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BIRDS CAUSE NET HETEROTROPHY IN SHALLOW LAKES

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Primary production, community respiration, and net C load from aquatic birds were studied in two Hungarian turbid soda pans during 2002. The studied water bodies were hypertrophic. The gross primary production/respiration (GPP/R) ratios were usually below 1, which indicated that these soda pans were net heterotrophic during the study period. The respiration did not correspond with the production but showed strong correlation with net carbon loading from aquatic birds, which pointed out the important role of allochtonous organic matter. Considering the relationship between bacterio- and phytoplankton, the studied soda ponds formed a separated group among lakes, which indicated that the bacterioplankton depends mainly on the net carbon load of aquatic birds instead of primary production. In spite of the well-accepted approach that lakes above 17 μg l^{-1} chlorophyll *a* concentration are net autotrophic, these hypertrophic soda pans (maximum chlorophyll $a > 75$ μg l^{-1}) proved to be net heterotrophic. The main factor causing net heterotrophy in these shallow soda ponds is the large organic carbon load (14.8 g C m^{-2} $year^{-1}$ in the "Kelemen-szék" pan and 35.6 g C m^{-2} $year^{-1}$ in the "Zab-szék" pan) of aquatic birds.

Key words: production, respiration, net heterotrophy, aquatic birds, soda pans

INTRODUCTION

Primary production and respiration are the major metabolic pathways by which organic matter is produced and destroyed. Net ecosystem production (NEP) is the difference between gross primary production (GPP) and ecosystem respiration (R) (ODUM 1969). If the NEP is positive, ecosystems are net autotrophic and production is greater than respiration, while net heterotrophic systems have greater respiration than production. Externally produced organic (allochtonous) carbon and its bacterial utilisation are considered to be the main factors causing net heterotrophy (ODUM 1957, COLE *et al.* 2000).

Over the past decade, it has been shown that oligotrophic regions of the ocean and unproductive lakes worldwide are net heterotrophic because bacterial respiration of allochtonous organic carbon causes community respiration to exceed primary production (DEL GIORGIO *et al.* 1997, GONZÁLES *et al.* 2001, PALSSON *et al.* 2005, HANSELL *et al.* 2004), whereas it has been supposed that the role of allochtonous dissolved organic carbon (DOC) is less pronounced in more productive lakes because bacterial production mainly depends on autochtonous DOC

(DEL GIORGIO & PETERS 1994). Numerous studies have reported that the relative importance of external carbon inputs to overall plankton metabolism should decline as phytoplankton production increases, along the trophic gradient of lakes: planktonic P/R ratios are generally <1 in oligotrophic and mesotrophic lakes and are >1 in eutrophic lakes (DEL GIORGIO & PETERS 1993*a*, DEL GIORGIO & PETERS 1994, BIDDANDA *et al.* 2001). Plankton respiration exceeds algal photosynthesis in oligotrophic lakes, and P/R rises above unity only when chlorophyll concentrations are above 17 mg m^{-3} (DEL GIORGIO & PETERS 1993*a*).

The controlling factors of bacterio- and phytoplankton, and relationships between pelagic algae and bacteria are important for understanding the functioning of the pelagic ecosystem (COVENEY & WETZEL 1995, KISAND *et al.* 1998). Several authors have attempted to describe the nature of the relationship between phytoplankton and bacterioplankton by means of empirical models: the abundance (or production) of heterotrophic bacteria positively correlated with the biomass of phytoplankton (chlorophyll-*a* concentration) or the primary production (BIRD & KALFF 1984, FUKSA 1990, CURRIE 1990, DEL GIORGIO & PETERS 1993*b*, JEPPENSEN *et al.* 1997, ZINABU & TAYLOR 1997, KONCZ *et al.* 1999).

