

Relationships between Short-Term and Long-Term Responses of Phytoplankton to Eutrophication of the Largest Shallow Lake in Central Europe (Balaton, Hungary)

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Summary

As a result of the increased phosphorous load, the originally mesotrophic Lake Balaton underwent rapid eutrophication that began in the 1960s-1970s. Because most of the nutrient load is received by the western basin, a sharp trophic gradient developed in the lake: the western part is hypertrophic, while the eastern remains meso-eutrophic. The paper describes the phytoplankton changes in the last four years (1989-1992) both in the hypertrophic and meso-eutrophic parts of the lake. Floristic changes of the last 60 years, long term trends of quantitative changes and short-term (daily) responses of phytoplankton to weather changes are discussed with special attention to *Cylindrospermopsis raciborskii*, a key species in the lake. The paper concludes that the management program that was started in 1983 to restore the lake and during which the external P load was reduced by about 40 % has so far not resulted in significant improvement in water quality, for the P accumulated in the sediment in the period of high external load still supports the development of high late summer algal crops.

1. 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 that began in the 1960s-1970s [1]. Because the majority of the nutrient load is received by the western basin, a sharp trophic gradient developed in the lake: the western part is hypertrophic, while the eastern is still meso-eutrophic. Between 1975 and 1981 the total phosphorus load was estimated as 2.47 g m⁻² year⁻¹ in western part of the lake, and 0.31 g m⁻² year⁻¹ in the eastern part; biologically available phosphorus was estimated as 55% and 58 % of the above values [2].

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In 1983, a large scale management program has started to slow down and reverse eutrophication of the lake. This included, among others, (1) the elimination of the most dangerous point-like sources; (2) establishing a more efficient sewage treatment together with a sewage transfer system around the eastern part and (3) the construction of two protecting reservoirs on the western tributaries. So far the program has resulted in about 40 % reduction of the biologically available phosphorus load of the lake [3]. Increase in trophic state of the lake was reflected in each of the biological variables [4] with a characteristic lag: the variables of phytoplankton responded earlier than those of other groups of plankton. Remarkable changes were observed in size and structure of fish population which are considered to have been caused by individual or combined effects of overfishing, interspecific competition with non-native species and loadings of nutrients and pesticides [5, 6].

This paper describes the phytoplankton changes in the last four years (1989-1992) both in the hypertrophic and meso-eutrophic parts of the lake. In relation to

- i) floristic changes that had occurred in the last 60 years;
- ii) long term trends of change and
- iii) the short-term (daily) response of phytoplankton to weather changes which are discussed with special attention to *Cylindrospermopsis raciborskii* WOLOSZ., a key species in the lake.

II. Material and Methods

Samples were taken in the Keszthely Bay and Tihany region of the lake (Fig. 1) with a vertical tube sampler. The sampling frequency was roughly biweekly in the Keszthely Bay except the vegetation period in 1992, when samples were taken twice a week. In the Tihany region samples were taken twice a week during the vegetation periods of 1990, 1991 and 1992; in cold seasons and in 1989 the sampling was weekly or biweekly. Samples were preserved with Lugol's Iodine, and phytoplankton was counted under an inverted microscope with a counting accuracy of $\pm 10\%$. Since January 1992, Hamilton's [7] computerized counter method was used for numbers and biomass estimates. Biomass records in the paper are wet-weights and were calculated from biovolumes. Several early works on phytoplankton of the lake are used in the paper to assess the long-term changes. The sources of the data are detailed in Padisák & G.-Tóth [8]. Meteorological data were measured in the Siófok (Fig. 1) Observatory of the Hungarian Meteorological Service and are from Monthly Weather Report [9].

