Insight into the hidden bacterial diversity of Lake Balaton, Hungary

E. Tóth1 · M. Toumi1 · R. Farkas1 · K. Takáts1 · Cs. Somodi1 · É. Ács2,3

Received: 22 May 2020 / Accepted: 17 August 2020 / Published online: 7 September 2020
© The Author(s) 2020

Abstract
In the present study, the prokaryotic community structure of the water of Lake Balaton was investigated at the littoral region of three different points (Tihany, Balatonmáriafürdő and Keszthely) by cultivation independent methods [next-generation sequencing (NGS), specific PCRs and microscopy cell counting] to check the hidden microbial diversity of the lake. The taxon-specific PCRs did not show pathogenic bacteria but at Keszthely and Máriafürdő sites extended spectrum beta-lactamase-producing microorganisms could be detected. The bacterial as well as archaeal diversity of the water was high even when many taxa are still uncultivable. Based on NGS, the bacterial communities were dominated by Proteobacteria, Bacteroidetes and Actinobacteria, while the most frequent Archaea belonged to Woesearchaeia (Nanoarchaeota). The ratio of the detected taxa differed among the samples. Three different types of phototrophic groups appeared: Cyanobacteria (oxygentic phototrophic organisms), Chloroflexi (anaerobic, organotrophic bacteria) and the aerobic, anoxic photoheterotrophic group (AAPs). Members of Firmicutes appeared only with low abundance, and Enterobacteriales (order within Proteobacteria) were present also only in low numbers in all samples.

Keywords Lake Balaton · Bacterial diversity · Archaea · Bacteria · Next-generation sequencing (NGS)

Introduction
Lake Balaton is the biggest lake of Central Europe, a shallow water ditch, with an average depth of 3.0–3.6 m. The open water of the lake is almost permanently homogenized by wind, resulting concomitant resuspension of the sediment. The lake has a great importance also due to its touristical use. The quality of the water is regularly tested, and monitoring has started already in the 1960s (Szabó 1999; Kiss et al. 2005). In 2006, Hungary joined the water quality assessments in line with the EU Water Framework Directive (EU WFD). In it, the definitions of biological variables were given a much stronger role than before. Moreover, till that time many studies had revealed the state of the water (Istvánovics et al. 2008; Bolla et al. 2010; Hatvani et al. 2014; Maasz et al. 2019).

The first microbiological investigations aimed at studying the prokaryotic diversity of the lake showed that members of the genus Bacillus (Firmicutes) are dominant at some regions (Langó 1982). Different Actinobacteria were also isolated from the water of Keszthely Bay, e.g. Streptomyces and Micromonospora species (Farkas 1982). In 1985, the presence of Enterobacteria (indicating faecal pollution) was found in Keszthely Bay, and Enterobacter agglomerans, Escherichia coli, Kluyvera cryocrescens and Klebsiella oxytoca were detected in high number among the cultivated bacterial strains (Bognár, 1990).

Tóth (1995) has studied the bacterial communities of the open water in the Balatonfüred region and found the dominance of many Gram-negative organisms belonging to the genera Aeromonas, Pseudomonas and Acinetobacter. Bacterial partners of Eudiaptomus gracilis (important member of the zooplankton of the lake) were also studied (Homonnay et al. 2011) as well as the microbiology of big-headed carps (Borsodi et al. 2017). The first detailed reports about aerobic anoxygenic phototrophs (AAPs) of the lake showed that their abundance as compared to heterotrophic bacteria is between 1 and 7% (Szabó-Tugyi et al. 2019).
All of these studies are very important, but most of them were based on cultivation techniques, and it is known that less than 1% of bacteria are cultivable from natural aquatic habitats (Amann et al. 1995).

The aim of the present study was to reveal the prokaryotic community structure of the water of the lake at the littoral region (where the water is subjected also to strong human influence due to bathing) by cultivation independent methods [next-generation sequencing (NGS) and microscopic cell counting]. By using specific PCRs, the presence of some hygienically important bacteria was tested. Our results show the hidden prokaryotic diversity of the lake which has never been revealed until now, and provide information about the potential health risks of bathing.

Materials and methods

Sampling

Sampling was carried out in 30. 08. 2018 at three points of the lake: Tihany (65.91900 N; 17.88903 E), Keszthely (46.76014 N; 17.25448 E) and Balatonmáriafürdő (46.70725 N; 17.38276 E) (later: Máriafürdő), from the littoral water region. The water samples (1–1 L) were aseptically collected into sterilized screw-capped flasks from 10 cm subsurface according to ISO 19458:2006. Samples were transported to the laboratory in a cooler bag (at 4 °C) and processed within 4 h after sampling.