In the present study, we examine the net metabolism and relation between gross phytoplanktonic primary production and planktonic respiration in two shallow, turbid alkaline pans in Hungary. These water bodies are both extremely turbid hypertrophic pans with little Secchi-disk transparency. The pans have hyposaline water dominated by Na^+ and HCO_3^- ions, and high conductivity and pH. By quantitative examination of phytoplankton and bacterioplankton as well as production and respiration measurements, this study adds to the limited knowledge of the role of bacteria and allochtonous C in hypertrophic, turbid lakes.

MATERIALS AND METHODS

Study sites and sampling

Samples for production and respiration measurements were collected monthly from two turbid soda ponds (“Kelemen-szék” pan and “Zab-szék”pan) after the melting of the ice in March 2002 until the ponds dried out in August 2002 in “Kelemen-szék” pan and in July 2002 in “Zab-szék” pan. “Kelemen-szék” pan and “Zab-szék” pan are the most characteristic and largest turbid soda pans in Hungary. Samples for bacterial measurements were collected monthly from eight soda ponds from August 2004 to October 2004 (Table 1). These intermittent shallow alkaline pans frequently dry out entirely by the end of summer. The average water depth of the studied ponds varied between 7 and 24 cm except Kastély-pond, which has a relatively large water-depth (110–150 cm). Kastély-pond is a relative clear soda pond with higher Secchi-disk transparency, however the other ponds are typical turbid shallow pans with very low Secchi-disk transparency (1–5 cm), which was due to high concentrations of suspended particles and dissolved coloured (humic) substances. Their salinity varies be-

Table 1. Selected physical and chemical parameters of the studied water bodies

Lake	Coordinates N	Coordinates E	Surface area (ha)	Water depth (cm)	Secchi-disc (cm)	pH	Conductivity (µS cm^{-1})	Dominant ions
“Böddi-szék” pan, Dunatetétlen	46°46’	19°8’	117	< 40	4	9.3	7900	Na; HCO_3 > Cl
“Zab-szék” pan, Szabadszállás	46°50’	19°10’	100	< 40	1	9.1	3200	Na; HCO_3 > Cl
“Kastély pond”, Dunatetétlen	46°46’	19°08’	1	~ 100	25	9.1	5000	Na; HCO_3 > Cl
“Kelemen-szék” pan, Fülöpszállás	46°49’	19°11’	120	< 40	2	9.1	4300	Na; HCO_3 > Cl
“Büdös-szék” pan, Szabadszállás	46°52’	19°10’	30	< 40	1	9	3100	Na; HCO_3 > Cl
“Büdös-szék” pan, Pusztaszer	46°33’	20°2’	50	< 40	3	9	2600	Na; HCO_3
“Bogárzó-szék” pan, Solt	46°48’	19°08’	20	< 40	2.5	9	4700	Na; HCO_3 > Cl
“Fehér-tó” pan, Kardoskút	46°28’	20°37’	70	< 40	1	9.1	2900	Na; HCO_3 > Cl

tween hypo- and mesosaline ranges corresponding to the season and water level with conductivity values between 1800–13000 µS cm^{-1}. These water bodies are characterized by the dominance of Na$^+$, HCO_3^-, and Cl$^-$ ions with pH values between 9 and 10 (Table 1).

Measurements

The total abundance of autotrophic picoplankton (APP) was enumerated by epifluorescence microscopy. In freshly collected samples the cells were filtered onto black polycarbonate membranes (Millipore, 0.4 µm pore size) and the filter was embedded into 50% glycerol. Slides were investigated with a Nikon Optiphot-2 epifluorescence microscope equipped with a SPOT RT camera. The cells were enumerated with blue-violet (BV 2A) and green (G 2A) excitation light. Using this experimental procedure, the red fluorescencing phycocyanin-rich cyanobacteria and eukaryotic (phycobiliprotein lack) cells were distinguished (MacIsaac & Stockner 1993).

