Lake stratification in the Carpathian basin and its interesting biological consequences

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Abstract

Stratification of small temperate lakes of the Carpathian basin was studied. Values of Schmidt stability and Lake Number indicated stable summer stratification. Depending on their depth and wind shelter, the lakes could be characterized by various stratification patterns. A near-linear stratification was observed in the Malom Tisza oxbow where in summer during midday the whole water column belonged to the metalimnion. Mixing of the upper water layer was generated by nocturnal cooling. Stable stratification had pronounced consequences for the vertical distribution of chemical variables and phytoplankton. Concentration of sestonic chlorophyll showed bimodal distribution produced by algae in the upper and purple bacteria in the deeper layers. These results revealed that processes and phenomena associated with deep stratified lakes can be observed in shallow basins.

Key words: DCM, fetch length, lake-surface area, Lake Number, Schmidt stability, Thiopedia

Introduction

Thermal stratification of lakes was demonstrated almost 2 centuries ago (de la Beche 1819) and has been considered the most important limnological feature of deep lake ecosystems affecting both the chemical heterogeneity of the water column and the composition of lake biota (Birge 1904, Wetzel 2001).

Because of its crucial role in the functioning of lake ecosystems, much effort has focused on finding relevant characteristics of the lakes and their environments that control the depth and stability of the thermocline (Gorham and Boyce 1989, Imberger and Patterson 1990, Stevens and Imberger 1996). Mixing regime and thermal structure is basically determined by lake morphology such as surface area, mean length, and maximal depth (Mazumder and Taylor 1994), as well as by weather, landscape, and climatic conditions (Gorham and Boyce 1989). Several models were developed to quantify the relationship between the lake geometry and thermocline/mixing depth (Kalff 2002). In these models the most important parameters are surface area, length and width of the lakes, or fetch length.

The positive correlation between thermocline depth and fetch length (active surface area for wind action) was demonstrated for both temperate (Gorham and Boyce 1989, Mazumder and Taylor 1994) and tropical (Kling 1988) lakes. Kling (1988) also demonstrated that mixing depth is often deeper in tropical lakes than in temperate ones, explained by the smaller density differences in layering by warmer water. Gorham and Boyce (1989) showed that the stronger the wind, the deeper the water column is affected because of exposure to larger mechanical energy. During an extensive study on Canadian large lakes, Mazumder and Taylor (1994) demonstrated that fetch length plays an important role in determining the epilimnion depth. For small lakes, however, it has been found that fetch length is a slight
indicator for the mixed-layer depth if fetch is <10 km (Mazumder et al. 1990). All these models are based on the assumption that the mixing/thermocline depth depends primarily on the strength of wind-induced water currents. In addition to the wind-driven effects, nocturnal heat loss also generates currents that play a role in lake stratification, especially in lower latitudes (Lewis 1996).

While stratification of large, deep lakes has been extensively studied for decades (Sundaram and Rehm 1973, Berman and Pollingher 1974, Salmaso 2002), development of stratification in shallow lakes has provoked scientific discussions only in recent years (Padisák and Reynolds 2003, Scheffer and Nes 2007, Branco and Torgersen 2009), possibly due to the lack of clear definition of shallow and deep lakes. From a practical point of view, Scheffer (1998) proposed the term “shallow” for lakes <3 m in average depth, while the functional-based approach of Padisák and Reynolds (2003) suggested a 5 m depth to separate shallow and deep lakes. Padisák and Reynolds (2003) also concluded that absolute depth alone is not adequate to define shallow or deep lakes because various stratification patterns might develop in shallow lakes. Most shallow lakes are polymictic (Hutchinson and Löffler 1956, Lewis 1983, Scheffer 1998) because wind-induced turbulence prevents the onset and persistence of stratification (Padisák et al. 1990, Pithart and Pechar 1995). Survey results, however, indicated that shorter periods of stratification might also develop in shallow temperate waterbodies (Mischke 2003, Teszárné Nagy et al. 2003, Branco and Torgersen 2009, Krasznaí et al. 2010, Borics et al. 2011) in subtropical (MacIntyre 1993) and tropical lakes as well (Fonseca and Bicudo 2008).

