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AUTOTROPHIC PICOPLANKTON (APP) IN FOUR LAKES OF DIFFERENT TROPHIC STATUS: COMPOSITION, DYNAMICS AND RELATION TO PHYTOPLANKTON

ABSTRACT: Abundance and dynamics of autotrophic picoplankton (APP) were studied in four temperate lakes: oligo-, meso- and eutrophic, as well as dystrophic lake. Orange fluorescing cyanobacteria prevailed in APP community in all four lakes, but in spring and autumn eukaryotic contribution increased. The densities of APP ranged between 2×10^4 ml^{-1} and 9.5×10^5 ml^{-1}. There was a trend of increase of APP numbers along classical trophic gradient, but its share in total phytoplankton biomass was decreasing showing decreasing importance of picoplankton with eutrophication.

Two types of APP seasonal patterns were described. One characterised by only one, spring-early summer peak, was found in mesotrophic and eutrophic lake. The second pattern described for humic lake was characterised by two peaks, in spring and autumn.

KEY WORDS: autotrophic picoplankton, abundance, seasonality, trophic gradient, lakes

1. INTRODUCTION

Phytoplanktonic algae can be divided into three size classes: microplankton <20 μm, nanoplankton 20–2 μm and the smallest fraction called picoplankton with a size range 2.0–0.2 μm. Among these classes picoplankton is less known. Large numbers of picoplanktonic algae were discovered in oceans in late 1970's after application of epifluorescence microscopy (Stockner and Antia 1986, Stockner 1988). Autotrophic picoplankton (APP) in oceans and fresh waters comprises small, unicellular algae; mainly prokaryotic blue-green algae – Cyanobacteriae (Johnson and Sieburth 1979, Waterbury *et al.* 1979) and eukaryotic green algae usually described as *Chlorella*-like cells (Johnson and Sieburth 1982). Prochlorophytes, discovered later, can be very abundant in the oceans (Chisholm *et al.* 1988), and although their presence in freshwaters is still discussed, the first reports about *Prochlorococcus*-like particles in an eutrophic reservoir have occurred (Corzo *et al.* 1999). Recently Komárek (1998) proposed new classification for solitary living cyanobacteria based on cytomorphological, molecular and biochemical approaches. According to this new taxonomy most of picocyanobacteria classified until now as *Synechococcus* belong to *Cyanobium* group.

Stockner and Antia (1986) and Stockner (1988) stated in their revues that in low productive waters APP is generally dominated by orange fluorescing cyanobacteria from genus *Synechococcus* and/or *Synechocystis*, which contain phycoerythrin as a dominant accessory pigment. However, in coloured or in more eutrophic lakes red fluorescing cyanobacteria, with phycocyanin as the main accessory pigment, as well as *Chlorella*-like eukaryota prevail (Fahnenstiel *et al.* 1991, Vörös *et al.* 1991, 1998).

The numbers of APP in lakes varies between 10^4 and 10^6 ml^{-1} (Stockner 1991); in boreal lakes the numbers are usually slightly lower – like 10^3–10^5 ml^{-1} (Fahnenstiel *et al.* 1986). The abundance of autotrophic picoplankton usually increases along with the trophic gradient, but its importance, that is, share in the total phytoplankton biomass and production decreases (Stockner 1991, Stockner and Shortreed 1991, Vörös *et al.* 1998). In oligotrophic lakes and ultraoligotrophic regions of the oceans, picophytoplankton can account for up to 90% of the total phytoplankton biomass and production (Craig 1984). In more eutrophic habitats, its share in the total biomass and production of phytoplankton is much lower, sometimes negligible (Fahnenstiel *et al.* 1986, Stockner 1991, Søndergaard 1991, Weisse 1993). However, it was found out that even in more productive waters, in some periods autotrophic picoplankton dominates in number, biomass and production of phytoplankton (Happey-Wood 1991, 1993, Vörös *et al.* 1991).

However, not much is known about seasonality and factors controlling abundance and distribution of autotrophic picoplankton in lakes. Autotrophic picoplankton is known to be very competitive in utilising nutrients, especially phosphorus (Platt and Li 1986), but it is sensitive to low water temperature (Caron *et al.* 1985, Stockner and Porter 1988). On the other hand Kukkonen *et al.* (1997), in a study done in Finnish lakes, found out that in deep, and/or coloured lakes picoplanktonic algae could reach higher numbers only during prolonged periods of stratification, when they were less exposed to darkness in deeper parts of lakes.

The aim of this study, carried in four temperate lakes forming trophic gradient, was to:

I) identify the main APP groups and the abundance, seasonal patterns and vertical distribution of APP,

II) find out the relation between trophic status of a lake and biomass of phytoplankton and picophytoplankton and assess importance of APP in phytoplankton communities,

III) compare changes in APP and larger phytoplankton caused by eutrophication.

The key factors controlling and influencing abundance and seasonality of APP as well as their production are the subject of another publication.

2. STUDY SITE

The study lakes are situated in north-eastern Poland in Masurian Lakeland. The lakes are characterised by trophic gradient from oligo-mesotrophic Lake Hańcza, mesotrophic Lake Majcz to eutrophic Lake Mikołajskie, additionally dystrophic, humic Lake Flosek was selected for studies. The main physical and chemical features of studied lakes are presented in Table 1. Lake Hańcza, deepest lake in Poland (108.5 m) falls with its chemical (TP = 0.045 mg l^{-1} and

Table 1. The main physical and chemical features of studied lakes, SD (Secchi depth) – range for whole year, TP and NK (Kjeldahl nitrogen i.e. organic and ammonium nitrogen) – mean summer values in epilimnion, Phyt. Biom. (Phytoplankton Biomass) – mean annual values

Lake	Hańcza[1]	Majcz[2]	Mikołajskie[2]	Flosek[3]
area (ha)	311	163	498	4
mean, max depth (m)	39 (109)	6 (16)	11 (27)	3 (7)
SD (m)	5.5–8.5	3.5–5.5	0.5–2.0	1.8–4.0
TP (mg l^{-1})	0.045	0.040	0.080	0.050
NK (mg l^{-1})	0.90	1.36	1.63	1.88
Chl. *a* (μg l^{-1})	2.5	5	35	7.5
Phyt. Biom. (mg l^{-1})	0.5	2.0	7.0	3.2

[1)]Hillbricht-Ilkowska, Wiśniewski 1993; [2)]Hillbricht-Ilkowska 1989; [3)]Hillbricht-Ilkowska *et al.* 1998.

biological (mean Chl *a* = 2.5 μg l^{-1}, max. Chl *a* (4.8 μg l^{-1}) characteristics between oligotrophy and mesotrophy (Vollenweider 1989). However, especially the biological features have typical oligotrophic character and thus further in this study the lake was classified as oligotrophic. Phytoplankton of this lake is dominated by small, nanoplanktonic Bacillariophyceae and by small forms of Cryptophyceae and Chlorococcales. Dinophyceae, especially *Ceratium hirundinella* and *Peridinium* spp., are important part of phytoplankton in contrary to Cyanobacteriae, which biomass was negligible (Jasser unpublished data).

