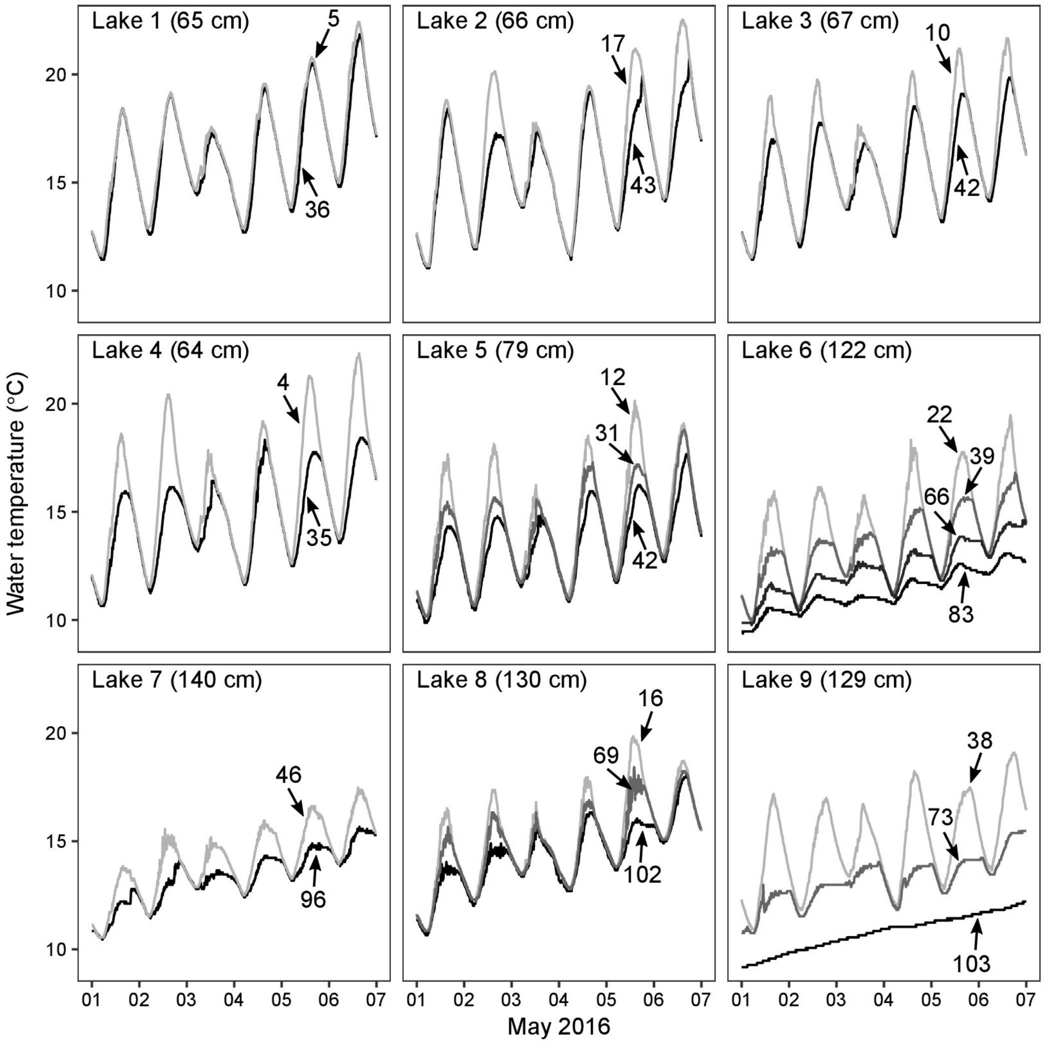

Fig. 4 Water temperature (°C) at two to four vertical positions in the nine investigated lakes from May 1 to May 7 2016. Depth (cm) of temperature measurements is denoted next to the graphs and the total water depth at measurement site is shown in parenthesis

