Multiple extreme environmental conditions of intermittent soda pans in the Carpathian Basin (Central Europe)

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Abstract

Soda lakes and pans represent saline ecosystems with unique chemical composition, occurring on all continents. The purpose of this study was to identify and characterise the main environmental gradients and trophic state that prevail in the soda pans (n=84) of the Carpathian Basin in Central Europe. Underwater light conditions, dissolved organic matter, phosphorus and chlorophyll *a* were investigated in 84 pans during 2009–2010. Besides, water temperature was measured hourly with an automatic sensor throughout one year in a selected pan. The pans were very shallow (median depth: 15 cm), and their extremely high turbidity (Secchi depth median: 3 cm, min: 0.5 cm) was caused by high concentrations of inorganic suspended solids (median: 0.4 g L^{-1}, max: 16 g L^{-1}), which was the dominant (>50%) contributing factor to the vertical attenuation coefficient in 67 pans (80%). All pans were polyhumic (median DOC: 47 mg L^{-1}), and total phosphorus concentration was also extremely high (median: 2 mg L^{-1}, max: 32 mg L^{-1}). The daily water temperature maximum (44 °C) and fluctuation maximum (28 °C) were extremely high during summertime. The combination of environmental boundaries: shallowness, daily water temperature fluctuation, intermittent hydroperiod, high turbidity, polyhumic organic carbon concentration, high alkalinity and hypertrophy represent a unique extreme aquatic ecosystem.

Highlights

- Soda pans can be highly turbid, alkaline, polyhumic, and hypertrophic habitats.
- Some pans are among the most turbid aquatic ecosystems in the world.
- Due to their shallowness, water temperature undergoes high daily fluctuations.
- The combination of environmental boundaries creates an extreme aquatic ecosystem.

Abbreviations

CHL, chlorophyll *a*; CDOM, chromophoric dissolved organic matter; DOC, dissolved organic carbon; K_d: vertical attenuation coefficient; SRP, soluble reactive phosphorus; TP, total phosphorus; TSS, total suspended solids; TSS-Alg, suspended solids without algae; Z, water depth; Z_{eu}, euphotic depth; Z_{mix} Z_{eu}^{-1}, ratio of mixed and euphotic depth; Z_S, Secchi disc transparency.

Key words

alkaline; hypertrophic; intermittent; polyhumic; turbid; water temperature fluctuation

1. Introduction

Most inland saline waters are shallow with unique physical and chemical conditions. Soda lakes and pans can be found on all continents, but they are much less frequent than other types of saline waters (Hammer, 1986). Soda lake formation depends on low levels of dissolved calcium and magnesium and the dominance of bicarbonate (HCO_3>>Ca+Mg). They represent the most stabile high-pH environments (pH>9) on Earth, which clearly distinguishes them from other inland saline waters (Grant, 2004; 2006; Warren, 2006; Brian et al., 1998).

Soda lakes are interesting also for evolutionary biology. Zavarzin (1993) argued that alkaline soda lakes have ancient prokaryotic communities. According to Brian et al. (1998), the "Precambrian explosion" of prokaryote diversity might had taken place in alkaline environments. The Archaean ocean was perhaps dominated by Na-Cl-HCO_3, and did not resemble the Na-Cl ocean of today (Kempe and Degens, 1985; Maisonneuve, 1982). According to this so-called "soda ocean hypothesis", this early Archaean hydrosphere might had a chemistry similar to that found in modern soda lakes (Warren, 2006). This hypothesis however remains controverial.

European soda pans were formed on various geological substrates by specific climatic, geologic and hydrologic conditions in the groundwater discharge areas of the Carpathian Basin at the end of Pleistocene and the beginning of Holocene. These relatively old habitats were strongly influenced by human impacts in the last two centuries, leading to the disappearance of the majority of soda pans (Boros et al., 2013). According to available knowledge, European soda pans are restricted to the Carpathian Basin (in Austria, Hungary and Serbia). Due to their unique conditions and biota, as well as the significant decline in their number and territory, soda pans are listed in the habitat directive (92/43/EC) as “Pannonian steppes and salt marshes” with high protection priority in the Natura 2000 network of the European Union (Boros et al., 2013). In addition, several of these habitats are listed as Ramsar sites or Important Bird Areas, and most soda pans in Austria are part of a UNESCO World Heritage site.

The most frequent ionic type of soda pans is the basic alkaline type (Na-HCO_3), which represents more than half of the natural soda pans in the Carpathian Basin, being widely distributed on the lowland part of the region. The second most frequent subtype is the chloride subtype (13% of all pans), which is concentrated to the Danube Valley in Central Hungary, while the third is the sulphate subtype (11%), which is rather frequent in Seewinkel (Austria). Magnesium can sometimes be a secondary dominant cation beside sodium. The high number of ionic subtypes reflects the chemical diversity of alkaline soda pans within the relatively small territory of the Carpathian Basin. Salinity varies between sub- and hypersaline ranges, with pH in the alkaline range (Boros et al., 2014).

The intermittent soda pans of the Carpathian Basin are very shallow compared to other saline lakes of the World (Boros et al., 2014), which is a key feature of these pans. Because of their shallowness, water temperature strongly follows air temperature, and notable daily temperature fluctuations can occur. Furthermore, polymixis and high turbidity are also usual conditions in most shallow lakes, and they are also key physical factors in the soda pans (Hammer, 1986).

In contrast with the known prevalence of strong environmental stress gradients due to extreme local conditions (salinity, pH, turbidity, desiccation), there are only a relatively few recent studies that have investigated the effect of this environment on the local biota. According to them, benthic and planktonic communities reflect a strong structuring role of salinity, turbidity and trophic state (e.g. Wolfram et al. 1999; Horváth et al., 2013a, 2014, 2015; Stenger-Kovács et al., 2014, 2016).

Zavarzin (1993) observed that endorheic soda lakes have a closed nutrient cycling, where carbon and nitrogen input is predominantly dominated by CO_2 and N_2 fixation by cyanobacteria. However, others argue that soda lakes are not entirely closed systems, due to large populations of waterbirds (Brian et al., 1998; Sorokin et al., 2014). Apart from the apparent role of local conditions, aquatic communities of soda pans are also strongly linked to waterbirds in two ways: habitats with a high zooplankton biomass attract more planktivorous waterbirds (Boros et al., 2006; Horváth et al., 2013b), while waterbirds (especially large-bodied herbivorous species e.g. geese) provide a high nutrient input, regulating trophic relationships, causing net heterotrophy, and a generally high trophic state (Boros et al., 2008a, 2008b; Vörös et al., 2008).

Although data are available on a selected number of European soda pans and their physical and chemical conditions, a large-scale evaluation of multiple environmental conditions together with the respective trophic state is still missing. It is currently also unknown whether the major ionic composition, which shows some geographical pattern in the region (Boros et al., 2014), has any relationship with other physical and chemical variables.

The purpose of this study was to identify and characterise the main environmental gradients and trophic state that prevail in the natural soda pans of the Carpathian Basin. For this, we used a dataset covering all natural intermittent soda pans (Boros et al., 2013) in the Carpathian Basin (Austria, Hungary, Serbia). Secondly, we also aimed to study the seasonal and daily water temperature fluctuations in a selected typical shallow soda pan, which can pose another type of stress for the biota developing on a daily basis.

