



Photoautotrophic picoplankton – a review on their occurrence, role and diversity in Lake Balaton

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Abstract

Occurrence of the smallest phototrophic microorganisms (photoautotrophic picoplankton, APP) in Lake Balaton was discovered in the early 1980s. This triggered a series of systematic studies on APP and resulted in the setting of a unique long-term picoplankton dataset. In this review, we intend to summarize the obtained results and to give a new insight on APP ecology and diversity in Lake Balaton. According to the results, APP dynamics depends on trophic state, temperature, nutrient, and light availability, as well as grazing pressure. APP abundance in Lake Balaton decreased to a low level ($1\text{--}2 \times 10^5$ cells mL⁻¹) as a consequence of decreasing nutrient supply (oligotrophication) during the past more than two decades, and followed a characteristic seasonal dynamics with higher abundance values from spring to autumn than in winter. Concomitantly, however, the APP contribution to both phytoplankton biomass and primary production increased (up to 70% and 40–50%, respectively) during oligotrophication. Regarding annual pattern, picocyanobacteria are dominant from spring to autumn, while in winter, picoeukaryotes are the most abundant, most likely due to the different light and temperature optima of these groups. Within picocyanobacteria, single cells and microcolonies were both observed with mid-summer dominance of the latter which correlated well with the density of cladocerans. Community-level chromatic adaptation (i.e., dominance of phycoerythrin- or phycocyanin-rich forms) of planktonic picocyanobacteria was also found as a function of underwater light quality. Sequence analysis studies of APP in Lake Balaton revealed that both picocyanobacteria and picoeukaryotes represent a diverse and dynamic community consisting several freshwater genotypes (picocyanobacteria: *Synechococcus*, *Cyanobium*; picoeukaryotes: *Choricystis*, *Stichococcus*, *Mychonastes*, *Nannochloris*, and *Nannochloropsis*).

Keywords Picocyanobacteria · Picoeukaryotes · Abundance · Contribution · Primary production · Diversity

First years: discovery of photoautotrophic picoplankton in Lake Balaton

Photoautotrophic picoplankton' (APP)—smallest photosynthetic organisms in the size range of 0.2–2 or 3 μm —is a major fraction of the biomass of primary producers in many aquatic ecosystems, particularly in oligotrophic lakes

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and oceans (Platt et al. 1983; Stockner and Antia 1986). Its global incidence was discovered in the late 1970s and early 1980s in several parts of the world, such as in Hungary (Johnson and Sieburth 1979; Waterbury et al. 1979; Vörös 1987–1988; Vörös 1991; Vörös et al. 1991). In Lake Balaton, the abundance of APP was found higher by two orders of magnitude than that of nano- and microphytoplankton, which revealed that the dominant fraction of the phytoplankton community had been neglected previously (Vörös 1987–1988). This led to a paradigm shift and a series of thorough studies on picoplankton in Lake Balaton (Table S1).

Altogether, three types of picoalgal cells were found: yellow fluorescent, phycoerythrin-rich; red fluorescent, phycocyanin-rich picocyanobacteria; and red fluorescent, picoeukaryotic algae.

Abundance of picocyanobacteria (CyAPP) usually shows a bimodal pattern with abundance maxima in spring and

autumn and with lower abundances in summer when phytoplankton is dominated by filamentous N_2 -fixing cyanobacteria (Vörös 1991; Mózes et al. 2006). Picoeukaryotes (EuAPP) are present from autumn to spring and their biomass in winter is comparable to that of CyAPP in summer (Mózes et al. 2006; Vörös et al. 2009; Somogyi et al. 2016). Several studies have been performed to investigate the occurrence, role and diversity of APP in Lake Balaton and here we intend to summarize the main findings of those investigations. First, we provide a brief description on the physical and chemical environment in Lake Balaton, which largely determines the dynamics of APP.

Physical and chemical environment in Lake Balaton

Lake Balaton is the largest lake in Central Europe with a surface area of 596 km² and a mean depth of 3.2 m. The dominant ions in lake water are Ca^{2+} , Mg^{2+} , and HCO_3^- ; whose concentration also primarily determines the observed high conductivity (650–1050 $\mu S\ cm^{-1}$) and pH (7.5–9.5) values (Table 1, Herodek 1988). Water temperature of Lake Balaton ranges from 0 to 29 °C with an annual average of 15 °C (Table 1). In winter, the lake is usually covered by ice for 42 ± 27 days, but years without ice cover can also occur (Vörös et al. 2009) with increasing probability. There is a characteristic depth and trophic gradient along the longitudinal axis of the lake, which latter results in a higher algal biomass concentration in the western parts of the lake as compared to the eastern one (Felföldi et al. 2011a; Vörös

et al. 2009). The trophic gradient has been formed by the fact that River Zala, carrying approximately half of the water and nutrient supply of the lake (Herodek 1988) enters the westernmost point of the lake. Moreover, the depth and trophic gradient causes and coincides with significantly higher inorganic turbidity (total suspended solid, TSS) and colored dissolved organic matter (CDOM) concentration in the western parts of the lake as compared to the eastern one, which, in turn, results in different water transparencies (Table 1). As a consequence, the vertical light attenuation coefficient is higher in the western (ranges from 0.54 to 6.01 m^{-1} , annual mean: 2.1 m^{-1}) as compared to the eastern basin (0.35–4.87 m^{-1} , annual mean: 1.3 m^{-1}) (Table 1). Besides the decrease in the light penetration from the east to the west, the spectral composition of the underwater light is concomitantly also changes (Fig. S1). Selective light absorption of the dissolved, yellowish-brownish (humic) substances (which are a major portion of CDOM) and phytoplankton (which has the highest absorption in the blue region) together causes a ‘redshift’ of the available light, i.e., orange/red light dominance in the western basin, which light climate significantly differs from the green light dominated eastern basin (Fig. S1; Kirk 1994; Vörös et al. 1998; Balogh et al. 2000; Wetzel and Likens 2001; Kürthy et al. 2012).