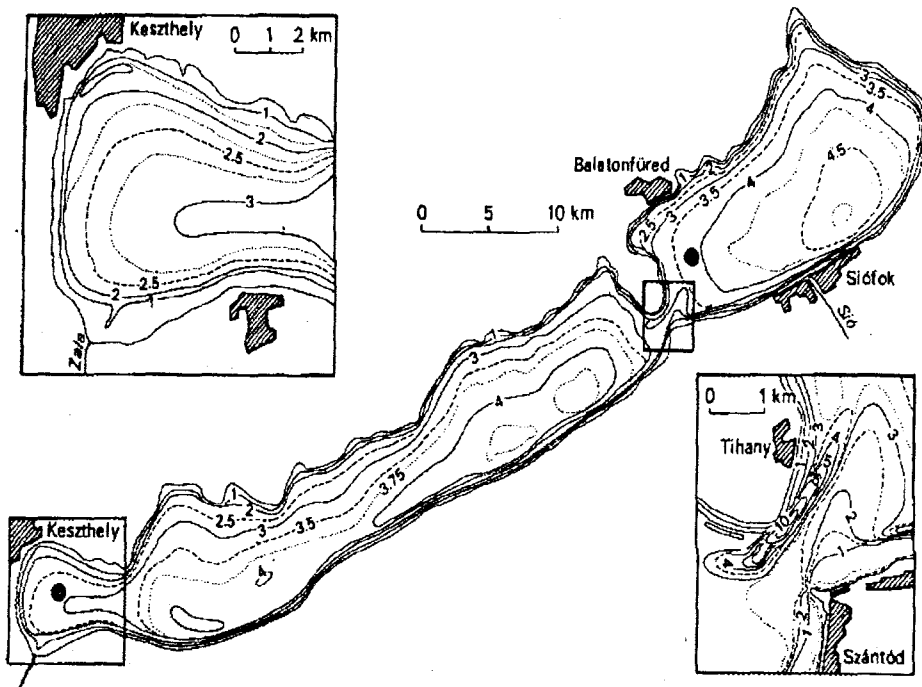


Fig. 1: The isobathic map of the lake.

Sampling sites are indicated with full circles

III. Results and Discussion

Long-term quantitative changes

Quantitative phytoplankton data from the Tihany region have been obtained since 1933 and those of Keszthely Bay have been available since 1962. The annual average and maximal biomasses of phytoplankton showed a sharp increase (Fig. 2). In the meso-eutrophic Tihany region of the lake both the annual average and maximum of biomass started at several hundreds of $\mu\text{g l}^{-1}$ in the early decades of the century; similar data were recorded in the middle sixties. Then a trendlike increase began up to several thousands (annual average) and several ten-thousands (maximum) $\mu\text{g l}^{-1}$. Beside the overall increasing tendency there are characteristic pulses (see subgraph of Fig. 2) in phytoplankton biomass. These can be attributed to *Cylindrospermopsis raciborskii* which occasionally blooms in the region. It is impossible to reconstruct the phytoplankton biomass in the Keszthely region of the lake for the early decades of the century, but, the initial data from the middle sixties are somewhat higher than those in the eastwestern part of the lake. The increase in phytoplankton biomass was very sharp in the 70s and early 80s, however, it seems to have reached some plateau. *Cylindrospermopsis* blooms, which regularly occur in the region, do not appear as sharp pulses (Fig. 2; subgraph).

