

Differential response of blue-green algal groups to phosphorus load reduction in a large shallow lake: Balaton, Hungary

Judit Padisák and Vera Istvánovics

Introduction

Lake Balaton is the largest shallow lake in Central Europe. The elongated lake (length: 77.9 km; average width: 7.2 km) has a surface area of 593 km², and has a mean depth of 3.14 m (maximum: 11 m). The theoretical retention time is 3–8 years. The catchment area of the lake is 5182 km²; the Zala River itself drains an area of 2622 km². As a result of the increased phosphorous load, the originally mesotrophic lake underwent rapid eutrophication in the 1960s–1970s (HERODEK 1984). Between 1975 and 1981, the total P load was estimated as 2.47 g m⁻² year⁻¹ in the western part of the lake, and 0.31 g m⁻² year⁻¹ in the eastern part (SOMLYÓDY & JOLÁNKAI 1986). As a consequence of the morphometric and loading conditions, a sharp trophic gradient has developed in the lake.

In the early 1980s, a large-scale eutrophication management program was started (ISTVÁNOVICS et al. in press). So far, the program has resulted in about 30% reduction of the biologically available P (BAP) load of the lake. This load reduction was expected to reduce slightly the phytoplankton development in the lake (HERODEK 1984).

This paper describes phytoplankton changes between 1989 and 1994 in two basins of the lake (Siófok Basin and Keszthely Basin) that are different in their trophic status. Special attention will be paid to *Cylindrospermopsis raciborskii*, a bloom-forming subtropical blue-green alga.

Material and methods

Phytoplankton samples were taken by a vertical tube sampler in the open water of the hypertrophic Keszthely Basin and in the less eutrophicated Siófok Basin. In 1989–1990, samples were taken biweekly. Later, at least one sample was taken each week in both areas during the vegetation period, while sampling was bi-weekly, sometimes monthly during the cold seasons. See map of the lake and its protecting reservoirs in ISTVÁNOVICS et al. 1997. Phytoplankton was counted under an inverted microscope (error: ±10%). Annual average data were calculated as follows:

1. Each not present data were set to zero biomass (the matrices were filled in with zero values).

2. Monthly averages of each species were calculated in order to eliminate the error that may come from unequal sampling frequency.
3. Annual averages were calculated from monthly averages.

In July–August 1994 concentrations of SRP, TP, NO₃-N, NO₂-N and NH₄-N were measured daily according to the FBA (1978) standards.

Results

Between 1989 and 1990, seasonal succession of phytoplankton was consistently monomodal in the hypertrophic Keszthely Basin: a sharp peak of blue-green algae developed each year (Fig. 1a).

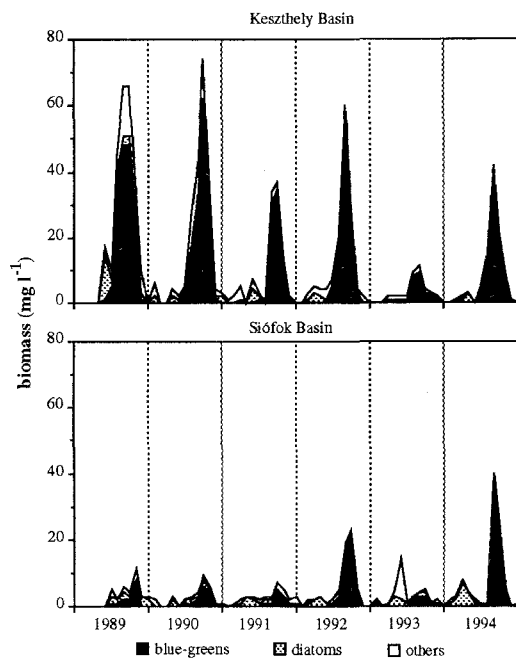


Fig. 1. Biomass (mg L⁻¹) of the dominant phytoplankton groups in the (a) Keszthely and (b) Siófok Basins of Lake Balaton between 1989 and 1994. Data are monthly averages.

Table 1. Annual average biomass of different phytoplankton groups and annual average contribution of the most important species in the Keszthely and Siófok Basins of Lake Balaton between 1990 and 1994.