The lake underwent a strong eutrophication during the 1970s–1990s: The external phosphorus load of the lake, supplied mainly by River Zala (see above), increased largely which led to a huge biomass increase of filamentous nitrogen-fixing (diazotrophic) cyanobacteria (Herodek 1979; Vörös and Nagy Göde 1993; Padisák and Szabó 1997). This highly eutrophic period was

Table 1 Physical and chemical characteristics of Lake Balaton as well as picoplankton abundance and composition between 2003 and 2018 (Re-analysis of data from Mózes et al. 2006; Vörös et al. 2009; Somogyi et al. 2016, 2017, expanded with unpublished results)

	Western basin			Eastern basin		
	Min	Max	Average	Min	Max	Average
WT (°C)	0	29	15	0	29	15
pH	7.48	9.37	8.47	7.90	9.48	8.55
EC ($\mu S\ cm^{-1}$)	647	855	749	698	1050	805
CDOM (mg Pt L ⁻¹)	6.50	45.94	17.17	0.63	11.54	4.44
TSS (mg L ⁻¹)	1.88	72.04	22.19	1.86	60.50	14.39
$K_{d\ PAR}$ (m^{-1})	0.54	6.01	2.10	0.35	4.97	1.31
Chl ($\mu g\ L^{-1}$)	1.89	61.13	14.24	0.85	20.73	5.16
PE CyAPP abundance ($10^3\ cells\ mL^{-1}$)	0	454	61	0	711	155
CyAPP abundance ($10^3\ cells\ mL^{-1}$)	2	956	234	0	773	197
col CyAPP abundance ($10^3\ cells\ mL^{-1}$)	0	374	49	0	576	42
EuAPP abundance ($10^3\ cells\ mL^{-1}$)	0	376	25	0	121	9
CyAPP biomass ($\mu g\ L^{-1}$)	1	501	123	0	405	103
EuAPP biomass ($\mu g\ L^{-1}$)	0	746	52	0	244	19

WT water temperature; EC electrical conductivity; CDOM colored dissolved organic matter; TSS total suspended solid; $K_{d\ PAR}$ vertical attenuation coefficient of photosynthetically active radiation (PAR, 400–700 nm); Chl Chlorophyll *a* concentration; PE CyAPP phycoerithrin-rich picocyanobacteria; CyAPP picocyanobacteria; col CyAPP colonial forms of picocyanobacteria; EuAPP picoeukaryotes

characterized by peak chlorophyll *a* (Chl) concentration of up to 200–260 $\mu\text{g L}^{-1}$ in the western basin, where it was lasted until mid-1990s (Fig. 1). In the eastern basin, the eutrophication began later and had a lower magnitude with peak chlorophyll *a* concentrations of 30–90 $\mu\text{g L}^{-1}$ (Fig. 1). By the period of 2013–2018, the lake returned to its meso-eutrophic character with summer chlorophyll *a* maxima of 30–40 $\mu\text{g L}^{-1}$ and 5–10 $\mu\text{g L}^{-1}$ in the western and eastern basins, respectively (Fig. 1). Similarly to the pattern of APP abundance (see above), the overall density of phytoplankton biomass also often shows a bimodal annual pattern with a lower spring peak, attributed to diatoms, and a higher summer peak, due to filamentous diazotrophic cyanobacteria and/or planktonic dinoflagellates. This seasonality is usually much more prominent in the western basin as compared to the eastern one. In winter, phytoplankton is usually dominated by EuAPP, small

flagellates and green algae (Vörös et al. 2009; Dokulil et al. 2014; Somogyi et al. 2016; Bullerjahn et al. 2019).

Abundance of APP in Lake Balaton

The occurrence and dynamics of APP in aquatic ecosystems is controlled by both bottom-up and top-down processes (Callieri 2008; Raven et al. 2005 and references therein). For this reason, their abundance and biomass density varies in a wide range among different water types. In Lake Balaton, APP abundance and biomass density have been changing considerably both along the longitudinal axis of the lake and over the years due to variations in trophic level. Highest abundance values were observed during the highly eutrophic period in the western basin (Fig. 2). In parallel with the oligotrophication, the APP abundance decreased continuously

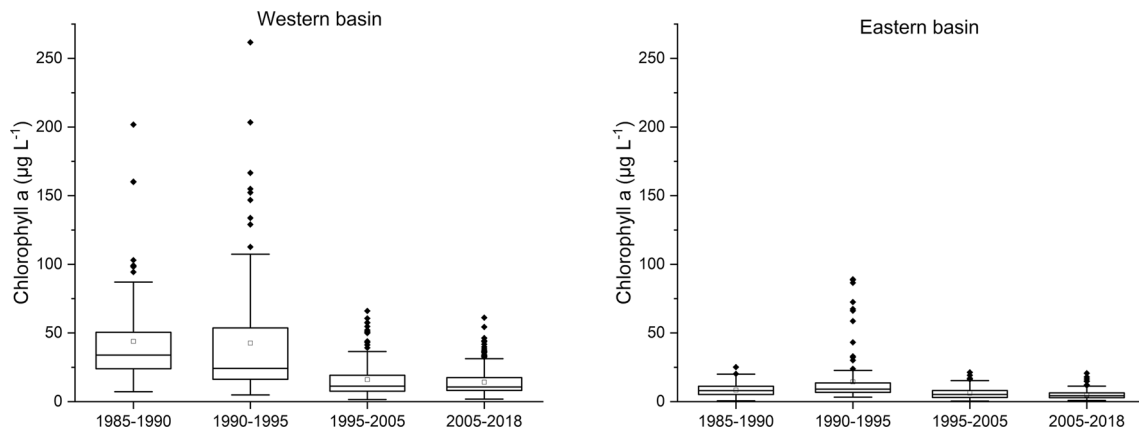


Fig. 1 Chlorophyll *a* concentration in Lake Balaton between 1985 and 2018. (Re-analysis of data from Vörös and Nagy Göde 1993; Padišák and Szabó 1997; Vörös et al. 2009; Somogyi et al. 2017, completed with unpublished results). The plotted rectangles represent

the 25th to 75th percentiles of individual measurements while the lines across the rectangles represents the median. Outliers are marked with black diamonds and mean values with squares