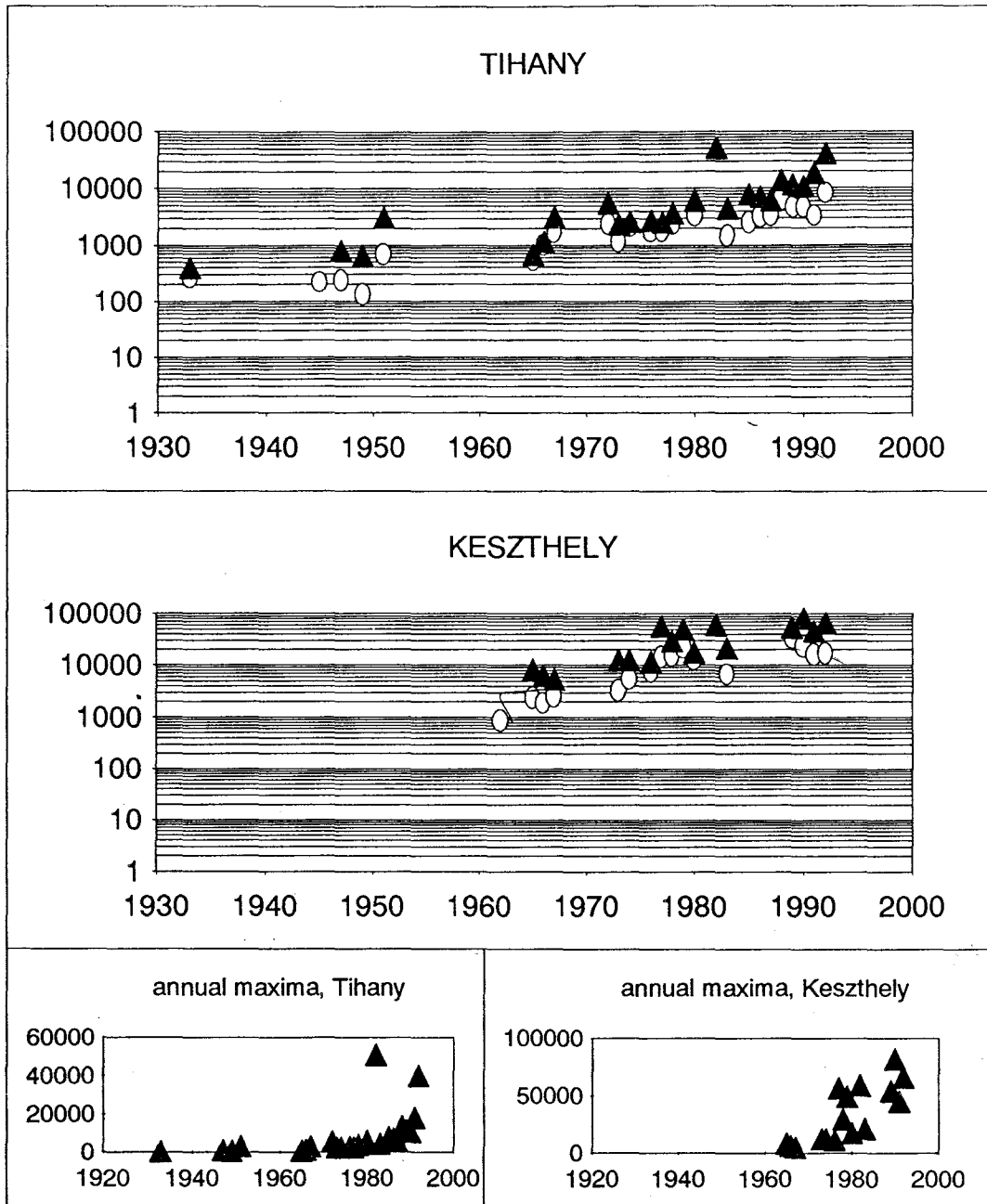


Fig. 2: Long-term changes of annual average (O) and maximal (▲) biomass in the Tihany and Keszthely regions of Lake Balaton.

Main graphs: logarythmic scales; lower subgraphs: maxima on linear scales.

Long-term compositional changes

The biomass increase was paralleled by basic compositional changes in phytoplankton in both parts of the lake. In the 60s-70s *Cyclotella comta* KÜTZ. dominated in the spring bloom and by late summers *Aulacoseira granulata* (EHR.) SIM., *A. granulata* var. *angustissima* (O. MÜLLER) SIM. and *Ceratium hirundinella* (O. F. MÜLLER) BERGH became