Lake Majcz is a small, stratified lake situated in forested area. Biological and chemical features indicate its mesotrophic state according to Vollenweider scale (Table 1). In spring and autumn the phytoplankton of this lake is dominated by Chrysophyceae, especially *Dinobryon* spp. and by Bacillariophyceae, while in summer by Dinophyceae like *Ceratium hirundinella* and *Peridinium* spp. Cyanophyceae, although present in summer and autumn, are still a marginal phytoplankton group in this lake (Spodniewska 1983a, Jasser unpublished data). Zooplankton biomass is low (5 mg l^{-1}) with dominant species characteristic for mesotrophic lakes (Węgleńska *et al.* 1983).

Lake Mikołajskie is one of the Great Masurian Lakes; the lake is moderately large, stratified and highly eutrophic (Table 1). It is situated in agriculture area and experiences strong urban and tourist influence. Bacillariophyceae dominates in the phytoplankton in spring, while in summer and autumn filamentous Cyanobacteriae and Dinophyceae prevail. Nanoplankton contribution to total phytoplankton biomass is small (only few percent) similarly like in other eutrophic lakes (Spodniewska 1976, Jasser unpublished data).

Lake Flosek, the smallest and the shallowest among studied lakes, is low to moderately productive, slightly humic but not acid lake (Table 1). Originally the lake was slightly acid, however in 1970's it has been limed so now the pH is around 8 and calcium concentration is up to 15.5 mg l^{-1} and water colour about 30 mg Pt l^{-1}. The lake is situated in forested area dominated by coniferous trees. Although the lake is shallow (mean depth 3 m) with light reaching the sediment it is stratified in the deepest part. Various *Chrysophyceae* from genus *Dinobryon* and *Syncrypta* as well as *Dinophyceae* with *Gymnodinium* predominate in this lake (Hillbricht-Ilkowska *et al.* 1998).

3. METHODS

Lakes Majcz and Mikołajskie have been sampled monthly in 1993 since February till November and in 1994 since February till December. Lake Flosek has been investigated in 1992 and 1993 since April till October. Lake Hańcza has been sampled four times in 1994: in April during spring mixing, during summer stagnation in June and in October and after beginning of autumn mixing in November.

Samples were taken from various depths, that is, 1, 5, 10 m in Lakes Majcz and Mikołajskie, 1 m in Lake Flosek and 1, 5, 10, 20, 40 and 90 m in Lake Hańcza. The samples were always collected in three replicates. Depths 1 and 5 m in Lakes Majcz and Mikołajskie corresponded to epilimnion and the depth of 10 m to hypolimnion. In Lake Hańcza only samples from 20 m and below corresponded to hypolimnion. A 5-L tube sampler (Bernatowicz) was used to collect the samples. The sub samples were divided for APP (50 ml), nano- + microphytoplankton (100 ml) and chemical analyses (500–1000 ml).

Fresh APP samples were brought to the laboratory in cooled, black boxes and preserved with pre-filtered, buffered formaldehyde to final concentration 1%. They were examined by fluorescent microscope within one week according to Malinsky-Ruszansky and Berman (1991), but in few cases within two weeks, however checking before if fluorescence does not fade.

Samples for APP were analysed in dark room under 1000 × magnification using 50 W halogen lamp and set of filters: blue B-2A (DM 510 nm, Ex 450–490 nm and BA 520 nm), as well as green G-2A (DM 580, Ex 510–560 and BA 590). APP cells has been counted on average on 20 fields or until 400 cells have been reached.

Nano- and microphytoplankton (larger phytoplankton) samples have been fixed with formaldehyde (2% final concentration) and Lugol solution according to Spodniewska (1974). The samples were concentrated by gradual gravitate sedimentation and removing water from above sedimentated material, and investigated according to Simm (1985) under light microscope NIKON Optiphot 2 in Fuchs-Rosenthal 0.125-ml volume glass camera for blood cells counting.

The abundance of APP and larger phytoplankton was calculated for 1 ml. The biomass was calculated based on abundance and volume of geometrical shapes corresponding to the investigated taxa and assuming that the mean density of phytoplankton cells is 1.1 mg fresh biomass × 1 mm^{-3} (Simm 1985, Kawecka and Eloranta 1994).

Concentrations of basic nutrients such as PO_4-P, NK – Kjeldahl Nitrogen (NH_4^+-Norg) as well as TP (total phosphorus) and TN (TKN+N-NO_3) were analysed according to standard methods Golterman and Clymo (1978) and Dowgiałło (1984), using spectrophotometer Shimadzu UV 160 A. The humic matter content in Lake Flosek was assessed from absorbency at 254 nm correlated to water colour in units of milligrams of Pt per litre based on equation A(254) = 0.04669 + 0.00289 col. (with R = 0.987, P = 0.05) and was ~ 30 mg Pt l^{-1}. In statistical analysis t-test and non-parametrical tests: Mann-Whitney and Wilcoxon, have been used. Probability threshold (α) of 5% ($P \leq 0.05$) was considered as statistically significant unless other stated.

4. RESULTS

4.1. COMPOSITION OF APP COMMUNITY

In all four studied lakes autotrophic picophytoplankton has been found. The APP was represented mainly by cyanobacteria rich in phycoerythrin, that is, fluorescing orange in blue light and by green algae, which thanks to chlorophyll *a* were fluorescing red in blue and green light. Orange fluorescing cyanobacteria were slightly rod shaped with diameter between 0.8 to 1.5 μm and were dividing in one plane, which suggests that cyanobacteria with such features belong to *Cyanobium* group (Komárek 1998) previously identified as *Synechococcus* group. Eukaryotic, *Chlorella*-like cells represented the second common group of picoalgae. They were bigger then picocyanobacteria, round with diameter 1.8–2.2 μm and were characterised by bright red fluorescence under blue light and dark, faded red in green light. The third group of picoalgae noticed occasionally were phycocyanin-rich cyanobacteria fluorescing red in blue and green light. However, the red fluorescence of the last group in blue light was usually very pall, while in green light they were indistinguishable from the more abundant phycoerythrin-rich cyanobacteria. Thus, unless they were well visible in blue light, they were counted together with phycoerythrin-rich cells in green light, and are not separated from them in further results.