Analysis of physical and chemical parameters

To measure the physical and chemical parameters, the following standards were used: MSZ 448-32:1977 (conductivity), MSZ ISO 5813:1992 (dissolved oxygen, DOC), MSZ 1484-13:2009 (nitrate concentration), MSZ 448-13-1983 (sulphate concentration), MSZ ISO 10260:1993 (chlorophyll a). The measures were done by the Central Transdanubian Water Authority, and we got it via the National Directorate of Water Management (OVF); data were obtained from the office except values of water temperature and pH which were measured on site.

Determination of microscopy cell counts

Determination of bacterioplankton abundance (microscopy cell counts) was carried out as described by Kéki et al. (2019) using Nikon80i epifluorescent microscopy and NisElements program package. For the investigations, 10 mL water samples were filtered on sterile polycarbonate filters (Millipore, Billerica, MA, USA) and fixed with 2% paraformaldehyde solution.

DNA extraction from the water samples

For DNA extraction, 0.25L water samples were filtered through 0.22 μm pore size, mixed cellulose filter (type GSWP; Millipore, Billerica, MA, USA) using the Ultraclean® PowerSoil DNA Isolation Kit (MoBio, Carlsbad, CA, USA) according to the manufacturer’s instructions.

Specific PCRs

Taxon-specific PCRs were applied for the following bacterial groups: Pseudomonas spp. and Pseudomonas aeruginosa according to Lavenir et al. (2007), Legionella spp. according to Cloud et al. (2000), Legionella pneumophila according to Fiume et al. (2005), Acinetobacter baumannii according to Tsai et al. (2018) and Stenotrophomonas maltophilia according to Filho et al. (2004).

At the sampling sites there were no people at the time of sampling (it was late pm), but the sites were subjected to bathing in the previous days, therefore, the bacterial community was tested also for extended spectrum beta-lactamase (ESBL)-producing and macrolide-resistant bacteria.

The presence of ESBL genes was tested by multiplex PCRs in the water samples according to Trung et al. (2015) and macrolide-resistance genes following the protocol described by Zmantar et al. (2011), testing five genes (ermA, ermB, ermC, msrA and mefA) simultaneously.

Next-generation DNA sequencing and data analysis

For the identification of bacterial and archaeal taxa, the 16S rRNA gene of the DNA samples was amplified with PCRs in separate, triplicate reactions using primers with the following target-specific sequences: Bact_341F (5′-CCT ACG GGN GGC WGC AG-3′) and modified Bact_805R (5′-GAC TAC NVG GGT ATC TAA TCC-3′) for bacteria (Herlemann et al. 2011), and A519F (5′-CAG CMG CCG CGG TAA-3′) and Arch855R (5′-TCC CCC GCC AAT TCC TTT AA-3′) for Archaea (Klindworth et al. 2013). DNA sequencing was performed on an Illumina MiSeq platform using MiSeq standard v2 chemistry by the Genomics Core Facility RTSF, Michigan State University, USA. Sequencing and the description of bioinformatic analysis were done according to Benedek et al. (2019). OTUs were determined at the species-level delineation based on Tindall et al. (2010). Sequence reads were deposited in the NCBI SRA database and are accessible through the BioProject PRJNA628507, Biosample ID SAMN14732963 (Tihany), SAMN14732959 (Máriafürdő) and SAMN14732964 (Keszthely). Diversity indices were calculated using mothur (Schloss et al. 2009),
and reads were subsampled to the read number of the sample having the lowest sequence count.

Results

Physico-chemical and biological parameters

The physico-chemical parameters together with the cell count values of the samples of the Lake Balaton are given in Table 1. Data of the three sampling sites showed similarities though some differences could be detected: the quantity of total organic carbon (TOC), total organic nitrogen (TON), total organic phosphorous (TOP) as well as chlorophyll-a concentration were the lowest in the Tihany region. Most TOC appeared in dissolved form (DOC), and the water was aerated at all sites.

Specific PCRs

The taxon-specific PCRs showed (Table 2) that *Pseudomonas* spp. and *Legionella* spp. were present at all sites, but pathogenic *L. pneumophila* and *P. aeruginosa* as well as *Acinetobacter baumannii* could not be detected. At Keszthely and Máriafürdő sites ESBL-producing bacteria could also be detected.

Amplicon sequencing

NGS results showed that diversity indices of Keszthely and Máriafürdő samples were similar in case of all types of indices, while Tihany sample (despite the fact that cell counts were high even at that site) produced much lower values. The Chao indices (abundance-based estimator of species richness) were 747.5 in case of Tihany, 1433.4 in case of Keszthely and 1509 in case of Máriafürdő sample, respectively.

The distribution of the different bacterial phyla and dominant classes among the samples is given in Fig. 1.