dominant. Blue-green algae did not dominate the late summer phytoplankton and their < 20% contribution was given mostly by coccal species (*Snowella lacustris* KOM. & HIND., *Microcystis* spp.). An increasing number of occasional moderate *Microcystis* blooms in the 60s can be considered as the first sign of the eutrophication [10, 11, 12]. New species of heterocytic blue-green algae appeared in the flora in the early 70s [13, 14, 15]. In the western part of the lake heterocytic blue green algae (*Aphanizomenon flos-aquae* [L.] RALFS, *A. issatschenkoi* [USS.] PROSH.-LAVR., *Anabaena spiroides* KLEB. and *A. aphanizomenoides* FORTI) became dominant regularly by late summer [16], while at that time *Ceratium* was still dominant in the eastern part. *Cylindrospermopsis raciborskii* was found first in 1978 and soon became a key species in the lake. By the late 80s blue green algae became the dominant group in the lake. However, their contribution to total annual biomass differs in the western and eastern parts of the lake on one hand, and on the other it depends on the actual annual crop of *Cylindrospermopsis*. The latter is the main reason for dividing the results from the last four years into two groups (Table 1): despite 1992, in years 1989-1991 there was no overall *Cylindrospermopsis* bloom in the lake.

	KESZTHELY				TIHANY			
	1965-67	1972-74	1989-91	1992	1965-67	1972,1974	1989-91	1992
blue-green algae	18	13	15	84	8	6	42	77
euglenophytes	2	3	3	1	5	2	1	1
dinoflagellates	25	41	33	1	46	13	5	2
cryptophytes	0	11	5	5	0	3	6	1
chrysophytes	1	1	1	1	0	0	6	2
centric diatoms	41	14	28	2	19	41	23	9
pennatae	13	13	13	3	17	23	5	6
diatoms								
green algae	1	5	3	3	3	13	12	2

Table 1: Percentage contribution of different algal groups to total phytoplankton biomass at the Keszthely and Tihany regions of Lake Balaton.

Seasonal development of phytoplankton in 1989-1992

In the meso-eutrophic part of the lake each group of blue-green algae form a summer - autumn maximum. Coccal blue-green algae (Fig. 3) provide a peak midsummers. In 1989-1991 *Snowella lacustris* was the most frequent species, while the higher biomass in 1992 was due to *Microcystis aeruginosa* KÜTZ. Heterocytic blue-green algae are late-