The total abundance of bacteria (TB) was determined by the acridine orange direct count method (Hobbie *et al.* 1977). Subsamples fixed with formaldehyde (final concentration 1.5%) were filtered through black, 0.2 µm pore-sized polycarbonate filters (Millipore). Slides were investigated with a Nikon Optiphot-2 microscope equipped with a SPOT RT camera. More than 400 cells were counted with blue (B 2A) excitation light.

The chlorophyll *a* concentration of the phytoplankton samples was determined spectrofluorometrically after hot methanol extraction (Wetzel & Likens 1991).

Primary production (GPP) and community respiration (R) was measured by the “light-dark bottle” method (Vollenweider 1969) monthly in two alkaline turbid lakes: “Kelemen-szék” pan and “Zab-szék” pan. The measurements started after ice melting in March 2002 and lasted 6 months till the ponds dried out in summer 2002. To estimate the rates of net production and dark community respiration, water samples were transferred into 300 ml Karlsruhe-bottles. For each station, 4 bottles were placed into an opaque plastic box (dark bottles) and 4 bottles were placed into a lake water filled basin at in situ irradiance. The bottles were placed upside down into the basin, the bottom of the bottles reached the water surface, and the height of the Karlsruhe-bottles exceeded the euphotic depth of the ponds. The in situ temperature-insuring lake water was changed hourly. Incubations lasted for 5 hours between 9 and 14 h. Measurements of dissolved oxygen before and after the incubation were made with WTW Oxi 539 dissolved oxygen meter with TriOxmatic 300 electrode.

Respiration rate (R) and gross primary production (GPP) were calculated as mg O_2 m^{-2} $hour^{-1}$. Daily GPP was calculated from the hourly values assuming that $GPP_{daily} = GPP_{hourly} \times$ (daylight hours – 2) while the respiration was calculated assuming that R_{day} = R hourly × 24.

The birds were counted by means of binoculars (8×42) and field scopes (30×75) weekly or biweekly on the opened water bodies of the pans in 2002 in order to estimate the carbon excretion of aquatic birds. The daily numbers of the birds were considered by average of weekly or biweekly counting data per each month. The net C inputs of the lakes from the aquatic bird guilds were estimated by the daily net C excretion for all species (see the details in BOROS *et al.* 2008).

RESULTS

Phytoplankton biomass and composition

During the study period both "Kelemen-szék" pan and "Zab-szék" pan was hypertrophic (OECD) with 95 μg l^{-1} maximum chlorophyll *a* concentration for "Kelemen-szék" pan and 348 μg l^{-1} for "Zab-szék" pan (Fig. 1). The average chlorophyll *a* concentration was 29 μg l^{-1} in "Kelemen-szék" pan and 145 μg l^{-1} in "Zab-szék" pan. The phytoplankton of the studied ponds was almost exclusively dominated by pico-sized algae (autotrophic picoplankton, APP). Picoeukaryotic green algae constituted the APP in spring (from March to May) while red-fluorescent phycocyanin containing picocyanobacteria dominated in summer. The maximum abundance of eukaryotic picoalgae was relative high (23×10^6 cells ml^{-1}) in "Zab-szék" pan at the end of April, while it was lower in "Kelemen-szék" pan (2.6×10^5 cells ml^{-1}) in March. The maximum abundance of picocyanobacteria was also high (30×10^6 cells ml^{-1}) in "Zab-szék" pan in June, as well as in "Kelemen-szék" pan (10×10^6 cells ml^{-1}).

Primary production and respiration

The maximum production (GPP) was measured in July (3750 mg O_2 m^{-2} d^{-1}), while the minimum GPP was measured in April (5 mg O_2 m^{-2} d^{-1}) in "Kelemen-szék" pan. The maximum production value was 2510 mg O_2 m^{-2} d^{-1} for "Zab-szék" pan, which was measured in June, while there was no measurable GPP in July (Fig. 1). The average GPP was 920 mg O_2 m^{-2} d^{-1} in "Kelemen-szék" pan and 740 mg O_2 m^{-2} d^{-1} in "Zab-szék" pan. The total gross primary production (TGPP) was 131 g

