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PhD thesis

**The significance of picoeukaryotic algae in shallow lakes: winter dominance
and taxonomic uniqueness**

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Balaton Limnological Research Institute of the Hungarian Academy of Sciences,

Tihany

2010

Introduction

The autotrophic picoplankton is a size classification, which comprises small ($<2\ \mu\text{m}$) prokaryotic picocyanobacteria and eukaryotic phototrophs (Stockner & Antia, 1986). Its widespread incidence was discovered in the late seventies and early eighties in several parts of the world, including Hungary (Johnson & Sieburth 1979; Waterbury *et al.*, 1979; Vörös, 1987-88; Vörös, 1991). It was soon established that pico-sized algae contribute significantly to planktonic primary production in oligotrophic oceans ($>90\%$) and can also play an important role in more productive aquatic environments (Platt *et al.*, 1983; Stockner & Antia, 1986). In Lake Balaton (Hungary), picoalgae provide more than 50% of the total planktonic primary production in the summer; their winter contribution is, however, not known (Vörös *et al.*, 1991; Somogyi & Vörös, 2006). The small size and simple morphology of picoalgae make their identification impossible by traditional microscopic methods, which left their taxonomic position unknown for a long time. Recent culture-based and culture-independent molecular taxonomic methods have allowed their reliable identification (Callieri, 2008; Vaultot *et al.*, 2008). As early studies had focused exclusively on the summer period, the fact that autotrophic picoplankton show characteristic seasonal dynamics was only later observed. Studies demonstrate that in the temperate zone picocyanobacteria dominate the picoplankton in the summer, while picoeukaryotes are dominant from autumn to spring (Pick & Agbeti, 1991; Malinsky-Rushansky *et al.*, 1995). The reasons for the seasonal dynamics, however, are not known entirely. Furthermore, the eukaryotic component of picophytoplankton has received much less attention than picocyanobacteria in fresh waters (Callieri, 2008; Vaultot *et al.*, 2008). New researches have revealed that picoeukaryotic algae belong to several different taxonomic groups despite their morphological similarity. In open oceans picoeukaryotes belong to Chlorophyta, Cryptophyta, Haptophyta and Heterokontophyta (Vaultot *et al.*, 2008). In fresh waters and saline lakes, the diversity of picoeukaryotic algal assemblages is scarcely known; the majority of the studied picoeukaryotes belong to Chlorophyta (Callieri, 2008). The existence of rich picophytoplankton communities dominated by picoeukaryotes was observed during the ice cover in Lake Balaton in winter 2003 (Mózes *et al.*, 2006). The winter picoalgae of other Hungarian shallow lakes have not been studied yet, even though the picophytoplankton-rich turbid soda lakes, which are unique in the European Union, are characteristic of Hungary (Vörös *et al.*, 2005).

Aims

The overall objective of the work was to investigate and determine the occurrence, ecology and taxonomy of picoeukaryotic algae in shallow lakes.

The detailed goals were the following:

1. To determine the occurrence and seasonal dynamics of picoeukaryotic algae in Lake Balaton (Hungary), in Lake Fertő/Neusiedlersee (between Hungary and Austria) and in shallow turbid soda pans in the Danube-Tisza Interfluvium (Hungary) with special respect to the winter.
2. To determine the influence of light and temperature on the observed seasonal dynamics by means of field measurements and laboratory experiments.
3. To determine the contribution of winter picoplankton to the total planktonic primary production in Lake Balaton and in Lake Fertő/Neusiedlersee.
4. To get information about the diversity of picoeukaryotic algal assemblages in Hungarian soda pans.

Materials and methods

The quantitative and qualitative investigation of autotrophic picoplankton was carried out biweekly in Lake Balaton between 2006 and 2010, monthly/bimonthly in soda pans in the Danube-Tisza Interfluvium between 2006 and 2007, bimonthly in 2004 and biweekly between 2008 and 2009 in Lake Fertő/Neusiedlersee. Water temperature, pH, conductivity and underwater light (Secchi-disk transparency or vertical attenuation coefficient) were measured at every sampling station and date. The chlorophyll *a* concentration in Lake Balaton and Lake Fertő was determined spectrophotometrically according to Németh (1998) and in soda pans spectrophotometrically according to Wetzel & Likens (2001). The abundance and composition of autotrophic picoplankton was determined by epifluorescence microscopy (MacIsaac & Stockner, 1993).

The contribution of the autotrophic picoplankton to total planktonic photosynthesis was determined using the ^{14}C method (Steemann-Nielsen 1952). The photosynthesis-irradiance (P-I) curves of picoplankton, nanoplankton and total phytoplankton were fitted with the model of Eilers & Peeters (1988) to obtain the photosynthetic parameters (P_{\max} , I_k , α and I_{opt}). The daily, surface related primary production of the different size fractions ($<3 \mu\text{m}$

and $>3 \mu\text{m}$) of phytoplankton were estimated based on the experimentally obtained P-I curves, daily global radiation, vertical attenuation coefficient and water depth.