2. Methods

2.1 Study sites

The Carpathian Basin is influenced by Continental, Atlantic and Mediterranean climate, with the predominance of Continental climate on the lowland steppe territories where the soda pans are located. Yearly mean air temperature is between +10 and +11 °C and the yearly sum of rainfall is between 500–600 mm on the lowlands. Daily air temperature fluctuation is the lowest in December (4–6 °C), and the highest in July (10–11 °C), based on the mean of 30 years (1971−2000), but the occurrence of irregular extremes is significantly increasing during the last decade. The time of sunshine is relatively high (1800−2000 hours per year) and the yearly mean of windy days (wind speed > 10 m s^{-1}) is 122 (www.met.hu). All these climatic conditions contribute to the high water level fluctuation and summer drying out of the soda pans.

The biomass of phytobenthos is low in soda pans, because of strong underwater light limitation (Boros et al., 2013), and previous studies have found that picophytoplankton is one of the fundamental contributors to planktonic primary biomass production (Keresztes et al., 2010). Macrophytes are relatively scarce because of the extreme conditions. Marshland (*Bolboschoeno-Phragmitetum*) and wet meadow vegetation (*Lepidio crassifolii* –

Puccinellietum limosae) are the most typical around the shoreline, while submerged macrophytes are sparse or absent. More details on the ecology and overall characteristics of soda pans were recently published by Boros et al. (2013).

The study area covers the whole lowland territory of the Carpathian Basin (Pannonian Plain), where the natural intermittent soda pans are located. This involved the survey of the Seewinkel region of Austria, the Great Hungarian Plain of Hungary and the Vojvodina region of Serbia. In this way, we included all the characteristic soda pans of the Pannonian ecoregion (Fig. 1).

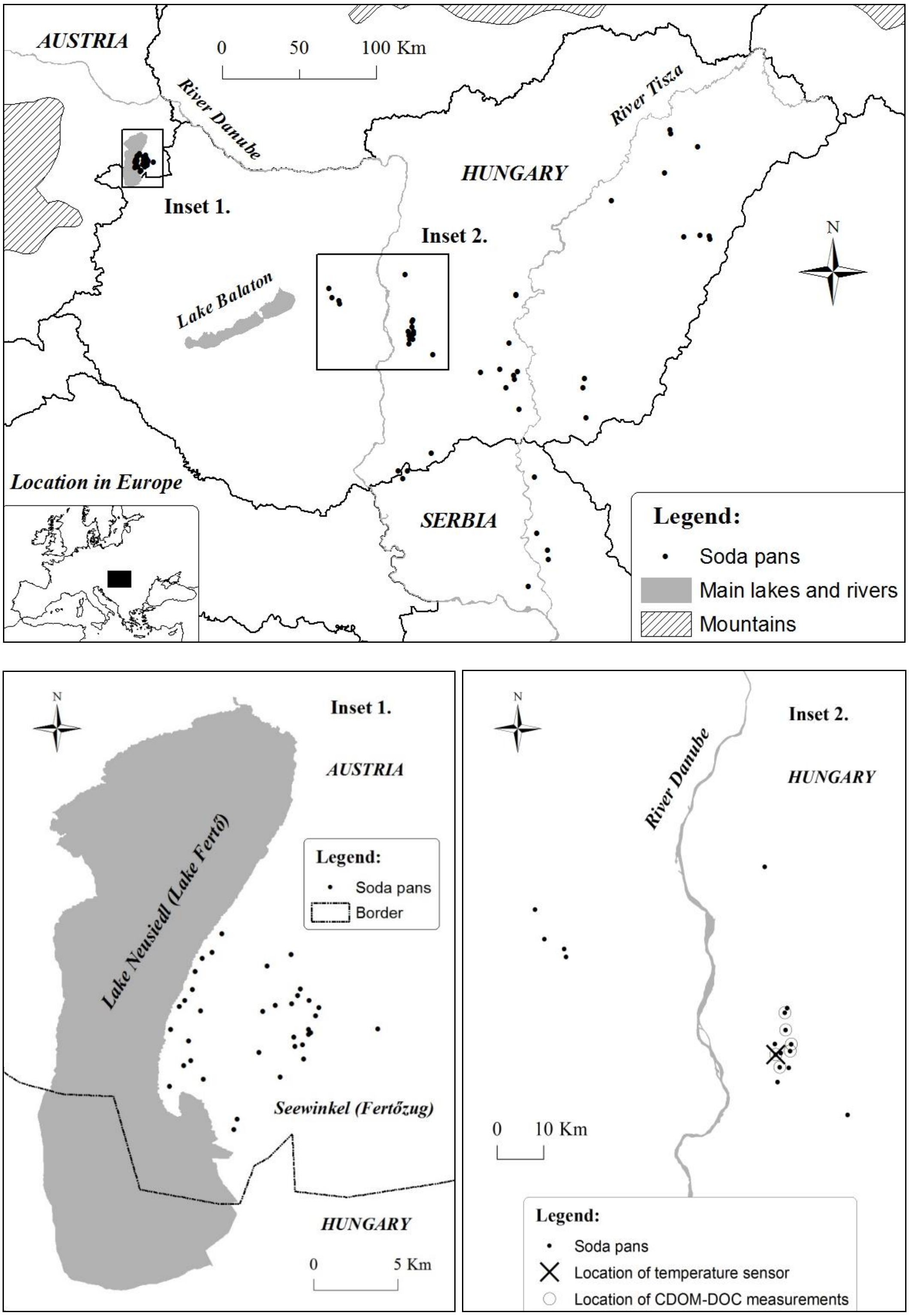

Fig. 1. Geographic location of the 84 investigated soda pans and position of the water temperature logger in the Carpathian Basin. (Inset 1. Seewinkel region; Inset 2. Danube Valley region in central Hungary, where the water temperature logger was positioned and the CDOM-DOC relationship measurements were carried out)

2.2 Water sampling and field measurements

The survey of intermittent soda pans took place from March 2009 to August 2010. Each pan (Appendix 1) was sampled once during this period. In spite of a single observation per habitat, the large spatial scale with the complete dataset of existing natural (n=84) soda pans in the region can give a representative overview on environmental conditions and trophic state. The exact position of sampling sites was obtained with a GPS device. Details on measuring the open water area are given in Boros et al. (2014). Water samples were taken from the open water area of the pans taking particular care not to disturb the sediment, by filling plastic containers with water subsequently analysed in the laboratory in triplicates. Water depth (Z) was measured at each sampling location with a centimetre-scale pole.

Underwater light conditions were measured on the field with a Secchi disc (Z_S), except when the lake bottom was visible (n=14). We used a Secchi disc constructed specifically for these turbid systems: the disc was a round tray (with a rim), with a measuring stick attached to its centre. In most habitats, we used it by immersing into the water, while in the most turbid habitats, we took some water from the surface layer (1-2 cm) and by pouring it on the tray, we could measure transparency with an accuracy of 0.5 cm. Electrical conductivity was measured with a WTW Multiline field instrument with a TetraCon 325, and pH with a SenTix 41 electrode on site. Salinity was calculated from conductivity (with a multiplying factor of 0.8) based on a formerly established experimental relationship (Boros et al., 2014).