Results show that on the level of phyla the samples are similar: Proteobacteria, Bacteroidetes and Actinobacteria were the most abundant members of the communities at each site and many unclassified bacteria: Planctomycetes, Cyanobacteria and Patescibacteria also occurred. Abundance of Firmicutes was relatively low in case of each sample. On the other hand, the ratio and composition of the different lower-level taxa differed among the samples. Most abundant orders among Alphaproteobacteria were Rhizobiales, Azospirillales, Rhodobacterales, Rhodospirillales and members of SAR11 clade (Azospirillales and Rhodospirillales were present only at Tihany region), among Deltaproteobacteria, Bdellovibrionales, Myxococcales and many sulphate-reducing bacteria (SRB) appeared, while Gammaproteobacteria

| Sampling site | T°C | Conductivity (μS/cm) | pH | Dissolved oxygen (mg/L) | DOC (mg/L) | ATOC (mg/L) | TON (mg/L) | TOP (μg/L) | Chlorophyll a (mg/mL) | NO₃⁻ (mg/L) | SO₄²⁻ (mg/L) | Cell count/mL |
|---------------|-----|----------------------|----|------------------------|-----------|-------------|-------------|-------------|----------------------|-------------|--------------|--------------|
| Tihany        | 22  | 680                  | 8.6| 9.14                   | 7.7       | 0.646       | 0.084       | 0.076       | 3.2                  | 119         | 6.3E+06      | 6.3E+06      |
| Máriafürdő    | 22.3| 610                  | 8.5| 9.52                   | 9.6       | 0.956       | 0.100       | 0.086       | 3.9                  | 94          | 6.1E+06      | 2.7E+06      |
| Keszthely     | 23.4| 600                  | 8.4| 10.03                  | 9         | 0.766       | 0.076       | 0.100       | 7.7                  | 91          | 8.7E+06      | 8.7E+06      |
(giving more than 60% of Proteobacteria at each site) were represented by the abundance of unclassified Burkholde-
riaceae, Methylococcales (was not present at Tihany sam-
ples), Betaproteobacteriales, Pseudomonadales and Xan-
thomonadales. Enterobacteriales were present only in low
numbers in all samples.

From the phylum Actinobacteria members of Micro-
trichales, Frankiales and Micrococcales appeared in high
number, their ratio was higher at Máriafürdő and at Kes-
zhely. Among Bacteroidetes, the orders Chitinophagales,
Cytophagales, Flavobacteriales and Sphingobacteriales were
abundant, at Tihany sample, less orders were identified than
in the other two samples.

Three different types of phototrophic metabolisms
appeared in the samples: Cyanobacteria are oxygenic
phototrophic organisms, Chloroflexi are anaerobic,
organotrophic bacteria and the aerobic, anoxic photohet-
erotropic group (AAPs). Their distribution among the
samples and the ratio of different Cyanobacteria are dis-
played in Fig. 2.

Among Cyanobacteria, ratio of Nostocales was high at
Keszthely and Máriafürdő samples, while members of Syn-
echococcales were more abundant in the Tihany region, and
they are represented by the dominance of Cyanobium (pico-
cyanobacterium). Among Chloroflexi, members of the order
Anaerolineales were the most abundant, but they did not
appear in Tihany sample.

In case of Archaea, the diversity indices showed simi-
ter tendencies than in case of bacteria, Chao indices were
108.27 in case of Tihany, 178.9 in case of Keszthely and
119.02 in case of Máriafürdő sample, respectively, and val-
ues were much lower than in case of bacteria.

---

**Table 2** Results of the taxon-specific, ESBL-producing and macrolide resistance genes by PCRs

| Sampling site | Pseudomonas spp. | P. aeruginosa | Legionella spp. | L. pneumophila | Stenotrophomonas maltophilia | Acinetobacter baumannii | ESBL-production | Macrolide resistance |
|---------------|------------------|--------------|----------------|---------------|-------------------------------|------------------------|-------------------|---------------------|
| Tihany        | +                | −            | +              | −             | +                             | −                      | −                 | −                   |
| Máriafürdő    | +                | −            | +              | −             | +                             | −                      | +                 | −                   |
| Keszthely     | +                | −            | +              | −             | +                             | −                      | +                 | −                   |

---

**Fig. 1** The distribution of the different bacterial phyla and the ratio of dominant classes among the samples of Lake Balaton
The archaeal phyla appearing at the samples are shown in Fig. 3.

