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Phytoplankton and bacterioplankton production in a reed-covered water body

Lajos Vörös*, Katalin V.-Balogh, Eszter Koncz, Attila Kovács

Balaton Limnological Research Institute of the Hungarian Academy of Sciences, P.O. Box 35, H-8237 Tihany, Hungary

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Abstract

Between 1996 and 1998 phytoplanktonic primary production and bacterioplankton production were measured monthly at five sampling stations in the lower Kis-Balaton reservoir. The open water area of the reservoir was rich in phytoplankton and had hypertrophic characteristics, but inside the reed stand (80% of the surface area) phytoplankton biomass and production were substantially (30–50 times) lower. The algal removal efficiency of the lower Kis-Balaton reservoir was 96%. The reservoir had a considerably smaller effect on bacterioplankton removal than on the phytoplankton. The decrease of biomass and production of bacterioplankton in the through-flowing water was approximately 60%. Inside the reed stand the biomass and the production of planktonic bacteria exceeded that of the phytoplankton by several times, suggesting that the release of biodegradable dissolved organic (humic) substances from macrophytes stimulated the metabolism of bacterioplankton. The significant reduction of phytoplankton inside the dense reed stand was primarily the result of the shading effect of the reeds. In the open water area a shading experiment demonstrated that a 1-week residence period for planktonic algae in the reed-covered area was sufficient for their complete elimination. The decomposition of planktonic algae, reed material and the lack of primary production inside the reed stand created oxygen-deficient and phosphorus-rich conditions during the vegetative period. These results suggest that reed-covered water bodies can effectively retain suspended solids and planktonic algae, but because of decomposition processes they cannot retain biologically-available phosphorus.

Keywords: Shallow reservoir; *Phragmites australis*; Shading effect; Humic substances; Phytoplankton; Bacterioplankton; Phosphorus retention

* Corresponding author. Tel.: +36-87-448244x118; fax: +36-87-448006.
E-mail address: vorosl@tres.blki.hu (L. Vörös).

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1. Introduction

During the last two decades the relationship between phytoplankton and bacterioplankton has become the focus of much research. In marine and freshwater pelagic ecosystems planktonic algae are the major source of substrates for planktonic bacteria. Large scale intersystem studies show that bacterial abundance and productivity are consistently related to algal abundance and productivity. Several independent estimates on marine and freshwater pelagic ecosystems have shown that bacteria utilise a large fraction (up to 90%) of primary production (Bird and Kalff, 1984; Cole et al., 1988; Lavandier, 1990). While numerous studies have focused on pelagic ecosystems, research exploring how the submerged and emerged macrophytes affect the structure and functioning of phytoplankton and bacterioplankton has been relatively limited (Komárková and Komárek, 1975; Kleppel et al., 1980; Middelboe et al., 1998; Mitamura and Tachibana, 1999; Reitner et al., 1999; Scheffer, 1999; Theil-Nielsen and Sondergaard, 1999).

Lake Balaton is a large shallow lake situated in western Hungary. By the 1970s, the south-western areas of the lake became hypertrophic, and summer blooms of filamentous nitrogen-fixing cyanobacteria created environmental problems with consequences for the water supply and recreation (Herodek, 1986).

Several measures have been taken since 1980 to reduce the nutrient load of the lake. The Kis-Balaton Water Protection System at the mouth of the Zala River was constructed for the non-point source nutrient—mainly phosphorus—control of Lake Balaton (Pomogyi, 1993a,b). This system has two large shallow reservoirs, of which the upper one was flooded in 1984 and the lower one in 1992. The surface area of the upper Kis-Balaton reservoir is 18 km^2 with a mean depth of 1.1 m. This reservoir is almost free of submerged and emerged macrophytes and has a hypertrophic character due to the mass development of planktonic algae (cyanobacteria, diatoms and green algae). The lower Kis-Balaton reservoir is designed to have a surface area of 51 km^2, and a mean depth of 1.2 m. In 1992, a 16 km^2 experimental area of this second reservoir was flooded. Approximately 80% of its area was covered by macrophytes, almost exclusively by reed (*Phargmites australis* (Cav.) Trin. ex Steud.). The lower Kis-Balaton reservoir was expected to retain both phosphorus and large phytoplankton biomass derived from the upper reservoir.