2.3 Measurement of TSS, TSS-Alg, CDOM, SRP, TP, CHL

The concentration of total suspended solids (TSS) was measured gravimetrically. Water samples of 100–150 ml were filtered through a previously dried and pre-weighed GF-5 glass fibre filter (nominal pore size=0.4 μm), then dried for 2 hours at 105 °C, then weighted again. The concentration of total suspended material was calculated based on the volume of the filtered sample.

Concentration of the chromophoric dissolved organic matter (CDOM) was measured spectrophotometrically at 440 nm according to the method of Cuthbert and del Giorgio (1992); CDOM is given in Pt units (mg Pt L^{-1}).

The concentration of soluble reactive phosphorus (SRP) was determined from filtrates of precombusted GF-5 glass fibre (nominal pore size=0.4 μm) based on the method of

Murphy and Riley (1962), while total phosphorus (TP) was measured from unfiltered water samples, with a potassium-persulfate digestion (Menzel and Corwin, 1965).

For chlorophyll *a* (CHL) measurements, 5–100 ml of water (depending on turbidity) was filtered through a GF–5 glass fibre filter (nominal pore size=0.4 µm) in the field, which then was frozen in test tubes. In the laboratory, CHL concentration was determined spectrophotometrically with hot methanol extraction (Wetzel and Likens, 1991).

The concentration of suspended solids without algae (TSS-Alg) was calculated by assuming a 1:100 ratio between CHL concentration and the dry weight of phytoplankton (Reynolds, 1984). Subtracting this value from the TSS concentration yielded the TSS-Alg content of the samples.

2.4 Estimation of K_d and DOC

The calculation of vertical attenuation coefficient (K_d) of the photosynthetically active radiation (PAR: 400−700 nm) for shallow lakes (including soda pans) in the Carpathian Basin is based on an empirical multiple regression equation [1], describing the relationships between light-absorbing components (CHL, CDOM, and TSS-Alg):

$$K_d\ (\mathrm{m}^{-1}) = -0.0255 + 0.0141 \times \mathrm{CHL}\ (\mu\mathrm{g\ L}^{-1}) + 0.0172 \times \mathrm{CDOM}\ (\mathrm{mg\ Pt\ L}^{-1}) + 0.0924 \times \mathrm{TSS\text{-}Alg}\ (\mathrm{mg\ L}^{-1}) \quad [1]$$

(V.-Balogh et al., 2009)

The euphotic depth (Z_{eu}) was calculated based on estimated K_d (m^{-1}) values (Kirk, 1996). Because of the shallowness of the soda pans, Z is regularly equal to mixed depth (Z_{mix}). With the help of these values, we calculated the ratio of mixed and euphotic depth ($Z_{mix}\ Z_{eu}^{-1}$) in each pan.

The relationship between CDOM and DOC was identified in a smaller data set: CDOM and DOC concentrations were simultaneously measured in water samples on six characteristic soda pans (Büdös-szék and Zab-szék at Szabadszállás, Kelemen-szék and Fehér-szék at Fülöpszállás, as well as Böddi-szék and Sósér at Dunatetétlen; Fig. 1, Inset 2) once or twice in each month (n=136) from April of 2013 to December of 2014. The concentration of DOC was measured in water samples filtered through a precombusted GF-5 glass fibre filter (nominal pore size is 0.4 µm), acidified (to pH=2 with HCl) and bubbled to remove dissolved inorganic carbon. Acid-washed glassware was used for organic carbon determination using an Elementar High TOC analyser. CDOM concentration was measured with the method of Cuthbert and del Giorgio (1992). According to this dataset, significant correlation [2] was found between measured CDOM and DOC in the soda pans:

$$\mathrm{DOC}\ (\mathrm{mg\ L^{-1}}) = 0.09102 \times \mathrm{CDOM}\ (\mathrm{mg\ Pt\ L^{-1}}) + 18.429 \quad [2]$$

($n=136$; $df=133$; $r^2=0.837$; $p<0.0001$)

The concentration of DOC was calculated by equation [2] from CDOM for all soda pans of Carpathian Basin in 2009−2010 period.

2.5 Daily water temperature fluctuation in a selected habitat

We measured water temperature with an automatic logger in hourly intervals (Hobo Pendant temperature data logger) throughout a year from 1 September 2014 to 31 August 2015 (the pan was dry before September 2014) in a typical shallow (median: 15 cm) soda pan ("Sósér" 46° 47' 18.62" N; 19° 8' 39.71" E) in the central territory of the Carpathian Basin (Fig. 1). The sensor was placed into the middle section of the water column in the central place of open water. We calculated the monthly mean of daily water temperature (°C) fluctuation (max−min) based on the data logger measurements.

2.6 Data analysis

We used a multiple linear regression to analyse the effects of light-absorbing components (CHL, CDOM, TSS-Alg) on Z_s, as well as linear regression to analyse the relationship between Z_S and K_d. The regressions were carried out in OriginPro 9 based on ln transformed variables with significance levels of $p<0.05$.

To show possible relationships between ionic types based on Boros et al., (2014) and the measured other local parameters (apart from Z_S, which was not measurable on the field when it was larger than Z), we carried out a Principal Component Analysis (PCA) in R (R Core Team, 2015). For this, we ln transformed all variables (apart from pH), in order to normalise their distribution, and used a zero mean and unit variance standardization.

The geographic data analyses were performed with ArcMap 9.3.1 GIS software. The geographical variation was investigated by the spatial autocorrelation function, “hot-spot” analyses, and Ordinary Least Squares tests based on ln transformed variables.

3. Results

3.1 Multiple environmental conditions

Median Z (n=84) was very low (15 cm), with the maximum not even exceeding 100 cm, and the measured minimum was 2 cm. Z_S was below 10 cm in 67% of the pans (n=56). Median Z_S was low (3 cm) because of high turbidity. The minimum (0.5 cm) was observed in some pans of the Austrian Seewinkel (Appendix 1), and the maximum did not exceed 38 cm.

Salinity varied from sub- to hypersaline (1–27 g L^{-1}), with its median value of 3 g L^{-1} in the hyposaline range, and the pH varied in alkaline range (7.7−10.4) with 9.5 median value.

As expected from low Z_S, median TSS-Alg concentration was generally high (0.4 g L^{-1}), with an extremely high maximum (16 g L^{-1}). Median CDOM concentration was relatively high (310 mg Pt L^{-1}), and according to the calculated DOC concentration, all habitats were above the 16 mg C L^{-1} polyhumic boundary. Based on their CHL concentration, 19 (23%) of the investigated pans were hypertrophic, 14 (17%) eutrophic, 19 (23%) mesotrophic, while 32 (37%) had oligotrophic character. The maximum (1.3 mg L^{-1}) was far more than the hypertrophic threshold of aquatic systems (75 µg L^{-1}).

Similarly, median TP concentration was extremely high (1.9 mg L^{-1}), 45 times more than the hypertrophic threshold (<100 µg L^{-1}) according to OECD (1982), moreover the maximum (31.7 mg L^{-1}) exceeded approximately 316 times the hypertrophic threshold. In line with the TP, the median of SRP was also considerable in the pans (0.9 mg L^{-1}), and it was 46% of TP concentration (Table 1).

