



Microbial communities of soda lakes and pans in the Carpathian Basin: a review

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Abstract

In this review, I would like to summarize the current knowledge on the microbiology of soda lakes and pans of the Carpathian Basin. First, the characteristic physical and chemical features of these sites are described. Most of the microbiological information presented deals with prokaryotes and algae, but protists and viruses are also mentioned. Planktonic bacterial communities are dominated by members of the phyla Actinobacteria, Bacteroidetes and Proteobacteria; small-sized trebouxiophycean green algae and *Synechococcus/Cyanobium* picocyanobacteria are the most important components of phytoplankton. Based on the current knowledge, it seems that mainly temperature, salinity, turbidity and grazing pressure regulate community composition and the abundance of individual microbial groups, but the external nutrient load from birds also has a significant impact on the ecological processes.

Keywords Bacterioplankton · Algae · Extreme environment · Alkaline habitat · Food web

Introduction

Soda lakes are athalassic saline aquatic habitats with a dominance of sodium and (hydrogen) carbonate ions, and they have usually lower salinity than other types of saline lakes but stable alkaline pH (Hammer 1986; Boros and Kolpakova 2018). Probably the most well-known representatives of these environments are lakes in the East African Rift Valley (e.g. Lake Natron, Lake Magadi and Lake Bogoria) and the Mono Lake in the USA (Grant 2004; Schagerl 2016; Sorokin et al. 2014). On the other hand, many soda lakes and pans can be found in the Eurasian Steppe; the most western occurrence of these habitats is within the Carpathian Basin (Boros et al. 2013; Boros and Kolpakova 2018) (Fig. 1). Furthermore, according to our current knowledge, the only occurrence of these habitats within Europe is the Carpathian Basin.

Although the alkaline character of the water seems to be a good indicator for ‘soda type’ inland waters, recently, Boros and Kolpakova (2018) proposed a more straightforward

definition for soda lakes: ‘ Na^+ and $\text{HCO}_3^- + \text{CO}_3^{2-}$ are the first in the rank of dominant ions (> 25e%)’. They also draw attention to the fact that several studies published dealing with the microbiology of soda lakes (also from the Eurasian Steppe) were carried out on sites that do not belong to the ‘soda type’ according to this definition. The daily fluctuation of pH (e.g. due to photosynthetic activity) only adds ad hoc alkalinity to these saline lakes, while in the case of true soda lakes, the pH is buffered with carbonates and remains constantly high irrespectively of diurnal and seasonal changes in the water (Kirschner et al. 2002; Vörös and Boros 2010; Wetzel 2001). Additional information about water chemistry and about the genesis of soda lakes and pans is given elsewhere (Boros et al. 2014, 2017; Boros and Kolpakova 2018; Schagerl 2016).

Currently, there are approximately 80–100 soda lakes and pans (including reconstructed and semi-natural lakes and pans) in the Carpathian Basin (Boros et al. 2013). These sites are *ex lege* protected areas in Hungary, and many of them are part of the UNESCO world heritage in Austria; some of them are also protected in Serbia. They have high protection priority in the Natura 2000 network of the European Union, several of them are Ramsar sites, since they are important continental stopover wetland sites of migrating birds, and many of them are situated within national parks (Boros et al. 2013, 2014, 2017; Gavrilović et al. 2018).

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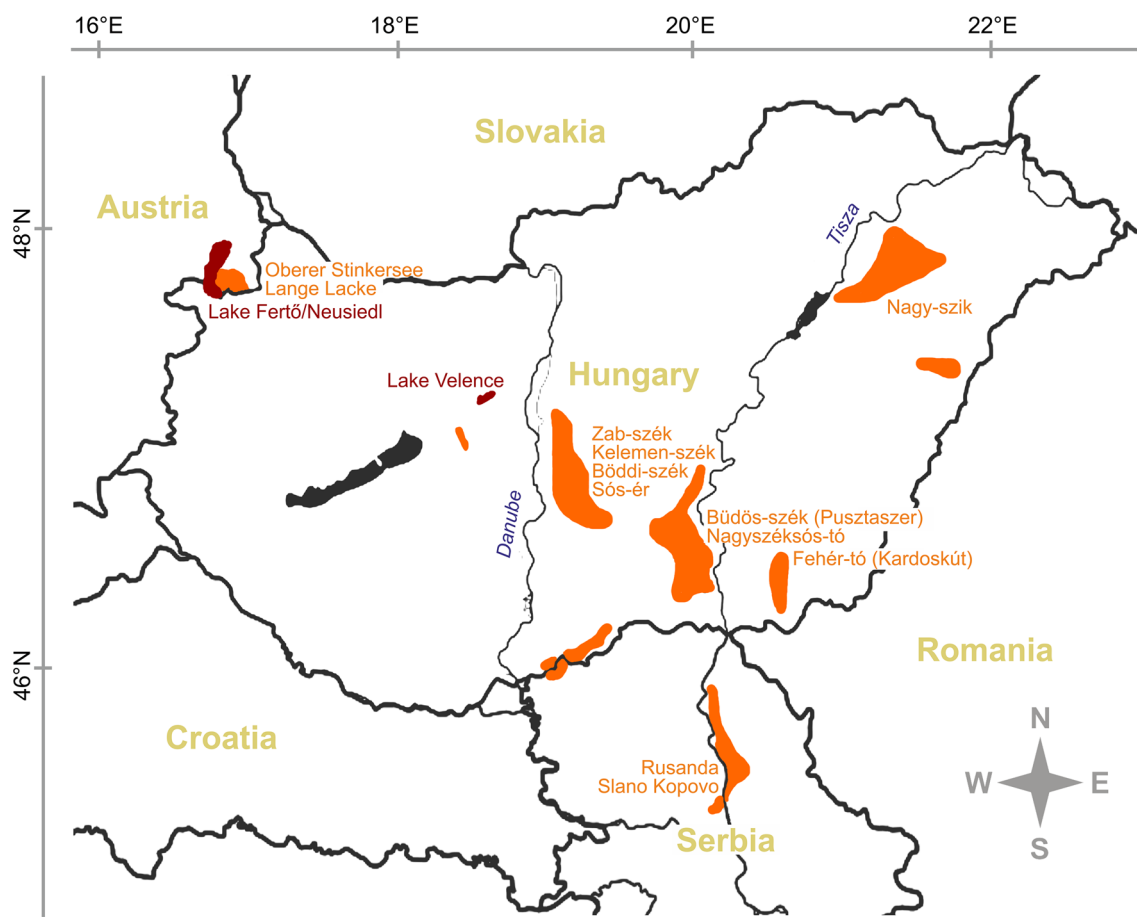