The aim of the study was to evaluate the mechanisms and effect of the dense reed stand of the lower Kis-Balaton reservoir on the phyto- and bacterioplankton biomass and production in the through-flowing water in connection with the required water protection role of the system.

2. Material and methods

2.1. Study sites and sampling

Between 1996 and 1998, regular monthly sampling were carried out from April to October from four stations. Station 1 (46°38′13″N, 17°11′00″E) was situated at the outlet of the upper Kis-Balaton reservoir (the inlet of the lower one) and Station 2 (46°39′22″N, 17°11′39″E) was situated at the upper open water area of the lower reservoir. The Station 3 (46°40′46″N,

17°12′21″E) and Station 4 (46°39′53″N, 17°13′12″E) were located inside the dense reed stand of the reservoir (Station 3 was the central part and Station 4 was the outlet of the lower Kis-Balaton reservoir). The Station 4 was near the mouth region of the Zala River, the main tributary of Lake Balaton.

2.2. Phytoplankton biomass and production

At the sampling stations, downwelling fluxes of photosynthetically active radiation (PAR) were measured with a Li-Cor, Inc. Model LI 185B radiometer equipped with 2π underwater and air quantum sensors. Phytoplanktonic chl *a* concentration was determined spectrophotometrically after hot methanol extraction (Iwamura et al., 1970). The phytoplankton biomass was calculated from the chl *a* concentration values assuming that the chl content is 0.5% of the fresh weight (Vörös and Padisák, 1991).

Primary production of phytoplankton was measured with the ^{14}C technique (Vollenweider, 1969). The water samples of 50 ml with 0.4 MBq sodium-^{14}C-bicarbonate were kept for 2 h in an incubator system (photosynthetron) at lake temperature at seven irradiances between 10 and 460 $\mu mol\ m^{-2}\ s^{-1}$. The exponential saturation equation of Webb et al. (1974) was used to describe the light dependence of photosynthesis. In the open water Stations 1 and 2 surface related photosynthesis was calculated using light attenuation coefficients of the water columns and actual global radiation data, integrated over each hour from sunrise to sunset, through 0.1 m layers in the water column (Présing et al., 1999). At sampling Stations 3 and 4, the actual global radiation was lowered by the measured light absorption of the reed stands. Forty-eight percentage of the global radiation was considered photosynthetically active radiation (Wetzel and Likens, 1990).

2.3. Bacterioplankton abundance and production

Bacterioplankton abundance was determined by acridine orange staining and epifluorescence microscopy (Hobbie et al., 1977). Bacterial cell volumes were estimated from length and width measurements and geometric formulas. The total biovolume of bacterioplankton assemblages was converted to fresh weight (biomass) assuming a specific gravity of 1.0. For thymidine incorporation studies, the procedure of Fuhrman and Azam (1982) was followed. Subsamples of 20 ml were incubated at the original water temperature for 0.5 h with [methyl-^{3}H]thymidine (specific activity 42 Ci $mmol^{-1}$; Amersham Life Science) at a final concentration of 20 nmol l^{-1}. After the incubation period uptake was stopped with formaldehyde addition. The bacterial uptake of thymidine was converted to cell production by the factor 2.0×10^{18} cells mol^{-1} thymidine. To calculate the bacterial carbon production from the cell production, 20 fg C per cell was used (Lee and Fuhrman, 1987). Bacterial growth efficiency was assumed to be 30% (Sorokin, 1999).