Picoeukaryotic algal strains were isolated from Zab-szék pan, Böddi-szék pan and Büdös-szék pan by serial streaking on agar plates and single colony isolations. For maintenance, the cultures were kept in a modified BG11 medium, at 21°C and $60 \mu\text{mol m}^{-2} \text{sec}^{-1}$ on a 10: 14 hour dark: light cycle (Rippka *et al.*, 1979). Molecular phylogenetic identification of the strains was carried out based on their 18S rDNA sequences using universal primers (Moon-van der Stay *et al.*, 2000; Yamamoto *et al.*, 2003). Strains ACT 0604, ACT 0605, ACT 0606, ACT 0607, ACT 0610, ACT 0621, ACT 0901 and ACT 0902 were also analysed based on their *rbcL* gene sequences according to Fawley *et al.* (2005). A detailed morphological analysis of strain ACT 0608 was done by scanning and transmission electron microscopy.

To clarify the role of light and temperature in the seasonal dynamics of picophytoplankton, photosynthesis measurements of one picoeukaryotic (ACT 0608) and one picocyanobacterial (ACT 0616) strain were carried out between $7 - 30^\circ\text{C}$ under various irradiance conditions ($5-1280 \mu\text{mol m}^{-2} \text{sec}^{-1}$) by light-dark bottle oxygen method.

Results and Discussion

1.a. We have found, that the seasonal dynamics of autotrophic picoplankton in Lake Balaton show an annual regular pattern, which reinforces earlier results concerning this and other lakes in the temperate zone.

During the study period (2006-2010), autotrophic picoplankton was composed by picocyanobacteria showing phycoerythrin or phycocyanin pigment dominance and picoeukaryotic algae in Lake Balaton. The same seasonal dynamics was observed in both lake basins (Keszthely and Siófok basin): the dominance of picocyanobacteria in the summer and that of picoeukaryotes in the winter. The contribution of picoeukaryotic algae to the biomass of the total picoplankton was, however, higher in the Keszthely basin than in the Siófok basin. Besides their opposite seasonal dynamics, the main difference between the two groups was that picoeukaryotes disappeared totally in the summer, while picocyanobacteria were present also in the winter, although with lower abundances.

1.b. The autotrophic picoplankton of turbid soda pans in the Danube-Tisza Interfluve showed a seasonal dynamics characteristic to lakes in the temperate zone: summer dominance of picocyanobacteria and winter dominance of picoeukaryotes. The abundance maximum of picoeukaryotes (10^8 cells ml⁻¹) in winter 2006-2007 was the highest ever found in an aquatic environment.

The autotrophic picoplankton showed similar seasonal dynamics to Lake Balaton: picocyanobacteria dominated in all pans in July 2006, picoeukaryotes became dominant in the autumn, and no picocyanobacteria were found in the winter. The picoeukaryotes reached their abundance maximum in late winter/early spring 2007, and their abundance decreased with the approaching summer. The abundance maximum of picoeukaryotes ($46 - 100 \times 10^6$ cells ml⁻¹) was the highest ever found in an aquatic environment and contradicts the widely accepted view that the abundance of picoeukaryotes is usually one magnitude lower than that of picocyanobacteria (Callieri, 2008).

1.c. The open water and the inner ponds of Lake Fertő/Neusiedlersee were rich in picophytoplankton, while its magnitude was negligible inside the reed belt. Picoeukaryotes were observed in the inner ponds and within the reed belt, but were not found in the open water.

High picoplankton abundances (10^6 cells ml⁻¹) were detected in the open water and the inner ponds of Lake Fertő/Neusiedlersee between April and October 2004, while in the artificial canal inside the reed belt their abundance was negligible. Earlier studies described similarly high picoplankton abundance values in the open water of the lake (Padisák & Dokulil, 1994). Picoeukaryotic algae were found only in the inner ponds and in the artificial canal during the study period.

1.d. The autotrophic picoplankton in the inner pond of Lake Fertő/Neusiedlersee showed similar seasonal dynamics to Lake Balaton and the soda pans in the Danube-Tisza Interfluve. In contrast, picoeukaryotes did not occur in the open water of the lake even in the winter which is unprecedented in the literature.

The autotrophic picoplankton showed different seasonal dynamics in the open water and in the inner pond (Ruster Poschen) of Lake Fertő/Neusiedlersee in a one-year study (2008-

2009). In the inner pond, it followed the general trend of the dominance of picocyanobacteria in the summer and of picoeukaryotes in the winter. In the open water, however, the seasonal dynamics differed from the findings in Lake Balaton and in the soda pans. Picoeukaryotic algae were not found at all in the winter, and the abundance of picocyanobacteria increased rather than decreased at the end of the summer. Their abundance maximum was observed in March, and their quantity decreased with the approaching summer. To our best knowledge, this phenomenon is unique in the literature.

2.a. Our field measurements indicate that light and temperature have a crucial role in the seasonal dynamics of autotrophic picoplankton.