4.2. SEASONAL PATTERN AND DENSITIES OF APP

The share of eukaryota and prokaryota varied seasonally and between the lakes, however in all the lakes picocyanobacteria most of the time dominated in APP assemblages. The highest mean share of eukaryotic APP was noticed in Lake Majcz (24%) and the lowest (4%) in humic Lake Flosek (Table 2) and seemed to be not connected with trophic status of a lake. Generally, the share of eukaryota was high in the spring time until thermal stratification occurred and in autumn, after beginning of mixing, when water temperature was low (Fig. 1). In Lake Hańcza eukaryota accounted for higher percentage of APP biomass only in spring, while in summer and autumn, their share was low. The highest contribution of eukaryota into APP biomass in Lake Majcz was noticed in November and December and in Lake Mikołajskie in April when it reached about 60% of total APP biomass. In Lake Flosek eukaryota accounted maximally for 12%. In summer months eukaryota share in all studied lakes was low, between 0.1 and 13% depending on the lake and it was significantly lower than in other periods ($0.008 < P < 0.04$).

During the study period the highest maximal abundance of APP was noticed in 1993 at the 10 m depth in the most productive lake, Lake Mikołajskie, where it reached 9.5×10^5 cells ml^{-1}. However the highest APP number in this lake calculated as a mean

Table 2. The mean and maximal share (%) of eukaryota in total APP biomass (annual values in four lakes)

Lake	Mean (%)	Maximal (%)
Hańcza	13	36
Majcz	24	63
Mikołajskie	18	53
Flosek	4	12

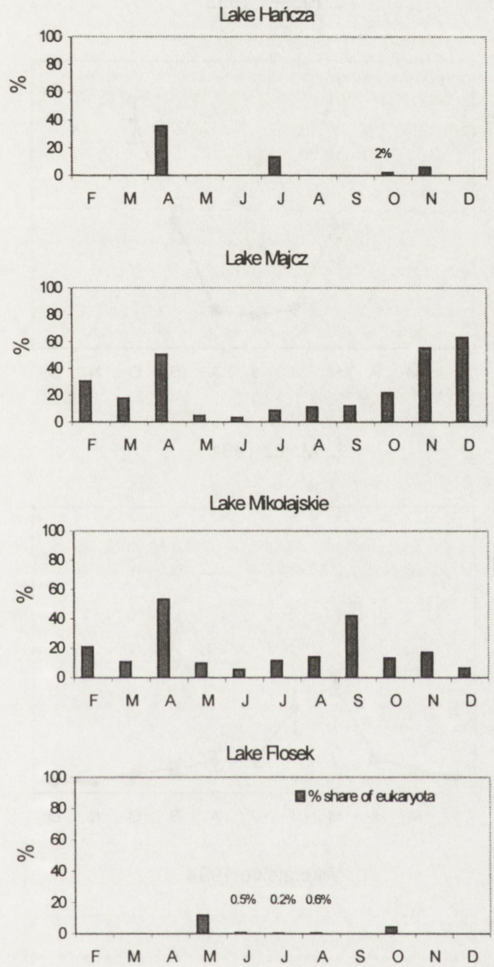

Fig. 1. The percentage share (%) of eukaryota in total APP biomass. Mean monthly values in Lake Hańcza for 1–90 m, Lakes Majcz and Mikołajskie 1–10 m and Lake Flosek 1 m

value for water column (1–10 m) in 1993 was 7×10^5 cells ml^{-1} and 6×10^5 ml^{-1} in 1994. In humic Lake Flosek, where APP was sampled only at 1m depth, maximal abundance of APP reached 8×10^5 cells ml^{-1} placing this lake together with the most productive lake as the richest with APP. During both years of study moderately productive, clearwater Lake Majcz was characterised by inter mediate values of maximal APP abundance (Table 3), while the lowest abundance of APP was noticed in the least productive lake, Lake Hańcza (0.9×10^5 ml^{-1}). However, in this last lake low sampling frequency did not allow to observe APP peak. The differences between maximal numbers in lakes representing clas-

Table 3. The abundance and biomass of APP in studied lakes. Mean monthly values for studied periods: Lake Majcz and Lake Mikołajskie Feb.–Nov. in 1993 and Feb.–Dec. in 1994, Lake Hańcza Apr., July, Oct. and Nov. in 1994 and Lake Flosek May–Oct. in 1993

Lake	APP mean abundance cells 10^5 ml^{-1}	APP mean biomass mg l^{-1}	APP max. biomass mg l^{-1}
Hańcza 1994	0.90	0.095	0.16
Majcz 1993	1.23	0.13	0.30
Majcz 1994	1.26	0.14	0.39
Mikołajskie 1993	2.27	0.20	0.71
Mikołajskie 1994	1.46	0.16	0.63
Flosek 1993	3.21	0.27	0.54

sic trophic gradient were statistically significant ($P<0.01$).

The mean seasonal numbers of APP in all studied lakes exhibited similar pattern like in case of maximal numbers, with the highest mean values recorded in Lakes Flosek and Mikołajskie and lowest in Lake Hańcza. The differences between lakes in this case were however not statistically significant, which resulted from high variability in APP abundance in each lake during sampling period.

The seasonality of APP in both regularly sampled lakes (Majcz and Mikołajskie) was repeatable in two study years and exhibited similar seasonal pattern in both lakes (Fig. 2). The APP numbers was low during winter period. In April or May APP abundance increased rapidly forming spring peak. In 1993 in Lake Majcz this peak occurred already in April, when water temperature was about 5°C. In 1994 in Lake Majcz and 1993 and 1994 in Lake Mikołajskie the highest APP abundance was noticed in May, when surface water temperature has just reached 10°C. The peaks persisted for about two months, however in second month the numbers have been already lower. After the peak APP abundance dropped sharply in both lakes, however the numbers were varying. In Lake Mikołajskie a slight tendency to increase of APP numbers was noticed towards autumn.