2.4. Water quality monitoring data

To evaluate the differences between the inflowing (Station 1) and outflowing (Station 4) water quality of the lower Kis-Balaton reservoir the weekly measured soluble reactive

phosphorus (SRP), total phosphorus (TP) and dissolved oxygen (DO) concentration data of the West Transdanubian Water Authority (Szombathely, Hungary) were used.

2.5. Enclosure experiment

At the end of July 1994, three enclosures were installed in the upper region of the 1 m deep open water area of the lower reservoir. The diameter of the plastic enclosures was 1.5 m and were open to the sediment which their rigid walls were sunk in. One of them was open to the air, two of them were shaded by grey plastic sheets. The water surface of the first unshaded enclosure received the total PAR, the second one received 5%, and the third one only 1% of the PAR. At the beginning of the experiment and after 24, 40, and 144 h, the phytoplankton biomass (chl *a*), DO (HI 9143 Microprocessor DO meter), and SRP concentration (Murphy and Riley, 1962) were measured in the enclosures and in the surrounding water.

3. Results

3.1. Changes of phytoplankton and bacterioplankton biomass through the reservoir

During the 3-year period, in the outlet of the upper reservoir (Station 1) and the open water area of the lower reservoir (Station 2) the highest phytoplankton biomass (estimated from the chl *a* measurements) was found in August with averages of 52 ± 5 and $45 \pm 2\,mg\,l^{-1}$, respectively. Leaving Station 2 the water reached the reed-covered area and flowed approximately 2 km through the dense reed stand before reaching Station 3. Here, the phytoplankton biomass decreased significantly, the summer maximum occurred in July, with an average of $9 \pm 2\,mg\,l^{-1}$. In the outlet, from May to October the monthly averages ranged between 0.47 ± 0.04 and $1.06 \pm 0.22\,mg\,l^{-1}$ at Station 4. (Fig. 1). The average phytoplankton retention of the reservoir was 96%.

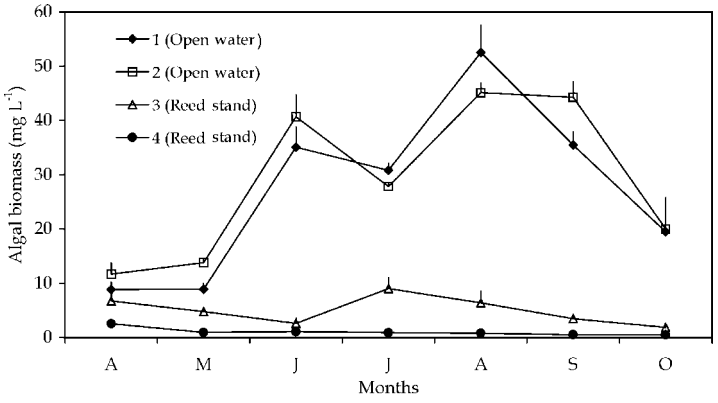

Fig. 1. Seasonal changes of the phytoplankton biomass in the lower Kis-Balaton reservoir in 1996–1998 (3-year averages and standard deviation).

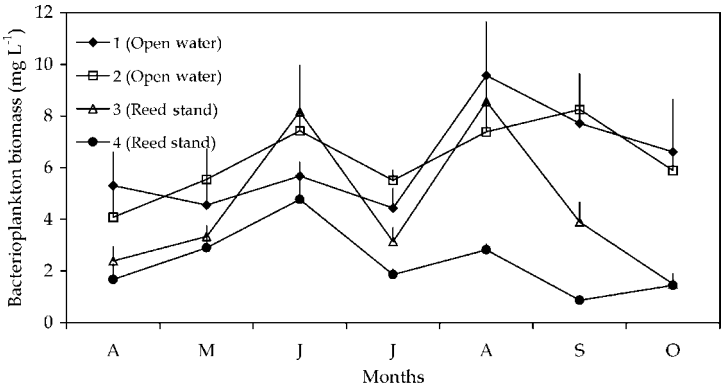

Fig. 2. Spatial and temporal changes of the bacterioplankton biomass in the lower Kis-Balaton reservoir in 1996–1998 (3-year averages and standard deviation).