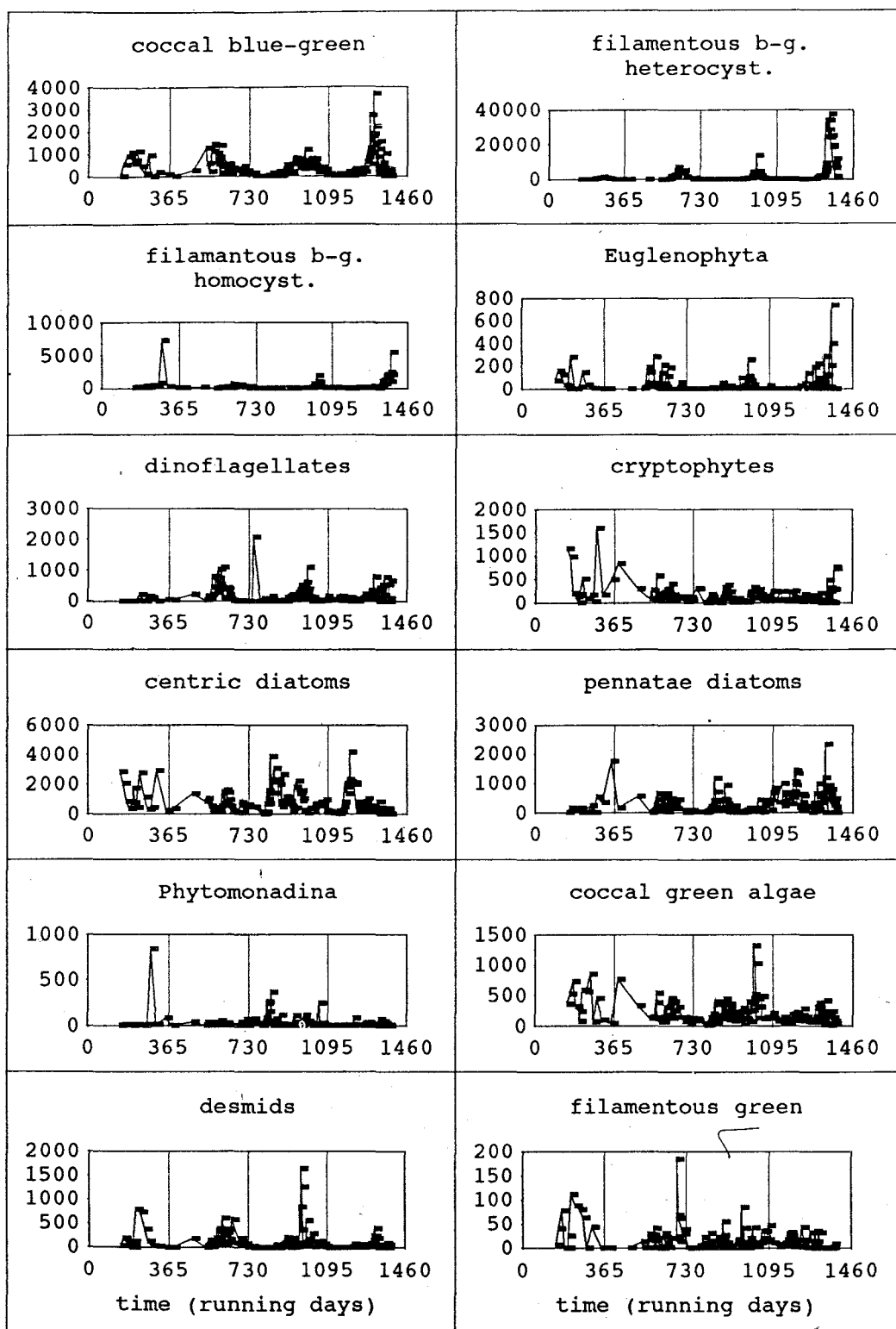


Fig. 3: Biomass ($\mu\text{g/l}$) of different algal groups in the Tihany region of Lake Balaton between 1989 and 1992.

Vertical gridlines separate years.