Table 1. Number of observations, minimum, first quartile (25%), median, third quartile (75%), and maximum of the investigated parameters

Parameters:	**N**	**Min**	**1st Qu.**	**Median**	**3rd Qu.**	**Max**
Area (ha)	84	0.2	3	5	20	200
Water depth (cm)	84	2	5	15	29	100
Secchi disc transparency (cm)	70	0.5	2	3	8	38
Euphotic depth (cm)	84	0	4	10	27	130
$Z_{mix}\,Z_{eu}^{-1}$	84	0.1	0.5	1.5	3.3	20
Suspended solids without algae (mg L^{-1})	84	12	82	400	990	16300
Salinity (g L^{-1})	84	1	2	3	6	27
pH	84	7.7	9.1	9.5	9.7	10.4
Coloured dissolved organic matter (mg Pt L^{-1})	84	20	170	310	650	7100
Dissolved organic carbon (mg L^{-1})	84	20	34	47	78	660
Total phosphorus (µg L^{-1})	84	67	700	1900	6300	31700
Soluble reactive phosphorus (µg L^{-1})	84	21	200	870	3100	26100
Chlorophyll *a* (µg L^{-1})	84	1	6	16	66	1300

According to the PCA (Fig. 2, Table 2), water depth was negatively related to TSS-Alg (which was the major contributor to low water transparency), pH, salinity, TP, and CHL. Hence, the shallowest habitats were at the same time the most turbid, saline, and alkaline pans with the highest concentrations of phosphorus and CHL. Local environmental conditions (even water depth) were independent of the size of habitats, in spite of the high variability in surface area (0.2–200 ha). According to the PCA ordination plot (Fig. 2), the measured environmental conditions were also independent of the ionic subtypes of the pans, with no clear separation of any of the major subtypes. Distribution of site scores along the first PCA axis (explaining most of the variation, 36%) showed no difference among the ion type groups, and only a slight separation could be observed along the second axis, which latter was due to a few Na-HCO_3 type habitats with high CDOM values.

Table 2. Loadings (scores) of the variables used in the PCA ordination (Fig. 2)

	PC1	PC2
Area	0.231	0.001
Z	-1.388	-0.388
Salinity	0.930	0.922
pH	0.761	1.333
TSS-Alg	1.453	-0.625
CDOM	0.343	-1.418
CHL	1.318	0.104
TP	1.415	-0.815

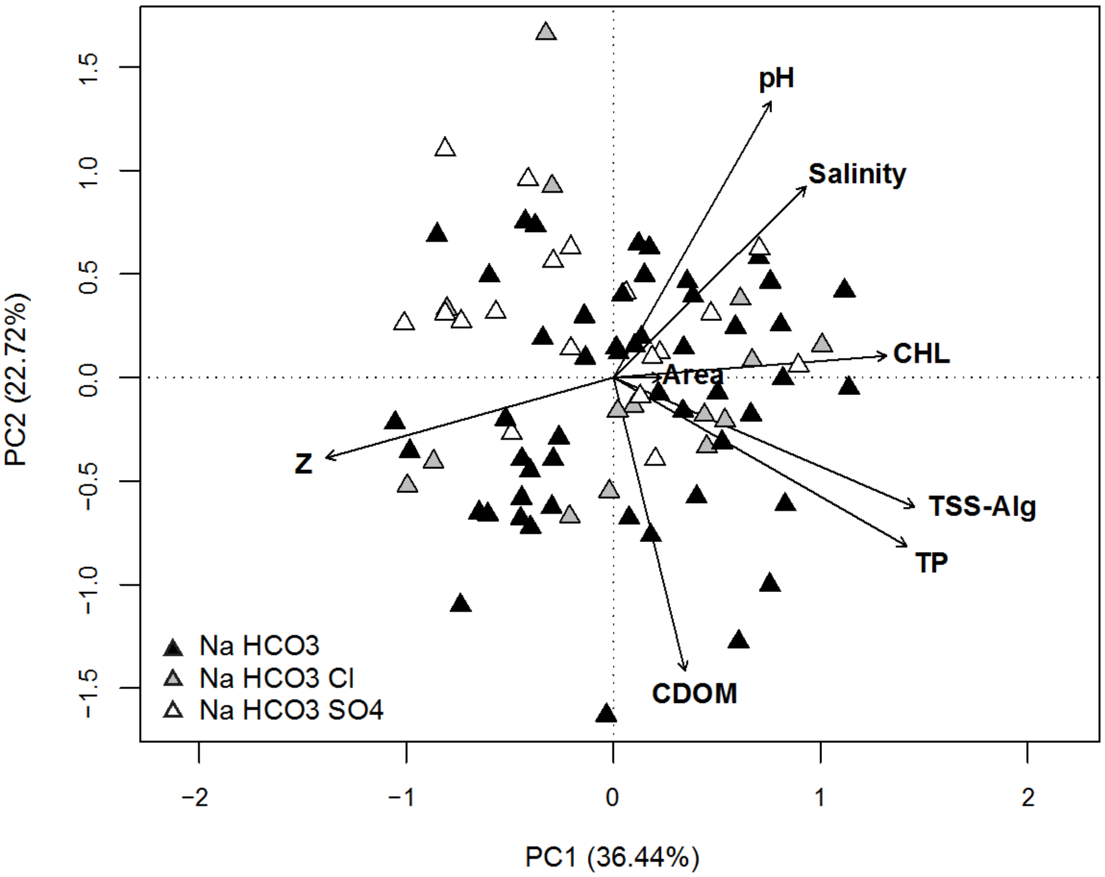

Fig. 2. Principal component analysis (PCA) of the measured environmental parameters. Colour coding illustrates the basic ionic types of soda pans

3.2 Underwater light conditions

Z_S and K_d had a strong negative linear relationship (n=70; df=68; r^2=0.701; p<0.001). According to the multiple regression between Z_S and the concentrations of the light-absorbing components (CHL, CDOM, TSS-Alg), only TSS-Alg had a significant effect on Z_S (n=70; df=66; r^2=0.733; p<0.001).

Median Z_{eu} (10 cm) calculated from K_d did not exceed median water depth, and the median of Z_{mix} Z_{eu}^{-1} ratio was 1.5. There was no significant relationship between Z_{mix} Z_{eu}^{-1} ratio and CHL concentration, and high phytoplankton biomass (160 µg L^{-1}) were detected up to very high 20 Z_{mix} Z_{eu}^{-1} ratio value.

TSS-Alg contributed with more than 50% to the light attenuation (K_d) in 80% of the pans (67). CDOM exceeded 50% contribution only in 19% of the pans (16), while CHL contribution was never dominant (max=41%) in the light attenuation (Fig. 3).