The absolute dominance of Nanoarchaeota was obvious in all samples, and Woesearchaeia dominated each sample among them: representing more than 65% of each community. Crenarchaeota (e.g. Bathyarchaeia) and Euryarchaeota (e.g. Methanobacteria and Thermoplasma) were very less abundant in Tihany sample, and Asgardeota did not even appear there. Unclassified Archaea were present in all of the three samples.
Discussion

The quality of the surface waters (e.g. lakes, rivers, streams) is very important, they often serve as basis for drinking waters or act as touristic sites, also for bathing purposes. In the nature, complex systems exist, where the characteristics of the given habitat are determined by inside and outside effects, influenced by interacting microbial populations as well as anthropogenic effects (e.g. bathing or any contamination). Studies using next-generation sequencing (NGS) technologies are providing new insights into the ecology of microbially mediated processes that influence freshwater quality.

Among the three sampling sites at Lake Balaton, only small differences could be revealed in the composition of bacterial communities, and all can probably be explained, e.g. by the small shifts and differences in the organic material (TOC, TON, TOP) content or the light access of the different sampling sites. Though the water body is aerobic (the dissolved oxygen content was always high), being a shallow lake, the wind can easily stir the whole water column, so anaerobic microbes can originate also from the sediment. Moreover, microbes can live in microhabitats where the oxygen concentration can differ strongly that of the water column.

In case of Lake Balaton, based on the chemical and biological parameters all the three sampling sites are low nutrient content habitat, seemed to be oligotrophic (https://www.vizugy.hu/index.php?module=vizstrat&programelemid=149; Borics and Kiss 2015) at time of samplings, though to state it, more investigations should be done (e.g. checking macrozoobenthos, macrophyton, etc.). But our result shows that even at the end of a summer period, when anthropogenic effect is higher due to bathing, the self-purification of the lake is adequate. Studying the seasonal dynamics of the phytoplankton, Somogyi et al. (2016) revealed a west-east trophic gradient in the longitudinal axis in the lake, similar to the previous years.

In 2018, the tendency is similar, though the cell counts of bacteria were in the same magnitude of all sampling sites. At the same time, the diversity indices (based on amplicon sequencing) showed the bacterial communities are less diverse in the Tihany region. It is also true that the DOC values as well as TON and TOP were the less at that site; if the amount of the available substrates is lower, most probably their concentration is limited, and these circumstances favour the reproduction of fewer types of organisms (Howarth and Marino 2006).

Taxon-specific PCRs did not show pathogenic microbes among the studied ones, but the presence of ESBL-producing bacteria at Keszthely and Máriafürdő may indicate anthropogenic effect or other faecal contamination (De Boeck et al. 2012; Blaak et al. 2014), since these regions are strongly affected by bathers.

If we check the composition of bacterial communities, we can immediately see that the diversity of the lake is much higher than we have ever thought. NGS results have not only shown the presence of many non-cultivable taxa but indicated also that those bacteria which previously were thought to be dominant, occur in the lake only with low frequency. Since, that our results are based on molecular data comparisons with previous studies is not really applicable, it is worth mentioning: members of Firmicutes appeared only with low abundance in the water of the lake at each sampling sites (e.g. Bacillus, Exiguobacterium species) though they were frequently isolated earlier (Langó 1982; Homonnay et al. 2011).

Among Proteobacteria, mainly different Pseudomonas, Aeromonas and Acinetobacter species were detected previously (Tóth, 1995), their seasonal abundance was also remarkable.

The present studies showed that in the water there are several bacteria which can be responsible for N₂ fixation (Rhizobiales, Azospirillales, etc.) which phenomenon can be very important in low nutrient content environments, where the nitrogen is often in limited concentration (Howarth and Marino 2006). Nitrogen fixation was documented also in case of Lake Balaton earlier (Kovács et al. 2012; Borics et al. 2016), authors revealed that during eutrophication processes nitrogen-fixing, filamentous cyanobacteria became frequent in the western part of the lake. This time also the heterotrophic, free living nitrogen-fixing bacteria were identified.

Based on literature data, bacteria belonging to SAR11 have an oligotrophic lifestyle with slow but efficient nutrient uptake at low substrate concentrations (Salcher et al. 2011). The concentration of TOC was low at each sampling site, which could have a positive effect on the abundance of subgroup III of SAR11.

The presence of Bdellovibrionales and Myxococcales (and even that of Vampirovibrionales) shows that even predator/parasite prokaryotes are present in the water body (Li et al. 2014).

Actinobacteria were also detected earlier in Lake Balaton (Szabó, 1982; Farkas, 1982; Tóth, 1995), they are often described in freshwaters and sediments of lakes. Hofmefldt et al. (2009) demonstrated that the prevalence of the clades of different Actinobacteria has changed in relation to total phosphorus (TOP) and Chl A, respectively. In our studies, several actinobacterial taxa were detected, among them Frankiales with the abundance of the hgcI clade. Though the exact role of these bacteria in Lake Balaton has to be defined by later studies, it is known that they can play a dominant role in degradation processes. Members of hgcI clade are common and abundant in a wide range

© Springer
of freshwater habitats (Warnecke et al. 2004); they have also the potential to utilize sunlight via actinorhodopsin which might promote anaplerotic carbon fixation (Ghylin et al. 2014). Ghai et al. (2014) studying a freshwater lake in Spain by metagenomic analysis showed a remarkable potential of their genomes to transform calcite carbonated plant detrital material (e.g. lignin-derived compounds). Moreover, they detected that the abundances of Actinobacteria correlate inversely to those of Cyanobacteria that can be responsible for prolonged damage to freshwater ecosystems.