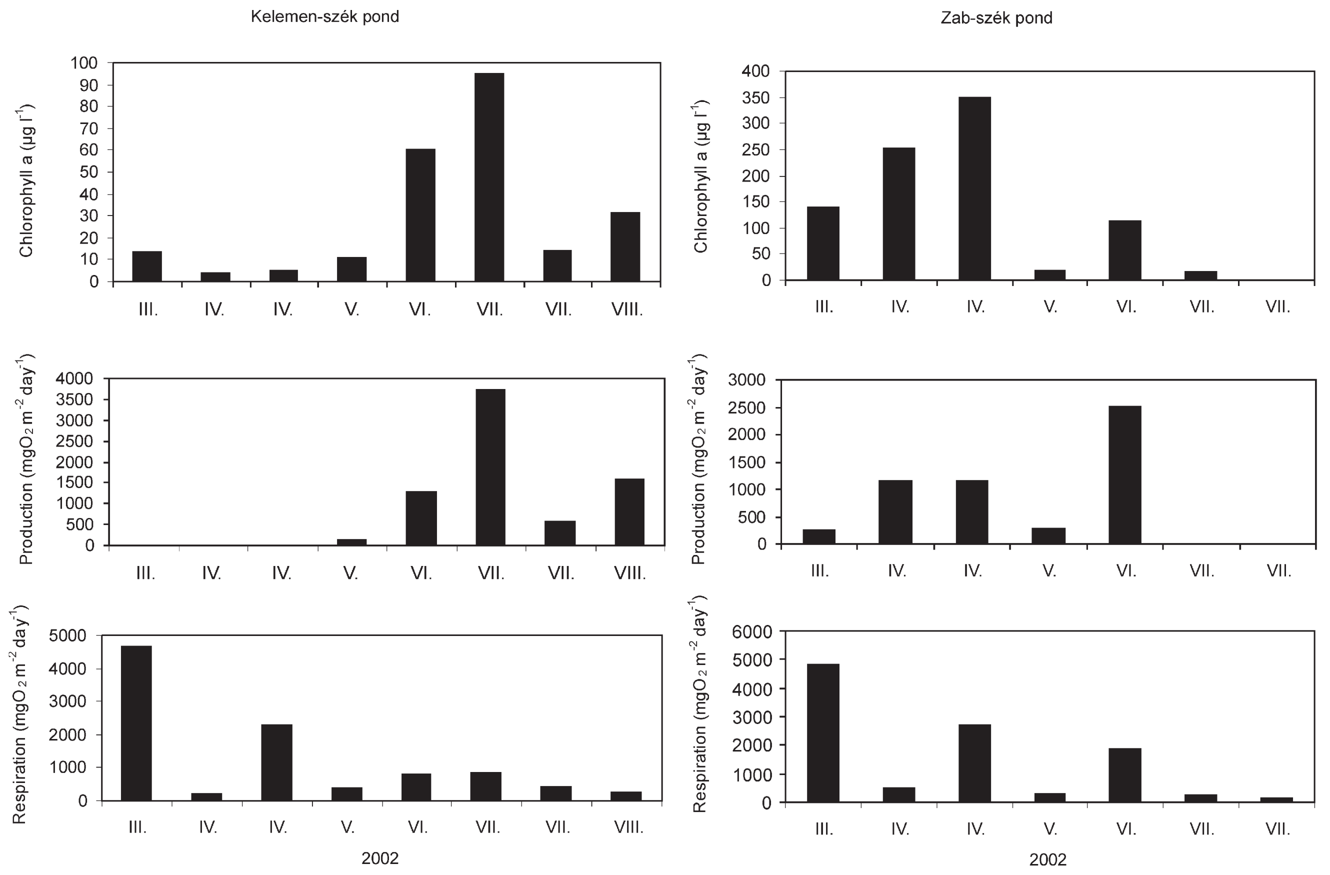

Fig. 1. Chlorophyll *a* concentration, surface-related gross primary production, and community respiration in "Kelemen-szék" pan and "Zab-szék" pan from March 2002 to August 2002