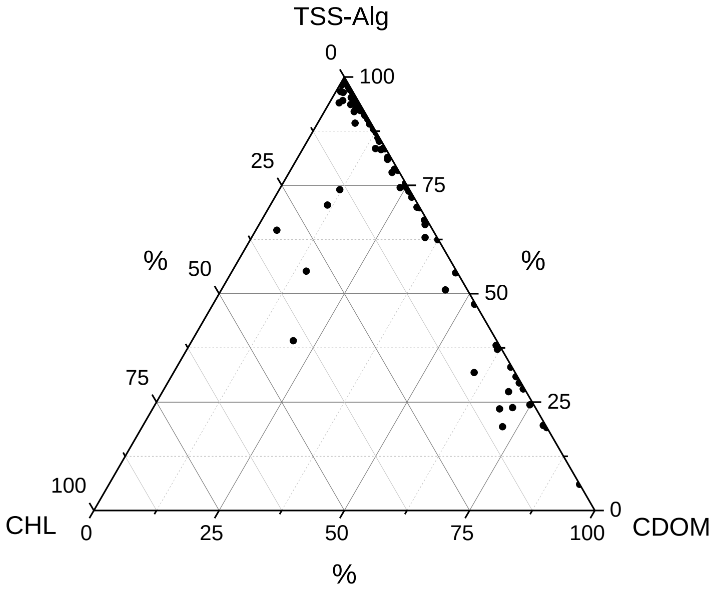

Fig. 3. Percentage contribution of suspended solids without algae (TSS-Alg), chromophoric dissolved organic matter (CDOM) and chlorophyll *a* (CHL) to the light attenuation (K_d) of the investigated soda pans in the Carpathian Basin. As these three parameters add up to 100%, their contribution can be illustrated on a ternary plot.

3.3 Geographical variation

Based on GIS spatial autocorrelation, Z_S, pH, TSS-Alg, CDOM and CHL (ln transformed data) had non-random spatial distribution. The “hot-spot” GIS analyses showed that both for pH and CHL, the highest values were concentrated in the northwestern region (Seewinkel, Austria, Fig. 1) of the Carpathian Basin. The highest values of Z_S and CDOM were concentrated in the central part of Hungary (Kiskunság) in the region. Although the TSS-Alg concentrations had non-random spatial distribution by autocorrelation, highly turbid pans (based on values of TSS-Alg) can be found in all parts of the region. All other variables had random spatial distribution.

3.4 Daily temperature fluctuation

The daily water temperature fluctuation was highest during summertime, in August (mean: 19 ±SD 7 °C; max: 28 °C in August), lowest from November to January (mean: 1 ±SD 1 °C; max: 3 °C; Fig. 4). The daily maximum temperature was also extremely high (44 °C, measured in 12 August 2015), while the minimum was close to freezing point (0.1 °C, measured in 29 December 2014). The yearly mean of daily fluctuation was 5 °C (±SD: 6 °C).

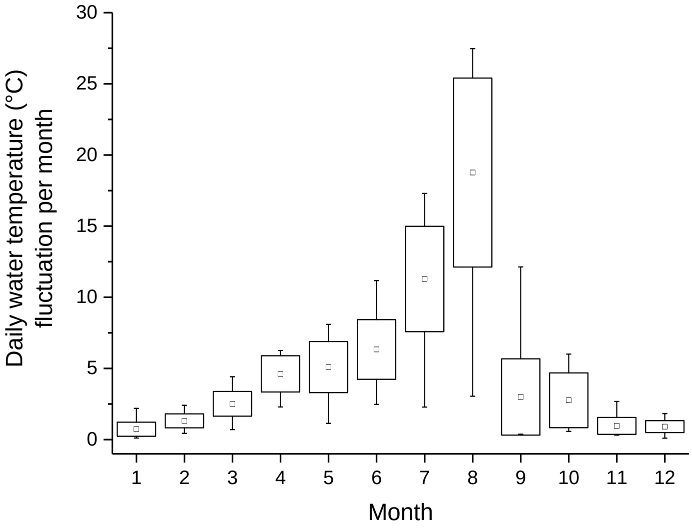

Fig. 4. Monthly mean (square), standard deviation (box: ±SD) and range (whiskers: min−max) of daily water temperature (°C) fluctuation in a characteristic shallow (Z_{median}=15 cm) soda pan in 2014−2015.

4. Discussion

We found multiple extreme conditions in the soda pans. Although Secchi depth (Z_S) is not the most accurate indicator of light penetration into the water, it is easy to measure, and therefore it is more frequently reported than other units of transparency. The low Z_S and high turbidity was mostly caused by large amounts of inorganic suspended solids. We compared available data on low Z_S values (below 20 cm) caused by inorganic suspended solids all around the World in Table 3. Townsend (2002) recorded the lowest Z_S (~0.5 cm) in opaque white clay pans with bicarbonate and calcium rich waters of Longreach Waterhole (Australia), which is the same as our lowest value. This is most probably the lower detection limit of transparency with a Secchi disc in the field.

Table 3. Low Secchi disc caused by inorganic suspended solids recorded in different parts of the World

Region	Secchi disc min (cm)	Reference
Lake Chapala (Mexico)	20.0	Dávalos and Owen, 2001
*Lake Aktas (Turkey)	16.8	Özbay and Kilinc, 2008
*Lake Neusiedl/Fertő (Austria and Hungary)	8.0	Löffler, 1979
*Pampa and Patagonia region (Argentina)	7.0	Gonzalo et al., 2010
*Lake Baringo (Kenya)	7.0	Odour et al., 2003
Temporary pools (Hungary)	6.0	Boven et al., 2008
South Africa	3.0	Hammer, 1986
Western Victoria (Australia)	1.0	Deckker and Williams, 1988
Longreach Waterhole (Australia)	0.5	Townsend, 2002
*Carpathian Basin (Austria and Hungary)	0.5	present study

*Soda pans and lakes

Swamps, marshes and bogs often have concentrations of DOC from 10 to 60 mg L^{-1} or even higher (Thurman, 1985). The DOC concentration in all the investigated pans was more than the polyhumic (>16 mg C L^{-1}) threshold (DOC range: 20−660 mg L^{-1}; CDOM range: 20−7100 mg Pt L^{-1}), while the maximum DOC value was 41 times higher, which means these soda pans have extremely polyhumic waters. Dissolution of humic substances is promoted at higher pH (Tipping and Hurley, 1988; Andersson et al., 1999, 2000; Kalbitz et al., 2000; Nicolas et al., 2005; Farook et al., 2012). However, this relationship was not supported by our data, most likely because vegetation cover along the shoreline of the investigated pans was scarce at higher pH (9.5<).

Scheffer (1998) reported that in shallow lakes, the euphotic depth can be calculated by multiplying Z_S by 1.7 – a value relatively close to the one we found in soda pans [2]. However, in spite of the strong physical control on underwater light in the soda pans, algae occurred up to high (20) mixing and euphotic ratios ($Z_{mix}\ Z_{eu}^{-1}$), and hypertrophic conditions based on CHL can be found until the value of 16. In deep lakes, algae cannot grow above 5−6 $Z_{mix}\ Z_{eu}^{-1}$ ratio (Talling, 1971), and only the gas-vacuolated cyanobacteria may prevail under these light conditions (Naselli-Flores, 2013). In the shallow (holomictic) Lake Baringo, where the daily resuspension of the sediment attributed to high turbidity, and the $Z_{mix}\ Z_{eu}^{-1}$ ratio was approximately 19, some net photosynthesis was still recorded. This was attributable to the primary production by the buoyant *Microcystis* spp. under these poor light conditions (Schagerl and Odour, 2003).

All pans are categorized as hypertrophic according to the high TP concentration and in some cases (23%), also according to their CHL concentration based on the OECD (1982) classification. The inlet of HCO_3 rich water may result in a pH rise in poorly buffered water systems, leading to an increased phosphorus release from the sediment (Scheffer, 1998). In line with this phenomenon, we have already proven that the SRP level significantly depends on soda dominated salinity and we also found correlation between phosphorus loading of aquatic birds and TP concentration of soda pans (Boros et al., 2008b). Soda pans, similarly to several other shallow lakes (Moss, 2015) exemplify that aquatic habitats can be naturally high in nutrients, with eutrophic or hypertrophic conditions representing the natural state of these systems.