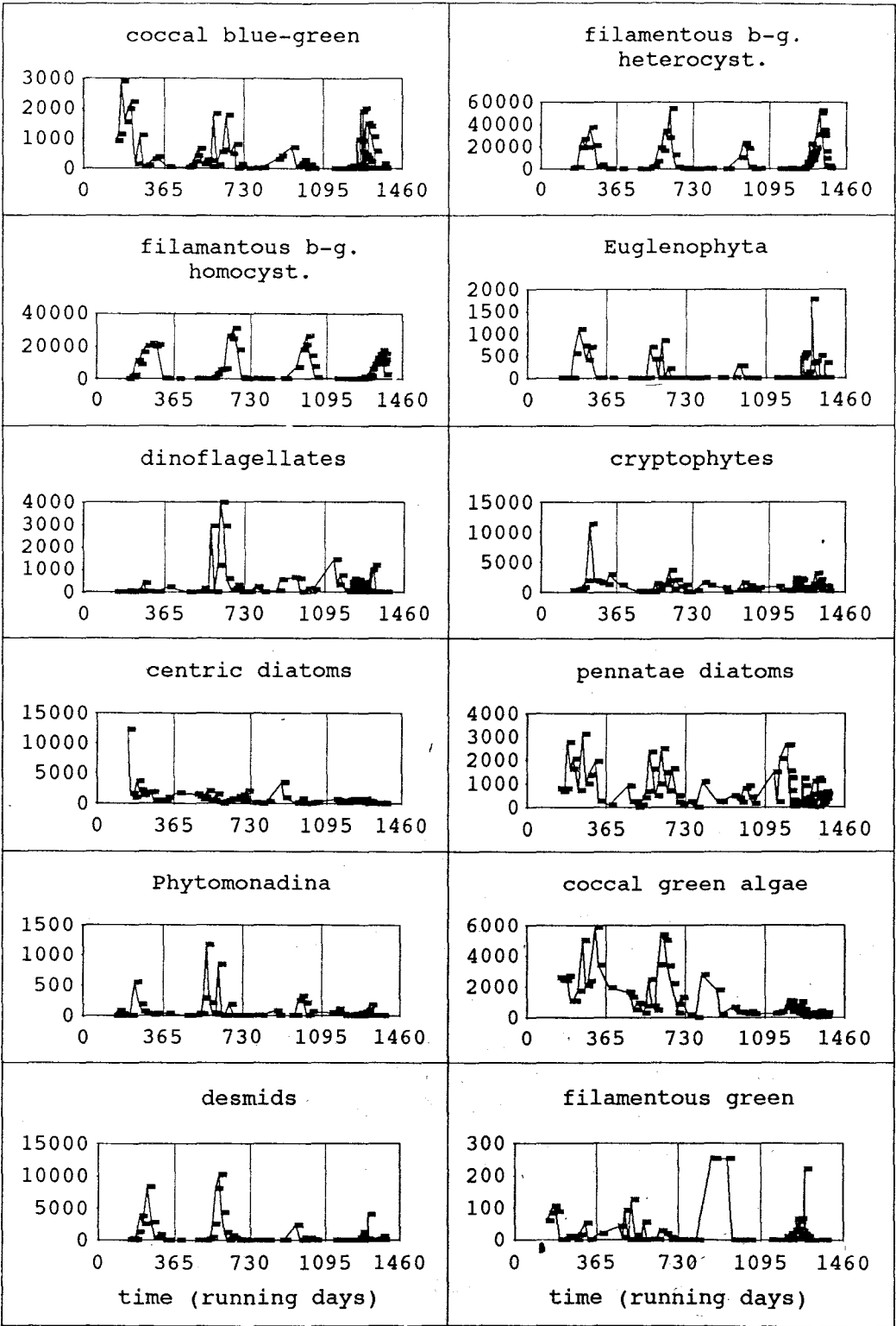


Fig. 4: Biomass (µg/l) of different algal groups in the Keszthely Bay of Lake Balaton between 1989 and 1992.

Vertical gridlines separate years.

summer - autumn species: in years without *Cylindrospermopsis* bloom *Aphanizomenon flos-aquae* is the most frequent species. A large population consisted of probably several different species of filamentous blue-green algae without heterocytes develops by late autumn; the most frequent form can be identified as *Planktothrix agardhii* (GOM.) ANAGNOSTIDIS & KOMÁREK. Like in the 60s-70s, centric diatoms, most notably *Cyclotella comta* and *C. ocellata* PANT. characterized the spring peak of phytoplankton. The latter provided a summer peak in 1991. Euglenophytes, dinoflagellates and desmids were typical summer species; other groups of phytoplankton are rather erratic in their seasonal behaviour.