	Keszthely					Tihany				
	1990	1991	1992	1993	1994	1990	1991	1992	1993	1994
	annual average biomass ($\mu\text{g L}^{-1}$)									
coccal blue-green	359	179	151	154	191	451	275	309	302	39
blue-greens with heterocytes	6701	2634	6649	1245	5111	800	526	3370	482	5043
blue-greens without heterocytes	5353	4413	2484	293	1156	117	117	387	226	513
Euglenophyta	105	23	54	77	42	28	11	36	26	71
dinoflagellata	536	194	284	185	218	172	133	113	83	212
cryptophytes	856	710	947	375	751	281	114	99	122	188
Xanthophyceae	8	710	0	0	12	0	0	0	0	8
chrysophytes	182	144	154	103	112	51	546	146	1136	57
centric diatoms	1076	689	285	242	260	686	802	507	543	875
pennate diatoms	703	396	492	368	309	202	184	389	414	515
phytomonadina	131	53	21	15	11	15	36	6	1	27
coccal green algae	1802	762	300	280	89	290	201	106	130	134
desmids	1042	226	70	26	40	114	99	31	44	31
other filamentous green algae	22	84	7	21	9	16	11	8	17	10
total biomass	18877	10508	11899	3385	8312	3223	3053	5506	3525	7722
	annual average contribution (%) of the dominant species to the total biomass									
<i>Snowella lacustris</i>	0.15	0.91	0.91	4.06	1.69	9.01	6.84	4.87	6.97	0.35
<i>Aphanizomenon klebahnii</i>	6.96	5.85	9.78	16.24	10.68	9.75	5.13	8.52	7.16	4.25
<i>A. issatschenkoi</i>	0.67	1.87	1.49	6.48	3.45	0.03	0.22	0.55	0.14	1.16
<i>Cylindrospermopsis raciborskii</i>	23.34	15.09	40.62	7.44	44.17	14.30	11.58	51.00	6.29	59.10
<i>Planktothrix agardhii</i>	22.21	33.87	18.33	3.65	11.14	0.01	1.99	1.16	1.49	5.05
<i>Ceratium hirundinella</i>	–	1.14	0.09	2.23	0.11	4.79	3.47	0.85	1.47	0.19
<i>Chrysochromulina parva</i>	0.28	0.39	0.43	1.17	0.60	0.57	15.68	1.64	1.74	0.04
<i>Dinobryon sociale</i>	0.66	–	<0.01	0.02	<0.01	2.05	<0.01	<0.01	30.16	<0.01
<i>Rhodomonas minuta/lacustris</i>	1.23	2.21	3.74	7.04	2.83	7.14	1.90	1.14	2.10	1.48
<i>Cyclotella radiosa</i>	1.61	4.04	0.33	1.62	2.47	10.77	15.68	6.45	10.56	9.87
<i>C. ocellata</i>	0.86	1.35	0.37	1.38	<0.01	7.53	9.40	1.53	3.91	0.92
<i>Synedra acus</i>	1.23	1.71	1.90	2.85	1.27	0.14	2.71	3.55	6.50	4.62
<i>Mougeotia</i> spp.	5.06	1.87	0.14	–	–	0.01	1.83	–	0.16	–

Phytoplankton biomass peaked characteristically in August at $38\text{--}75\text{ mg L}^{-1}$ (monthly average). The only exception was 1993, when a peak monthly average biomass of 13.5 mg L^{-1} was registered. Spring development of phytoplankton was insignificant. Despite the rather uniform appearance of the summer blue-green algal blooms, species composition of the blooms varied from year to year (Table 1). In 1992 and 1994, *Cylindrospermopsis raciborskii* was monodominant in the late summer peak; at an annual level it contributed 41 and 44 % to the total biomass.

Annual standing crop of non-heterocytic blue-green algae, most notably *Planktothrix agardhii*, decreased in the study period in both absolute and relative terms. This species

reached its highest biomass in the Keszthely Basin in 1991. At a longer scale (1978–1994), this group showed parallel changes with the $\text{NO}_3\text{-N/SRP-P}$ loading ratio (Fig. 2a).

Biomass of heterocytic blue-green algae, other than *Cylindrospermopsis raciborskii*, decreased with the decreasing BAP load of the Keszthely Basin (Fig. 2b). However, their relative contribution increased twofold (Table 1). Within this group, *Aphanizomenon klebahnii* and *A. issatschenkoi* were the most frequent.

The appearance of *Cylindrospermopsis raciborskii* blooms was independent of both external BAP-load and N/P ratio (Fig. 2c).