The contribution of picocyanobacteria and picoeukaryotes to the biomass of the total picoplankton changed significantly with the water temperature in Lake Balaton, in the inner pond of Lake Fertő/Neusiedlersee and in the studied soda pans. Picocyanobacteria were the dominant picoplankters under high temperatures in the summer, while picoeukaryotes dominated under low temperature conditions in the winter. Not only the temperature but the incoming solar radiation is also much lower in the winter than in the summer. The contribution of picoeukaryotes decreased with the increasing water temperature at all the above mentioned sampling stations, but their contribution was lower in the Siófok basin, than in the Keszthely basin, and in the latter it was lower than in the inner pond (Ruster Poschen) of Lake Fertő/Neusiedlersee in the winter. According to our hypothesis, these differences result from the differing underwater light climate (light intensity, spectral composition) in these water bodies.

2.b. Different light- and temperature preference of picoeukaryotes and picocyanobacteria were confirmed by means of photosynthesis measurements of isolated strains, which helped to explain the opposite seasonal appearance of these groups.

The obtained P-I curves help to understand the characteristic seasonal dynamics of picophytoplankton. Since ca. 15 °C appeared to be a turning-point temperature below which the maximum photosynthetic rate (P_{max}) and light utilization parameter (α) of the picoeukaryotic strain exceeded that of the picocyanobacterial strain. The lowest temperature (7 °C) in our experiments, which was close to the midday temperature of the pans in winter 2006-2007, was not optimal for the picoeukaryotic strain, but its production exceeded that of

the picocyanobacterial strain. The results indicate that low winter temperatures provide a competitive advantage to picoeukaryotes. Besides temperature, however, light is also a significant controlling factor: at low temperatures, the picoeukaryotes can utilize low light intensities more efficiently than picocyanobacteria. The winter predominance of picoeukaryotes and the summer predominance of picocyanobacteria seem to be caused by different optima of these groups for light and temperature.

3. The contribution of winter picophytoplankton to the primary production of the total phytoplankton was determined in Lake Balaton and Lake Fertő/Neusiedlersee for the very first time. In Lake Balaton the importance of picoplankton was similarly high in the winter than in the summer. The contribution of picoplankton was significant both in the open water and in the inner pond of Lake Fertő/Neusiedlersee in winter.

The obtained P-I curves show that the light saturation parameter (I_k) and the optimal light intensity (I_{opt}) of picoplankton were lower than that of nanoplankton, which suggest the better low light acclimatization of picoplankton. The contribution of picoplankton to the total planktonic primary production showed diurnal and depth-dependence variation in connection with the changing irradiance both in Lake Balaton and in Lake Fertő/Neusiedlersee. Their contribution was lower at noon in the surface regions and higher in the morning or at the evening. The contribution of picoplankton to the primary production of phytoplankton was 25-28% in the Siófok basin at all sampling date. Their contribution was 41-44% in Keszthely basin in winter 2009 and in summer 2009, but it was as little as 15% in February 2010. The picoplanktonic contribution was 44% in the open water of Lake Fertő/Neusiedlersee, and it was 40% in the inner pond (Ruster Poschen) in February 2010. The importance of picoplankton in the primary production was as high in the winter as in the summer in Lake Balaton and their importance was also significant in the winter also in Lake Fertő/Neusiedlersee.

4.a. The picoeukaryotic algal assemblages of the soda pans in the Danube-Tisza Interfluve were represented by green algae (Chlorophyta). The presence of three different taxa was verified by molecular phylogenetic methods.

Thirteen picoeukaryotic algal strains were isolated from the soda pans in the Danube-Tisza Interfluve. The morphological identification of these strains was not possible because of the

small size and simple morphology of the cells. The strains belonged to three major green algal (Chlorophyta) lineages based on their molecular phylogeny (18S rDNA sequences): two strains (ACT 0617 and ACT 0619) were the member of the *Mychonastes/ Korschpalmella/ Pseudodictyosphaerium* (Chlorophyceae) clade, eight strains (ACT 0604, ACT 0605, ACT 0606, ACT 0607, ACT 0610, ACT 0621, ACT 0901 and ACT 0902) belonged to the genus *Choricystis* (Trebouxiophyceae) and three strains (ACT 0608, ACT 0622 and ACT 0602) formed a distinct, new lineage within the Chlorophyta. *Choricystis* strains formed two distinct groups based on their *rbcL* sequence data, and these groups were well differentiable from previously studied *Choricystis* strains. The picoeukaryotic algal community of the soda pans proved to be diverse despite of the extreme conditions (pH, conductivity) in these water bodies.

4.b. A novel green alga was found in the soda pans in the Danube-Tisza Interfluve. It was fully described and named *Chloroparva pannonica* (Trebouxiophyceae, Chlorophyta) based on the detailed morphological investigation (electron microscopy) and 18S rDNA sequence analysis of strain ACT 0608.

The picoeukaryotic strain ACT 0608 formed a new distinct lineage within the Trebouxiophyceae based on its entire 18S rDNA sequence. The sequence analysis of ACT 0608 revealed that this isolate is distantly related to *Nannochloris eucaryotum* UTEX 2502 and *Chlorella minutissima* C-1.1.9 and SAG 1.80 (97,5-97,6%), therefore the phylogenetic position of the new chlorophyte confirms that a new genus was found. The novel algal species was described as *Chloroparva pannonica* after carrying out detailed morphological investigations (scanning and transmission electron microscopy).

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