In the open water bodies of the upper and lower Kis-Balaton reservoirs (Stations 1 and 2) seasonal changes of bacterioplankton biomass followed the alterations of algal biomass. At Station 1 the highest bacterial biomass was found in August, $9.6 \pm 0.71\ mg\ l^{-1}$. At Station 2, the maximum bacterioplankton biomass was found in September, $8.3 \pm 1.4\ mg\ l^{-1}$. The lowest bacterial biomasses were usually found in spring. Inside the reed stand, at Station 3, the bacterioplankton biomass decreased in spring and autumn, but there was no significant decrease in summer. At Station 4, the bacterioplankton biomass showed moderate decrease during the whole period (Fig. 2). The average decrease of the bacterioplankton biomass in the reservoir was 58%.

3.2. Changes of phytoplankton and bacterioplankton production through the reservoir

The phytoplanktonic primary production increased from April to August than decreased to October, showing a typical seasonal pattern at Stations 1 and 2. The summer maximum reached the value of $11.2\ g\ C\ m^{-2}$ per day in August when the monthly averages were 7.2 ± 1.2 and $5.4 \pm 0.68\ g\ C\ m^{-2}$ per day, respectively. At Stations 3 and 4 the primary production dramatically decreased, and the seasonal dynamics also changed. The production values steadily decreased from April to August (Fig. 3). The average decrease of phytoplanktonic primary production was 98% in the reservoir.

In the open water areas (Stations 1 and 2) the bacterial production was as high as the phytoplankton production and showed similar seasonal pattern. The summer maximum reached the value of $12.0\ g\ C\ m^{-2}$ per day. Inside the reed zone (Stations 3 and 4) the decrease of bacterioplankton production was less significant, than the decrease of the algal production. At Station 3 the monthly average bacterial production values ranged between 1.06 ± 0.13 and $2.6 \pm 0.22\ g\ C\ m^{-2}$ per day, while at Station 4 they ranged between 0.51 ± 0.17 and $2.14 \pm 0.72\ g\ C\ m^{-2}$ per day (Fig. 4). The average decrease of the bacterioplankton production was 64% in the reservoir.

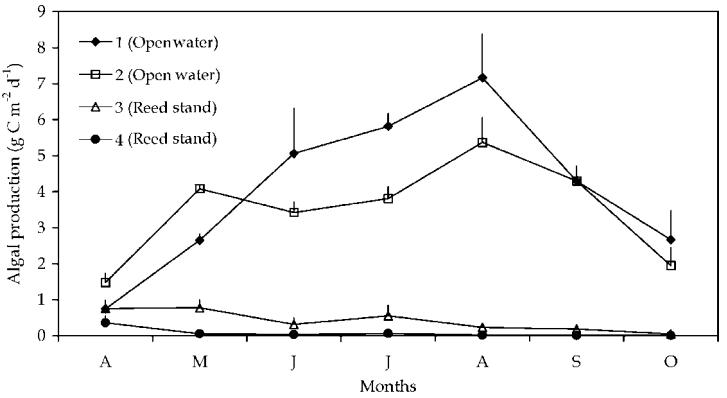

Fig. 3. Spatial and temporal changes of the phytoplankton production in the lower Kis-Balaton reservoir in 1996–1998 (3-year averages and standard deviation).

3.3. Changes of phytoplankton biomass and phosphorus concentration during the shading experiment

At the end of the week-long field experiment, in the open enclosure the phytoplankton biomass was $62 \pm 9\,mg\,l^{-1}$ and the SRP concentration $118 \pm 5\,\mu g\,l^{-1}$. The algal biomass and SRP concentration values were identical in the surrounding water. However, the light reduction resulted in rapid and significant changes of them. Two days of 95% shading resulted in 30%, 6 days already 90% decrease of phytoplankton biomass, while the SRP concentration increased three times at the end of the experiment. The almost complete (99%) shading had more drastic effect. In this enclosure the algal biomass decreased of 90% in 2 days, while only 3% of the initial biomass remained at the end of the experiment. At the same time the SRP concentration was one order of magnitude higher, than that in the open water or in the open enclosure (Fig. 5).