Several metrics have been proposed for measuring the stability of lake stratification, among which Lake Number (Lₜ; Imberger and Patterson 1990) has become widely accepted and used in recent years (MacIntyre et al. 1999, Read et al. 2011). As long as the value of this dimensionless metric is >10, the wind can stir the upper water layer but cannot affect the thermocline. In the case of strong winds, the value of Lₜ drops below 10, which indicates that currents cause mixing across the thermocline.

Despite the accumulated information, uncertainties persist in understanding the vertical inhomogeneity of shallow water columns and stability of shallow lake stratification.

The objectives of this study were (1) to study the various stratification patterns of small lakes in the Carpathian basin; (2) to describe the stratification with its associated processes in a wind-sheltered shallow lake; and (3) to find an empirical model to predict the mixing depth as a function of fetch length.

We hypothesized that in wind-sheltered conditions, shallow standing water would present a vertical temperature profile similar to those reported for large deep lakes.

**Material and methods**

**Selection of study sites**

We selected 13 lakes for this study, all located in the lowlands of the Carpathian Basin (80–140 m a.s.l.). The mean air temperature in the region is 10–12 °C (21–23 °C in summer), and the annual precipitation is ~450–600 mm. In addition to the shallow oxbow lakes characteristic for the region (Borics et al. 2014), several deeper gravel- and sand-pit lakes were included in our study. Overall, the 13 lakes selected had surface areas between 0.1 and 2.2 km² and maximum depths between 6 and 31 m (Table 1). A wind-sheltered oxbow lake (Malom-Tisza) of the middle Tisza valley was selected to study the stability and vertical patterns of stratification (length 4.6 km, mean depth 3 m, maximum depth 8 m; Krasznaí et al. 2008; see Borics et al. 2011 for nutrients and chemicals).

**Sampling and field measurements**

Lake depth was determined by a HUMMINBIRD 350TX fish sonar. Fetch lengths of pit lakes were considered to be equal to the maximum lake length, measured using Google Earth, with an accuracy of 10 m. For the Malom Tisza oxbow, the fetch length was approximated by the longest linear distance fitted to the sampling points in each meander. Direction of prevailing wind in the Carpathian basin shows diverse patterns during summer (Kakas 1960); therefore, it was not considered for determination of fetch length.

Vertical sampling was conducted with a Ruttner type (HYDRO-BIOS) sampler at each 1 m interval; the thermometer of the sampler was used to measure water temperature. Pit lake samplings were carried out at the deepest part of the lakes in September 2007. The planar thermocline depth was defined as the depth where the temperature gradient was maximal (Hutchinson 1957). Determination of the top and bottom of the thermocline was based on the density differences of the layers (Read et al. 2011). Metalimnion was defined as the layer between the thermocline top and bottom, and top of the thermocline was considered as epilimnion depth.

To study the temporal pattern of lake stratification and the vertical distribution of chemical and biological variables in the Malom-Tisza oxbow, monthly sampling was performed between May 2007 and September 2010. At a smaller temporal scale, the diurnal variation of strati-
Lake stratification was studied during a 3 h sampling interval over a 24 h period from 22 to 23 July 2007. Photoautotrophic organisms were sampled using a tube sampler equipped with outlets at each 0.25 m interval. Samples were fixed by Lugol’s solution and counted according to Lund et al. (1958) and Utermöhl (1958). Biovolume was determined based on specific volumes, estimated by appropriate geometric forms for each taxon (Hillebrand et al. 1999).

Water temperature (°C), pH, and conductivity (µS cm⁻¹) were measured in situ by LT lutron DO-5509 and WTW MultiLine P4 instruments, while chemical parameters (NO₃⁻-N, NO₂⁻-N, NH₄⁺-N, soluble reactive

<table>
<thead>
<tr>
<th>Lake Name</th>
<th>Location</th>
<th>Area (km²)</th>
<th>Z max (m)</th>
<th>Z mean (m)</th>
<th>Fetch (m)</th>
<th>Z Epilim. (m)</th>
<th>Z Therm. (m)</th>
<th>Schmidt stability (J - m²)</th>
<th>Wind speed necessary to break stratification (m s⁻¹)</th>
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<td>112</td>
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<td>13.5</td>
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phosphorus [SRP], total phosphorus [TP], and chlorophyll a [Chl-a]) were determined according to Hungarian National Standards (MSZ 12750-17:1974; MSZ 448-12:1982; MSZ ISO7150-1:1992). Water transparency was measured by Secchi disk; the euphotic depth was estimated by a multiplier of 2.5 for oxbows and 2.7 for pit lakes. Light attenuation coefficient was estimated by the modified Poole-Atkins (1929) formula: $K_d = 1.65/ \text{Secchi depth}$. (Giesen et al. 1990), which is applicable to natural waters of low colour and varying turbidity. Mean wind speed data for the April–October period (3 m s$^{-1}$) were used to calculate metrics used for characterizing the stability of stratification.