Our results connected to other phototrophic bacteria showed that their abundance is high in the water of Lake Balaton, which is not new. Kovács et al. (2012) described the effect of irradiance on the germination of N-fixing, filamentous cyanobacteria in the sediment of Lake Balaton with varying phosphorous supply. They focused their studies on the most invasive Cyanobacteria of the lake (Cylindrospermopsis raciborskii and Aphanizomenon flos-aquae). Somogyi et al. (2016) detected the dominance of picocyanobacteria in the summer and dominance of picoeukaryotes in the winter period. Cyanobia (Synechococcales) which are picosized cyanobacteria were observed also in the open water of Lake Fertő (Somogyi et al. 2010); we showed they are dominant in the Tihany region in the summer of 2018, and the abundance of these bacteria is not surprising. Felföldi et al. (2011) demonstrated also the diversity and seasonal dynamics of photoautotrophic picoplankton in Lake Balaton.

The members of Anaerolineales (Chloroflexi) are strictly anaerobic, organotrophic organisms, they are often found in freshwater sediments (Wise et al. 1997) and they can be responsible for metabolizing even different organic substrates.

Aerobic anoxic photoheterotrophic bacteria (e.g. Rhodobacterales) are a diverse group of bacteria that produce bacteriochlorophyll a in the presence of oxygen (Ruiz-González et al. 2020). They are facultative photoheterotrophic bacteria being able to gain energy also from the utilization of light, which gives them an advantage over obligate heterotrophic bacteria (Szabó-Tugyi et al. 2019).

Cytophaga–Flavobacterium group and Chitinophagales are Gram-negative, chemoheterotrophic organisms (Kirchman, 2002), often able to degrade polymer substrates as cellulose, and chitin even degrade calcite carbonated organic substrates (Berg et al. 2009).

In case of Archaea, our knowledge is still less connected to their possible role as most of the novelty discovered phyla do not have any cultured representatives (Castelle and Banfield 2018). On the basis of 16S rDNA sequence comparisons, the phylum “Nanoarchaeota” represents a deep lineage within the Archaea. The predominant archaeal group of our water samples belonged to Woesearchaeia; they are widely distributed in nature, anaerobic, fermentative, syntrophic bacteria that contribute significantly to the biogeochemical cycles of iron and methane (Gayner 2018).

Members of Bathyarchaeota (phylum Crenarchaeota) are generalists, which appear in various environments. They are incorporated in Feammox processes-anabiotic ammonium oxidation coupled to Fe(III) reduction (Rios-Del Toro et al. 2018). Some of them are involved in anaerobic methane oxidation. Evans et al. (2015) presumed also the syntrophy between Bathyarchaeota and sulphate-reducing bacteria (SRB) towards anaerobic oxidation of methane.

Conclusions for future biology

As a conclusion, we can state that the bacterial as well as archael diversity of the water of Lake Balaton is high and even when many taxa are uncultivable, the novel molecular studies can reveal their hidden diversity. Prokaryotes are organized in complex communities, they can be involved in many different metabolic processes, chemotrophic as well as phototrophic organisms were also detected, just as bacteria involving many oxidation/reduction reactions, etc. The microbial communities we have revealed can be responsible for many steps in the biogeochemical cycles of carbon, nitrogen, sulphur but also that of phosphorous or iron; to discover it in details, further investigations are necessary. It is true that the diversity and abundance of bacterioplankton depend on the phytoplanktonic primary production, but heterotrophic bacteria most probably are involved also in degradation of the residuals of different chemical contaminations which have been detected in the lake (Simon-Delso et al. 2015; Avar et al. 2015; Maasz et al. 2019), these can be removed by the help of these complex bacterial communities. Though the self-purification of the water is strong, humans must consider keeping the water quality safe for further use.

Funding Open access funding provided by Eötvös Loránd University. This work was completed in the ELTE Institutional Excellence Program supported by the National Research, Development and Innovation Office (NKFH-1157-8/2019-DT).

Data accessibility Sequence reads were deposited in the NCBI SRA database and are accessible through the BioProject ID SAMN14732963 (Tihany), SAMN14732959 (Máriafürdő) and SAMN14732964 (Keszthely). Data of physical and chemical analysis were collected from the official database of National Directorate of Water Management.