The seasonal pattern identified for Lake Flosek was different, as two distinguished peaks of APP abundance were noticed. One of them occurred similarly like in both other lakes, that is, in spring, in May, when water

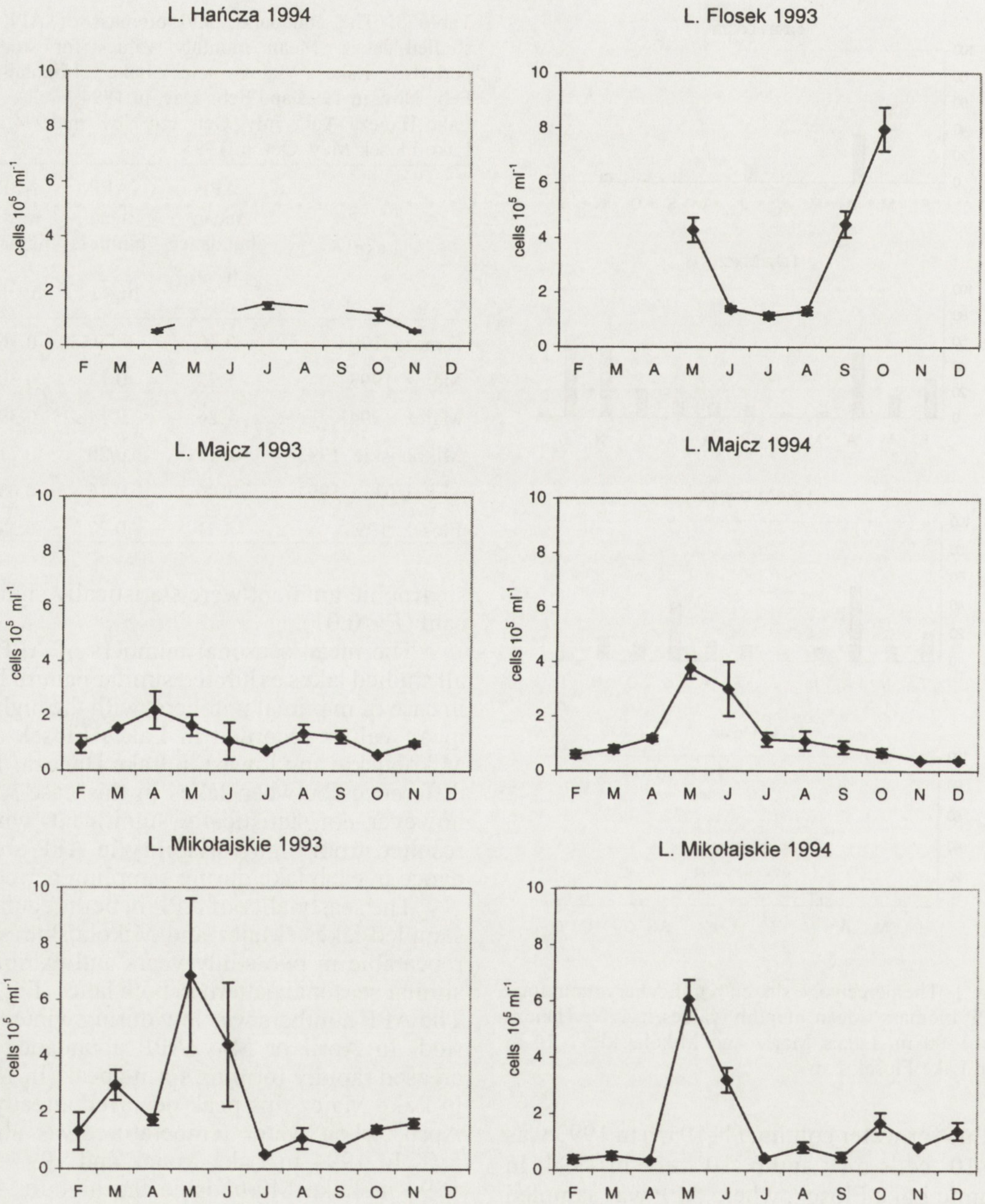

Fig. 2. The mean abundance of APP in studied lakes in water column: Lake Hańcza 1–90 m, Lake Majcz and Lake Mikołajskie 1–10 m, Flosek 1 m

temperature also reached 10ºC. The second, an autumn peak, was noticed in October, and was significantly higher ($P = 0.05$) than the spring one. During summer APP abundance was low and stable. In Lake Hańcza, because of low sampling frequency, no distinguished seasonal pattern of APP was identified. It was noticed however that during mixing period, when waters temperature was low, APP abundance was much lower than during summer stratification.

4.3. BIOMASS OF APP AND LARGER PHYTOPLANKTON

The highest value of maximal biomass of APP was noticed, similarly like for numbers, in most productive Lake Mikołajskie (0.71 mg l^{-1}) followed by the value observed in