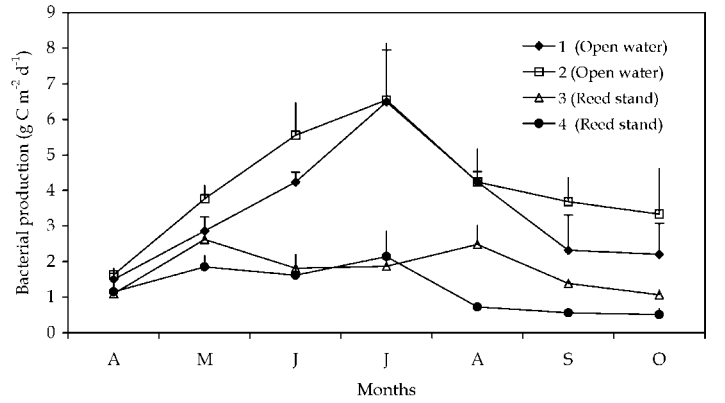

Fig. 4. Spatial and temporal changes of bacterioplankton production in the lower Kis-Balaton reservoir in 1996–1998 (3-year averages and standard deviation).

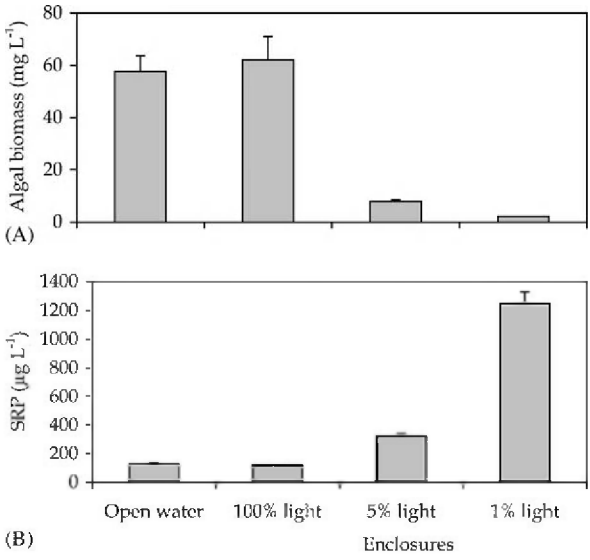

Fig. 5. Phytoplankton biomass (A) and soluble reactive phosphorus (SRP) concentration (B) in different experimental variants at the end of the 6-day long enclosure experiment.

In the experimental enclosures, parallel with the decrease of phytoplankton biomass and increase of the SRP concentration, the DO concentration also significantly decreased. At the end of the experiment, the open water and the open enclosure were supersaturated with oxygen around noon, while the shaded enclosures were oxygen-deficient (10 and 5% of saturation) at this time.

3.4. Changes of dissolved oxygen and phosphorus concentration in the reservoir

During winter and spring, when the shading effect of the reed stand was moderate, DO concentration was higher due to the production of planktonic and benthic algae. However, in summer and autumn, when the shading was stronger the DO concentration was very low, indicating oxygen deficiency in the reservoir. At Station 1 the annual average DO concentration was 7.6 ± 2.4 mg O_2 l^{-1}, at Station 2 it was 6.9 ± 2.0 mg O_2 l^{-1}. In the reed-covered area at Station 3 DO concentration was 4.0 ± 2.1 mg O_2 l^{-1} and in the outflowing water it was only 2.3 ± 1.5 mg O_2 l^{-1}.