O_2 m^{-2} 6 $months^{-1}$ for “Kelemen-szék” pan and 124 g O_2 m^{-2} 6 $months^{-1}$ for “Zab-szék” pan. The maximum values of community respiration (R) were measured in both ponds in March (Fig. 1): it was 4600 mg O_2 m^{-2} d^{-1} for “Kelemen-szék” pan and 4800 mg O_2 m^{-2} d^{-1} for “Zab-szék” pan. The minimum R was 240 mg O_2 m^{-2} d^{-1} in “Kelemen-szék” pan in August and 150 mg O_2 m^{-2} d^{-1} in “Zab-szék” pan in July. The average community respiration was 1230 mg O_2 m^{-2} d^{-1} for “Kelemen-szék” pan and 1510 mg O_2 m^{-2} d^{-1} for “Zab-szék” pan. The total respiration (TR) was 240 g O_2 m^{-2} 6 $months^{-1}$ for “Kelemen-szék” pan and 270 g O_2 m^{-2} 6 $months^{-1}$ for “Zab-szék” pan.

The GPP/R ratios were usually below 1 except during the most productive period of the ponds. The P/R ratios calculated from the TGPP and TR values was 0.55 for “Kelemen-szék” pan and 0.46 for “Zab-szék” pan.

Organic carbon from aquatic birds

The maximum C load of “Kelemen-szék” pan produced by aquatic birds was 4300 mg C m^{-2} $month^{-1}$, while the minimum was 159 mg C m^{-2} $month^{-1}$. The maximum C load of “Zab-szék” pan originating from aquatic birds was 13600, the minimum was 100 mg C m^{-2} $month^{-1}$. The maximum values were measured in November, while the minimum values were measured in May. The average monthly carbon load derived from aquatic birds was 1230 mg C m^{-2} $month^{-1}$ in “Kelemen-szék” pan and 3230 mg C m^{-2} $month^{-1}$ in “Zab-szék” pan. The annual absolute carbon load of the ponds produced by aquatic birds in 2002 was 10350 kg in “Kelemen-szék” pan and 14770 kg in “Zab-szék” pan. The surface-related load from

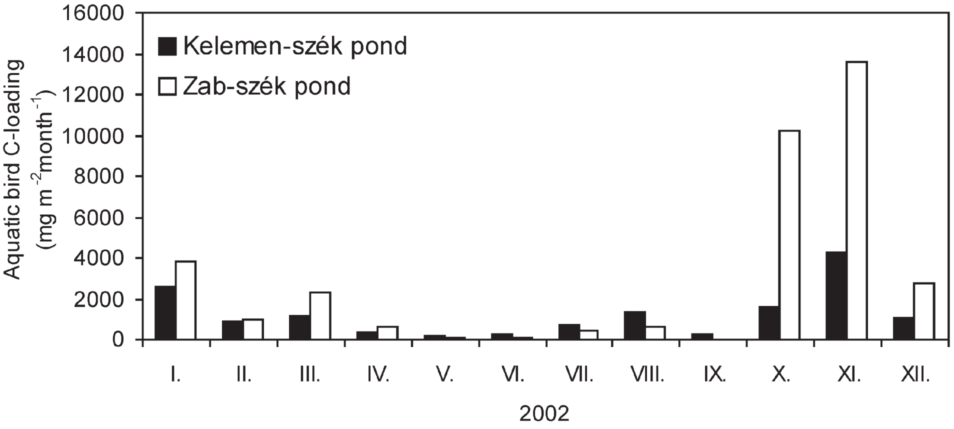

Fig. 2. Allochtonous organic carbon load of “Kelemen-szék” pan and “Zab-szék” pan released from aquatic birds in 2002

aquatic birds was 14.8 g C m^{-2} $year^{-1}$ in "Kelemen-szék" pan and 35.6 g C m^{-2} $year^{-1}$ in "Zab-szék" pan.