**Metrics of water column stability**

Several metrics have been developed for characterization of the stability of lake stratification, such as the Schmidt stability (Schmidt 1928, Idso 1973), Wedderburn number (Thompson and Imberger 1980), Lake Number (Imberger and Patterson 1990), and Brunt–Väisälä frequency (Turner 1973). In the present study, 2 metrics, Schmidt stability and Lake Number, were applied.

Schmidt stability, $S_T$, is the amount of work needed for a water column to overcome thermal stratification without further addition or subtraction of heat. This metric was calculated by the Idso’s formula (1973):

$$S_T = \frac{\int_0^{Z_T} (Z-Z_p) \rho A \, dZ}{A_g}$$

Lake Number ($L_N$) is a dimensionless index that expresses the dynamic stability of the water column. $L_N$ is the ratio of the strength of stratification to the effect of the wind stress (equation 2). If $L_N > 10$, wind stirs the uppermost region of a lake; for $L_N > 3$ and $< 10$, the thermocline partially tilts, and shear and shear-induced mixing increases across the thermocline; for $L_N = 1$, full upwelling occurs; for $L_N = 0.1$, the upwelling is more extensive; and for $L_N < 1$, the lake will mix (MacIntyre et al. 2009): 

$$L_N = \frac{S_T(Z_T+Z_h)}{2 \rho_h U^2 A_s Z_p}$$

where $g$ is the acceleration due to gravity; $A_s$ is the surface area of the lake; $A_s$ is the area of the lake at depths $Z$; $Z_p$ is the maximum depth of the lake; $Z_r$ is the depth to the centre of volume of the lake; $\rho_h$ is the density of the hypolimnion; $Z_i$ and $Z_h$ are the depths to the top and bottom of the metalimnion; and $u^*$ is the water friction velocity due to wind stress.

The metrics were calculated by the Lake Analyzer program (Read et al. 2011).

**Statistical methods**

A general least-squares linear regression (in Matlab) was used to study the relationship between the fetch and thermocline depth. To illustrate the vertical differences of variables in the water column, data were standardized by dividing each value by the maximum.

**Results**

**Thermal stratification of the lakes**

The vertical temperature profiles indicated stable stratification (Fig. 1). The lakes showed high variation in depth of metalimnion and the planar thermocline. The lake characterized by the deepest surface mixed layer had a deep ($Z_{therm} > 10$ m) planar thermocline. Deepening of the mixed layer reduced the thickness of the metalimnion, especially apparent in Lake Hegyeshalom, where thickness of the metalimnion was <2 m. In the case of most lakes, a typical 3-layered stratification could be observed; however, several lakes were characterised by a near-linear stratification. In these lakes the thickness of the surface mixed layer was minimal or zero; thus, the whole upper part of the water column belonged to the metalimnion.

The stability of the lakes varied by a factor of 10, with low values on the order of ~ 100 J m$^{-2}$ and high values exceeding 1000 J m$^{-2}$. Because $S_T$ is primarily a measure of the heat content of the lake, the highest values were found in the deeper lakes. $L_N$ computed using mean wind speeds of 3 m s$^{-1}$ for the region all exceeded 10, and most were >50. These high numbers indicate that wind mixing would be restricted to a shallow near-surface layer during summer stratification, and any deepening of the upper mixed layer would occur by nocturnal cooling or cooling during cold fronts. Internal wave motions would likely be linear and not likely to cause mixing (Horn et al. 2001). The wind speeds that would cause $L_N$ to drop to 10 and initiate thermocline tilting and some shear ranged from 4 to 30 m s$^{-1}$, with the lower values tending to occur for lakes with longer fetches. The oxbow lake, Malom-Tisza, had the highest value, attesting to its considerable resistance to wind mixing and a possible reason for the near-linear stratification that developed.