Fig. 1 Geographic location of soda lakes and pans in the Carpathian Basin. Soda lakes are marked in brown, and characteristic areas with soda pans are marked in orange. Selected examples of soda pans are also given for these areas. Based on the data of Boros et al. (2013, 2014, 2017)

Although studies on microbial communities started decades ago in this region, detailed information about the taxonomic composition of bacteria and small-sized algae became available with the introduction of cultivation-independent (particularly high-throughput DNA sequencing) methods. In this review, I summarize the current knowledge on the abundance, composition and ecology of microorganisms inhabiting these special alkaline aquatic habitats.

Habitat types: the physical and chemical environment

Lakes can be defined as continental water bodies that have a distinct shoreline habitat, but ‘true’ soda lakes are rarely found in the Carpathian Basin (Lake Fertő/Neusiedl and Lake Velence), since most of these endorheic aquatic ecosystems could be regarded as pans with extremely shallow water and no characteristic shoreline habitat (Figs. 1, 2; water depth ~5–30 cm; area ~3–20 ha; Boros et al. 2014). Precipitation, groundwater upwelling and evaporation (the

annual amount of sunshine hours is ~2000 h; Boros et al. 2017; Kiss 1976) play the most important role in their water balance. In other words, hydrogeological and meteorological conditions determine their water regime. Due to these and the extreme shallowness of the pans, their salinity changes drastically throughout the year, but usually remains within the sub- and hyposaline range, within 1–20 g/L salinity values. This means that the salt content of these lakes and pans is typically less than half of that of seawater (35 g/L); therefore, in some manner they are similar to ‘brackish’ waters (Boros et al. 2014, 2017; Table 1). The high number of windy days (~120 days, Boros et al. 2017) in this plain area (a major part of the corresponding region is also called the Great Hungarian Plain) contributes to the continuous resuspension of sediment and the high inorganic turbidity of the water. Probably due to the high turbidity, the dynamic fluctuation of water level (and, therefore, lake area) and the high salinity, submerged macrophytes are sparse or absent from these lakes, while at the shores marshland vegetation may be present (Boros 1999; Boros et al. 2013). At some sites, expanded shoreline vegetation [mainly bayonet grass



Fig. 2 Landscapes and important macroscopic characters of the soda pans in the Carpathian Basin. **a** Aerial view of a turbid soda pan (Fehér-tó near Kardoskút; photo: Erika Greipel). **b** Migrating birds flying over a soda pan [common crane (*Grus grus*) at Bűdös-szék near Pusztaszer]. **c** Shoreline of a turbid soda pan (Rusanda). **d** Waves generated by the strong wind in a turbid soda pan (Zab-szék).

e Water samples collected from a turbid pan and a coloured soda pan (Zab-szék and Sós-ér). **f** Sample collection from a turbid soda pan (Kelemen-szék). **g** Mosaic of suspended and settled turbid water in buffalo footprints highlighting the high dissolved organic matter content (brown) of turbid-type soda pans (Nagyszéksós-tó). For the geographic location of these sites, see Fig. 1

Table 1 Physical and chemical characteristics of some soda lakes and pans of the Carpathian Basin

	Lake Fertő/Neusiedl	Lake Velence	Zab-szék	Kelemen-szék	Sós-ér
Type	Turbid	Turbid	Turbid	Turbid	Coloured
Area (km ²)	309	24	1.82	1.90	0.03
Depth (cm)	60–140	50–150	0–45*	0–40*	0–50*
Secchi depth (cm)	2.5–30	40–58	0.5–7	1–4	1.5–25
pH	8.9–9.3	7.5–9.6	8.9–10.2	8.9–9.5	8.3–10.1
Salinity (g/L)	1.8–2.4	0.7–2.6	1.9–17.0	1.4–11.2	1.5–18.9
TSS (mg/L)	20–260	18–40	150–8000	700–2200	3–340
TOC (mg/L)	20–100	20–25	35–405	40–70	85–1200
TP (mg/L)	0.02–0.1	<0.01–1.7	2.0–17.7	3.1–3.3	0.3–4.0

Based on data presented in Bell et al. (2018), Boros et al. (2008b, 2016, 2020), Borsódi et al. (2007), Bullerjahn et al. (2020), Somogyi et al. (2009, 2010), Szabó et al. (2020) and Szabó-Tugyi et al. (2019). If salinity data were not available, values were calculated from conductivity based on the equation of Boros et al. (2014). Physicochemical data are given for open water areas in the case of large soda lakes

*Astatic pan that could completely dry out

(*Bolboschoenus maritimus*) and common reed (*Phragmites australis*)] hinders sediment resuspension, which results

in a lower inorganic suspended matter content in the water body (Table 1). Furthermore, groundwater and the decaying

biomass of emergent macrophytes supply coloured dissolved organic matter (humic substances), which results in the polyhumic character of these pans (Boros et al. 2013, 2017, 2020).