Bacterioplankton

The abundance of bacteria varied between 5 – 659 × 10^6 cells ml^{-1}, the chlorophyll *a* concentration ranged between 5.7 and 332 µg l^{-1} from August to October in 2004 in the studied eight turbid, alkaline lakes. The highest chlorophyll *a* concentration value was measured in "Büdös-szék" pan, Szabadszállás in October, while the lowest was measured in "Kelemen-szék" pan in September. The highest bacterial abundance (659 × 10^6 cells ml^{-1}) was measured in "Böddi-szék" pan in October, while the lowest (5 × 10^6 cells ml^{-1}) was measured in "Fehér-tó" pan, Kardoskút in August. All studied ponds showed higher bacterial abundance values in autumn than in summer, which was independent from chlorophyll *a* concentration (Fig. 3).

DISCUSSION

During the study period, "Zab-szék" pan proved to be more productive than "Kelemen-szék" pan, although both ponds were hypertrophic. The observed picoalgal abundance values correspond well to the measured chlorophyll *a* concentra-

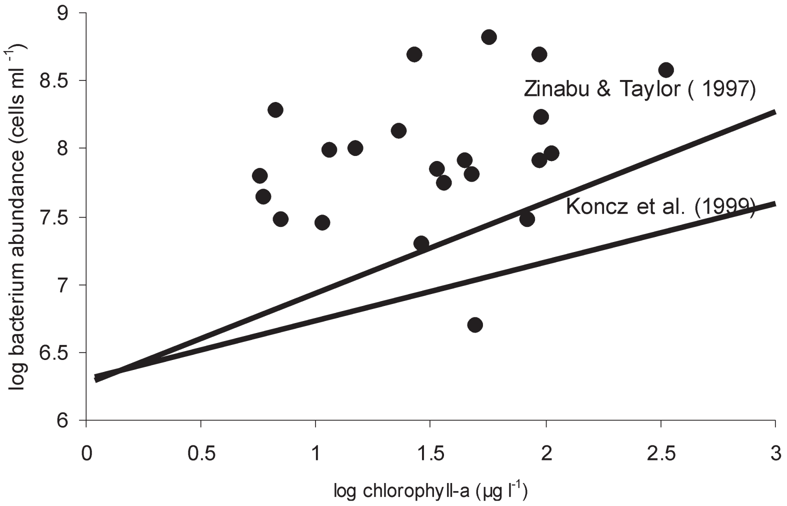

Fig. 3. Bacterium abundance versus chlorophyll *a* concentration in Hungarian soda pans in 2004 comparing with ZINABU and TAYLOR's (1997) equation based on Ethiopian soda ponds and empirical shallow lake model of KONCZ *et al.* (1999)

tions. The chlorophyll *a* concentration increased from March to the end of April in “Zab-szék” pan, while it decreased rapidly when the picoeukaryotic algae disappeared. In summer, the chlorophyll *a* concentration increased again as the picocyanobacteria grew until the pond was dried out. There was not such a high picoeukaryotic algal peak in “Kelemen-szék” pan in spring, but in summer the pond showed a similar tendency: the chlorophyll *a* concentration increased with the growing of picocyanobacteria until August, when the pond dried out (Fig. 1).

The measured GPP was in good connection with chlorophyll *a* concentration. In “Kelemen-szék” pan GPP was very low (5–8 mg O_2 m^{-2} d^{-1}) in spring, than it increased with the chlorophyll *a* concentrations following its changes (Fig. 1). In “Zab-szék” pan GPP was relative high in spring (300–1150 mg O_2 m^{-2} d^{-1}) but not as much as the maximum chlorophyll values indicated, which was surely due to the low water temperature (Fig. 1). In summer GPP also increased with the increasing chlorophyll-a concentration. The respiration didn’t correspond with the chlorophyll *a* changes, the maximum respiration values were measured in early spring when the chlorophyll *a* concentration was lower, which refers to the presence of allochtonous organic matter. The maximum respiration values were much higher than the maximum values of GPP, which also shows the importance of allochtonous organic matter.