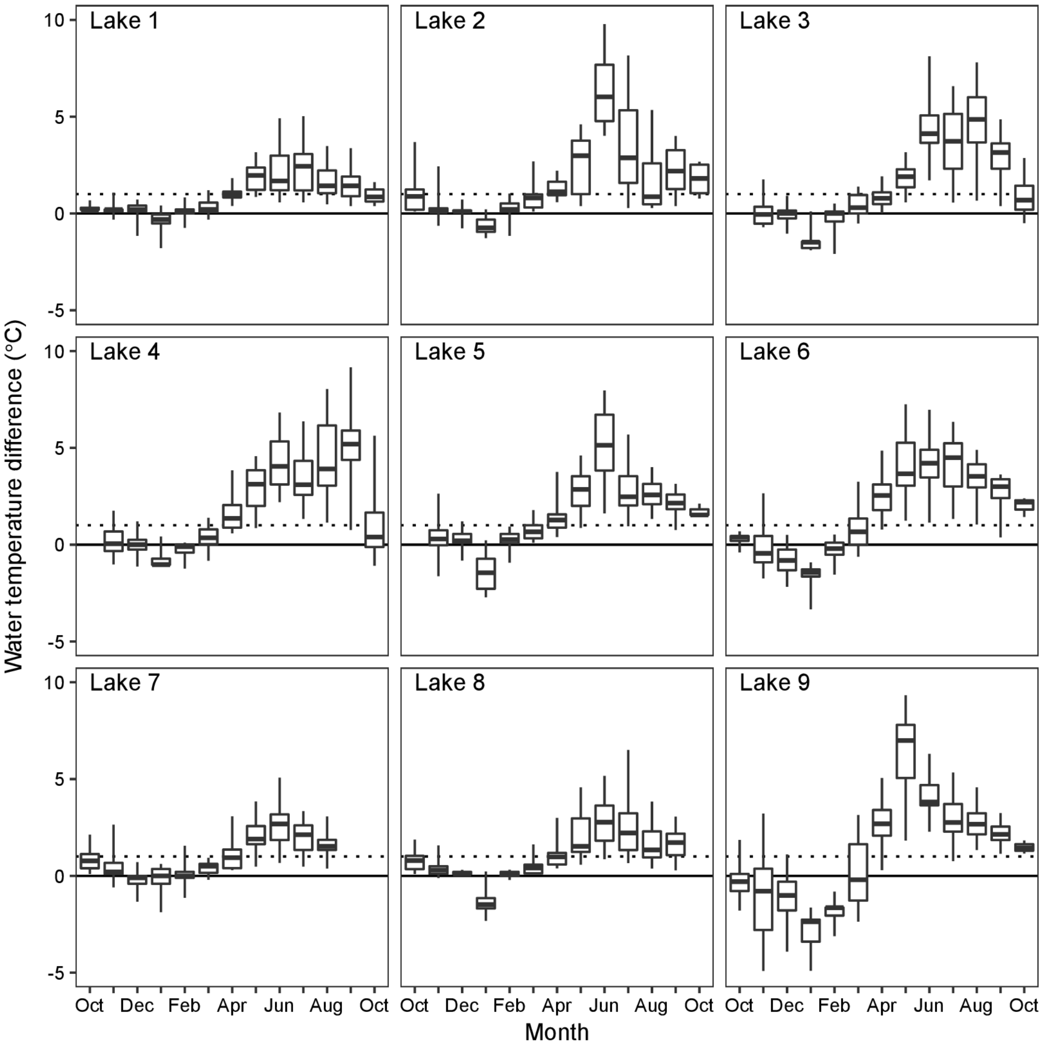

Fig. 5 Seasonal dynamics of vertical differences in water temperature in nine investigated lakes of increasing maximum water depth. Maximum diel differences in water temperature between surface and bottom sensors are summarized in monthly box-plots showing median (solid horizontal line), 25 % and 75 % quartile (upper and lower hinge) and maximum and minimum values (upper and lower whisker). The dotted horizontal line is the 1 °C stratification threshold