Therefore, two different optical water types can be distinguished with the naked eye: the ‘turbid’ and the ‘coloured’ type (Boros et al. 2013, 2017; Fig. 2). Turbid-type waters have a characteristic greyish colour due to the high amount of suspended inorganic particles, while the brownish colour is a result of the high concentration of dissolved humic substances in the case of the coloured type. Both of the largest shallow soda lakes (Lake Fertő/Neusiedl and Lake Velence) in this region belong to the turbid type, and this type is more common also among the soda pans (Boros et al. 2013). However, it should be noted that these types are not always distinct categories; pans with intermittent character can also be found, and in the case of larger turbid lakes, the water of inner ponds within the reed belt resembles a coloured type soda pan (Boros et al. 2013; Dokulil 1979; Somogyi et al. 2010).

Taken together, these aquatic habitats can be considered as multiple extreme environments with stable alkaline pH and high water turbidity, and in the case of the soda pans, a fluctuating daily temperature (up to 28 °C difference) and intermittent (astatic) character (Boros et al. 2017; Kirschner et al. 2002). Furthermore, the concentration of several nutrients is also high throughout the year (e.g. the orthophosphate concentration is usually between 0.2 and 3.0 mg/L, and the average of dissolved organic carbon is 90 mg/L, in the range of 20–1000 mg/L; Boros et al. 2017, 2020; Table 1), which supports the growth of algae and bacteria. On the other hand, there is a relatively low N/P ratio in the water, partially due to the volatilization of ammonia under alkaline conditions (Boros et al. 2008b), which can significantly influence the microbial metabolic processes. Moreover, it should be noted that high local geographical diversity exists with respect to the physicochemical conditions, which can be explained by the differences in connectivity with groundwater, precipitation and other meteorological and geological features (Boros et al. 2017).

Prokaryotes

The abundance of planktonic bacteria is around 10^6 – 10^7 cells/mL and 10^7 – 10^8 cells/mL in the soda lakes and pans, respectively (Eiler et al. 2003; Kirschner et al. 2002; Szabó et al. 2020; Szabó-Tugyi et al. 2019; Vörös et al. 2008), and they belong mainly to the phyla Actinobacteria, Bacteroidetes and Proteobacteria (Bell et al. 2018; Bullerjahn et al. 2020; Szabó et al. 2017, 2020; Fig. 3). Archaea represent a minor fraction (~ 10% on average) of the planktonic prokaryotic community (Szabó et al. 2017, 2020), probably

due to the fact that these sites have only moderate salinity compared to other saline lakes in the world.

At lower taxonomic level, the uncultured groups acIII-A1, acSTL and acTH1 and the genera *Nitrliruptor* and *Ilumatobacter* are the most characteristic planktonic Actinobacteria in the shallow soda pans; their abundance can reach the highest values ever reported in the literature (up to 89%; Szabó et al. 2020). Probably, these small-sized bacteria, which have a protective cell wall structure, are the survivors of grazing pressure during spring–summer (Szabó et al. 2017, 2020). The proportion of planktonic Betaproteobacteria (e.g. *Limnohabitans* and *Hydrogenophaga*), which are well-known planktonic bacteria in freshwaters (Newton et al. 2011), is the highest in periods with the lowest salinity (Szabó et al. 2020). Other important planktonic bacteria, like members of the classes Cytophagia, Flavobacteria and the order Rhodobacterales (Alphaproteobacteria), are associated with algal blooms (Bullerjahn et al. 2020; Korponai et al. 2019; Szabó et al. 2020). Based on shotgun metagenomic data, genes of the *TonB* receptor system, which is responsible for the uptake of phytoplankton-derived high molecular weight organic matter (Williams et al. 2013; Buchan et al. 2014), were the most abundant in the community gene pool (Szabó et al. 2017) in a turbid pan. In the rarely observable dual blooms, under a green algal surface layer, dense populations of purple bacteria composed of the genera *Rhodobaca* (Rhodobacterales), *Thiorhodospira* or *Ectothiorhodospira* (both Chromatiales, Gammaproteobacteria) can grow just above the sediment layer (Borsodi et al. 2013; Korponai et al. 2019). Most probably, such blooms can emerge if the weather is warm, sunny and calm (Korponai et al. 2019). Nevertheless, photoheterotrophic bacteria represent a significant fraction of the total planktonic bacterial community in the soda lakes and pans of the Carpathian Basin in general. Based on microscopic cell counts, the abundance of aerobic anoxygenic phototrophs is usually at the magnitude of 10^6 – 10^7 cells/mL and denotes 5–30% of heterotrophic bacteria (Szabó-Tugyi et al. 2019). According to the results of recent years, the previously frequently isolated *Aeromonas*, *Pseudomonas* and *Bacillus* species (Ács et al. 2003; Langó et al. 2002) denote only a negligible part of bacterioplankton (Fig. 3).