Based on the results of the PCA, water depth is one of the key physical factors that seems to determine several other environmental conditions in these very shallow intermittent pans (e.g. turbidity, salinity and trophic state). In most cases, the shallowest pans were the most saline and turbid habitats with hypertrophic state. Salinity and trophic state represent the most important environmental gradients for the local biota (Horváth et al., 2014), and they both had a random geographical distribution within the Carpathian Basin, similarly to water depth. The other variables with non-random geographical distribution might reflect local events (e.g. dilution by precipitation or mixing effect of local wind) or difference in the connectivity of the habitats to groundwater.

The daily water temperature maximum (44 °C) and fluctuation maximum (28 °C) were particularly high during the summertime in a characteristic shallow soda pan, which means notable physical stress for the biotic community. Although high fluctuation and intense warming up during summertime is not uncommon in shallow lakes (Hammer, 1986), the values we found were extremely high. Water temperature rarely exceeds 32 °C even in tropical lakes and rivers (Hutchinson, 1957; Ward and Stanford, 1982), while the daily maximum we found exceeded those measured in shallow African temporary pans under tropical climate (28–33 °C; Appleton, 1977; Meintjes, 1996) or intertidal habitats that are also known to warm up easily due to their extreme shallowness and small size (32 °C, Helmuth et al., 2002). Although salinity only rarely reaches hypersaline levels, excessive daily temperature fluctuation adds to the harsh environmental conditions. These daily changes are so far very little studied in shallow aquatic habitats, although they might also have a strong community shaping effect.

Organisms living in extreme environments are known as extremophiles. Do they thrive in these extreme environments, or do they simply tolerate it temporarily? As this may vary widely among species, the environmental conditions that define "extreme" therefore depend on the taxa being studied. Reese et al. (2014) suggested that those organisms surviving at the edge of a biosphere's habitable zone should be considered "boundary organisms". They also concluded that in general, organisms can cope with acidic environments better than with alkaline conditions. According to them, a true "extreme" environment for all life on Earth would be hot brine with very high pH. During summer, a very similar environment is formed in soda pans.

5. Conclusion

The investigated parameters of soda pans, such as the combination of shallowness, intermittent character (periodic desiccation), high turbidity, polyhumic concentration of dissolved humic substances, hypertrophic conditions, high daily water temperature fluctuation, and high alkalinity represent multiple environmental boundaries in the studied endorheic soda pans, which altogether create an extreme environment. These characteristics have evolved under specific climatic and hydrogeological conditions of the Carpathian Basin, that contributed to the development of a unique and extreme aquatic ecosystem.

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Appendix 1 List of geographical locations, names and values of investigated parameters in the soda pans

Latitude	Longitude	CO	Settlement	Name of pan	Ion type	Area	Z	Z_s	Z_{eu}	$Z_{mix}Z_{eu}^{-1}$	Salinity	pH	TSS-Alg	CDOM	DOC	CHL	TP	SRP
N	E					ha	cm	cm	cm		g L^{-1}		mg L^{-1}	mg L^{-1}	mg L^{-1}	µg L^{-1}	µg L^{-1}	µg L^{-1}
47° 46' 30.98"	16° 46' 9.90"	AT	Illmitz	Albersee	Na HCO_3 Cl	7.6	11	2.0	4	2.9	10	9.6	1200	140	31	350	5000	1200
47° 44' 41.10"	16° 46' 10.55"	AT	Illmitz	Herrnsee	Na HCO_3 SO_4	4.3	100		67	1.5	6	9.0	25	270	43	1	120	52
47° 49' 2.66"	16° 47' 59.54"	AT	Illmitz	Hochgstetten	Na HCO_3 SO_4	5.3	19	3.0	9	2.1	5	9.5	400	360	51	500	1200	360
47° 45' 31.33"	16° 47' 8.93"	AT	Illmitz	Kirchsee	Na HCO_3	4.7	2		4	0.5	3	9.9	1200	170	34	30	730	69
47° 45' 21.50"	16° 46' 49.86"	AT	Illmitz	Krautingsee	Na HCO_3 SO_4	0.4	24	13.0	19	1.3	3	8.9	50	1100	120	8	640	210
47° 48' 23.80"	16° 47' 13.35"	AT	Illmitz	Mittlerer Stinkersee	Na HCO_3	4.4	18	3.0	9	2.1	7	9.8	550	140	31	74	1000	180
47° 49' 37.74"	16° 48' 27.96"	AT	Illmitz	Obere Höllacke	Na HCO_3	6.6	5	3.0	6	0.9	14	9.8	900	120	29	180	5700	2400
47° 48' 49.73"	16° 47' 33.66"	AT	Illmitz	Oberer Stinkersee	Na HCO_3	49.9	3	0.5	1	3.1	13	9.8	5000	120	30	490	12600	6600
47° 47' 8.50"	16° 47' 34.02"	AT	Illmitz	Runde Lacke	Na HCO_3	3.3	17		40	0.4	7	9.9	90	180	35	3	200	52
47° 47' 15.68"	16° 46' 32.86"	AT	Illmitz	Seeuferlacke	Na HCO_3 SO_4	0.4	11		58	0.2	7	9.6	21	330	49	26	330	110
47° 47' 27.82"	16° 46' 47.063"	AT	Illmitz	Südlicher Silbersee	Na HCO_3 Cl	1.7	10		110	0.1	9	9.8	23	110	28	13	300	120
47° 44' 57.08"	16° 47' 47.12"	AT	Illmitz	Unterer Schrändlsee	Na HCO_3	0.2	4		43	0.1	2	9.5	37	380	53	62	470	210
47° 47' 48.58"	16° 47' 8.65"	AT	Illmitz	Unterer Stinkersee	Na HCO_3	35.6	40	16.0	41	1.0	4	9.7	80	220	38	7	90	45
47° 46' 5.28"	16° 47' 10.78"	AT	Illmitz	Zicklacke	Na HCO_3 SO_4	53.8	12		23	0.5	4	9.9	180	180	35	15	150	59
47° 43' 21.51"	16° 49' 19.19"	AT	Apetlon	Apetloner Meierhoflacke	Na HCO_3 SO_4	5.2	44	17.0	26	1.7	9	9.4	53	719	84	45	930	470
47° 47' 21.09"	16° 53' 12.90"	AT	Apetlon	Auerlacke	Na HCO_3	3.5	7	3.0	7	1.1	2	9.5	710	230	39	26	740	260
47° 47' 42.77"	16° 52' 10.79"	AT	Apetlon	Eszterházi-tó	Na HCO_3	2.6	3	1.0	1	6.0	2	9.2	8700	6300	600	81	8200	5800
47° 47' 10.27"	16° 50' 31.78"	AT	Apetlon	Große Neubruchlacke	Na HCO_3	23.5	14	0.5	2	9.3	7	9.5	3200	90	27	230	6300	1100
47° 47' 34.30"	16° 52' 43.35"	AT	Apetlon	Kühbrunnlacke	Na HCO_3	5.3	2	1.0	2	1.0	4	9.8	2300	590	72	120	7000	3700
47° 45' 40.88"	16° 52' 32.44"	AT	Apetlon	Lange Lacke	Na HCO_3 SO_4	97.3	33	4.0	8	4.1	3	9.7	600	52	23	83	2200	1100
47° 45' 51.39"	16° 50' 25.14"	AT	Apetlon	Neufeldlacke	Na HCO_3 SO_4	0.2	11	2.0	4	2.6	4	9.1	1000	1100	120	48	2700	1400
47° 46' 37.76"	16° 52' 44.16"	AT	Apetlon	Nord-Östlich Wörtenlacke	Na HCO_3 SO_4	0.5	4	4.0	11	0.4	5	9.7	400	180	35	95	6500	5600
47° 46' 8.05"	16° 52' 29.41"	AT	Apetlon	Östliche Hutweiden lacke	Na HCO_3 SO_4	5.4	5	4.0	8	0.6	7	10.0	400	140	31	1300	3600	1200
47° 46' 29.18"	16° 52' 44.80"	AT	Apetlon	Östliche Wörthenlacke	Na HCO_3 SO_4	23.3	36		130	0.3	2	10.3	32	38	22	2	73	39