In the less eutrophic area of the lake, seasonal periodicity of phytoplankton was consistently bimodal in the 6-year study period (Fig. 1b). In

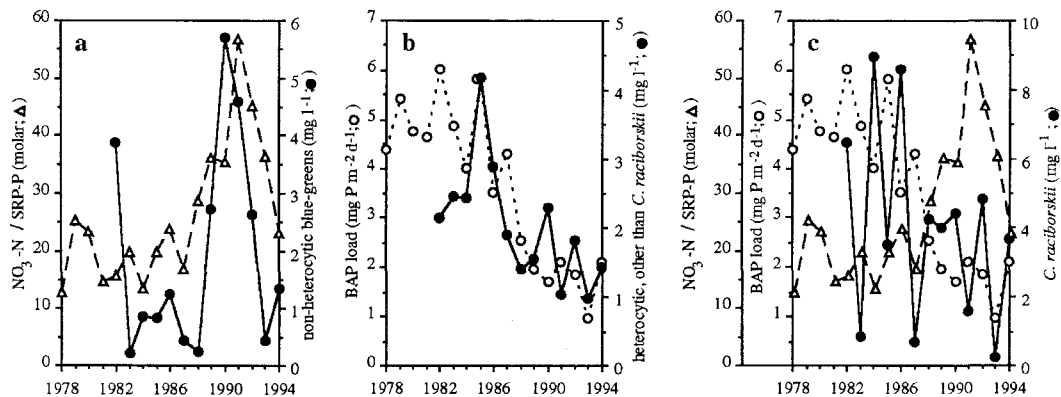


Fig. 2. Changes (a) in biomass of non-heterocystic blue-green algae and N/P loading ratio; (b) in biomass of heterocystic blue-green algae other than *Cylindrospermopsis raciborskii* and BAP loading; (c) in biomass of *C. raciborskii*, BAP loading and N/P loading ratio. Each data represent annual averages in the Keszthely Basin between 1978 and 1994.

general, *Cyclotella radiosa* and *C. ocellata* reached a spring peak average monthly biomass of 4–5 mg L⁻¹. Simultaneous development of *Synedra acus* increased the monthly average to 8 mg L⁻¹ in 1994. In 1993, a heavy bloom of *Dinobryon sociale* occurred in the eastern basin of the lake as a chance event (REYNOLDS et al. 1993) with no overall consequence for the long-term development of phytoplankton.

Blue-green algae dominated during the summer peaks (Table 1) in the eastern basin, too. In 1989–1991 and in 1993, *Snowella lacustris*, *Aphanizomenon klebahnii* and *Cylindrospermopsis raciborskii* were the most important species; however, none of them reached monodominance. In spite of the blue-green dominance, quite diverse phytoplankton assemblages were recorded. In these years, summer peaks were about 10 mg L⁻¹ as a monthly average. In late summers 1992 and 1994, *C. raciborskii* bloomed, as in the hypertrophic area.

In 1982, when this alga bloomed first in the lake (G.-TÓTH & PADISÁK, 1986), the net rate of population increase was 0.17 d⁻¹ (ln units) corresponding to a doubling time of somewhat longer than 4 days. In 1992, a growth rate of 0.24 d⁻¹ was calculated, i.e. doubling time was somewhat shorter than 3 days. In 1994, the net rate of growth was even quicker: 0.27 d⁻¹, which corresponds to a doubling every 2.6 days. The period when the biomass of *C. raciborskii* was higher than 10% of the peak biomass lasted for 57, 52 and 64 days in 1982, 1992 and 1994, respectively. In 1994, a small second peak occur-

red in the decreasing phase because some of the freshly developed akinetes began to germinate (microscopical observation). This phenomenon was even more pronounced in the hypertrophic area (data are not shown).

Correlation analysis between *Aphanizomenon/Cylindrospermopsis* biomass and the main inorganic nutrients during the lag and log phases of the population growth showed that both species were independent of the ambient concentrations of SRP-P, NO₃-N and NO₂-N, and showed a significant negative correlation with the NH₄-N concentration ($r_{\text{Aph}, \text{NH}_4\text{-N}} = -0.69$; $n = 9$; $P < 5\%$ and $r_{\text{Cyl}, \text{NH}_4\text{-N}} = -0.89$; $n = 9$; $P < 0.1\%$).