The ratio of planktonic primary production to community respiration (P/R) in these lakes was below 1, which indicates that under the study period these ponds were net heterotrophic. DEL GIORGIO and PETERS (1993*a*) showed that the P/R ratio varied systematically with lake trophy: oligotrophic lakes have been supposed to be net heterotrophic and 17 μg l^{-1} chlorophyll *a* concentration indicate the turning point, eutrophic and hypertrophic lakes have been supposed to be net autotrophic for the increase of primary production and the decrease of the role of allochtonous organic matter. These findings do not correspond with our results: in spite of the fact that the average chlorophyll *a* concentration of these ponds was far above 17 μg l^{-1}, these ponds proved to be net heterotrophs (Fig. 4).

The monthly carbon load deriving from aquatic birds shows characteristic seasonal dynamics: because of the absence of aquatic birds it is very low in summer; however it is a significant amount from autumn to spring due to the mass appearance of migratory and wintering birds. The amount of carbon load from aquatic birds was usually higher in “Zab-szék” pan especially under the more important autumn-winter period (the maximum carbon load was three times higher) than in “Kelemen-szék” pan. The higher productivity of “Zab-szék” pan can be related by the net N- and P-load from aquatic birds.

In spite of the high phytoplankton biomass of the ponds, respiration was not correlated with the chlorophyll *a* concentration, however a strong correlation was found between respiration and the net C loading from aquatic birds which clearly supports the determining role of allochtonous organic matter in these alkaline water bodies (Fig. 5).

Bacterioplankton play the main role in transformation and degradation of organic matter. The observed extreme high bacterial abundance values "per se" refer to the presence of huge amounts of dissolved organic matter. During the past decades several studies described extreme high bacterial abundance and chlorophyll *a* concentration values in turbid soda lakes (KILHAM 1981, EILER *et al.* 2003), however, our maximum bacterial abundance value (659×10^6 cells ml^{-1}) exceeded the values of the Ethiopian shallow alkaline ponds (KILHAM 1981).

Numerous empirical models have been published describing the relationship between bacterio- and phytoplankton in a wide range of water bodies. These empirical relationships (between log bacterial abundance (cells ml^{-1}) and log chlorophyll *a* concentration (µg l^{-1}) are very similar: the slopes of the curves are lower than 1 and the intercept of the y axis varies between 5.8–6.5 (BIRD & KALFF 1984, FUKSA 1990, CURRIE 1990, DEL GIORGIO & PETERS 1993*b*, JEPPENSEN *et al.* 1997, KONCZ *et al.* 1999).

ZINABU and TAYLOR (1997) described an empirical relationship between bacterial abundance and chlorophyll *a* concentration by data from Ethiopian soda ponds which was above the described regression lines. No relationship has been found between chlorophyll *a* concentration and bacterial abundance values in Hungarian shallow alkaline pans, which indicate, that other factors – for example allochtonous organic matter – play more important role controlling the bacterial population in these shallow soda pans than the planktonic primary production. The