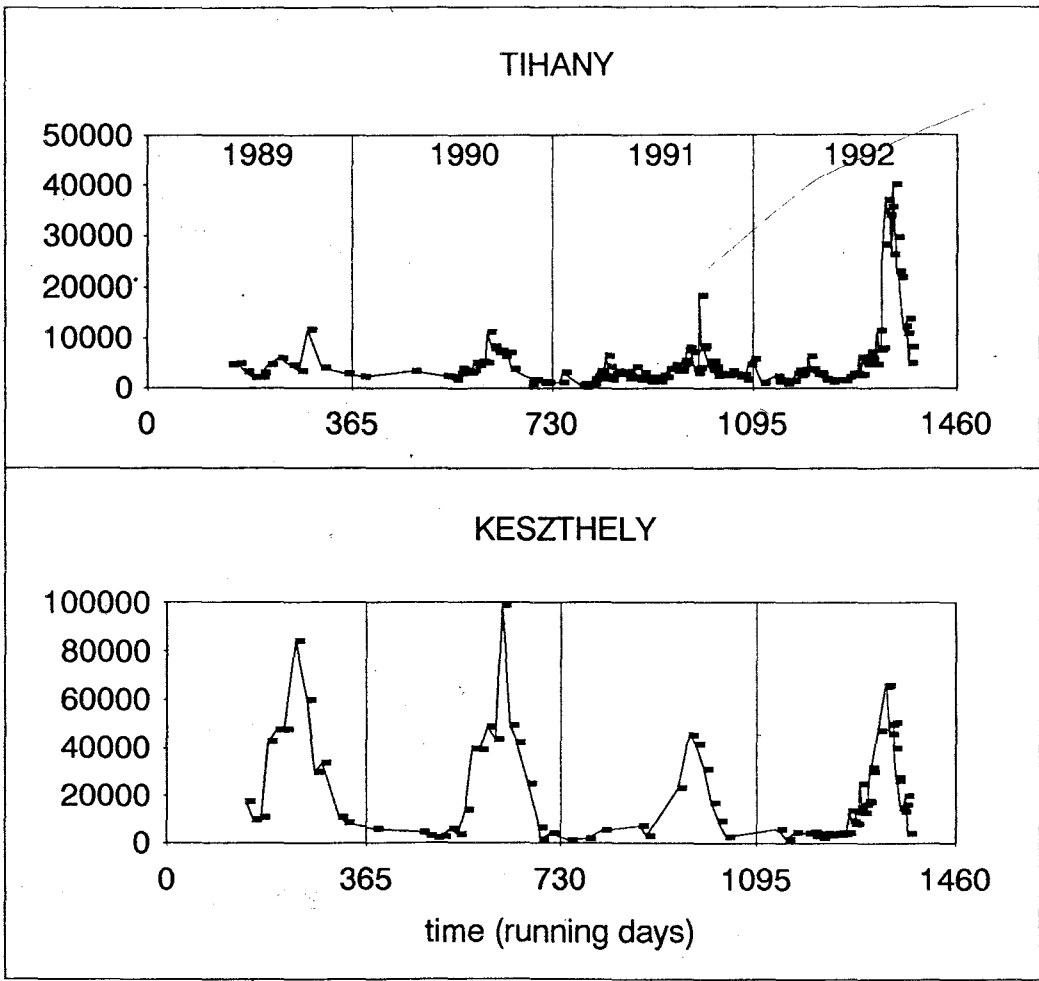


Fig. 5: Phytoplankton biomass ($\mu\text{g/l}$) in the Tihany region and in the Keszthely Bay of Lake Balaton between 1989 and 1992.

In the Keszthely Bay of the lake blue-green algae appear in a similar seasonal sequence and their dominance is much expressed (Table 1, Fig. 4). The heterocytic and homocytic

filamentous species widely overlap in time, and their seasonal maxima are very similar. Desmids (notably, *Mougeotia* sp.) provided a clear peak in 1989 and 1990. Other groups of algae are quantitatively less important, however, their annual development is similar to that in the mesotrophic part. In the Tihany region of the lake recent years (1989-1991) without *Cylindrospermopsis* bloom are compositionally in an intermediate state between the original composition and that in the Keszthely Bay. In the latter, years with or without overall *Cylindrospermopsis* bloom do not differ significantly.