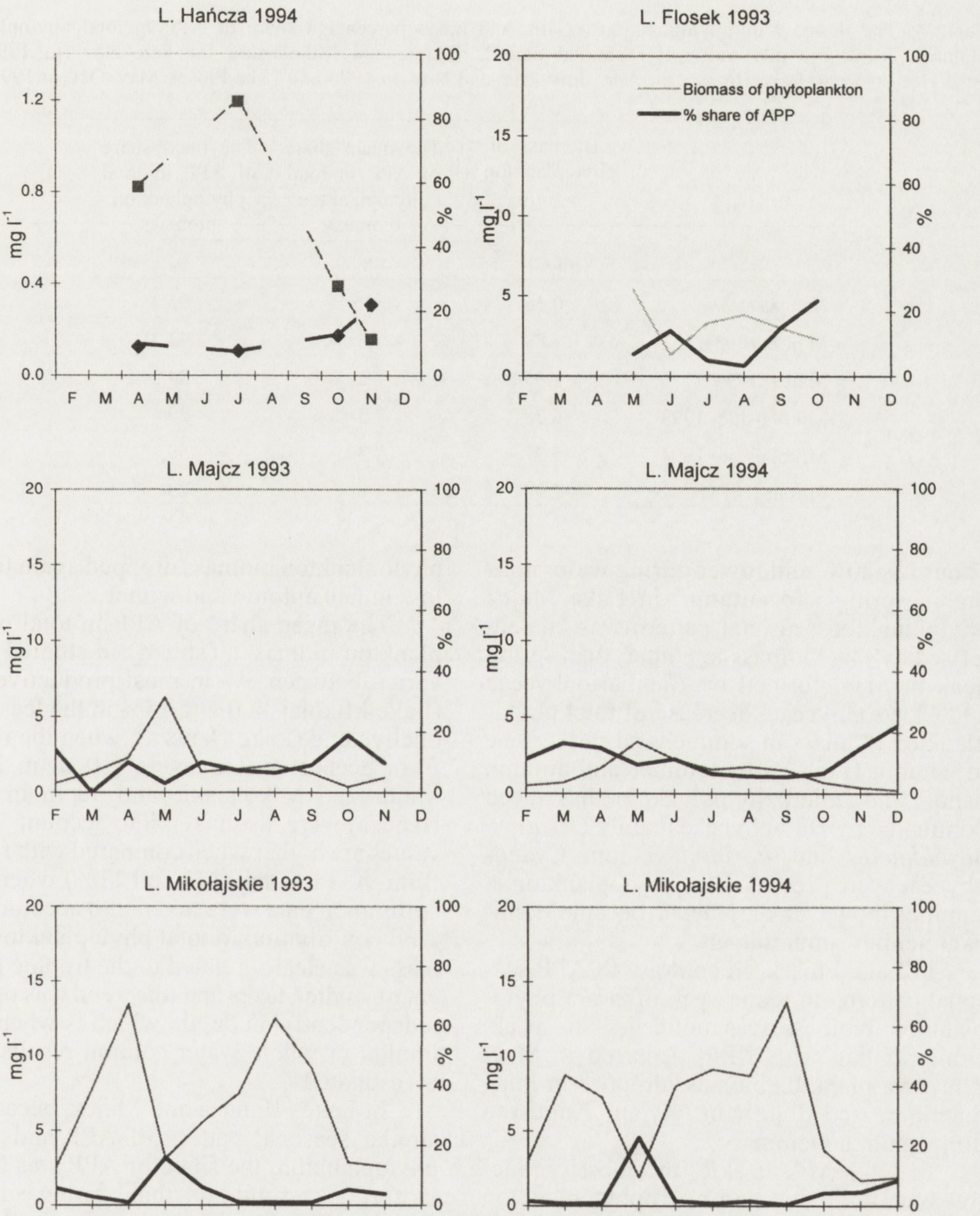

Fig. 3. Mean biomass (for water column) of total phytoplankton and the % share of APP in it. Mind the scale

shallow, humic Lake Flosek (0.54 mg l^{-1}). The lowest value of maximal biomass (0.16 mg l^{-1}) was observed in oligotrophic Lake Hańcza (Table 3). The mean monthly values for studied periods reflected the same pattern (Table 3). In most cases the biomass of APP community followed closely the seasonal pattern of abundance, with the exception of Lake Majcz. In April 1994 in this lake numbers of APP were still low, however APP biomass was considerably high. That was due to a peak of eukaryotic picophytoplankton, which occurred just at that time, while total APP abundance was still considerably low.

The seasonality of nano- and microphytoplankton exhibited various patterns in studied lakes. In both less productive lakes, oligotrophic Lake Hańcza and mesotrophic Lake Majcz, larger phytoplankton exhibited seasonal pattern similar to that of APP. In Lake Hańcza phytoplankton reached highest values in July, when water temperature was

Table 4. The biomass of phytoplankton >2 μm and mean percentage share of APP in total phytoplankton biomass. Mean monthly values for studied periods: Majcz and Mikołajskie for Feb.–Nov. in 1993 and Feb.–Dec. in 1994, Lake Hańcza for Apr., July, Oct. and Nov. in 1994 and Lake Flosek May–Oct. in 1993

Lake	Biomass of phytoplankton >2 μm	The mean share of APP in total phytoplankton biomass	The max. share of APP in total phytoplankton biomass
	$mg\ l^{-1}$	%	%
Hańcza 1994	0.56	15	55
Majcz 1993	1.83	6	43
Majcz 1994	1.35	8	34
Mikołajskie 1993	6.78	3	29
Mikołajskie 1994	5.97	3	59
Flosek 1993	2.94	8	23

about 18–20°C and lower during water mixing in spring and autumn. In Lake Majcz phytoplankton seasonal pattern was characterised by low biomass in winter, than spring peak in May, formed by Bacillariophyceae and Chrysophyceae, decrease of total phytoplankton biomass in summer and further one in autumn (Fig. 3). In summer and autumn nano- and microphytoplankton has been dominated by Dinophyceae mainly *Ceratium hirundinella* and *Peridinium* spp. Cyanophyceae were present in the phytoplankton in summer, however they never became dominant neither subdominant.

In Lake Flosek, in contrary to APP seasonal pattern, only one peak of larger phytoplankton biomass was noticed. This peak, similarly like with APP, occurred in May. The phytoplankton biomass dropped in June, than increased slightly in July and August to drop again in October.

In Lake Mikołajskie, the most productive one, the nano- and microphytoplankton seasonal pattern and APP pattern exhibited an opposite character (Figs 2 and 3). In this lake two peaks of phytoplankton biomass were noticed; the first one in March–April formed by Bacillariophyceae and was followed by severe decrease of phytoplankton biomass in May (*clear water phase*). After *clear water phase*, in June, the phytoplankton biomass started to increase gradually and reached maximum in August or September. During that time Cyanophyceae, Chlorophyceae and Dinophyceae became dominant. In both years of the study these second, late-summer peaks were significantly higher than those in spring. After late-summer maximum phytoplankton biomass dropped again to stay low in late autumn and winter.

The mean share of APP in total phytoplankton biomass (Table 4) in studied lakes varied between 3% in most productive lake (Lake Mikołajskie) and 15% in the least productive one (Lake Hańcza), when the results from deepest water layers (10 m in Lakes Majcz and Mikołajskie and 90 m in Lake Hańcza) were also taken into account. These values are higher when compared with results from the same lakes (1 and 11%) when only epilimnion data were taken into account. The APP contribution to total phytoplankton biomass was clearly related to the trophic gradient of studied lakes and this trend was present independently on depth, which is when epilimnion or whole water column results were investigated.

In Lakes Hańcza and Majcz, because of similar seasonal pattern of APP and larger phytoplankton, the share of APP was higher in spring and autumn than during summer months (Fig. 3) and the maximal share of APP was noticed not during their maximal abundance but in autumn when larger phytoplankton has already started to decline. At that time APP accounted in Lake Hańcza 55% of total phytoplankton biomass while in Lake Majcz 42 and 27% respectively in 1993 and 1994. During APP peaks in Lake Majcz APP contribution did not exceed 17% of total phytoplankton biomass. In Lake Flosek, where the average share of APP in total phytoplankton biomass was at the same level like in moderately productive Lake Majcz, the highest share of APP (23%) occurred during autumn peak when abundance and biomass of larger phytoplankton have already started to decline.

The largest differences in APP contribution to the total phytoplankton biomass have been found however in most productive Lake Mikołajskie (between 0.3 and 59%). In this lake seasonal pattern of APP and of larger phytoplankton had opposite character. Thus the highest share of APP in the total phytoplankton biomass coincided with their seasonal peaks similarly like in Lake Flosek. During APP peak the share of APP varied then in Lake Mikołajskie between 9 and 59% depending on the depth, while in other periods APP accounted from 0.3 to 6% of total phytoplankton biomass (Fig. 3).