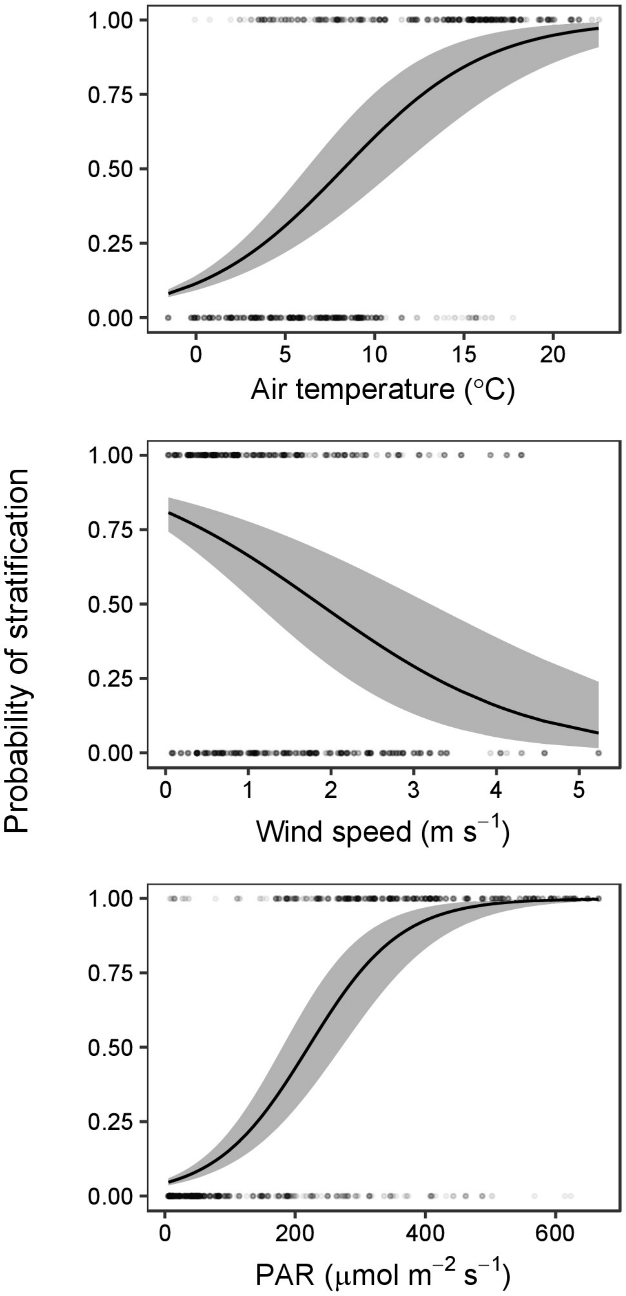

Fig. 6 Probability of stratification as a function of mean diel air temperature, wind speed and PAR. The observations (stratified = 1 and mixed = 0) used to fit the model are shown as points. The solid line is the logistic regression fit from the mixed effect model and the grey area is the 95 % confidence interval

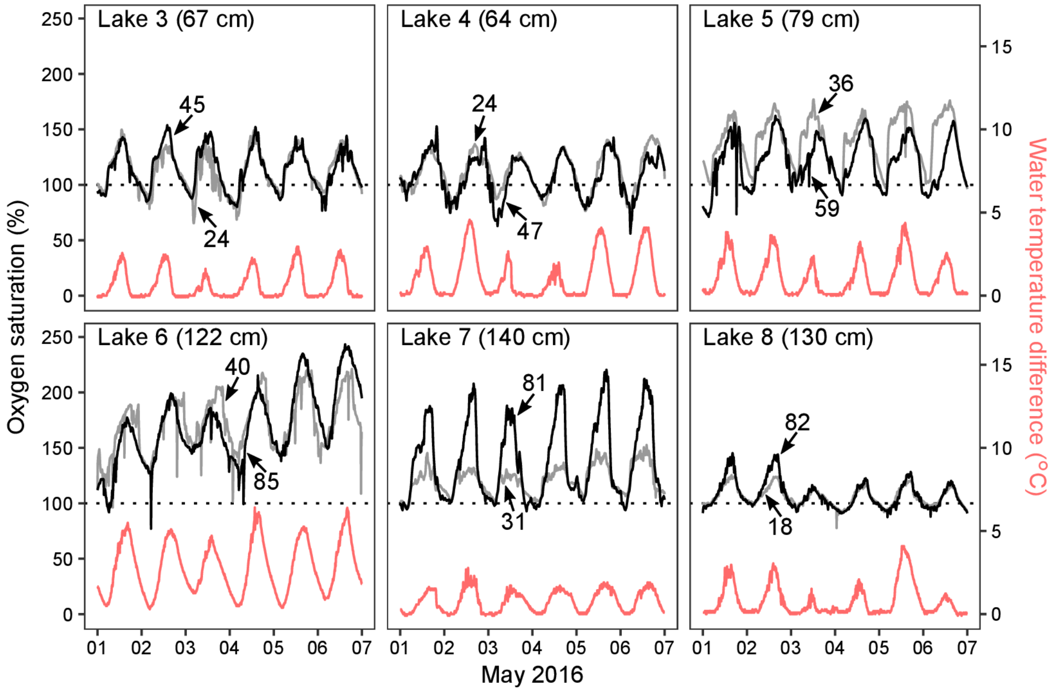

Fig. 7 Oxygen saturation (primary y-axis) in surface waters (grey) and bottom waters (black) in six of the lakes from May 1 to May 7. Depth (cm) of oxygen measurements is denoted next to the graphs and the total water depth at measurement site is shown in parenthesis and the dotted line is 100 % oxygen saturation. Also shown, is the water temperature difference (°C, red solid line, secondary y-axis) between top and bottom (Figure 4)

Tab. 1 Characteristics of the nine investigated lakes in terms of morphometry, percent plant cover on bottom and surface in July 2016 and chemical parameters from December 2015 to July 2016. Mean values with ranges in parenthesis. Number of determination in parenthesis in heading