**Thermal stratification of the Malom Tisza oxbow**

Based on both the vertical temperature profile and the $S_T$ and $L_N$ metrics, the Malom-Tisza oxbow showed stable thermal stratification between May and August in each year (Fig. 2 and 3). The maximum difference between the surface and bottom layers was 22.8 °C (July 2007); the...
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Fig. 1. Temperature profiles of study lakes. Field measurements were conducted 18 Aug 2007 to 4 Sep 2007 in the midday period (11:00–15:00 h).
temperature of the bottom layers never exceeded 11°C; and the temperature at the lake surface occasionally exceeded 30 °C. The stable stratification period lasted until late October, when homothermy established first at 11 °C in the whole water column and then cooled down to 4 °C. After the December homothermy (4 °C), ice cover developed each winter.

Temperature profiles of the Malom-Tisza oxbow imply a near-linear stratification of the water column (Fig. 3). The epilimnion, defined as the upper mixed layer with a uniform temperature, was observed only occasionally. In several cases, the depth of epilimnion was <1 m or 0; thus, the linear stratification started from the water surface, and the whole water column belonged to the metalimnion. Development of the classical 3-layered stratification was an exception rather than the rule.

**Diurnal thermal changes**

Diurnal changes in the vertical temperature profile were restricted to the upper 4 m layer (Fig. 4). At the immediate lake surface, the daily fluctuation was >6 °C while at lower depth (2 m) it was only 2.4 °C. The nocturnal surface cooling affected only the upper 2 m of the water column. Due to this process, the depth of the mixed layer changed considerably during the day (Fig. 4). As a result of the linear stratification of the water column, the epilimnion disappeared in the warmest hours of the day. The bottom of the metalimnion did not change notably.

Both stability metrics ($S_T$, $L_N$) showed similar tendencies (Fig. 5). Higher values were calculated for the warmest periods of the day. The $L_N$ calculated using mean winds of 3 m s$^{-1}$ indicated that wind only stirred the surface waters and that the stratification was so strong relative to wind that internal wave motions would be linear and produce little shear to cause mixing below the surface.

**Chemical stratification**

In the Malom-Tisza oxbow, vertical distribution of main chemicals demonstrated the presence of a characteristic chemocline in summer (Fig. 6). Dissolved oxygen dropped suddenly at <3 m depth, resulting in an oxic–anoxic interphase. Similarly, a considerable increase in the concentration of nitrate-nitrogen and the phosphorus forms occurred at 4 m depth. Paralleling chemicals, a slight increase in electrical conductivity was also observed. Although most of the chemoclines disappeared with homothermy in October, some variables continued to show vertical differences (Fig. 6; values of variables in Table 2).

**Vertical changes in algal biomass**

Differences in Chl-$a$ values in the various layers referred to a marked uneven vertical distribution of phytoplankton biomass in the water column (Fig. 7). After the development of stable stratification, a characteristic increase in Chl-$a$ was observed in deeper layers. In each
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In a case, a first peak of deep chlorophyll maximum (DCM) occurred at the bottom of the euphotic zone (between 2 and 3 m depth, dominated by filamentous cyanobacteria), which was followed by a second, more remarkable DCM positioning below the euphotic zone. This bimodal distribution of Chl-a could be observed in each year of the investigations (Fig. 7). Microscopic observations evidenced the dominance of the purple sulphur bacteria (predominantly *Thiopedia rosea*) in these layers (Fig. 8); however, these bacteria did not form a distinct layer, but occurred in high abundance in the aphotic zone and peaked ~2 m below the compensation zone.

Fig. 3. Temporal variation in the temperature profiles in the Malom-Tisza oxbow in 2007, 2008, 2009, and 2010: • • • = metalimnion top; • • • • = thermocline depth; --- = metalimnion bottom.
Values of thermocline, metalimnion, and the metrics used for characterising stability of stratification were calculated (Table 1). The least-squares linear regression indicated a significant ($p < 0.001$) increase in thermocline depth with fetch length (Fig. 9; $L_{\text{fetch}}$: $R^2 = 0.74$). The equation of this linear regression line reads: $Z_{\text{therm}} = 0.007 \times L_{\text{fetch}} + 3.7056$, whereby the intercept was at $\sim4$ m depth. Similarly, a significant relationship was also found between the fetch length and the depth of epilimnion (Fig. 10; $R^2 = 0.79$, $p < 0.001$). In this case, the intercept predicted a theoretic thickness of epilimnion of $\sim0$ m if fetch length approximates zero.