4.4. VERTICAL DISTRIBUTION OF LARGER PHYTOPLANKTON AND APP BIOMASS

In all three lakes, Majcz, Mikołajskie and Hańcza, where vertical distribution of phytoplankton and picophytoplankton has been studied, no clear relation between picophytoplankton densities and depth was found during whole vegetation period. However, in Lakes Majcz and Mikołajskie the highest abundance of APP in 1993 was noticed at 10 m depth in both lakes and in 1994 – in Lake Mikołajskie at 5 m ($P \leq 0.03$). The differences in cell number between depths have not persisted for longer period.

In contrary to APP larger phytoplankton biomass was gradually decreasing with depth and in almost all cases was lowest at the deepest sampling layers. Thus, as a result of this decrease, APP share in the total phytoplankton biomass in Lakes Majcz and Mikołajskie was increasing with depth (Fig. 4), and in both years of the study (R^2 was between 0.91 and 0.99). In Lake Hańcza, similarly like in the other two lakes, larger phytoplankton biomass was decreasing with depth, with an exception of occasional metalimnetic maximum, and was usually lowest at the two deepest layers. Thus APP share in the total phytoplankton biomass was changing and in April and July it tend to increase slightly with depth ($R^2 = 0.67$ and 0.51). Towards the end of the season however, in October, still during stratification, and in November, during autumn overturn, no trend has been found in APP contribution to the total phytoplankton biomass at various depths (Fig. 5).

5. DISCUSSION

Picocyanobacteria with phycoerythrin as the main accessory pigment dominated in APP assemblages in studied lakes regardless of their trophic status. The second biggest group of APP was eukaryota and its importance varied seasonally and between the lakes. The phycoerythrin-rich picocyanobacteria seemed to belong to Synechococcus group, however according to new classification of picocyanobacteria proposed by Komárek (1998) those coccoid and/or slightly rod shaped unicellular forms belong to genus *Cyanobium*. The eukaryotic component of APP represented *Chlorella*-like cells, the most common between eukaryotic picoalgae. The repeatable clear seasonal pattern of APP composition was described for all the lakes. It was characterised by higher contribution of eukaryota or even their dominance

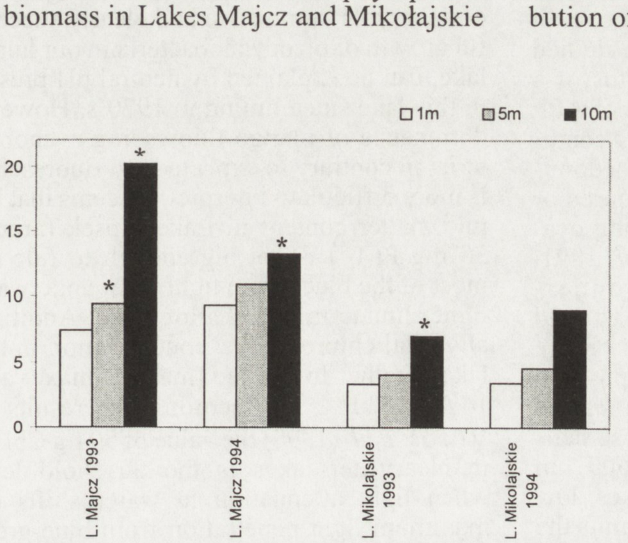

Fig. 4. The mean annual share (%) of APP in total phytoplankton biomass in Lakes Majcz and Mikołajskie in two years of the study and for different depths.
* – Indicates statistically significant higher values, mind the scale

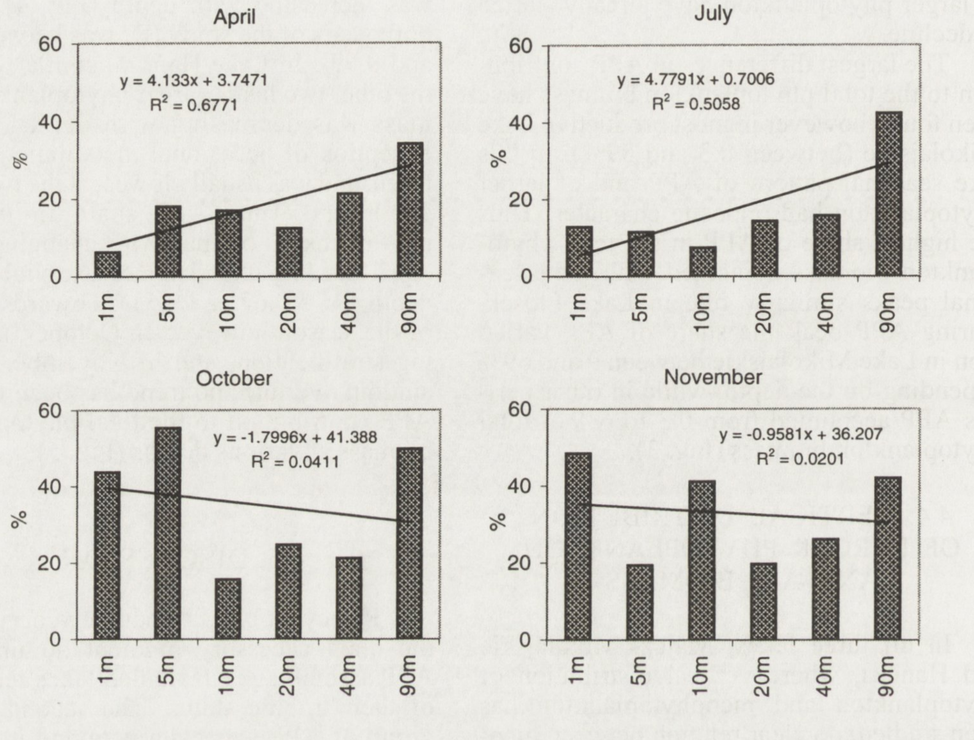

Fig. 5. The mean share (%) of APP in total phytoplankton biomass in Lake Hańcza in April, July, October and November 1994 at various depths. The lines indicate correlation with depth

in total APP biomass in spring and autumn (when water temperature was low) and by dominance of picocyanobacteria in late spring and during summer stratification. These results support other findings (Weisse 1993) that eukaryotic algae in contrary to cyanobacteria are less vulnerable to low temperatures and can outnumber picocyanobacteria in cold periods.