Remarkable diel changes in the planktonic microbial activity and abundance were also observed in the shallow soda pans, and external abiotic factors (diluting the effect of rainfall which decreases salinity, but also the grazing pressure and viral lysis, the wind-induced sediment resuspension, and daily fluctuations of temperature and irradiation) seem to have a regulating effect on them (Kirschner et al. 2002; Krammer et al. 2008). The generation time of bacteria in these environments can be as little as a few hours (Eiler et al. 2003; Krammer et al. 2008). Growth studies on planktonic bacterial isolates have shown that the type of

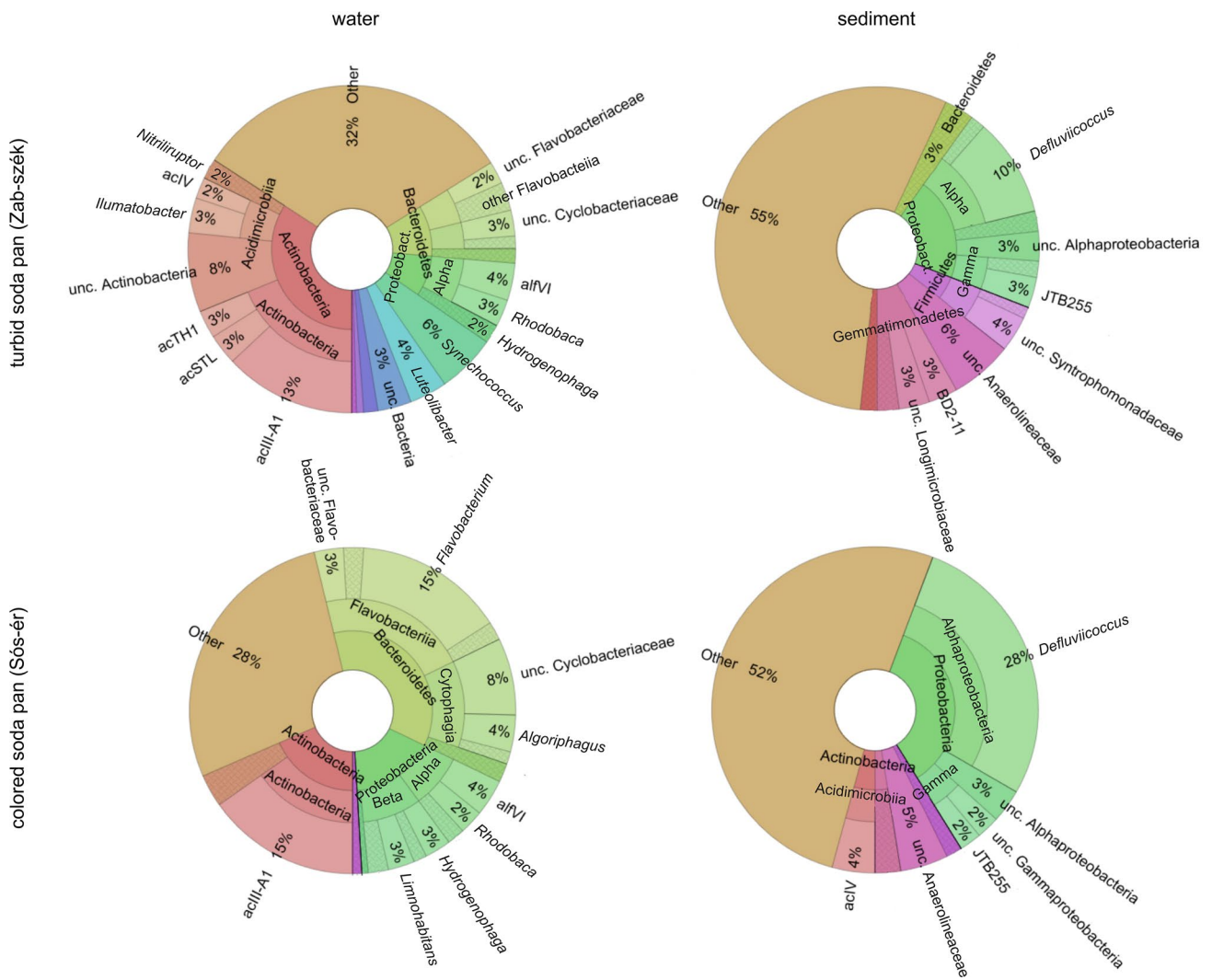


Fig. 3 Bacterial community composition of a turbid pan and a coloured soda pan from the Carpathian Basin. Based on the 16S rRNA gene amplicon sequencing data presented in Bedics et al. (2019) and

Szabó et al. (2020). Composite data are based on 16 and 13 planktonic samples in the case of Zab-szék and Sós-ér pans, respectively, and are based on 3–3 samples in the case of sediments

dominant anion determines the adaptation of prokaryotes, since strains isolated from soda pans grew better in media containing (hydrogen) carbonate than in media containing the same amount of chloride (Bedics et al. 2019).

Sediment bacterial communities of the soda pans in the Carpathian Basin are dominated by Proteobacteria, but the phyla Bacteroidetes, Actinobacteria, Gemmatimonadetes and Chloroflexi may also have significant contribution; and similarly to the bacterioplankton, remarkable differences are observable when comparing the turbid and the coloured pan (Bedics et al. 2019; Fig. 3). It seems that the abundant *Defluviicoccus* genus, which is capable of glycogen accumulation (Burow et al. 2007), has a special importance in the anaerobic biodegradation of organic material within the sediment. The number of lactate-utilizing sulphate-reducing bacteria was an order of magnitude higher in the reed

rhizosphere (i.e. in the vicinity of the macrophyte-derived organic carbon source) than in the sediment, and genera *Desulfovibrio*, *Desulfotomaculum* and *Desulfobulbus* have been detected in Lake Velence (Vladár et al. 2008). Furthermore, numerous moderately halophilic and alkaliphilic bacteria with a diverse metabolic profile have been isolated from the periphyton of reed (Borsodi et al. 2007; Rusznyák et al. 2008). The dominance of the phyla Proteobacteria (e.g. genera *Rheinheimera*, *Hydrogenophaga*, *Agrobacterium*) and Bacteroidetes (e.g. *Flavobacterium*) has been observed in these periphyton samples in cultivation-independent studies (Rusznyák et al. 2008).