Compliance with ethical standards

Conflict of interest The authors declare that there are no conflicts of interest connected to data of the paper.
Ethical statement  Our paper does not contain any experiments connected to humans or animals.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Amann RI, Ludwig W, Schleifer KH (1995) Phylogenetic identification and in situ detection of individual microbial cells without cultivation. Microbiol Rev 59:143–169

Avar P, Maasz G, Takács P, Lovas S et al (2015) HPLC-MS/MS analysis of steroid hormones in environmental water samples. Drug Test Anal 8(1):123–127. https://doi.org/10.1002/dta.1829

Benedek K, Bálint J, Máthé I et al (2019) Linking intraspecific variation in plant chemical defence with arthropod and soil bacterial community structure and N allocation. Plant Soil 444:383–397. https://doi.org/10.1007/s11104-019-04284-7

Berg KA, Lyra C, Sivonen K, Paulin L, Suomalainen S, Tuomi P, Rapala J (2009) High diversity of cultivated heterotrophic bacteria in association with cyanobacterial water blooms. Syst Microb Ecol J 3:314. https://doi.org/10.1038/sj.isme.2008.110

Blaak H, van Hoek AH, de Roda Husman AM, Schets FM (2014) Prevalence and characteristics of ESBL-producing E. coli in Dutch recreational waters influenced by wastewater treatment plants. Vet Microbiol 170(3–4):448–459. https://doi.org/10.1016/j.vetmic.2014.03.007

Bolla B, Borics G, Kiss KT, Resköné NM, Várbiró G, Ács É (2010) Recommendations for ecological status assessment of lake Balaton (largest shallow lake of central Europe), based on benthic diatom communities. Vie Et Milieu-Life Environ 60(3):197–208

Borics G, Kiss KT (2015) Módszertei utánumítató a Fitoplanktonon élőénycsoport VKI szerinti gyűjtéséhez és feldolgozásához Kézirat pp 22

Borics G, Ács É, Boda P, Boross E, Erős T, Grigorszky I, Kiss KT, Sz Lengyel, Reskóné NM, Somogyi B, Vörös L (2016) Water bodies in Hungary—an overview of their management and present state. Hung J Hydrol 96(3):57–67

Borsodi AK, Szabó A, Krett G, Felföldi T, Specziár A, Boross E (2017) Gut content microbiota of introduced bigheaded carps (Hypophthalmichthys spp.) inhabiting the largest shallow lake in Central Europe. Microbiol Res 195:40–50. https://doi.org/10.1016/j.micres.2016.11.001

Castelle CJ, Banfield JF (2018) Major new microbial groups expand diversity and alter our understanding of the tree of life. Cell 172:1181–1197. https://doi.org/10.1016/j.cell.2018.02.016

Cloud JL, Caroll KC, Pixton P, Erali M, Hillyard DR (2000) Detection of Legionella species in respiratory specimens using PCR with sequencing confirmation. J Clin Microbiol 38:1709–1712

De Boeck H, Miwanda B, Lunguya-Metlla O, Muyembe-Tamfun J, Stoberingh E, Glupczynski Y, Jacobs J (2012) ESBL-positive Enterobacteria in drinking water. Emerg Infect Dis 18(6):1019–1020. https://doi.org/10.3201/eid1806.111214

Evans PN, Parks DH, Chadwick GL, Robbins SJ, Orphan VJ, Goldberg SD, Tyson GW (2015) Methane metabolism in the archaeal phylum Bathyrarchaeota revealed by genome-centric metagenomics. Science 350:434–438. https://doi.org/10.1126/science.aac7745

Farkas I (1982) Cellulózbontó aktinomicéták a Keszthelyi-öbölben és a „Zala-hatás” bakteriológiai indikációjának kérése. MTA Biol Oszt Közl 25:191–200

Felföldi T, Duleba M, Somogyi B, Vajna B, Nikolausz M, Márialigeti K, Vörös L (2011) Diversity and seasonal dynamics of phototrophic picoplankton in Lake Balaton (Hungary). Aquatic Microbiol Ecol 63:273–287. https://doi.org/10.3354/ame01501

Filho da Silva LVF, Tateno AF, Velloso LF, Levi JE, Fernandes S, Bento CNO, Rodriguez JC, Ramos SRTS (2004) Identification of Pseudomonas aeruginosa, Burkholderia cepacia Complex, and Stenotrophomonas maltophilia in respiratory samples from cystic fibrosis patients using multiplex PCR. Pediatr Pulm 37:537–547. https://doi.org/10.1002/ppul.20016