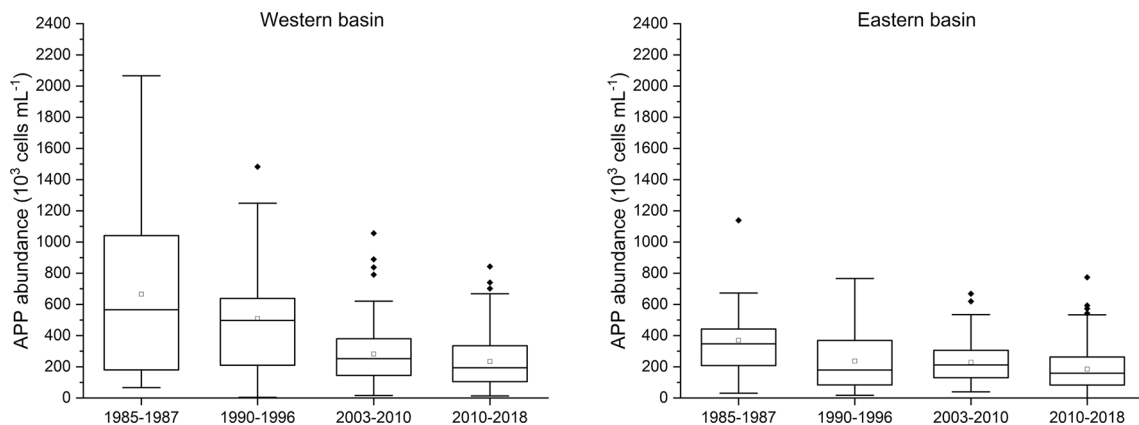


Fig. 2 Picoplankton (APP) abundance in Lake Balaton (Re-analysis of data from Vörös 1987–1988; Vörös et al. 1991, 2009; Mózes et al. 2006; Somogyi et al. 2017, completed with unpublished results). Marking as in Fig. 1

during the subsequent period in both basins. By the period of 2010–2018, the APP abundance reduced approximately to one-third in the western basin and to approximately half in the Eastern basin as compared to that of in the 1985–1987 period (Fig. 2, Table 1).

The decrease in APP abundance with decreasing nutrient supply is a well-documented phenomenon. Its usual values ranges from 10^2 to 10^4 cells mL^{-1} in oligotrophic waters, while much higher values (10^4 – 10^6 cells mL^{-1}) was observed in eutrophic systems (Stockner and Antia 1986; Burns and Stockner 1991; Stockner and Shortreed 1991; Weisse 1993; Szelag-Wasielewska 1997). Both temporal (long-term) and spatial changes in APP abundance of Lake Balaton fits well with other results and emphasize the fundamental role of nutrient supply on APP dynamics. Besides long-term changes, as stated above, APP follows also a characteristic seasonal dynamics in Lake Balaton with higher abundance values from spring to autumn as compared to winter season (Fig. S2). The only exception to trend is when the nanoplankton fraction in the summer period is dominated by filamentous diazotrophic cyanobacteria. In summer, filamentous N_2 -fixing cyanobacteria can outcompete other taxonomic groups including CyAPP and EuAPP, suggesting a possible nitrogen limitation of phytoplankton in Lake Balaton (Présing et al. 2001; Vörös et al. 2009).

APP contribution to phytoplankton biomass in Lake Balaton

APP contributes significantly (up to 70%) to phytoplankton biomass in Lake Balaton. However, this contribution follows an opposite trend than that of the abundance: It increases from the west to the east along the longitudinal axis (and parallel with decreasing trophic level) of the lake (Fig. 3). The reason of this paradox is the better nutrient supply of

the western part, which affects not only the picoplankton fraction but also the nano- and microplankton. During warm periods, filamentous diazotrophic cyanobacteria seems to have a competitive advantage over CyAPP. Hence, the most likely explanation for low summer contribution of CyAPP observed in many freshwater lakes is that they are nitrogen limited (Vörös et al. 2009). In marine environments, CyAPP were shown to fix atmospheric nitrogen (Rippka et al. 1979), but in freshwaters it has not been detected yet (Postius and Böger 1998; Présing et al. 2001). During the highly eutrophic 1985–1996 period, APP mean contribution was about 7% (ranging from 0.2 to 24%) and 13% (ranging from 1.5 to 40%) in the western and eastern basin, respectively (Fig. 3). In parallel with the subsequent oligotrophication, this contribution increased significantly: to 14% (ranging between 0 and 73%) and to 19% (ranging between 0 and 70%) in the western and eastern basin, respectively (Fig. 3). This clearly shows that APP contribution in Lake Balaton largely depends on the actual trophic state and increases with decreasing phytoplankton biomass (Fig. S3). This is in good agreement with previous findings in other aquatic ecosystems (Stockner and Antia 1986; Stockner 1991; Callieri and Stockner 2002; Szelag-Wasielewska 1997).