Cyanobacteria are discussed in the section on algae of this review, since they perform photosynthesis with chlorophyll-a and, therefore, belong to the same functional group as eukaryotic algae; furthermore, in limnological practice,

their amount is determined together with that of microalgae as ‘bulk’ chlorophyll-a concentration.

Algae

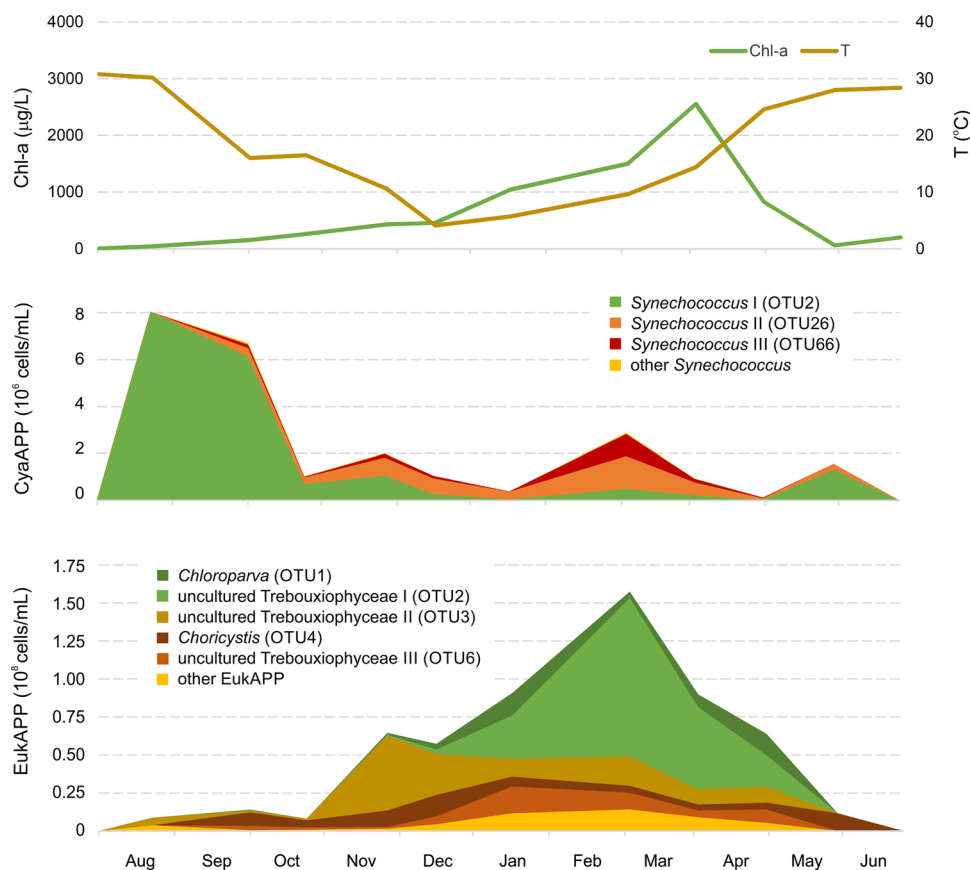
The high inorganic turbidity and the high concentration of humic compounds result in very low euphotic depth values in the soda lakes and pans of the Carpathian Basin (~5–25 cm; Boros et al. 2017). Nonetheless, phytoplankton biomass is high (the chlorophyll-a concentration typically in the range of 5–200 µg/L), which means meso-, eu- and hypertrophic conditions; most of the shallow soda pans are hypertrophic (Boros et al. 2017; Somogyi et al. 2009, 2010, 2017).

At these sites, pico-sized algae (<3 µm; APP, photoautotrophic picoplankton or picophytoplankton) typically contribute to the total phytoplankton biomass with 50–100%, and their abundance is around 10^6 – 10^7 cells/mL, but it can reach the highest values ever reported (up to 10^8 cells/mL; Keresztes et al. 2010; Somogyi et al. 2009, 2017; Fig. 4). APP are the most predominant in pans where the inorganic turbidity is higher than 50 mg/L, since it is hypothesized that in these turbid waters, the low underwater light intensity (which is circumvented with the high surface-to-volume

ratio of the cells; Raven 1998) and the reduced grazing pressure have a promotional effect on their ecological success (Somogyi et al. 2017). In general, within this group, picocyanobacteria dominate when the water temperature is higher than 15 °C, while eukaryotic algae are the main APP members during the cooler period of the year (Somogyi et al. 2009; Fig. 4). Photosynthetically active algae (APP and nanoplankton) were recently detected even in the ice of Lake Fertő/Neusiedl, with an abundance of around 10^4 APP cells/mL (Bullerjahn et al. 2020). Only phycocyanin-rich picocyanobacteria (with a greenish colour) may prevail at these sites (Felföldi et al. 2009; Somogyi et al. 2009, 2016), since the high turbidity and the high amount of coloured dissolved organic matter create a ‘red shift’ in the underwater light spectrum (Stomp et al. 2007; Vörös et al. 1998).