Fiume L, Bucca SMA, Poda G (2005) Detection of Legionella pneumophila in water samples by species-specific real-time and nested PCR assays. Lett Appl Microbiol 41:470–475. https://doi.org/10.1111/j.1472-765X.2005.00779.x

Gayner NJ (2018) River bank inducement influence on a shallow groundwater microbial community and its effects on aquifer reactivity. University of Wisconsin Milwaukee, UWM Digital Commons, Theses and Dissertations, pp 1–138

Ghai R, Mizumo CM, Picazo A, Camacho A, Iguez-Valera SR (2014) Key roles for freshwater Actinobacteria revealed by deep metagenomic sequencing. Mol Ecol 23:6073–6090. https://doi.org/10.1111/mec.12985

Ghylin TW, Garcia SL, Moya F, Osyerman BO, Schwientek P, Forrest KT et al (2014) Comparative single-cell genomics reveals potential ecological niches for the freshwater acI Actinobacteria lineage. ISME J 8(12):2503–2516. https://doi.org/10.1038/ismej.2014.135

Hatvani IG, Clement A, Kovács J, Székely-Kovács I, Korponai J (2014) Assessing water-quality data: the relationship between water quality amelioration of Lake Balaton and the construction of its mitigation wetland. J Great Lakes Res 40:115–125. https://doi.org/10.1016/j.jglr.2013.12.010

Herlemann DP, Labrenz M, Jürgens K, Bertilsson S, Waniek JJ, Andersson AF (2011) Transitions in bacterial communities along the 2000 km salinity gradient of the Baltic Sea. ISME J 5:1571–1579. https://doi.org/10.1038/ismej.2011.41

Holmfeldt K, Dziallas C, Titelman J, Pohlman K, Grossart HP, Riemann L (2009) Diversity and abundance of freshwater Actinobacteria along environmental gradients in the brackish northern Baltic Sea. Environ Microbiol 11(8):2042–2054. https://doi.org/10.1111/j.1462-2920.2009.01925.x

Homonay ZZ, Kéki Z, Márialigeti K, Tóth EM (2011) Bacterial communities in the gut of the freshwater copepod Eudiaptomus gracilis. J Basic Microbiol 52(1):86–90. https://doi.org/10.1002/jobm.201100052

Howarth RW, Marino R (2006) Nitrogen as the limiting nutrient for eutrophication in coastal marine ecosystems: evolving views over three decades. Limnol Oceanogr 51(1):364–376. https://doi.org/10.4319/lo.2006.51.1_part_2.0364

Istvánovics V, Honti M, Kovács Á, Osztics M (2008) Distribution of submerged macrophytes along environmental gradients in large, shallow Lake Balaton (Hungary). Aquat Bot 88:317–330. https://doi.org/10.1016/j.aquabot.2007.12.008

Kéki ZS, Márialigeti K, Tóth E (2019) Critical point analysis and biocide treatment in a microbiologically contaminated water purification system of Lake Balaton.
a power plant. SN Appl Sci 1:820–831. https://doi.org/10.1007/s42452-019-0740-9

Kirchman DL (2002) The ecology of Cytophaga–Flavobacteria in aquatic environments. FEMS Microbiol Ecol 39(2):91–100. https://doi.org/10.1111/j.1574-6941.2002.tb00910.x

Kiss G, Gy Dévai, Töthmérezs B, Szabó A, Resköné Nagy M (2005) A vízminőségi állapot hosszú távú változásainak többlévő elemzése a Balaton példáján. Hidrológiai Közlöny 35(6):57–59

Klingworth A, Puersche E, Schweer T, Pepiles J, Quast C, Horn M, Glöckner FO (2013) Evaluation of general 16S ribosomal RNA gene PCR primers for classical and next-generation sequencing-based diversity studies. Nucleic Acid Res 41:1–11. https://doi.org/10.1093/nar/gks808

Kovács AW, Tóth VR, Vörös L (2012) Light-dependent germination and subsequent proliferation of N2-fixing cyanobacteria in a large shallow lake. Ann Limnol Int J Lim 48:177–185. https://doi.org/10.1051/limn/2012100

Langó ZS (1982) A Balaton északi parti régiója Bacillus populációjának számítógépes analízise. MTA Biol Osz Közl 25:313–326

Lavenir R, Jocktan D, Laurent F, Nazaret S, Cournoyer B (2007) Improved reliability of Pseudomonas aeruginosa PCR detection by the use of the species-specific ecfX gene target. J Microbiol Meth 70:20–29. https://doi.org/10.1016/j.mimet.2007.03.008

Li H, Chen C, Sun Q, Liu R, Cai J (2014) Vampirovibrio chlorellavorus is related to the family Bdellovibrionaceae, which has been described as Bdellovibrio and like organisms or BALOs. Bdellovibrio and like organisms enhanced the growth and survival of Panaeus monodon and altered community rearing structures in its rearing water. Appl Environ Microbiol 80(20):6346–6354. https://doi.org/10.1128/AEM.01737-14