Each of the three summers (1982, 1992 and 1994) when *C. raciborskii* bloomed in the total lake area of almost 600 km² of Lake Balaton were exceptionally calm and warm (Table 2). In 1982, the long calm period began in mid-August and continued in September; the bloom developed by mid-September (Fig. 3). In August 1992, the mean monthly air temperature exceeded the 30-years average by 4.5 °C. The bloom developed sooner than in 1982 and peaked in the last days of August. In 1994, the warm weather began in June, by July, monthly air temperature had been 3.2 °C higher than the 30-years average. Exponential growth of *C. raciborskii* was observed in the first days of August and the peak biomass had been reached by mid-August.

In both 1992 and 1994, quite dense populations (maxima about 5 mg L⁻¹) of *Aphanizome-*

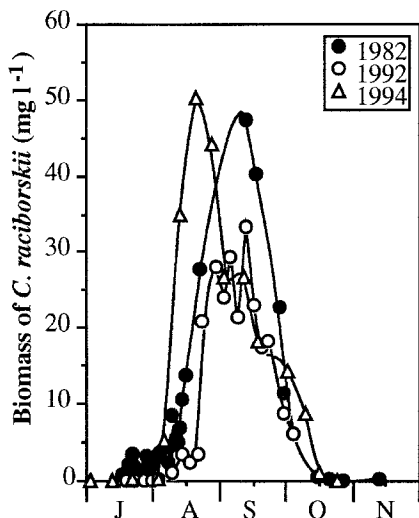


Fig. 3. Population dynamics of *Cylindrospermopsis raciborskii* in the Siófok Basin of Lake Balaton in the summers of 1982, 1992 and 1994.

Table 2. Mean monthly air temperatures and their deviation from the 30 years average in July, August and September of 1982, 1992 and 1994. As recorded by the Siófok Meteorological Station. Data are from the Monthly Weather Reports of the Hungarian Meteorological Service.

	mean monthly air temperature (°C)			temperature deviation from the 30 years average (°C)		
	July	Aug.	Sept.	July	Aug.	Sept.
1982	21.5	20.9	19.3	+0.2	+0.1	+2.6
1989	22.0	20.5	16.6	+0.7	-0.3	-0.1
1990	20.8	21.5	15.3	-0.5	+0.7	-1.4
1991	22.9	21.5	17.8	+1.6	+0.7	+1.1
1992	22.4	25.4	17.2	+1.1	+4.6	+0.5
1993	20.6	21.5	16.4	0	0	0
1994	24.3	22.8	19.1	+3.2	+2.5	+2.6

non klebahnii developed prior to the *Cylindrospermopsis raciborskii* blooms, so that some morphological characters of the two populations could be compared (Table 3). We compare the periods when the respective populations were denser than 10 % of their maximal biomass, either in the increasing or in the decreasing phase. Of the *Aphanizomenon klebahnii* biomass, 5.1 % was found in heterocytes in both years. Akinetes represented 0.7 % in 1992

and 1.3 % in 1994. The biomass that could be attributed to *Cylindrospermopsis raciborskii* heterocytes was 1.9 (1992) and 1.4 %. *C. raciborskii* akinetes represented 6.3 % (1992) and 2.9 % (1994) of the biomass. Taking the absolute biomass values into consideration, the following ratios can be estimated (Table 3):

1. Biomass of the common *C. raciborskii* filament-cells exceeded that of common *Aphanizomenon klebahnii* filament-cells by a factor of 8.5 in 1992 and 15.7 in 1994. The common cells contribute more than 90 % to total population biomass in both species.

2. Despite its much higher abundance, *Cylindrospermopsis raciborskii* produced only 2 (1992) and 3.5 (1994) times higher heterocyte biomass.

3. Microscopical observations evidenced that *C. raciborskii* began to produce a huge number of akinetes when the population was at its maximum biomass. *Aphanizomenon klebahnii* akinetes began to appear in much smaller numbers and only at the decreasing phase of the population development. This difference led to a 45-fold (1992) and 23.6-fold (1994) higher akinete biomass of *Cylindrospermopsis raciborskii*.

Discussion

Lake Balaton's phytoplankton has undergone profound changes during the last several decades. Phytoplankton seasonal periodicity used to be bimodal in the originally mesotrophic lake: a higher spring peak of diatoms was followed by a late summer peak during which *Snowella lacustris*, *Ceratium hirundinella* and centric diatoms, especially *Aulacoseira* spp., dominated. By 1989–1994, the previously dominant species had become subdominants (*Snowella*, *Ceratium*) or insignificant (*Aulacoseira*) in the Siófok Basin, while in the hypertrophic area they have almost completely been replaced by blue-green algae that appeared in the flora during the 1970s. Because phytoplankton of the lake was strongly P deficient, the increased P loads during the 1960s–1970s led to an increase in phytoplankton biomass as predicted by the VOLLENWEIDER (1968) model. Increased P availability led to occasional N-deficiency, especially in late summers evidenced by the appearance of N₂-fixing blue-green algae in the flora of the lake (PADISÁK 1992) followed by their continuous biomass increase (VÖRÖS & NÉMETH 1980).