The picocyanobacterial community in these lakes and pans is dominated by small coccoid solitary cells (Somogyi et al. 2009, 2010), which belong to various non-marine *Synechococcus*/*Cyanobium* groups of the picophytoplankton clade sensu Urbach et al. (1998) (Bell et al. 2018; Felföldi et al. 2009, 2011; Szabó et al. 2020). In the case of Lake Fertő/Neusiedl, most picocyanobacteria belong to the *Cyanobium gracile* cluster (Group A) of the above-mentioned clade (Somogyi et al. 2010). Planktonic eukaryotic picoalgae are composed of members of the genera *Choricystis* and

Fig. 4 Seasonal changes in the picophytoplankton community in a turbid soda pan. Amplicon pyrosequencing data combined with microscopic cell counts of picocyanobacteria and eukaryotic picoalgae (Zab-szék pan). Analysis based on the data presented in Szabó et al. (2020). For the phylogenetic position of each OTU, see also Szabó et al. (2020)



Chloroparva and other uncultured green algal (mainly trebouxiophycean) taxa, which have characteristic seasonal dynamics (Bell et al. 2018; Somogyi et al. 2011, 2016; Fig. 4).

Regarding the composition of larger planktonic algae in the soda lakes of the Carpathian Basin, Cyanobacteria (*Planktothrix*, *Microcystis*, this latter often causes toxic bloom in Lake Velence), green algae (*Monoraphidium*), diatoms and euglenids are characteristic in the open turbid water, while in the coloured inner ponds, Cryptophyta (*Rhodomonas*, *Cryptomonas*), Dinophyta (*Peridinium*) and diatoms (*Campylodiscus*, *Cyclotella*, mainly meroplanktonic species) are the most common groups (Ács et al. 2003; Bell et al. 2018; Bullerjahn et al. 2020; Dokulil et al. 2014; Padišák 1992; Padišák and Dokulil 1994; Somogyi et al. 2010, 2016).

In the coloured shallow pans, during summer, the cyanobacterial genera *Aphanizomenon* and *Anabaenopsis* may form even blooms (Boros et al. 2013). In the turbid soda pans, nanoplanktonic eukaryotic algae (e.g. *Cryptomonas*) are only rarely observed due to the dominance of APP, while in the coloured pans euglenids (*Euglena*, *Phacus*) and chlamydomonads (*Carteria*, *Chlamydomonas*) may even present with biomass values as high as 3–30 mg/L (Gavrilović et al. 2018; Szabó et al. 2020). Occasionally, dual planktonic blooms can be observed in the shallow pans with an upper layer dominated by a green alga (*Oocystis submarina*) and a deeper layer with purple bacteria (Borsodi et al. 2013; Korponai et al. 2019). Contrary to this, a winter bloom under the snow and ice cover was composed of several uncultured green algal genotypes with pico-sized cells (Pálffy et al. 2014). Neuston blooms of euglenids and the green alga *Nautococcus* have also been reported (Boros et al. 2013).

In the shallow nearshore areas of the pans, filamentous green algae (e.g. *Cladophora*, *Oedogonium* and *Gongrosira*) or members of the class Xanthophyceae (e.g. *Triboinema* and *Vaucheria*) may develop and grow in the entire water body. If the water level decreases, these algal mats dry, and the result is irregular paper scrap-like structures, the so-called meteor paper (Boros et al. 2013; Fehér 2010; Kiss 1971, 1976). Benthic algal mats of nitrogen-fixing *Nodularia* (Cyanobacteria) species can be observed, but only when the water depth is extremely shallow (< 5 cm) and sufficient light reaches the sediment surface, while in the deeper regions of the turbid pans, the role of benthic algae is negligible (Boros et al. 2013; Vörös and Boros 2010). The benthic diatom communities of the soda pans are mainly composed of *Nitzschia* and *Navicula* species, also including fast-moving species (Gavrilović et al. 2018; further details can be found in the beautifully illustrated paper of Stenger-Kovács and Lengyel 2015).

The periphyton community of Lake Fertő/Neusiedl and Lake Velence is dominated by diatoms (mainly Pennales,

like *Achnanthes*, *Nitzschia*, *Synedra*, *Fragilaria*, *Gomphonema* and *Cymbella*; Ács et al. 2003; Buczkó 1989; Buczkó and Ács 1998).

Protists, viruses and fungi

Most heterotrophic nanoflagellate (HNF) species are relatively small (~ 5–10 µm in diameter), and they are supposed to be the main protozoan grazers of bacteria and picophytoplankton (Weisse 1993). Using classical microscopy, it is relatively complicated to enumerate and identify HNFs from these turbid environments; therefore, only a few studies have been conducted to date. However, the abundance of HNFs may be around 10⁴–10⁵ cells/mL (Krammer et al. 2008), and as it was revealed recently by an 18S rRNA gene-targeted high-throughput sequencing study, the most important flagellate genera in the soda pans of the Carpathian Basin are *Spumella*, *Jakoba*, *Ochromonas* and *Andalucia* (Márton et al. 2019).

Ciliates were studied intensively at these sites decades ago (mainly sessile forms; Gelei 1950; Stiller 1963; Szabó 1999), several novel species and genera have been described, and a diverse community was revealed (with genera *Epistylis*, *Vorticella* and *Maryna*), but unfortunately no detailed recent data on their abundance and composition are available. Ciliates have approximately one magnitude larger cell size than the HNF species (~ 50–200 µm in diameter) and possibly contribute to a lesser extent to the planktonic food web, since Krammer et al. (2008) found no ciliates in the water samples collected from small soda pans near Lake Fertő/Neusiedl, which supported that planktonic ciliates are a negligible fraction of the microbial community and their role in benthic habitats may be much more pronounced.

According to the above-mentioned 18S rRNA gene-based amplicon sequencing study (Márton et al. 2019), fungi can, in some cases, be important members of the planktonic community. Due to their saprophytic lifestyle, alkalitolerant fungi may contribute also to the mineralization of organic matter, e.g. after the collapse of summer algal bloom or during the decline of zooplankton populations.