47° 47' 26.49"	16° 51' 54.50"	AT	Apetlon	Östliche-Fuchslochlacken	Na HCO_3	11.9	17		30	0.6	2	10.4	150	95	27	4	200	47
47° 47' 5.25"	16° 53' 4.23"	AT	Apetlon	Sechsmahdlacke	Na HCO_3	9.3	10	4.0	11.7	0.9	5	10.3	400	160	33	16	1500	400
47° 47' 55.73"	16° 52' 18.35"	AT	Apetlon	Stundlacke	Na HCO_3	5.5	3	3.0	6.7	0.4	2	9.6	700	240	40	64	1900	58
47° 45' 5.41"	16° 51' 27.80"	AT	Apetlon	Südliche Martenhofenlacke	Na HCO_3	3.7	4	1.5	0.3	13.2	4	10.0	16300	160	33	170	2900	240
47° 46' 31.70"	16° 52' 51.31"	AT	Apetlon	Süd-Östlich Wörtenlacke	Na HCO_3 SO_4	1.9	3	1.0	1.7	1.8	5	9.4	2900	160	33	470	18100	13300
47° 43' 41.21"	16° 49' 27.68"	AT	Apetlon	Unterer Weißsee	Na HCO_3 SO_4	5.7	43	23.0	99.6	0.4	2	9.1	12	190	35	24	130	57
47° 46' 5.78"	16° 52' 7.96"	AT	Apetlon	Westliche Hutweiden lacke	Na HCO_3	1.5	2	3.0	13.1	0.2	2	9.8	270	600	73	13	710	220
47° 46' 22.28"	16° 52' 3.30"	AT	Apetlon	Westliche Wörthenlacke	Na HCO_3	22.6	44	35.0	67.6	0.7	2	9.6	61	64	24	3	67	40
47° 47' 23.25"	16° 51' 7.02"	AT	Apetlon	Westliche-Fuchslochlacken	Na HCO_3	12.6	6	0.5	0.4	14.3	2	9.4	11600	1200	130	280	11000	3800
47° 48' 38.73"	16° 50' 40.47"	AT	Apetlon, Illmitz	Ochsenbrunnlacke	Na HCO_3	20.6	2	3.0	0.4	4.9	5	9.9	12000	500	64	280	12400	6700
47° 46' 42.88"	16° 56' 3.24"	AT	St. Andrä	Baderlacke	Na HCO_3 SO_4	3.1	9	2.5	6.0	1.5	2	9.6	800	170	34	54	2600	500
47° 49' 1.52"	16° 51' 48.27"	AT	Podersdorf, Apetlon	Birnbaumlacke	Na HCO_3	19.3	8	0.5	0.4	20.1	1	9.0	11300	6400	600	160	7600	3600
47° 3' 37.09"	18° 27' 52.74"	HU	Aba	Fényes-tó	Na HCO_3 Cl	2.4	22	22.0	75.2	0.3	2	7.7	19	260	42	1	660	470
47° 8' 26.56"	19° 6' 57.26"	HU	Apaj	Alsó-Szúnyog	Na HCO_3	4.3	19	5.0	12.3	1.5	3	9.8	330	400	55	7	1380	520
46° 5' 48.14"	19° 19' 53.69"	HU	Bácsalmás	Sóstó	Na HCO_3	6.1	28	7.0	50.3	0.6	3	9.4	62	180	35	16	1400	1088
45° 59' 43.58"	19° 3' 14.79"	HU	Bácsszentgyörgy, Gara	Névtelen	Na HCO_3	0.6	23	4.0	9.1	2.5	1	8.4	500	250	41	12	1900	940
46° 44' 21.74"	19° 59' 40.56"	HU	Csongrád	Kis-sóstó	Na HCO_3	7.7	45	4.0	7.1	6.3	1	8.7	600	620	75	8	1900	1300
47° 20' 11.36"	21° 30' 49.07"	HU	Derecske	Bocskoros-szik	Na HCO_3	3.6	3	2.0	6.4	0.5	5	9.6	650	670	79	23	7800	4200
46° 45' 52.36"	19° 8' 13.68"	HU	Dunatetétlen	Böddi-szék	Na HCO_3 Cl	198.1	21	2.8	5.7	3.7	6	9.2	730	680	81	120	12700	8100
46° 47' 29.43"	19° 9' 29.45"	HU	Dunatetétlen	Fűzfa-szék	Na HCO_3	3.8	15	2.0	3.0	4.9	5	9.3	310	7100	670	6	4100	2700
46° 47' 18.62"	19° 8' 39.71"	HU	Dunatetétlen	Sósér	Na HCO_3 Cl	2.8	15	3.0	3.6	4.1	5	9.0	82	7000	650	2	2500	1400
46° 44' 20.19"	19° 8' 56.99"	HU	Dunatetétlen, Harta	Bába-szék	Na HCO_3 Cl	4.0	30	30.0	56.2	0.5	3	9.5	27	320	48	2	130	71
46° 48' 26.61"	19° 11' 12.20"	HU	Fülöpszállás	Fehér-szék	Na HCO_3 Cl	10.4	18	2.0	6.7	2.7	4	9.4	580	820	93	72	1000	200
46° 47' 42.02"	19° 11' 5.79"	HU	Fülöpszállás	Kelemen-szék	Na HCO_3 Cl	189.7	9	4.0	2.5	3.6	9	9.4	1900	680	81	6	7900	5600
47° 42' 46.90"	21° 21' 50.35"	HU	Hajdúböszörmény	Móricz-szik	Na HCO_3	0.8	26	6.0	11.9	2.2	1	9.1	200	1200	130	6	4100	2800
47° 19' 1.50"	21° 44' 9.84"	HU	Hosszúpályi	Fehér-tó	Na HCO_3	6.5	14	8.0	4.3	3.2	3	10.1	1100	350	50	6	2300	1400
47° 20' 17.49"	21° 43' 50.04"	HU	Hosszúpályi	Petrovics-lapos	Na HCO_3	1.4	4	2.0	9.5	0.4	3	9.4	410	580	72	21	2500	1200
47° 1' 3.87"	20° 3' 32.21"	HU	Jászkarajenő	Csukáséri-tavak-1	Na HCO_3	1.6	4	3.0	11.1	0.4	20	9.7	410	150	32	60	31700	26100