Table 3. Amounts of common filament cells, heterocytes and akinetes in *Aphanizomenon klebahnii* and *Cylindrospermopsis raciborskii* in the Siófok Basin of Lake Balaton in 1992 and 1994.

	<i>Aphanizomenon</i>	<i>Cylindrospermopsis</i>	Cyl/Aph biomass ratio
1992			
maximum biomass (mg L ⁻¹)	5.17	33.38	
10%–10% period	12 July–15 Sept.	17 Aug.–29 Sept.	
filaments	94.2%	92.7%	8.47
heterocytes	5.1%	1.0%	2.0
akinetes	0.7%	6.3%	45.0
1994			
maximum biomass (mg L ⁻¹)	5.19	50.26	
10%–10% period	18 July–6 Sept.	1 Aug.–4 Oct.	
filaments	93.6%	95.7%	15.7
heterocytes	5.1%	1.4%	3.5
akinetes	1.3%	2.9%	23.6

In 1985, the Zala river, which alone transported more than 90% of the nutrient load of the Keszthely Basin and contributed one-third of the nutrient load of the whole lake, was directed into a protecting reservoir (Upper Kis Balaton; surface area: 18 km²) where rapid planktonic eutrophication began. In 1992, the water of the protecting reservoir was transferred into a wetland area (Lower Kis-Balaton; 16 km²; ISTVÁNOVICS et al. 1997). In 1991, P-precipitation was introduced at the sewage treatment plant of the biggest city along the course of the river. These measures, which coincided with the drastic reduction of fertilizer application and an 8-years period of exceptionally low water discharge, resulted in a significant BAP load reduction of the Keszthely Basin. The N/P loading ratios were also significantly influenced (Fig. 2).

The annual average biomass of non-nitrogen-fixing blue-green algae, most notably *Planktothrix agardhii*, changed parallel with the N/P loading ratios. Growth of these species is as sensitive to N-deficiency than any other groups of phytoplankton. An additional reason for the increase of *P. agardhii* might have been the superior shade tolerance of this species in highly kinetic lakes (REYNOLDS 1994).

Biomass of nitrogen fixing blue green algae, other than *Cylindrospermopsis raciborskii*, decreased parallel with the external BAP load. The explanation is that these species are able to compensate for temporary N-deficiency by N₂-fixation, and thus they growth depends on the P-supply. This biomass decrease can be rec-

ognized as a first, though slight, sign of the success of the restoration programme.

In terms of total phytoplankton biomass, the trophic response to external nutrient load reduction has been obviously delayed as it was evidenced in other shallow lakes, too (SAS 1990). This delay is caused by internal recycling of the phosphorus that has accumulated in the sediments during the period of increased external loading. Based on mass-balance calculations, internal P load of Balaton could increase by a factor of 2–4 in the post-management period as compared to the pre-management period.

C. raciborskii, which certainly became a key species in the lake, behaves in a considerably independent way of the actual P-loading, as demonstrated in Fig. 2c for the Keszthely Basin. The same holds true for the Siófok Basin where sewage diversion has resulted in 65% BAP load reduction by 1988. For understanding the ecology of *C. raciborskii* in the lake, we have to find explanations (1) for the irregular nature of its blooms and (2) for its obvious independence of external P-loading.

(1) *C. raciborskii* is a subtropical blue-green alga, common in eutrophic waters. It developed blooms throughout Lake Balaton only in the exceptionally warm and calm summers recorded in 1982, 1992 and 1994. The bloom consistently occurred in the third to the fourth week of the continuously warm period in each of the three years irrespective of the timing of this period. Laboratory experiments (GORZÓ 1987) provide evidence that *C. raci-*

borskii akinetes have a high and surprisingly narrow (-22 – 24 °C) temperature optimum of germination as compared to other heterocytic blue-green algae (-17 – 26 °C) that are common in the lake. Warm conditions are essential for germination of this subtropical species. Such conditions are incidental in temperate Lake Balaton. This provides a sufficient explanation for the irregularity of the *C. raciborskii* blooms.