Virological studies on these environments are, similarly, very scarce. Bacteriophages, mainly Caudovirales, were detected by Szabó et al. (2017) in the plankton of a turbid pan, while members of Phycodnaviridae (viruses that infect algae; Larsen et al. 2008) were reported from Lake Velence (Bell et al. 2018). The number of viral particles was estimated to be around 10⁸–10⁹/mL in the water of some soda pans in the Carpathian Basin (Krammer et al. 2008).

Food webs

A schematic food-web structure for a soda pan is shown in Fig. 5.

Birds have dual roles (net importers or net exporters) on the trophic food web of these pans: some species (e.g. the herbivorous geese; e.g. *Anser* species) supply the water with a high amount of allochthonous nutrients through their excrements, while others (e.g. *Anas* species) feed on the large populations of zooplankton (Boros et al. 2006, 2008a, b, 2016). The contribution of birds to the external nutrient load was estimated to be 50, 35 and 70% in the case of organic carbon, nitrogen and phosphorous, respectively (Boros et al. 2008a, b). Furthermore, the continuous mixing by the wind does not allow the bird faeces to settle down to the bottom of the pans, and therefore, they can provide a nutrient supply directly to the planktonic organisms. The naturally high concentration of nutrients results in eutrophic or, in many cases, even hypertrophic conditions, which, in this case, is called guanotrophication (Boros et al. 2016).

In general, the growth of phytoplankton and heterotrophic bacteria is supplied with nutrients from external sources (bird excrements and groundwater) and from decomposing shoreline macrophytes (Boros et al. 2008b, 2016, 2020; Dokulil et al. 2014; Vörös et al. 2008). On decaying reed, the periphyton and bacterial community was different compared with ‘healthy’ green reed (Ács et al. 2008; Buczkó and Ács 1998), and bacteria with urease activity and capable of biopolymer utilization were also isolated (Rusznayk et al. 2008), which indicates the role of microorganisms in the mineralization of organic matter originating from shoreline vegetation and from

birds. Heterotrophic processes in plankton are much more pronounced than autotrophic ones (net heterotrophic systems; Boros et al. 2016; Vörös et al. 2008), and alkaline pH was also reported to having an accelerating effect on organic matter degradation (Krachler et al. 2009). So, it should be emphasized that contrary to the fact that soda pans are, in many cases, hypertrophic (even with visible blooms, e.g. Korponai et al. 2019; Pálffy et al. 2014), heterotrophic activity is more significant.

The most important consumers of bacteria and algae are probably HNFs and microcrustaceans, while a fraction of the planktonic heterotrophic bacteria can be particle attached, which may protect cells against grazing in turbid pans (Koblížek 2015; Szabó-Tugyi et al. 2019).

Fish are usually absent from soda pans due to the astatic character of these pans, which results in the high abundance of zooplankton (Boros et al. 2006; Horváth et al. 2013) and a relatively strong top-down control of bacterio- and phytoplankton (Szabó et al. 2020). Therefore, the main consumers of zooplankton in these soda pans are filter feeder bird species and not fish. Some of the organic carbon and nutrients can be released from the system even through emerging insects and dust transferred by the wind from the dried-up lake bottom (Boros et al. 2013). However, if conditions are appropriate (e.g. there is no desiccation through subsequent years), fish populations [Prussian carp (*Carassius gibelio*) or stone moroko (*Pseudorasbora parva*)] may survive (Boros et al. 2013). Furthermore, in the case of large soda lakes (Lake Fertő/Neusiedl and Lake Velence), a diverse fish community is continuously present (due to the constantly low salinity values and the artificially set relatively high water level); fishing is allowed, and it is a popular activity at these sites (Borics et al. 2016).

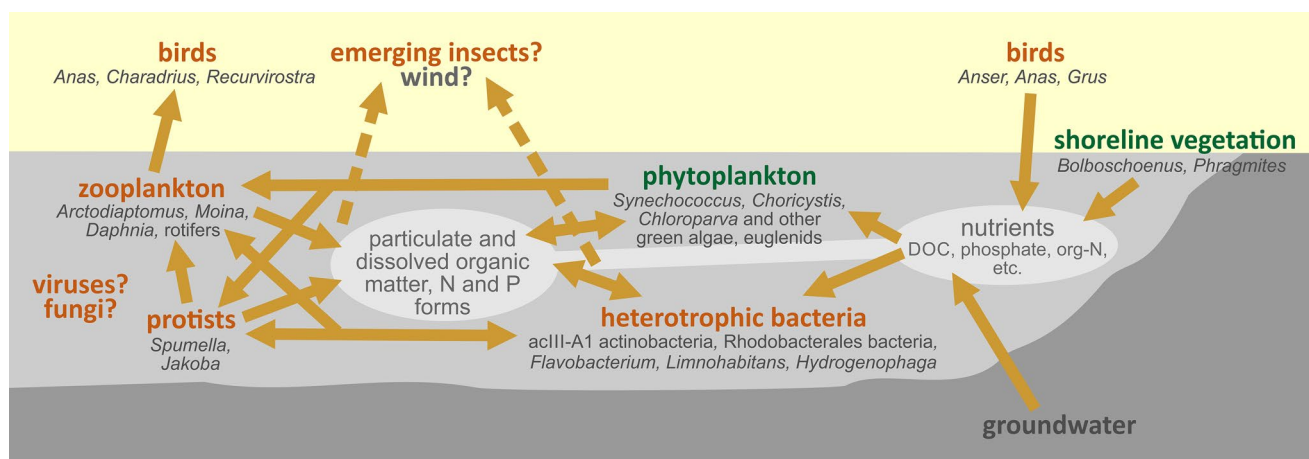


Fig. 5 Schematic planktonic food web structure of intermittent (astatic) soda pans in the Carpathian Basin. Arrows show the main flow directions of organic carbon and nutrients. For the sake of simplicity,

only major food web components are shown. Autotrophic organisms are marked with green, heterotrophs with brown letters. Characteristic genera are given for each group

For additional information about aquatic birds, shoreline vegetation and the composition and ecology of zooplankton communities, see Boros et al. (2013, 2016), Dokulil and Herzig (2009), Horváth et al. (2013, 2014, 2016, 2019) and Tóth et al. (2014).