**Fetch length vs. thermocline, and epilimnion depth**
Table 2. Chemical characteristics of Malom-Tisza oxbow in July and October 2007.

<table>
<thead>
<tr>
<th>Date</th>
<th>Depth (m)</th>
<th>Water temp (°C)</th>
<th>pH</th>
<th>Cond. (µS cm(^{-1}))</th>
<th>DO  (mg L(^{-1}))</th>
<th>NH(_4)-N (µg L(^{-1}))</th>
<th>NO(_2)-N (µg L(^{-1}))</th>
<th>NO(_3)-N (µg L(^{-1}))</th>
<th>PO(_4)-P (µg L(^{-1}))</th>
<th>TP (µg L(^{-1}))</th>
<th>Chl-a (µg L(^{-1}))</th>
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Fig. 6. Vertical distribution of main chemicals in the Malom-Tisza oxbow, 2007 (a–c) July; (d–f) October. Variables are standardised by maxima.
To estimate the stability of lakes, 2 metrics (S<sub>T</sub>, L<sub>N</sub>) were applied. The S<sub>T</sub> values of the lakes fell in the range of values characteristic for lakes of similar depth and size in Austria and North America (Wetzel 2001). We note, however, that the highest value calculated for Lake Vadna (1304 J m<sup>-2</sup>) is one order of magnitude larger than that given for Lake Findley, Washington, although concerning the lake morphology, these lakes are quite similar.

During calculation of the L<sub>N</sub> values, average wind speed (3 m s<sup>-1</sup>) data for the region were considered. The L<sub>N</sub> values calculated this way did not drop below values of ~10, which means that wind can stir the upper water column but cannot mix the thermocline or affect its depth (Imberger and Patterson 1990); thus, the lakes were stably stratified. These results are not in accordance with the strong positive relationship between the fetch length and thermocline depth (Fig. 9) and epilimnetic depth (Fig. 10). Considering that wind can affect the thermocline depth at a value of L<sub>N</sub> < 10, the critical winds speed values (when L<sub>N</sub> = 10) were calculated for each lake (Table 1). Although these values are higher than the summer average wind speed for the region, and somewhat higher values would
be required for greater tilting of the thermocline and enhanced shear, these are not exceptional because similar wind-speed values are often measured in the Carpathian basin in the summer period (www.idokep.hu homepage). Thus, the thermocline depth can be basically determined by the strengths of enduring strong winds, especially in lakes with less wind sheltering.

In addition to the classical 3-layered stratification of the lakes, additional stratification patterns could also be distinguished. Development of 2-layered stratification with an upper mixed and a lower metalimnetic layer were characteristic for the small shallow lakes. A 2-layered stratification also characterized Lake Ormosbánya, but in this lake the metalimnion reached the surface, and beneath that a homothermal hypolimnion was observed.

A near-linear stratification occurred in the Malom Tisza oxbow, where the whole water column belonged to the metalimnion. Malom-Tisza, characteristic of many oxbows in the Hungarian lowland, retains its naturally sheltering riparian vegetation (Pálfai 2001). The special, sinuous morphology and the natural sheltering both reduce the possibility of development of wind-induced turbulences. The observed 1-layered stratification is characteristic only for the warmest midday period, when the lake is progressively heated. After sunset, as a result of nighttime cooling, the upper layer of the water column cools convectively, resulting in the development of a surface mixed layer. Temperature of the surface layer decreased by 5 °C from noon to sunrise, and the impact of this nocturnal cooling was observed even at 2 m depth.

This kind of diurnal cycle of stratification has been observed in subtropical (Imberger 1985, Imberger and Patterson 1989) and tropical regions as well (Hare and Carter 1984, Lewis 1996, Talling and Lamoalle 1998). The phenomenon was also called a partial atelomixis of the epilimnion (Barbosa and Padisák 2002). This nocturnal mixing, and not wind, could set the depth of the mixed layer in small wind-sheltered lakes. In this case, the role of wind is not to create shear and generate turbulences, but rather to increase evaporation processes and thus enhance the cooling of the immediate surface layer (Kalf 2002).

The monthly stratification patterns of the Malom-Tisza oxbow and the values of the calculated metrics ($S_T$, $L_N$) demonstrated that stable thermal stratification of small-surfaced waterbodies is not an exceptional or temporal phenomenon. Despite its absolute shallowness (average depth ~3 m), the studied oxbow functioned as a typical temperate dimictic lake having a complex water column mixing only during spring and autumn.