The TP concentration showed more or less the same seasonal variations at Stations 1, 3 and 4 and did not alter significantly through the reservoir from the inflow to the outflow (Fig. 6). The SRP and TP concentration showed the same seasonal variation and did not differ significantly at Station 4, where the annual average SRP concentration was 156 ± 2 µg l^{-1} (Fig. 6). At Station 3, the SRP concentration was significantly lower, than that of the TP, the annual average was 82 ± 1.85 µg l^{-1}. At Station 1 the SRP concentration was extremely low, the values were below the detection limit almost during the half of the year, the maximum value was only 60 µg l^{-1} (Fig. 6).

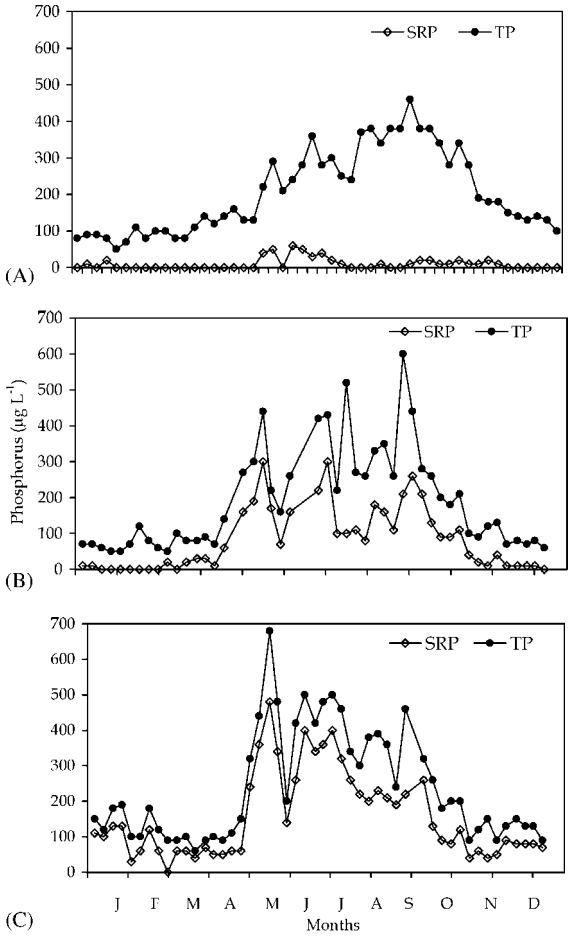

Fig. 6. Seasonal changes of total phosphorus (TP) and soluble reactive phosphorus (SRP) concentration, (A) in the inlet (Station 1); (B) in the reed zone (Station 3); (C) in the outlet (Station 4) of the lower Kis-Balaton reservoir (mean of triplicates).

4. Discussion

In marine and freshwater pelagic systems on average about one-half of the planktonic primary production is utilised by bacteria (Cole et al., 1988; Lavandier, 1990). The open water of the shallow Lake Balaton corresponds to this general finding where on the annual basis approximately 50% of the planktonic primary production was channelled through the bacterioplankton (Vörös et al., 1996a). The investigated water bodies of the lower Kis-Balaton reservoir presented a completely different picture.

In the open water areas, the planktonic primary production was as high as the bacterioplankton production. This alteration was most probably the result of the bacterial utilisation

of the additional (non phytoplanktonic) organic carbon source of planktonic bacteria. This reservoir is rich in dissolved humic substances and their bacterial utilisation could explain the relatively high bacterial production (V.-Balogh and Vörös, 1997). A similar situation was found in the Upper Bear Lake in Canada where the anthropogenic influences on water quality were minimal and the bacterioplankton biomass and production were higher than phytoplankton biomass and production. Here the allochtonous input of dissolved humic substances was the main organic carbon source of bacteria while the planktonic algae were seriously limited by inorganic N (Jansson et al., 2001). A stimulating effect of humic substances on growth and the abundance of bacteria is well known (Jones, 1992). Tranvik (1988) found that the productivity of natural bacterial assemblages from small Swedish lakes was highly positively correlated with DOC and humic matter under controlled laboratory conditions. Data from more than 600 freshwater lakes showed that epilimnetic bacteria production was four times higher in coloured (DOC rich) lakes than in clear waters (Nürnberg and Shaw, 1998). According to a comparative study in two oligotrophic Swedish lakes the ratio of bacterial secondary production to phytoplanktonic primary production was higher in the humic lake than in the clearwater lake, indicating that the bacterioplankton of the humic lake utilize allochtonous substrates, in addition to substrates originating from autochtonous primary production (Tranvik, 1989).