Conclusions for future biology

The large number of novel taxa described from various habitats of soda lakes and pans of the Carpathian Basin (Table 2) indicates that these sites are important sources of unexplored biodiversity. It has been argued that biodiversity is generally higher in soda lakes compared with other continental saline lakes due to their relatively lower salinity (Grant 2004). Bacteria isolated from these habitats may be important sources of bioactive molecules and enzymes in the future, as detergent additives originating from soda lakes are already applied to help domestic and industrial washing processes (Grant 2004; Kalwasińska et al. 2018; Rothschild and Mancinelli 2001). Microalgae inhabiting these sites may be applied in biofuel production and wastewater treatment and may represent important natural sources for the cosmetic and food industries (Aravantinou et al. 2016; Khan et al. 2018; Selvarajan et al. 2015). Furthermore, these sites also have balneotherapeutic potential; the only existing example in this region is the medical centre by Lake Rusanda (Melenci, Serbia).

Based on current knowledge, it seems that mainly temperature, salinity, turbidity and grazing pressure regulate community composition and the abundance of individual microbial groups in the soda lakes and pans of the Carpathian Basin (Somogyi et al. 2009; Szabó et al. 2020), but

the external nutrient load from birds also has a significant impact on the ecological processes (Boros et al. 2016; Vörös et al. 2008). The unusually high dissolved organic carbon and nutrient content results in hypertrophic conditions and a net heterotrophic system (Boros et al. 2008b, 2020; Somogyi et al. 2009; Vörös et al. 2008), where zooplankton have a special importance in the control of microbial plankton (due to the lack of fish in most of these habitats; Boros et al. 2013; Horváth et al. 2013; Szabó et al. 2020). The dual role of birds and special environmental conditions (high pH, low transparency, moderate salinity with special ionic composition) add further unique features to these protected sites (Boros et al. 2006, 2013, 2014, 2016, 2017).

On the other hand, the processes observed in these multiple extreme aquatic habitats can be regarded as analogues of global environmental problems, e.g. (1) due to their shallowness, these sites are very sensitive to changes of meteorological conditions; (2) due to rising sea levels, moderately saline environments are expected to become more common if saltwater intrudes into coastal freshwater habitats; (3) increased evaporation is expected to result in a shift in many lakes from freshwater to saline conditions (Jeppesen et al. 2015); and (4) the growing human population creates environments with a high concentration of nutrients with the introduction of wastewaters to surface waters.

Finally, it should be noted that a significant fraction of soda pans has disappeared (~80% habitat loss) in the region due to human activities during the last 60 years (Boros et al. 2013), which has resulted in notable species loss (Horváth et al. 2019). However, ongoing management, monitoring and protection actions (see, e.g. www.boddi.hu; www.hortobagyte.hu) are promising trends to save these unique aquatic habitats for the future.

Table 2 Examples of new bacterial and algal species recently described from the soda lakes and pans of the Carpathian Basin

Species name	Isolation source		Reference
	Site	Habitat	
Bacteria			
<i>Arundinibacter roseus</i> (gen. nov., sp. nov.)	Lake Fertő/Neusiedl	Lake water (inner pond)	Szuróczi et al. (2019)
<i>Bacillus alkalisediminis</i> (sp. nov.)	Kelemen-szék (KNP)	Upper sediment layer	Borsodi et al. (2011)
<i>Bacillus aurantiacus</i> (sp. nov.)	Kelemen-szék (KNP)	Upper sediment layer	Borsodi et al. (2008)
<i>Cellulomonas phragmiteti</i> (sp. nov.)	Kelemen-szék (KNP)	Reed periphyton	Rusznayk et al. (2011)
<i>Nesterenkonia pannonica</i> (sp. nov.)	Böddi-szék (KNP)	Lake water	Borsodi et al. (2017b)
<i>Nitrincola alkalilacustris</i> (sp. nov.)	Zab-szék (KNP)	Lake water	Borsodi et al. (2017a)
<i>Nitrincola schmidtii</i> (sp. nov.)	Unnamed pan (KNP)	Lake water	Borsodi et al. (2017a)
<i>Pannonibacter phragmitetus</i> (gen. nov., sp. nov.)	Lake Fertő/Neusiedl	Decomposing reed rhizome	Borsodi et al. (2003)
<i>Phragmitibacter flavus</i> (gen. nov., sp. nov.)	Lake Fertő/Neusiedl	Lake water from a reed-covered area	Szuróczi et al. (2020)
Algae			
<i>Chloroparva pannonica</i> (gen. nov., sp. nov.)	Böddi-szék (KNP)	Lake water	Somogyi et al. (2011)

The term ‘sp. nov.’ in parentheses indicates that the taxon was described as a new species, while ‘gen. nov.’ stands for a new genus described for the first time from these sites. Abbreviation: KNP—Kiskunság National Park, Hungary

Remember the proverb: *Varietas delectat* (Cicero).

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Compliance with ethical standards

Conflict of interest The author declares that there is no conflict of interest.

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