The above discussed observations were confirmed by the quantitative regression models of Bell and Kalff (2001), which well describes the relationship between AAP contribution and total phytoplankton biomass (expressed as chlorophyll *a* concentration) in both freshwater and marine ecosystems. The slope and intercept of such empirical relationship for Lake Balaton ($\log \text{APP}\% = 1.71 - 0.83 \log [\text{Chl}]$; Fig. S3) were somewhat different from the one determined by Bell and Kalff (2001) for freshwater environments (i.e., $\log \text{APP}\% = 1.56 - 0.53 \log [\text{Chl}]$). This difference, however, could arise from system morphometry, i.e., the freshwater environments studied by Bell and Kalff (2001) were mainly deep lakes with much lower inorganic turbidity than Lake

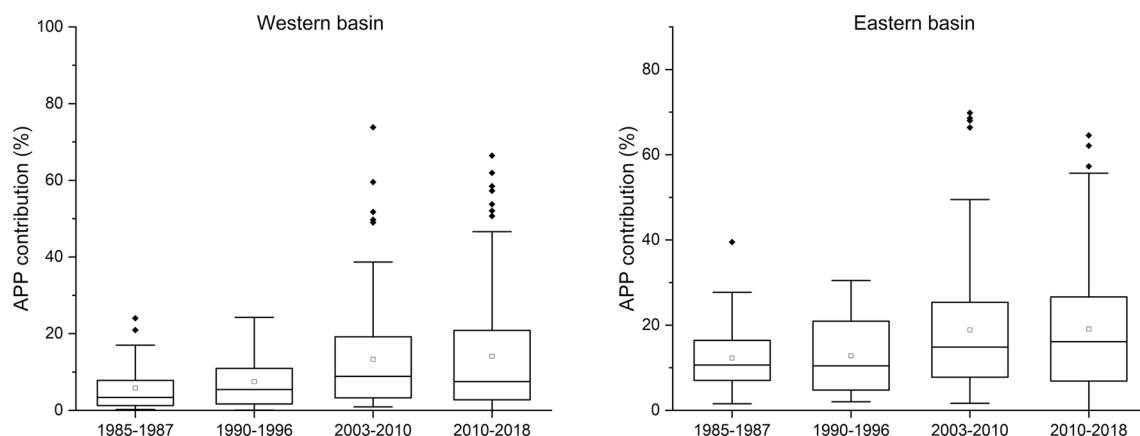


Fig. 3 Picoplankton (APP) contribution to total phytoplankton biomass in Lake Balaton (Re-analysis of data from Vörös 1987–1988; Vörös et al. 1991, 2009; Mózes et al. 2006; Somogyi et al. 2017, completed with unpublished results). Marking as in Fig. 1

Balaton. According to our previous findings, inorganic turbidity has a significant influence on APP contribution, resulting in higher values as compared to other freshwater lakes with the same total phytoplankton biomass (Somogyi et al. 2017). This higher contribution in turbid waters might be a consequence of lower underwater light intensities and/or reduced grazing pressure (Somogyi et al. 2017).

Primary production of APP in Lake Balaton

The contribution of APP to total phytoplankton primary production can be as high as or even exceed their biomass contribution, particularly in oligotrophic environments. Global estimates indicate that these microorganisms provide 39% of the planktonic primary production in the world's ocean: APP dominates phytoplankton biomass and production in nutrient-poor, warm (> 26 °C) waters, but it represents only a minor fraction in nutrient-rich and cold (< 3 °C) waters (Agawin et al. 2000). Despite the fact that the APP contribution could be as high as in marine waters, much less information is available for freshwater lakes (Bell and Kalff 2001). Primary production of the picoplankton in Lake Balaton, was determined in 1986, in 2005, in 2009 and additionally in winter of 2009–2014 (Vörös 1991; Somogyi and Vörös 2006; Somogyi et al. 2016). In general, summer rates were usually higher than those in spring and autumn (with the exception of a formation of a filamentous cyanobacterial bloom in the western basin), and the winter rates were considerably lower (Somogyi et al. 2016).

During the highly eutrophic 1985–1996 period, the contribution of APP to primary production varied between 43 and 56% in the less productive eastern basin and between 1 and 57% in the western basin (Vörös 1991). In the western basin, a strong seasonal trend was also observed with a minimum APP contribution of 1% during a summer bloom of filamentous diazotrophic nitrogen-fixing cyanobacteria. During the next two decades, the summer contribution of APP in primary production increased to 23–32% in this basin. In contrast, the more oligotrophic eastern basin, such contribution was constantly high, ranging from 24 to 54% (Somogyi and Vörös 2006; Somogyi et al. 2016). Thus, similarly to the contribution of APP to phytoplankton biomass, a strong increasing trend of APP contribution to primary production was also found with decreasing total phytoplankton biomass (Fig. S4). In winter the basin-dependent difference in APP contribution to primary production was abolished: It ranged between 16 and 41% in the western basin and between 13 and 46% in the eastern basin (Somogyi et al. 2016). Nevertheless, these values do not differ much from summer one, suggesting that trophic state has higher impact on APP contribution to primary

production than seasonality per se, in good agreement with literature data on aquatic ecosystems (Stockner 1991; Bell and Kalff 2001; Callieri 2008).