Variable Unit (n)	Max. depth (z_{max}) m (13-311)	Mean depth (z_{mean}) m (13-311)	Area m^2 (13-311)	Cover bottom % (1)	Cover surface % (1)	Total-P µg L^{-1} (6)	Ortho-phosphate µg L^{-1} (6)	Total-N µg L^{-1} (6)	Ammonium µg L^{-1} (6)	Nitrate µg L^{-1} (6)	*Chl a* µg L^{-1} (9)	pH (8)	Alkalinity meq L^{-1} (8)	$CDOM_{400}$ m^{-1} (8)
Lake 1	0.68 (0.26-1.03)	0.28 (0.15-0.38)	4336 (728-8350)	96	18	98 (60-165)	24 (8-59)	1672 (1011-2938)	60 (19-121)	1 (0-7)	19 (5-53)	8.1 (8-8.4)	2.9 (1.4-4.3)	7.3 (5.1-10.1)
Lake 2	0.68 (0.36-0.87)	0.34 (0.16-0.44)	483 (234-601)	0	0	477 (73-1176)	184 (11-572)	3613 (1415-7541)	179 (49-493)	13 (0-41)	134 (8-525)	8.2 (7.9-8.6)	3.9 (3.2-4.9)	7.6 (5.1-12)
Lake 3	0.69 (0.31-0.78)	0.49 (0.19-0.54)	704 (572-759)	95	35	28 (20-41)	3 (2-5)	935 (655-1370)	36 (16-63)	3 (0-15)	5 (3-9)	8.1 (7.7-9.1)	3.1 (1.2-4.7)	4.7 (3.5-6)
Lake 4	0.73 (0.4-1.3)	0.41 (0.13-0.53)	1062 (545-1354)	100	73	23 (16-31)	3 (1-5)	765 (678-864)	32 (10-57)	9 (0-52)	5 (1-11)	7.8 (7.5-8.1)	4.4 (3.8-4.9)	3.4 (2.8-4.4)
Lake 5	0.77 (0.59-0.89)	0.47 (0.33-0.58)	420 (378-431)	87	57	46 (26-66)	13 (2-29)	949 (697-1321)	47 (17-83)	7 (0-44)	21 (6-63)	7.8 (7.4-8.1)	4.1 (2.9-5)	4.3 (2.8-7.4)
Lake 6	1.27 (0.9-1.41)	0.73 (0.56-0.75)	503 (369-607)	100	68	48 (23-74)	6 (2-12)	1200 (941-1516)	78 (32-160)	82 (0-492)	25 (2-80)	7.8 (7.5-8.1)	3.2 (2.1-4.1)	3.5 (2.3-4.4)
Lake 7	1.36 (0.63-1.69)	0.82 (0.46-0.93)	577 (328-749)	90	22	20 (16-27)	2 (1-3)	1006 (599-2264)	45 (6-106)	14 (0-68)	4 (2-9)	8 (7.8-8.2)	4.1 (1.2-5.6)	3.4 (2.8-4.1)
Lake 8	1.54 (1.21-1.77)	0.79 (0.62-0.90)	2206 (1762-2553)	42	4	45 (21-90)	7 (1-13)	805 (589-1190)	56 (18-87)	3 (0-16)	7 (1-25)	8.1 (7.9-8.3)	3 (2.2-3.6)	3.2 (2.1-3.9)
Lake 9	1.69 (1.09-2.32)	0.75 (0.44-0.96)	682 (408-1080)	92	92	149 (106-188)	46 (21-65)	1903 (1667-2182)	75 (22-135)	2 (0-10.7)	68 (24-177)	7.9 (7.3-8.3)	4 (3.1-5.4)	8.2 (5.1-11.5)

Tab. 2 Logistic mixed-effect models for predicting daytime stratification-mixing status (binary response) of the investigated lakes (n = 1537). The table includes models within two AIC units of the best model. Each model includes "site" as a random effect. The table shows K (number of estimable parameters), AIC, AIC differences (Δ_i) relative to the best model, Akaike weights (ω_i) and the parameter estimates with standard error in parenthesis

Model	K	AIC	Δ_i	ω_i	Intercept	Area	z_{max}	Wind	PAR	Airtemp.
Wind + PAR + Airtemp.	5	739	0	0.29	0.33 (0.34)			-0.82 (0.11)	2.7 (0.17)	1.4 (0.13)
Wind + PAR + Airtemp. + Area + z_{max}	7	739.1	0.03	0.29	0.34 (0.24)	-0.48 (0.26)	0.37 (0.21)	-0.81 (0.11)	2.68 (0.17)	1.41 (0.14)
Wind + PAR + Airtemp. + Area	6	739.7	0.63	0.21	0.33 (0.28)	-0.38 (0.3)		-0.81 (0.11)	2.69 (0.17)	1.36 (0.13)
Wind + PAR + Airtemp. + z_{max}	6	739.7	0.65	0.21	0.35 (0.31)		0.31 (0.25)	-0.82 (0.11)	2.69 (0.17)	1.46 (0.14)
Null	2	2111	1371.9	0	0.02 (0.12)					