Inside the reed stand the phytoplankton production dramatically decreased. This decrease is explained by the rapid elimination of the planktonic algae under the severely light limited conditions of the water body of this wetland (Istvánovics et al., 1997). The decrease was lower in spring when the shading effect of the dead reed stand was moderate and it increased with the development of the new reed shoots (Figs. 1 and 2). When the young reed developed completely, usually less than 5% of the incoming PAR reached the water surface (Vörös et al., 1996b), which resulted in significant light inhibition of planktonic algae. It seems that the light deficiency of algae is one of the basic characteristic of the reed-covered water bodies because the dense stand of macrophytes can make the whole water column virtually aphotic (Ondok, 1978; Kirk, 1996). Our enclosure experiment clearly demonstrated the effect of shading on the open water phytoplankton. One week residence of planktonic algae in shaded environment resulted in almost complete elimination of them (Fig. 6). The average residence time of the river water in this wetland is 30 days, which could explain the highly efficient phytoplankton retention of this reservoir. In the lower Kis-Balaton reservoir the decomposition of planktonic algae, the oxygen consumption of dead reed material and the additional lack of primary production in the reed-covered water bodies create anoxic circumstances during the vegetation period, which resulted in an increased level of SRP in the outflowing water.

Inside the dense reed stand the bacterioplankton production significantly exceeded the planktonic primary production. In the middle of the reed stand it was 5 times and in the outlet it was 10 times higher than the phytoplankton production. In the reed-covered area the carbon source of planktonic bacteria derived from the particulate and dissolved organic carbon import from the open water areas, however the production of the above-ground biomass of the reed contributed significantly to the bacterially-available DOC pool of these waters. In the lower Kis-Balaton reservoir the organic carbon production of the above-ground biomass of the reed was as high as the phytoplanktonic primary production in the open waters 600–1200 g C m^{-2} per year (Szeglet, 1994) and its decompositon produced

significant amount of DOM (V.-Balogh et al., 1999). In the outflowing water of this reservoir system the average DOC concentration was $15 \pm 0.99\ mg\ l^{-1}$ while above these reservoirs in the inflowing Zala River the average DOC concentration was only $4.5 \pm 0.34\ mg\ l^{-1}$ (V.-Balogh and Vörös, 2001). There is experimental evidence that the conversion of vascular plant detritus into dissolved organic matter provides plant-derived carbon to populations of free-living bacterioplankton (Moran and Hodson, 1989).

A similar phenomenon was observable in Lake Neusiedl, a large shallow lake where approximately one-half of the surface area is covered by dense reed vegetation. Here the bacterioplankton carbon demand was always higher than carbon production of phytoplankton, indicating that bacterioplankton metabolism in Lake Neusiedl is heavily dependent on non-phytoplankton sources of DOC. This source is the production of the reed (*P. australis*) since there is no major allochtonous organic matter input from other sources (Reitner et al., 1999).

Our results suggest that the reed-covered water bodies of lower Kis-Balaton reservoir heterotrophic ecological systems are where the decomposition of the inflowing planktonic algae and the submerged and emerged macrophytes significantly exceed the light limited primary production. Due to the prevailing decomposition processes these wind-protected water bodies are permanently anaerobic or semi-anaerobic. At the same time the upstream water is oversaturated with O_2 during the day, but a temperature-dependent depletion occurs during the night (Istvánovics et al., 1997).

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