Morphotypes (single cells vs. colony forming) of planktonic picocyanobacteria in Lake Balaton

In aquatic environments, CyAPP exist either as single cells with different morphologies (cocci, rods, etc.) or form colonies (Stockner et al. 2000). Such microcolonies comprise a few to > 50 individual cells (Callieri 2008 and references therein). In Lake Balaton, microcolonies of both phycoerythrin-rich and phycocyanin-rich CyAPP were found (Vörös et al. 1991; Mózes et al. 2006; Felföldi et al. 2011a): Colonial forms are dominant in mid-summer, while from autumn to early summer, mainly single cells are present (Fig. S5). Several studies suggest that colonies could be more resistant against zooplankton grazing than individual cells (Stockner et al. 2000; Crosbie et al. 2003; Callieri et al. 2016). Microcolony formation, favoured by the formation of 'spinae' on the cell surface, thus, might be a defense strategy against grazing (Komárková 2002; Jezberová and Komárková 2007; Callieri et al. 2016). Microcolonies are also surrounded by a mucilaginous polysaccharide sheet, which, besides increasing the size of the colony, could provide additional protection (Pernthaler 2005). Microcolony formation of CyAPP under grazing pressure was also confirmed by laboratory experiments (Komárková and Šimek 2003; Callieri et al. 2016). Interestingly, predation pressure provokes strain-selective responses of CyAPP, possibly because of different cell characteristics (cellular size; ability to synthesize exopolysaccharides; Callieri et al. 2016). Yet, it should be noted that although colony formation can prevent grazing by small-sized grazers (e.g., nanoflagellates, ciliates, small rotifers), microcolonies might be grazed more efficiently by larger-sized zooplankton (e.g., cladocerans, copepods) than single cells (Pernthaler and Amann 2005; Callieri et al. 2016). In Lake Balaton, abundance of colonial CyAPP shows a tight positive correlation with the abundance of Cladocera (Fig. 4, Fig. S6). Enclosure experiments also showed that cladoceran grazing can effectively control picoplankton growth in Lake Balaton; however, in that study, colonial forms were not distinguished from single cells (Vörös et al. 1991).

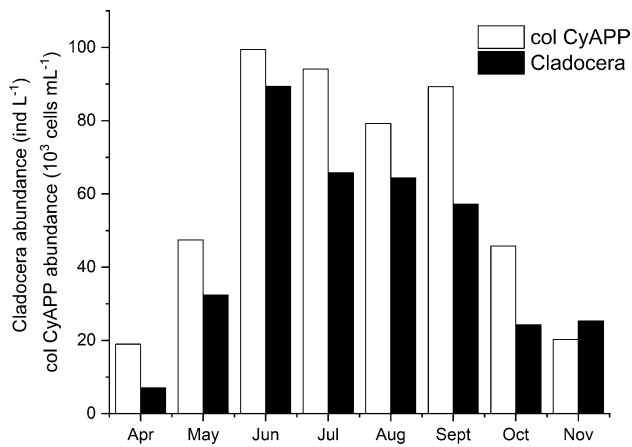


Fig. 4 Multiannual monthly averages of colonial picocyanobacteria (col CyAPP) and Cladocera between 2005 and 2015 (Re-analysis of data from Vörös et al. 2009 and Somogyi et al. 2017, completed with unpublished results)

Community-level chromatic adaptation of planktonic picocyanobacteria in Lake Balaton

CyAPP contains either phycoerythrin or phycocyanin (PE and PC, respectively) as major light harvesting phycobiliproteins (Callieri 2008, 2017 and references therein). In Lake Balaton, both PE-rich and PC-rich CyAPP are present, however, their distribution changes largely along the longitudinal axis of the lake (Vörös 1991; Vörös et al. 1998, 2009; Mózes 2008; Mózes et al. 2006; Felföldi et al. 2011a). In the western basin, PC-rich cyanobacteria predominate, constituting about 75% of the total CyAPP. In contrast, PE-rich CyAPP are dominant in the eastern basin, where their mean contribution is about 80% (Table 1, Fig. 5). The abundance ratio of

PE/PC-rich CyAPP decreases sharply with increasing phytoplankton biomass: under $\sim 12 \mu\text{g L}^{-1}$ chlorophyll *a* concentration PE-rich forms prevail, while above that threshold, PC-rich forms dominate (Fig. S7). Similar trends were found in various other aquatic ecosystems (Pick and Agbeti 1991; Stockner 1991; Callieri 2008). Picocyanobacterial pigment composition reflects the underwater light environment: The “redshift” of the available light in turbid environments (e.g., as shown for the western basin of Lake Balaton in Fig. S1) provides selective advantage for those cyanobacteria, which preferentially absorb orange-red light ($\sim 625 \text{ nm}$) due to their high PC content. In contrast, PE-rich CyAPP, which effectively absorb green light ($\sim 560 \text{ nm}$), prevail in clear lakes and oceans (as well as in the eastern basin of Lake Balaton), where the underwater light is dominated green color (Fig. S1; Calieri et al. 1996; Vörös et al. 1998; Camacho et al. 2003, Stomp et al. 2004, 2007; Katano et al. 2008; Haverkamp et al. 2009; Frenette et al. 2012). Laboratory experiments demonstrated that using mixed cultures, PE-rich and PC-rich CyAPP predominate under growing green and orange/red light, respectively. However, when they are grown together under white light, they can coexist, absorbing different parts of the light spectrum (Calieri et al. 1996; Stomp et al. 2004; 2007a).

Diversity of planktonic picocyanobacteria in Lake Balaton

Due to the lack of distinguishing morphological features, members of APP could taxonomically be identified by DNA sequence analysis. For prokaryotes, the most widely used marker is the 16S rRNA gene (Felföldi et al. 2011b; Callieri et al. 2013; Callieri 2017), which is also present in