Maasz G, Mayer M, Zrinyi Z, Molnar E, Kuzma M, Fodor I, Pirger Z, Takács P (2019) Spatiotemporal variations of pharmacologically active compounds in surface waters of a summer holiday destination. Sci Total Environ 677:545–555. https://doi.org/10.1016/j.scitotenv.2019.04.286

Rios-Del Toro EE, Valenzuela EJ, López-Lozano NE, Cortés-Martínez MG, Sánchez-Rodríguez MA, Calvario-Martínez O, Sánchez-Carrillo S, Cervantes FJ (2018) Anaerobic ammonium oxidation linked to sulfate and ferric iron reduction fuels nitrogen loss in marine sediments. Biodegradation 29:429–442. https://doi.org/10.1007/s10532-018-9839-8

Ruiz-González C, García-Chaves MC, Ferrera I, Niño-García JP, del Giorgio PA (2020) Taxonomic differences shape the responses of freshwater aerobic anoxic phototrophic bacterial communities to light and predation. Mol Ecol 29(7):1267–1283. https://doi.org/10.1111/mec.15404

Salcher MM, Pernthaler J, Posch T (2011) Seasonal bloom dynamics and ecophysiology of the freshwater sister clade of SAR11 bacteria ‘that rule the waves’ (LD12). ISME J 5:1242–1252. https://doi.org/10.1038/ismej.2011.8

Schloss PD, Westcott SL, Ryabin T, Hall JR, Hartmann M, Hollister EB et al (2009) Introducing Mothur: open-source, platform-independent, community supported software for describing and comparing microbial communities. Appl Environ Microbiol 75:7537–7541. https://doi.org/10.1128/AEM.01541-09

Somogyi B, Felföldi T, Dinka M, Vörös L (2010) Periodic picophytoplankton predominance in a large, shallow alkaline lake (Lake Fertő, Neusiedlersee). Ann Limnol Int J Limnol 46:9–19. https://doi.org/10.1051/limn/2010001

Somogyi B, Tugyi N, Vörös L (2016) Fitoplankton szennézési dinamikája a Balatonban MTA ÖK BLI. Elektronikus folyóirata 3:16–26

Szabó M (1999) A Balaton vízgazdálkodási fejlesztési programja. Hidrológiai Közlöny 79(1):2–10

Szabó-Tugyi N, Vörös L, V-Balogh K, Botta-Dukát Z, Bernát G, Schmera D, Somogyi B (2019) Aerobic anoxicogenic phototrophs are highly abundant in hypertrophic and polyhumic waters. FEMS Microbiol Ecol 95(8):1–9. https://doi.org/10.1093/femslec/fiz104

Tindall BJ, Rosselló-Mora R, Busse HJ et al (2010) Notes on the characterization of prokaryote strains for taxonomic purposes. Int J Syst Evol Microbiol 60:249–266. https://doi.org/10.1099/ijys.0.016940-0

Tóth E (1995) A Balatonfüredi-öböl nyílt vize oligotróf baktérium és mahogányből alakult élőhelye az adatok alapján. Elektronikus folyóirata 3:16–26

Trung NT, Hien TTT, Huyen TTT et al (2015) Simple multiplex PCR assays to detect common pathogens and associated genes encoding for acquired extended spectrum betalactamases (ESBL) or carbapenemases from surgical site specimens in Vietnam. Ann Clin Microbiol Antimicrob 14(1):23. https://doi.org/10.1186/s12941-015-0079-z

Tsai HC, Chou MY, Shih YJ, Huang TY, Yang PY, Chiu YC, Chen JS, Hsu BM (2018) Distribution and genotyping of aquatic Acinetobacter baumannii strains isolated from the Puzi River and its tributaries near areas of livestock farming. Water 10:1374. https://doi.org/10.3390/w10101374

Warnecke F, Amann R, Pernthaler J (2004) Actinobacterial 16S rRNA genes from freshwater habitats cluster in four distinct lineages. Environ Microbiol 6(3):242–253. https://doi.org/10.1111/j.1462-2920.2004.00561.x

Wise MG, McArthur JV, Shimkets LJ (1997) Bacterial diversity of a Carolina bay as determined by 16S rRNA gene analysis: confirmation of novel taxa. Appl Environ Microbiol 63:1505–1514

Zmantar T, Kouhi B, Miladi H, Bakhrouf A (2011) Detection of macrolide and disinfectant resistance genes in clinical Staphylococcus aureus and coagulase-negative staphylococci. BMC Res Notes 4(1):453. https://doi.org/10.1186/1756-0500-4-453