In addition to the stable thermal stratification, the considerable vertical differences in chemical variables might also be a characteristic feature of eutrophic oxbow lakes. Both the oxycline and the dramatic increase of ammonium observed at 3–4 m depths imply that, in addition to the diurnal mixing of the upper water layers, deeper mixing events occasionally affect the upper layers of the metalimnion.

High algal biomass is frequently observed in the shallow euphotic zone of oxbows (Grigorszky et al. 2003, Tészárné Nagy et al. 2003, Borics et al. 2011). These studies emphasized that because of the reduced mixing of the shallow euphotic layers, the phytoplankton of these waterbodies are dominated by populations of buoyant planktonic cyanobacteria having gas vesicles and/or flagellated algae capable of changing their position within the water column. Previous studies (Krasznai et al. 2010, Borics et al. 2011) demonstrated that phytoplankton of the Malom-Tisza oxbow also share these traits. These algae are responsible for the upper Chl-$a$ peak in the euphotic zone.

Our results are in accordance with the findings that development of high biomass phytoplankton in the euphotic zone is responsible for the enhanced light attenuation in the photic zone (Krause-Jensen and Sand-Jensen 1998) and coincides with high microbial activity in the deeper layers, quickly depleting the hypolimnetic oxygen reserves (Wood et al. 1984). The drastic depletion of oxygen results in lower values of phosphorus retention (Nürnberg 1984) and contributes to the increase of phosphorus forms and NH$_4$ ions in the deeper layers. These nutrient reserves become available for the plankton when the whole water column mixes again.

In our investigation, the algal biomass was not limited to the shallow euphotic zone but was also prominent in the deeper layer, resulting in a second DCM. Although the ethanol extraction method used for measuring Chl-$a$ con-
centrations in this study does not allow us to distinguish between Chl-α and bacteriochlorophyll, microscopic investigations clearly showed that a purple sulphur bacterium, *Thiopedia rosea*, dominated in the aphotic zone. Because this bacterium is strongly anaerobic and obligatory phototrophic, its occurrence is limited by the unavailability of hydrogen sulphide and by the lack of light. These sources determine the distribution of *Thiopedia* in the water column in both directions (i.e., toward the upper and lower layers).

Eichler and Pfennig (1991) demonstrated that growth of *Thiopedia rosea* is inhibited by light intensities $>150 \, \mu E \, m^{-2} \, s^{-1}$; therefore, the well-illuminated epilimnion cannot be considered a hospitable environment for these bacteria, partly because of the higher light intensity and the lack of sulphide. The increase of the biomass of *Thiopedia rosea* clearly indicates the depth of mixing layer. In the deeper layers, the low light intensity and high sulphide concentrations limit the growth of bacteria, but in this case it was expressed neither in Chl-α nor in biomass values. Photoautotrophic bacteria can use a wide range of the light spectrum and require lower light intensities for carrying out photosynthesis than algae and thus are able to thrive under very low light intensities (Takahashi and Ichimura 1970). An additional property of *Thiopedia rosea* is that this taxon can also migrate in the water column by changing its buoyancy (Kohler et al. 1984). These properties make these bacteria particularly successful in this environment (Guerrero et al. 1985).

In most of the models proposed to describe the relationship between the morphological characteristics of lakes and thermocline/mixing depth, the relationship is approximated by power equations (Kalff 2002). For the lakes involved in this study, a linear model could be applied. Despite the relatively low numbers of lakes, the proportion of explained variance was high (~0.8). Our results suggest that fetch length is a good predictor of mixing depth, even in the case of shallow, small waterbodies.

Although metrics used for assessing water column stability refer to a stable water column, stratification in shallow lakes is quite sensitive to changes in hydrological and meteorological processes. Global warming (or, as it should be called, “global weirding”; Friedman 2008, Bunnell 2010) coincides with extremities in temperature, precipitation, winter conditions, and other phenomena associated with climate change. These phenomena exert a pronounced influence on lake level and mixing regime (Blenckner et al. 2002, MacIntyre and Melack 2009, Berman and Pollingher 1974). This project was supported by the Hungarian National Science Foundation (OTKA Nr. K 75552 and OTKA104279), Bolyai Fellowship of the Hungarian Academy of Science and the EU Societal Renewal Operative Program (TÁMOP-4.2.2.A.11/1/KONV-2012-0064).

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