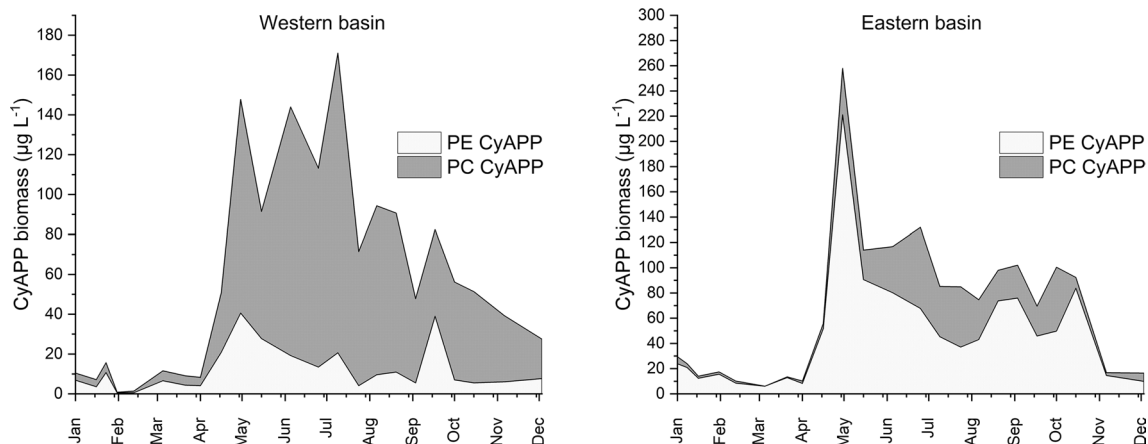


Fig. 5 Biomass of phycoerythrin-rich (PE) and phycocyanin-rich (PC) picocyanobacteria in Lake Balaton in 2011 (Re-analysis of data from Kürthy et al. 2012)

chloroplasts, therefore, could also be used for the identification of eukaryotic algae (e.g., Fuller et al. 2006).

Various PC- and PE-rich picocyanobacterial strains have previously been isolated from Lake Balaton, which belong to Group A (*Cyanobium gracile* cluster) and Group B (sub-alpine cluster D), respectively, of the non-marine lineages of the picophytoplankton clade sensu Urbach et al. (1998) (Fig. 6; Felföldi et al. 2011a, b). These two groups are among the most common genotypes of freshwater picocyanobacteria distributed worldwide in diverse types of lakes and ponds (e.g., Crosbie et al. 2003; Callieri et al. 2013; Huang et al. 2014; Vasileva et al. 2017).

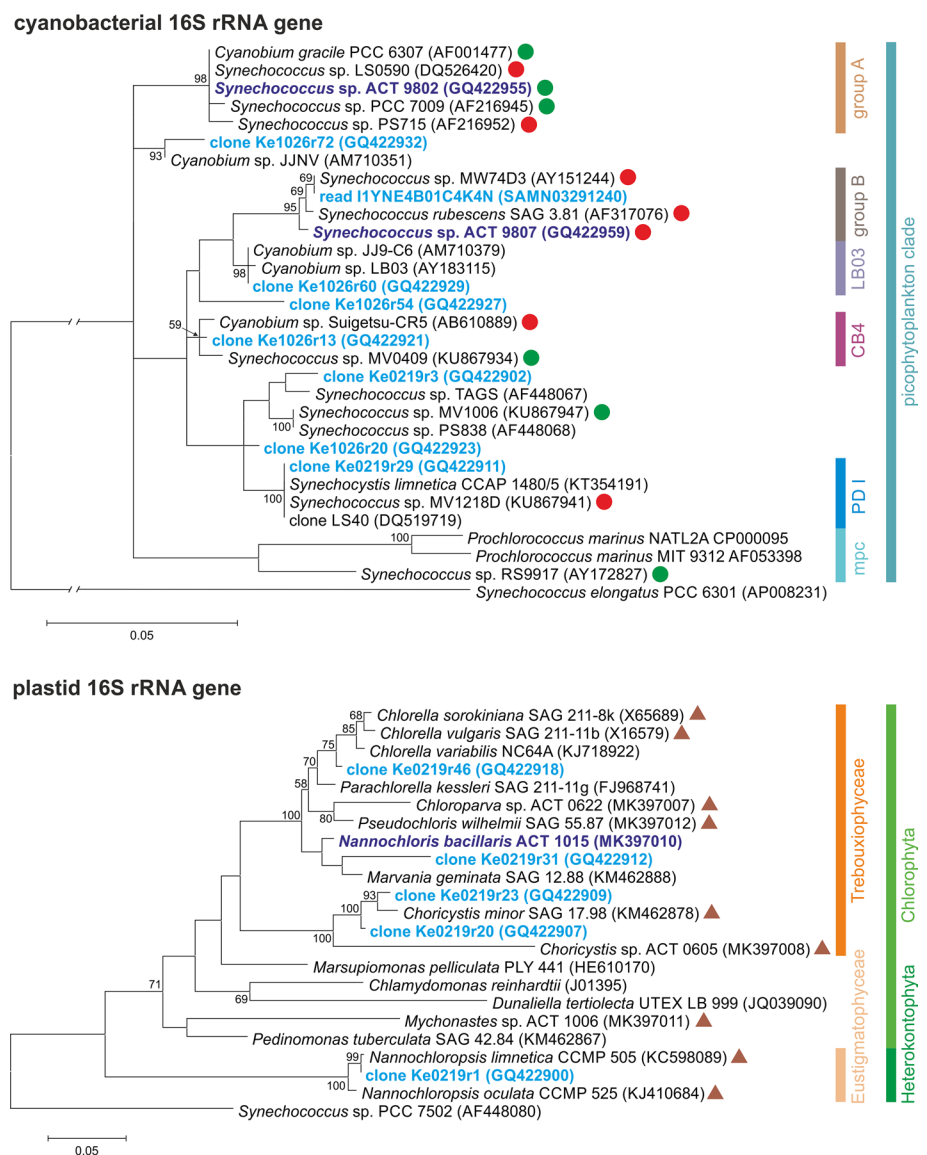
Phylogenetic analysis of uncultured sequences revealed the occurrence of several other picocyanobacterial groups (e.g., PD1, CB4, LB03) in Lake Balaton (Fig. 7). The relative abundance of the detected genotypes was basin-dependent, pronounced seasonal changes were also observed.