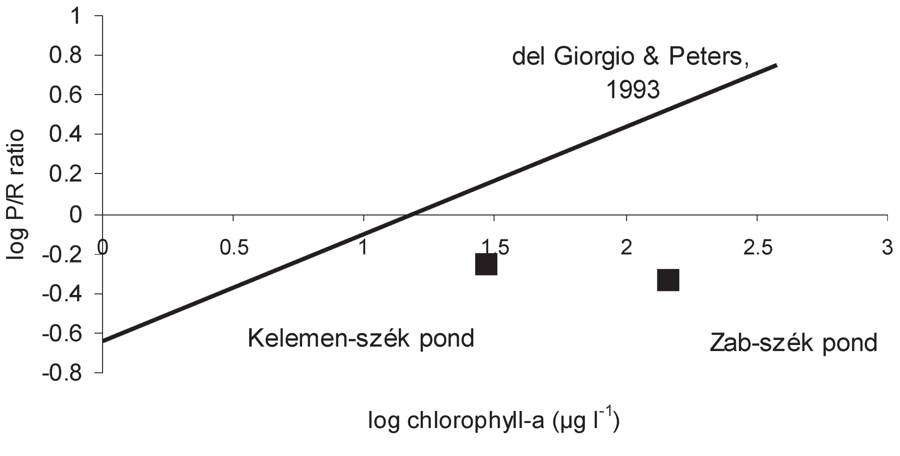

Fig. 4. Production/respiration ratio (calculated from the TGPP and TR values) versus chlorophyll *a* concentration in "Kelemen-szék" pan and "Zab-szék" pan comparing with empirical model of DEL GIORGIO and PETERS (1993)

measured chlorophyll *a* concentration-bacterial abundance values constitute a distinct data set above ZINABU and TAYLOR's (1997) empirical relationship (Fig. 3). This indicates that the bacterioplankton in these soda lakes depends mainly on the net carbon input from aquatic birds instead of planktonic primary production.

These characteristic Hungarian soda pans constitute a specific group among a wide range of water bodies, not only for their special chemical composition and high turbidity, but also in point of their nutrient-cycling processes: in spite of their hypertrophic relations, neither the bacterium abundance values, nor the rate of respiration correlate to the production or the biomass (chlorophyll *a* concentration) of phytoplankton. The explanation of this phenomenon is the huge amount of organic carbon load from migrating or overwintering aquatic birds, which cause extreme high bacterial abundance and community respiration. The intensity of the main ecological processes (primary production and respiration) is almost exclusively determined by aquatic birds in these shallow soda pans.

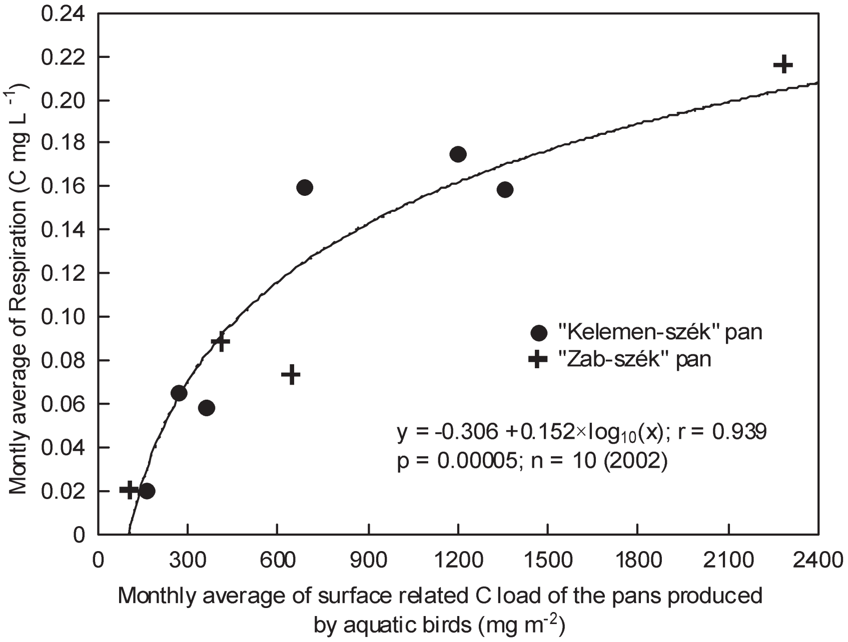

Fig. 5. Relationship between surface related aquatic bird C-loading and volume specific plankton respiration in the studied pans ("Kelemen-szék" pan and "Zab-szék" pan) in 2002

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