47° 1' 5.43"	20° 3' 40.74"	HU	Jászkarajenő	Csukáséri-tavak-2	Na HCO_3	2.4	30	10.0	15.4	1.9	1	9.5	200	650	77	3	2300	1700
46° 34' 4.11"	19° 45' 0.69"	HU	Jásszentlászló	Kerek-tó	Na HCO_3	2.7	45	4.0	15.7	2.9	1	8.5	250	430	58	7	1200	650
46° 28' 9.05"	20° 36' 58.30"	HU	Kardoskút	Fehér-tó	Na HCO_3	68.0	15	1.3	1.6	9.3	9	9.4	2800	1400	140	56	4300	2100
46° 40' 27.48"	19° 20' 44.30"	HU	Kaskantyú	Sárkány-tó	Na HCO_3	4.0	50	8.0	13.1	3.8	1	9.7	280	530	67	8	500	140
46° 17' 31.76"	20° 38' 6.89"	HU	Királyhegyes	Csikóspusztai-tó	Na HCO_3	8.6	15	1.5	2.6	5.7	3	9.3	1300	3100	300	6	7700	5200
46° 28' 39.70"	19° 57' 59.02"	HU	Kistelek	Tóalj Bíbic-tó)	Na HCO_3	3.8	48	38.0	74.4	0.6	1	8.3	16	270	43	3	580	400
47° 20' 24.37"	21° 39' 10.17"	HU	Konyár	Kerek-Szik-tó	Na HCO_3	3.3	3	2.0	6.3	0.5	4	10.3	710	440	59	12	1800	690
46° 31' 27.05"	20° 37' 46.71"	HU	Orosháza	Kis-sóstó	Na HCO_3	8.8	31	15.0	11.2	2.8	1	9.7	300	770	89	15	1200	800
46° 35' 12.81"	19° 54' 58.97"	HU	Pálmonostora	Pallagi-szék	Na HCO_3 Cl	2.8	62	31.0	52.8	1.2	2	8.3	36	310	47	4	750	600
46° 32' 46.20"	20° 2' 2.17"	HU	Pusztaszer	Büdös-szék	Na HCO_3	61.6	62	7.0	11.4	5.4	1	8.6	400	290	44	3	1300	900
46° 31' 25.46"	20° 2' 24.14"	HU	Pusztaszer	Vesszős-szék	Na HCO_3	10.0	18	15.0	18.4	1.0	2	9.2	80	1000	110	7	2400	1800
46° 59' 14.18"	18° 32' 48.66"	HU	Sárkeresztúr	Sárkány-tó	Na HCO_3 Cl	22.1	8		41.8	0.2	27	10.2	120	19	20	1	75	21
46° 58' 17.77"	18° 33' 11.31"	HU	Sárszentágota	Sóstó	Na HCO_3 SO_4	4.0	34		63.6	0.5	4	9.3	15	300	46	45	230	21
46° 48' 31.17"	19° 8' 30.82"	HU	Solt	Bogárzó	Na HCO_3 Cl	19.3	5	2.0	4.6	1.1	13	9.5	810	1500	150	4	15600	11400
46° 45' 48.85"	19° 10' 51.13"	HU	Soltszentimre	Névtelen	Na HCO_3 Cl	0.6	5	2.5	5.9	0.8	26	9.5	600	520	65	1000	30500	25700
47° 0' 17.89"	18° 29' 28.36"	HU	Soponya	Sóstó	Na HCO_3 SO_4	4.4	28		105.3	0.3	3	9.1	26	110	29	1	800	560
46° 52' 2.03"	19° 10' 11.51"	HU	Szabadszállás	Büdös-szék	Na HCO_3	70.3	4	2.0	2.0	2.0	6	9.5	2300	630	76	17	12700	6800
46° 52' 34.15"	19° 10' 35.66"	HU	Szabadszállás	Pipás-szék	Na HCO_3	6.4	12	1.0	2.0	6.0	6	9.5	1900	3300	320	7	10200	5700
46° 50' 5.09"	19° 10' 17.82"	HU	Szabadszállás	Zab-szék	Na HCO_3 Cl	181.7	5	2.0	3.1	1.6	10	9.5	1600	260	42	17	17000	11200
46° 20' 58.84"	20° 4' 19.34"	HU	Szatymaz	Fehér-tó	Na HCO_3	1.1	21		73.0	0.3	1	8.2	25	230	39	4	96	46
47° 33' 50.43"	20° 53' 24.77"	HU	Tiszafüred	Meggyes-lapos	Na HCO_3 Cl	12.6	11	9.0	19.3	0.6	2	9.4	190	330	49	27	4800	2700
47° 57' 45.69"	21° 25' 9.41"	HU	Tiszavasvári	Fehér-szik	Na HCO_3	28.6	6	3.0	4.5	1.3	5	9.2	1000	380	53	8	8000	4900
47° 56' 26.67"	21° 25' 36.79"	HU	Tiszavasvári	Göbölyös-szik	Na HCO_3	4.4	23	1.0	1.3	17.8	1	7.8	3400	2600	260	17	10300	8400
46° 33' 44.61"	20° 4' 31.70"	HU	Tömörkény	Dong-ér	Na HCO_3 SO_4	30.4	10		63.1	0.2	4	10.0	67	61	24	2	180	26
47° 51' 30.48"	21° 39' 30.02"	HU	Újfehértó	Nagy-Vadas-tó	Na HCO_3	43.0	15	13.0	14.5	1.0	3	9.9	320	130	30	16	2100	1000
45° 57' 10.47"	20° 11' 50.71"	RS	Coka	Csókakopó	Na HCO_3	8.5	25	4.0	11.6	2.2	1	8.6	370	320	47	9	1400	410
45° 28' 12.05"	20° 17' 59.91"	RS	Elemir	Okanj bara	Na HCO_3	96.5	60	8.0	8.8	6.8	1	8.0	440	650	78	3	1000	570
45° 30' 44.55"	20° 18' 6.79"	RS	Melenci	Jezero Rusanda	Na HCO_3 SO_4	160.8	49	5.3	12.5	3.9	13	9.2	350	250	41	5	25200	21600
45° 18' 54.85"	20° 8' 5.63"	RS	Mosorin	Jandena-jama	Na HCO_3	0.5	2	2.0	44.9	0.0	3	9.6	43	120	29	300	540	160
45° 56' 50.31"	19° 5' 24.46"	RS	Stanisics	Bela bara	Na HCO_3	4.4	25	5.0	10.4	2.4	1	8.7	440	180	35	16	1500	620

45° 59' 31.38"	19° 7' 59.79"	RS	Ridica	Medura	Na HCO_3	5.8	31	19.0	21.0	1.5	4	9.3	130	190	36	470	1800	570
45° 37' 32.86"	20° 12' 31.25"	RS	Novi Becsej	Slano Kopovo	Na HCO_3 Cl	119.3	38	2.0	2.6	14.6	2	8.8	1800	330	48	20	3800	2900

Notes: CO - Country - AT: Austria, HU: Hungary, RS: Serbia