According to the data, their abundance was primarily determined by temperature and availability of nitrogen forms (Felföldi et al. 2011a), however, other abiotic and biotic factors such as orthophosphate concentration, viral lysis, etc. (Becker et al. 2007; Mühling et al. 2005) may have also significant impact on it. In summary, planktonic picocyanobacteria in Lake Balaton represent a diverse and dynamic community, consisting of various genotypes of freshwater *Synechococcus* and *Cyanobium*.

APP in wintertime: dominance of picoeukaryotes in Lake Balaton

Occurrence of picoeukaryotic algae in Lake Balaton was first time observed in winter 2003 (Mózes and Vörös 2004; Mózes et al. 2006). From that time, APP studies have been

Fig. 6 Maximum likelihood phylogenetic trees of picoalgal strains and the most abundant uncultured planktonic genotypes from Lake Balaton based on 16S rRNA gene sequences. Re-analysis of sequence data from Felföldi et al. (2011a), Somogyi et al. (2016) and Borsodi et al. (2017). Uncultured genotypes were retrieved from samples collected in February 2003, October 2005 and June 2013. The cyanobacterial phylogenetic tree is based on 584, the plastid tree is based on 568 nucleotide positions, and in both cases the Kimura 2-parameter substitution model was applied. For methodological details of phylogenetic tree construction, see Kalwasińska et al. (2017). GenBank and Sequence Read Archive codes are given in parentheses. Bootstrap values higher than 50 are shown at the nodes. Lake Balaton strains are highlighted with purple and uncultured genotypes with light blue letters. Phycoerythrin-rich picocyanobacteria are marked with red, phycocyanin-rich picocyanobacteria with green circles, while eukaryotic algal species having cells smaller than 3 µm are marked with brown triangles. Cluster designation of picocyanobacteria follows the nomenclature of Crosbie et al. (2003), Chen et al. (2006) and Ivanikova et al. (2007). *Abbreviation: mpc* marine picophytoplankton clade



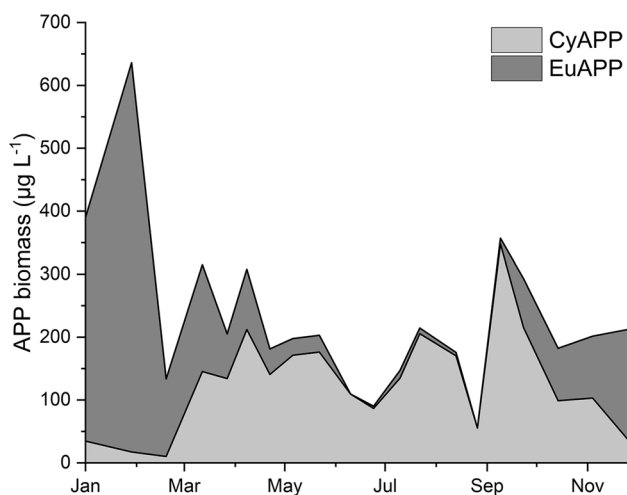


Fig. 7 Biomass of picocyanobacteria (CyAPP) and picoeukaryotes (EuAPP) in the western Basin of Lake Balaton in 2012 (Re-analysis of data from Somogyi et al. 2016)

extended to the winter season, which revealed a characteristic seasonal dynamics of APP (Vörös et al. 2009; Somogyi et al. 2012, 2016). In regards of CyAPP, their minimum biomass is usually found in winter, follows by an increase in spring and maxima are recorded in summer or in the beginning of autumn (Fig. 7; Vörös et al. 2009). In both basins, positive relationship was described between temperature and CyAPP abundance (Vörös et al. 2009), which is a general phenomenon in both marine and freshwater environments (Waterbury et al. 1986; Malinsky-Rushansky et al. 1995; Stockner et al. 2000; Callieri and Stockner 2002).

The annual pattern for picoeukaryotes (EuAPP) shows an opposite trend, i.e., starts to grow in autumn and attained its maxima in late winter or early spring, irrespective of the presence or absence of ice cover (Fig. 7; Vörös et al. 2009). In summer, EuAPP is almost undetectable (Fig. 7). The abundance of picoeukaryotes is much higher in the eutrophic western basin than in the mesotrophic eastern one (Table 1). The highest EuAPP abundances are found below 8 °C, and they became negligible above 15 °C (Fig. S8). The contribution of CyAPP and picoeukaryotes to the total picoplankton biomass also depends on water temperature: EuAPP contribution is high above 10 °C (Fig. S8). Thus, the seasonal pattern of EuAPP is similar in the shallow Lake Balaton to larger deep lakes, with a single population peak in spring or early summer (Stockner et al. 2000).

EuAPP and CyAPP cells are considerably different in terms of phylogeny, structure, and physiology. The winter and summer predominance of EuAPP and CyAPP, respectively, reflect the different light- and temperature optima of these microorganisms. EuAPP has competitive advantage over CyAPP under conditions characterized by low light and temperature, as was also observed at harsh polar

environments (Pálffy et al. 2014; Metfies et al. 2016). In general, EuAPP cells have a lower light demands as compared to CyAPP cells, although the latter group also includes low-light-adapted microorganisms (Callieri 2008). In the Pacific Ocean, for instance, CyAPP contribute more to the picoplankton productivity in the lower regions (1–7% of the surface irradiance) of the euphotic zone than in the well-lit region (> 15% of the surface irradiance) (Rii et al. 2016). In Lake Balaton, EuAPP-dominated winter communities have much lower light demands, than the CyAPP-dominated summer communities (Somogyi et al. 2016). Determination of the photosynthetic activities of CyAPP and EuAPP strains confirmed the crucial role of light and temperature in the seasonal dynamics of picophytoplankton: In agreement with field data, ca. 15 °C appeared to be the key temperature below which the maximum photosynthetic rate (P_{max}) and light utilization parameter (α) of the EuAPP strains exceeded that of the CyAPP strains (Somogyi et al. 2009).