In contrary to other findings (Søndergaard 1991, Vörös *et al.* 1998), an overall share of eukaryota in APP biomass in studied lakes was not related to trophic status of a lake. The differences in composition of APP in lakes are known to depend on light conditions and pH. In waters, where red light dominates in the light climate, like in coloured or highly eutrophic lakes, red fluorescing cyanobacteria (Pick 1991, Vörös *et al.* 1991, 1998) or eukaryotic algae prevail (Søndergaard 1991, Szeląg-Wasielewska and Gołdyn 1996, Jasser and Arvola in press). This is a result of their pigment composition as phycocyanin and/or chlorophyll *a*, the main photosynthetic pigments in these cells are better adapted to harvest the 600 nm wavelengths. However, in humic lakes, low pH additionally to light conditions, limits the occurrence of cyanobacteria including picocyanobacteria. In this way low pH favours the growth of eukaryotic picoplankton and rules out even those cyanobacteria, which are red fluorescing (Stockner and Shortreed 1991). In present study the biggest mean share of eukaryota was found in mesotrophic, clearwater lake and the smallest in humic, rather low productive lake, Lake Flosek, which is not in line with above findings. Lack of eukaryota dominance and clearly successful growth of picocyanobacteria in our humic lake, can be explained by neutral pH present in this lake since liming in 1970's. However dominance of orange fluorescing cyanobacteria, in contrary to expected red fluorescing, is more difficult to interpret. It seems that humic matter content in Lake Flosek (around 30 mg Pt l^{-1}) is not big enough to rule out most of the blue-green light from underwater light climate in this shallow lake. Additionally total chlorophyll *a* concentration in this lake is rather low value (mean 5, max. value 14 μg Chl. l^{-1}). According to results of Vörös *et al.* (1998) the value of 50 μg Chl. l^{-1} in clearwater lakes is the threshold level when light attenuation in water shifts the maximum light penetration from blue-green to red spectrum producing dominance of phycocyanin-rich over phycoerythrin rich algae. Thus, low humic matter content together with low chlorophyll a concentration and neutral pH in Lake Flosek still favour growth of phycoerythrin-rich picocyanobacteria. In eutrophic, clearwater Lake Mikołajskie phytoplankton biomass only seldom exceeded the value of 50 μg Chl. l^{-1} that also explains high proportion of phycoerythrin-rich cyanobacteria in this lake.

The densities of APP found in studied lakes, between 2×10^4 and 9.5×10^5 cells ml^{-1} for picocyanobacteria and between 3×10^2 and 10^4 × cells ml^{-1} for eukaryotic APP, are in accordance with other findings for temperate lakes (Stockner 1988, Weisse 1993). The maximal numbers of picocyanobacteria recorded in lakes belonging to classic trophic gradient in this study were related to their trophic status and the highest density was recorded in most productive Lake Mikołajskie and the lowest in the least productive Lake Hańcza. This is in line with a general concept that the numbers and biomass of APP correspond roughly to trophic status of a lake (Stockner 1991, Vörös *et al.* 1998). Surprisingly high APP densities, up to 8 10^5 ml^{-1}, were found in low productive, humic Lake Flosek. These numbers of APP exceed the values expected for lake of such productivity (Stockner 1991). However, there are records from other low or moderately productive but shallow lakes that picoplanktonic cyanobacteria occur there in very high densities. This was a case in oligo-mesotrophic Lake Neusiedlersee (up to 7×10^5 cells ml^{-1}) and in the mesotrophic part of Lake Balaton (up to 11×10^5 cells ml^{-1}) as reported Vörös *et al.* (1991), in oligo-mesotrophic, slightly acidic Lake Skrzynka 50×10^5 cells ml^{-1} (Szeląg-Wasielewska 1999) or in humic Lake Jylisjärvi (Jasser and Arvola in press). It is difficult to say now what factor is the main one causing such favourable conditions for picocyanobacteria growth in these lakes. One of the reasons might be unfavourable conditions for zooplankton grazing on APP due to constant mixing of water in these shallow lakes causing high turbidity. This explanation, may be especially reliable in case of the other shallow lakes (Nesiedlersee, Balaton and Jylisjärvi), which become occasionally very turbid but in case of Lake Flosek it needs further investigation.

Seasonal patterns of picocyanobacteria found in all three lakes investigated monthly (Lakes Majcz, Mikołajskie and Flosek) have shown certain similarities and in case of Lake Majcz and Lake Mikołajskie consistency within two years of study. In all three lakes prokaryotic APP exhibited spring-early summer peak, which in case of both deeper lakes was the only peak recorded during the year. Picoplanktonic cyanobacteria in these lakes started to increase when water temperature was between 5 and 10°C which is in line with findings that these algae are regulated by temperature and temperature around 10°C seems to be triggering for their growth (Kuosa 1991, Weisse 1993).

After peak in May, which was partially prolonged for June, the numbers of APP in three studied lakes (Majcz, Mikołajskie and Flosek) were low during summer stratification, the time of highest water temperature. This seasonal pattern is different than broadly described seasonality of APP in other temperate waters (Caron *et al.* 1985, Fahnenstiel *et al.* 1986, Søndergaard 1991). In those previously investigated lakes APP reached their highest abundance in summer during highest water temperatures. However Weisse (1988) in study done in prealpine, mesotrophic Lake Constance, Happey-Wood (1991) in mesotrophic Llyn Padarn and Szeląg-Wasielewska (1999) in oligo-mesotrophic Lake Skrzynka described pattern with high spring peak being also an annual maximum, however in those lakes APP used to form other smaller peaks again in late summer. In neither of our deeper lakes a late summer or an autumn peak was noted, which suggests that lakes Majcz and Mikołajskie represent another type of seasonal patterns of APP in temperate region.

Even more interesting is fact that in Lake Mikołajskie, in both years of the study, APP reached its maximal abundance during clear water phase, thus when biomass of bigger phytoplankton was lowest, as well as according to PEG (Plankton Ecology Group) model also biomass of protozooplankton (Sommer *et al.* 1986). Protozooplankton, i.e. heterotrophic nanoflagellates and ciliates, is known to be the main picoplankton grazer (Stockner 1988, Weisse 1993), and thus one can expect that decrease of its biomass should release APP from strong grazing pressure and stimulate increase of APP densities. However Weisse (1988) in his study in Lake Constance noticed actually very low densities of

APP, almost annual minimum, during clear water phase concluding that together with other components of microbial loop they might have been grazed down by bigger zooplankton. It is possible that APP in Lake Mikołajskie forms a peak during low grazing pressure of protozooplankton at the beginning of *clear water phase*. However, later APP becomes limited by bigger zooplankton, which caused its decrease observed in June. In this context the seasonality of APP described for Lake Mikołajskie needs still more attention and investigation.