(2) Some indirect evidence suggests that *C. raciborskii* may be able to utilize P that accumulated in the sediments of the lake in the recent past (ISTVÁNOVICS & HERODEK 1994).

i) P uptake experiments in *Gloeotrichia echinulata* showed (ISTVÁNOVICS et al. 1993) that P assimilation and growth are completely separated both in time and space. Growth was preceded by benthic P assimilation; the epilimnetic growth was based ultimately on internally stored P. The P pools of freshly recruited colonies were estimated to be sufficient for 3–4 subsequent doublings. The case of *G. echinulata* exemplifies that benthic P assimilation does exist as an evolutionary life strategy among Cyanobacteria.

ii) During the first *Cylindrospermopsis raciborskii* bloom in 1982 it was supposed that extraordinarily heavy rainfalls prior to the bloom induced such an increase of the external P load, that could cover P requirement of the algal bloom (G.-TÓTH & PADISÁK 1986). However, in 1992 and 1994 dry periods preceded the *C. raciborskii* bloom and the external P supply was only one-third of that in 1982.

iii) As in *Gloeotrichia echinulata*, *Cylindrospermopsis raciborskii* does not maintain long-lasting large planktonic populations in Lake Balaton; blooms occur as sharp pulses. Development and decline occupied a period of 52–57 days. A period of 64 days was observed only when immediate germination of freshly produced akinetes was microscopically detectable. This disflexibility of population dynamics can be indicative of a storage-dependent growth. Moreover, similar to *Gloeotrichia echinulata* and unlike other heterocytic blue-green algae in the lake, microscopic oil droplets were observed in newly developed akinetes of *Cylindrospermopsis raciborskii*. Oil droplets may represent a food reserve for subsequent growth (ROELOFS & OGLESBY 1970).

iv) GORZÓ (1987) clearly demonstrated the inverse relationship between the abundance of

heterocystic blue-green algal filaments in the plankton and that of the akinetes in the sediments in the period 1984–1986 in each basin of the lake.

v) The number of akinetes that *Aphanizomenon klebahnii* produces in Lake Balaton is certainly sufficient for the next year inoculation as evidenced by the regular appearance of this species. Why does *Cylindrospermopsis raciborskii* produce 24–45 times more akinete biomass? Noticeably, in terms of akinete number, the difference is even more pronounced because *C. raciborskii* akinetes are smaller than those of *Aphanizomenon klebahnii*. If akinetes of *Cylindrospermopsis raciborskii* do not merely serve as inocula for the next-year's population, but their benthic recruitment is a significant contribution to the population development, then akinete overproduction becomes understandable. In the case of *Gloeotrichia echinulata* benthic recruitment reached up to 40% of the population increase (ISTVÁNOVICS et al. 1993).

vi) It is commonly thought that the development of dense populations of N_2 -fixing blue-green algae, is favoured by N-deficiency. *Cylindrospermopsis raciborskii* in Lake Balaton produces much less of heterocytes than other blue-green algae. Moreover, close negative correlation between *C. raciborskii* and NH_4 -N allows us to suppose significant inorganic N-uptake. Indeed, PRÉSING et al. (1996) found that during the 1994 bloom NH_4 uptake covered 85% of the N demand in the Siófok Basin and 50% in the Keszthely Basin in spite of the ambient NH_4 concentrations below $3 \mu g l^{-1}$. The rest of the N requirement was supplied by N_2 -fixation. These observations suggest that *C. raciborskii* blooms in Lake Balaton are not induced primarily by N-deficiency.

Conclusively, in the post-management period it was impossible to outline a simple relationship between P-load reduction and blue-green algal biomass in Lake Balaton. However, if blue-greens are divided into groups we managed demonstrate that:

1. Non-heterocytic blue-green algae follow changes in the N/P loading ratio.

2. Heterocytic blue-greens, other than *Cylindrospermopsis raciborskii*, decrease parallel with the BAP load reduction.

3. *C. raciborskii* behaves independent of the actual loading conditions and this independence is most probably linked with its specific life-strategy.

Our results demonstrate the high diversity of adaptational strategies of blue green algae.

Acknowledgements

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- Authors' address:
- J. PADISÁK and V. ISTVÁNOVICS, Balaton Limnological Institute of the Hungarian Academy of Science, H-8237 Tihany, Hungary.