In summary, key factors controlling the abundance of picoeukaryotes differ from those ones controlling CyAPP (Vörös et al. 2009). Importantly, during the cold-water period, when both water temperature and irradiance are appropriate for picoeukaryotes, the concentrations of available nitrogen and phosphorus are the highest in Lake Balaton (Présing et al. 2001; Vörös et al. 2009). On the other hand, in summer, when both water temperature and irradiance are optimal for CyAPP, nitrogen limitation can occur (Vörös et al. 2009).

Diversity of eukaryotic picoalgae in Lake Balaton

Although the bacterial 16S rRNA gene is present in the chloroplast (see above), due to the limited number of available reference sequences, taxonomic identification of eukaryotic algae is usually carried out by the sequence analysis of the 18S rRNA gene, which latter provides limited resolution at distinguishing closely related species (Krienitz and Bock 2012).

The taxonomic composition of the picoeukaryotic phytoplankton community in Lake Balaton is similar to those in other freshwater lakes in the temperate zone. Isolated strains from Lake Balaton all belong to Chlorophyta and were taxonomically identified as *Choricystis* sp., *Stichococcus bacillaris*, *Nannochloris bacillaris*, and *Mychonastes* sp. (Somogyi et al. 2016), which corresponds well with previous findings showing green algal dominance in freshwater picoplankton. Community-level DNA-based studies of the phytoplankton community in Lake Balaton also suggests the dominance of chlorophytes within eukaryotic APP (Felföldi et al. 2011a, Fig. 7). The majority of the isolates were identified as members of the genus *Choricystis* (Somogyi et al.

2016), which is widely distributed in freshwater lakes in Europe, Asia and North-America (Belykh et al. 2000; Fawley et al. 2004; Hepperle and Krienitz 2001; Hepperle and Schlegel 2002). Members of the *Mychonastes* clade, which were also isolated from Lake Balaton, are also reported from various lakes worldwide (Hepperle and Krienitz 2001; Hepperle and Schlegel 2002; Krienitz et al. 1999; Fawley et al. 2004; Hanagata et al. 1999; Shi et al. 2019).

Interestingly, the heterokontophyte pico-sized green alga *Nannochloropsis* was also detected in Lake Balaton (Fig. 7). Members of this genus were identified from different freshwater and saline aquatic ecosystems (Krienitz et al. 2000; Suda et al. 2002; Karlov et al. 2017), and the diverse isolation source of sequences having > 99% nucleotide similarity to the clone retrieved from Lake Balaton (based on a GenBank search; jelly-like biofilm, Lake Baikal; sediment, West Lake Bonney, Antarctica; Nam Co Lake, China; winter hospital shower water, USA; Wanigawa River, Japan; freshwater, Baffin Island, Canada) suggests the high adaptation potential and widespread distribution of this uncommon member of APP.

Taken together the results of cultivation and culture-independent studies, it seems that *Choricystis* is the most abundant genus in Lake Balaton within eukaryotic APP, while the occurrence of members of genera *Stichococcus*, *Mychonastes*, *Nannochloris*, *Nannochloropsis* (and also some unidentified taxonomic groups) are also proven (Fig. 7). Apparently, many of the above-mentioned genera (e.g., *Choricystis*, *Mychonastes* and *Stichococcus*) isolated from Lake Balaton may contain oil droplets (Vörös et al. 2009; Wu et al. 2015; Selvarajan et al. 2016; Chen et al. 2017), which suggests their role as a valuable food source for heterotrophic flagellates and mesozooplankton on one hand and potential use of them in future biotechnological applications.

Conclusions for future biology

Picophytoplankton forms the base of the food web in most aquatic ecosystems. Essential role of APP in Lake Balaton was also clearly demonstrated, based on the analysis of a long-term phytoplankton dataset, covering the period from mid-1980s to the present. The overview provided by this review may help to understand better the role and diversity of APP and to identify the main drivers of their dynamics. Future studies should focus on the impact of global changes, i.e., how climate change will presumably affect their physiology, genetic diversity, as well as population dynamics, and, more generally, their exact ecological role in Lake Balaton. Addressing these questions is not simple: It has just been demonstrated that APP can answer positively (with elevated biomass values) to ocean warming (Flombaum et al. 2020).

As a result, warmer conditions can lead to elevated phytoplankton biomass in oceanic regions that are already dominated by APP, which contradicts to previous findings on worldwide declining phytoplankton biomass. This, together with niche partitioning of APP communities according to light and temperature gradients, will, expectedly lead to an altered genetic diversity.

Exploring the factors affecting APP dynamics is of major importance, as APP is the main primary producer in most of marine and freshwater environments and it is the key element of all aquatic food webs. In case of Lake Balaton, grazing is suggested to further studies influencing APP dynamics as bottom-up control is widely studied. Feeding experiments with natural lake water communities and algal isolates may provide novel data on the effect of grazing on the phytoplankton community with special attention to APP. Metagenomics of the gut content may serve further information on the feeding behavior of various zooplankton taxa. Allelopathic defense mechanisms of APP against grazer attack have also been poorly studied.

Another intriguing, yet understudied issue is the role of picoalgae on surface habitats, i.e., on sediment surface, lakeshore underwater surfaces, ice cover in winter, etc. in Lake Balaton. Moreover, to understand better the remarkable seasonal dynamics of APP in Lake Balaton, exploring the dormant forms of the APP cells will also be of interest.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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