Also APP in humic Lake Flosek seems to exhibit different seasonal pattern than commonly described for temperate lakes. It is because both, spring and autumn, maximum formed by prokaryotic APP occurred during periods of rather low temperature (about 10°C) and APP numbers during summer temperature maximum were very low.

The investigations of vertical distribution of APP and larger phytoplankton in three deeper lakes have revealed that while larger phytoplankton was generally decreasing with depth the APP distribution has not shown any clear trend. Although the highest numbers of APP were actually found at 10 or 5 m depths (in Lakes Majcz and Mikołajskie) but it did not last long and the differences between depths were not consistent. Also in Lake Hańcza no clear relation between APP densities and depth were noticed, but high abundances of living APP cells were found even at 90 m. These results from all three lakes support the previous findings that autotrophic picoplankton is well adapted to low light intensities (Glover 1985, Glover *et al.* 1986). However, high numbers of APP in the layers close to the surface, like at 1 m depth in Lakes Majcz and Mikołajskie and 1 and 5 m depths in Lake Hańcza suggest that APP can also be adapted to higher light intensities and thus can not be considered only as shadow-like organisms.

A consequence of these broad adaptation of APP to various light intensities and of the fact, that larger phytoplankton clearly decreases with depth, is that importance of APP increases with depth, especially in more productive lakes (Figs 4 and 5). In other words APP is out competed by larger phytoplankton in the environment optimal for the last one but it stands much bigger chances in less favourable conditions, like in meta- and hypolimnion. This in turn implies that, while APP is usually a marginal group in term of biomass in phytoplankton communities in epilimnion of temperate, moderately productive and productive lakes, its importance for these lakes is much bigger and should not be underestimated. This may be especially important in stratifying lakes with migrating zooplankton.

In the four studied lakes with trophic gradient autotrophic picoplankton contributed to total phytoplankton biomass on average between 3 and 15%. The lowest average contribution was found in most productive lake (L. Mikołajskie) and the highest in the least productive one (L. Hańcza). In both moderately productive lakes, mesotrophic Lake Majcz and dystrophic Lake Flosek, APP contribution to phytoplankton was intermediate (Table 4). These results show decreasing importance of APP along trophic gradient. It is in line with the general rule , which has been already described by other authors (Stockner 1991, Stockner and Shortreed 1991, Vörös *et al.* 1998). One can draw also similarities to changes described for nanoplankton occurring during eutrophication (Hillbricht-Ilkowska 1977, Spodniewska 1978, 1979), which consists in decreasing importance of nanoplankton along trophic gradient. In this case however additionally interesting is fact that the highest observed APP share in the total phytoplankton biomass occurred in the most productive lake (Mikołajskie) with the lowest average share of APP (3%). In this way, in most eutrophic lake APP contribution to total phytoplankton biomass undergoes the biggest variation (0.3–59.3%). This suggest further similarities to nanoplankton changes occurring with eutrophication. With overall decrease in nanoplankton importance in highly productive lakes occasional domination of nanoplankton in phytoplanktonic assemblages appears in these lakes. Such phenomenon was found i.e. in spring before summer peak of microplanktonic algae (Spodniewska 1983b).

6. SUMMARY

The abundance and dynamics of autotrophic picoplankton (APP) was studied in four temperate lakes of varying trophic status (Table 1). Three lakes represented the classical trophic gradient: oligotrophic (L. Hańcza), mesotrophic (L. Majcz) and eutrophic (L. Mikołajskie) while the fourth one was dystrophic, humic, however not acidic lake (L. Flosek). Orange

fluorescing cyanobacteria prevailed in APP community in all four lakes (Table 2), but in spring and autumn the contribution of eukaryotic APP used to increase and occasionally they were becoming dominant (Fig. 1).

The densities of APP in studied lakes ranged between 2×10^4 ml^{-1} and 9.5×10^5 ml^{-1}, which is well in line with previous findings (Stockner 1988, 1991), and when maximal densities were taken into account there was a trend of increase in APP densities along classical trophic gradient. The highest maximal abundance and biomass of picoalgae was noticed in most productive lake (L. Mikołajskie), while in a shallow, rather low productive, humic lake (L. Flosek) highest average abundance was found (Fig. 2). The mean monthly values for studied periods reflected the same pattern (Table 3).

Two types of APP seasonal patterns where found in studied lakes. The first pattern is characterised by only one, spring-early summer, density peak of APP and low densities during the rest of the year. This pattern was found in moderately (L. Majcz) and in highly productive (L. Mikołajskie) lakes and was different than any other previously described for temperate lakes, as the only APP peak occurred still during rather low water temperature (Weisse 1993). The second pattern, described for humic lake, exhibited two density peaks: in spring and autumn, with the last one being an annual maximum (Fig. 2). Also in this lake both APP peaks were noticed during rather low water temperature, first before, and second after maximum of water temperature. The peaks of APP in less productive lakes occurred during time of high phytoplankton biomass (with an exception of second, autumn APP peak in Lake Flosek) while in the most productive lake APP peaked in spring during low phytoplankton biomass, clear water phase (Fig. 3). As a consequence the highest APP share in less productive lakes was mostly result of decrease in biomass of larger phytoplankton while in the most productive lake it coincided with APP peak (Figs 2 and 3).

No clear and consistent relation between APP densities and depth were found in studied lakes, but in Lakes Majcz and Mikołajskie the highest abundance of APP in 1993 was noticed at 10 m depth in both lakes and in 1994 in L. Mikołajskie at 5 m. In contrary the share of APP in total phytoplankton biomass was clearly related to depth, due to vertical distribution of larger phytoplankton and was significantly increasing with depth in almost all cases (Figs 4 and 5).

Except for depth relation a trophic relation between APP share in total phytoplankton biomass was found. Autotrophic picoplankton contributed to the total biomass of phytoplankton on average between 3 and 15 % in studied lakes (Table 4), with the lowest contribution in the most productive lake (Mikołajskie) and the highest in the least productive one (Hańcza). This relation with trophic gradient shows decreasing importance of picoplankton with eutrophication, which is similar to one described for nanoplankton (Hillbricht-Ilkowska 1977, Spodniewska 1978, 1979). Also fact that APP share in the total phytoplankton biomass undergoes the biggest variations in the most productive lake (0.3–59.3%) suggest similarities to nanoplankton changes occurring during eutrophication. With an overall decrease in nanoplankton importance in highly productive lakes occasional domination of nanoplankton in phytoplanktonic assemblages, like in spring, occur (Spodniewska 1983b).

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