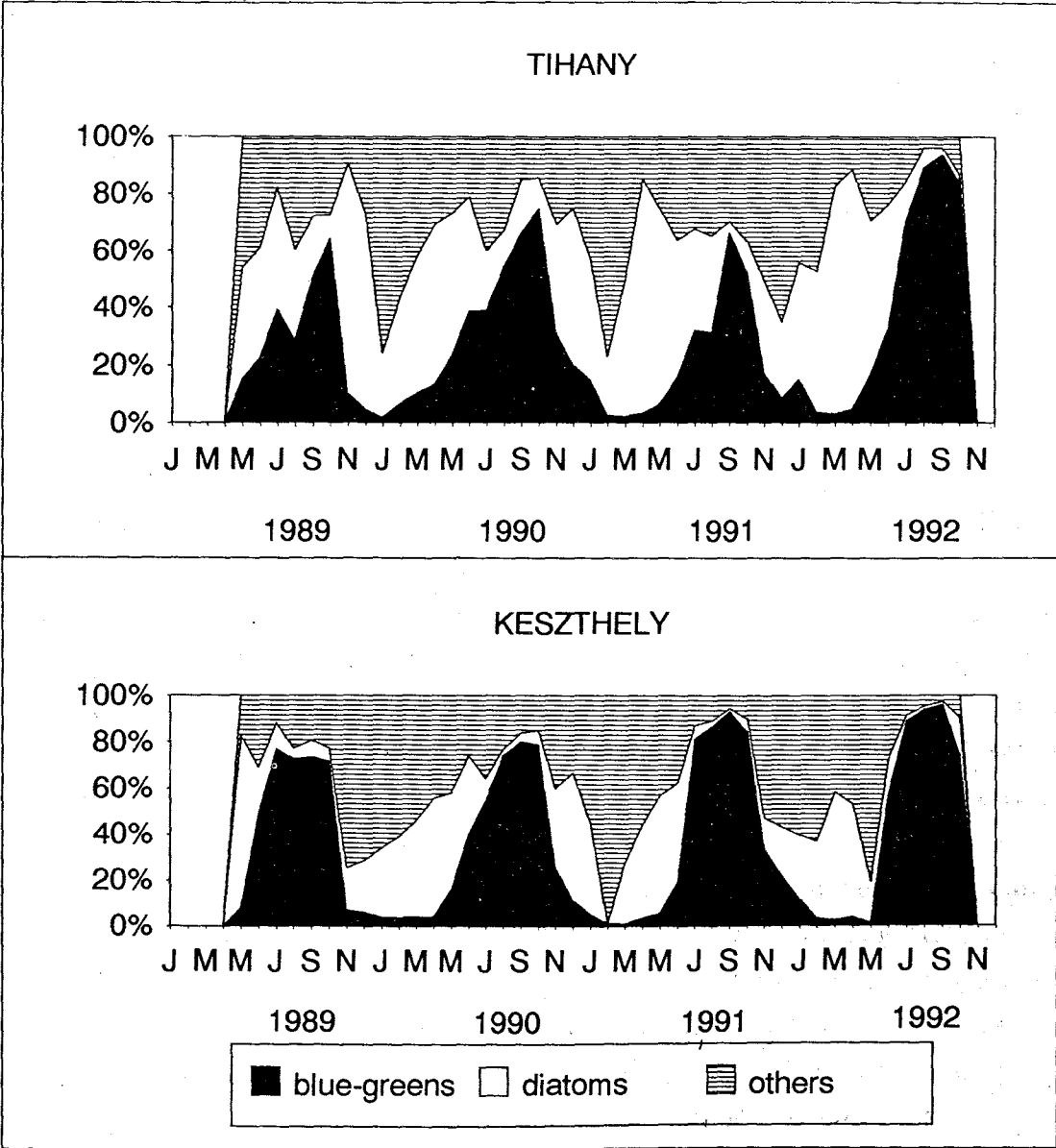


Fig. 6: Percentage contributions of different algal groups to total phytoplankton biomass in the Tihany region and in the Keszthely Bay of Lake Balaton between 1989 and 1992.

Data represent monthly averages.

In a comparison with early years, notable differences can be observed in the seasonal pattern of phytoplankton.

i) Seasonal development of phytoplankton in Tihany region was characterized by a spring and a late summer peak biomass before the early eighties. These two peaks were quantitatively often similar (for example in 1972, 1974), and in several years the spring peak exceeded the late summer one (for example in 1977, 1978, 1980, 1983; [17, 8]). So far as data exist, the summer peak always exceeded the spring one in the Keszthely region (the only known case when the spring biomass was higher is 1980; [8]). In the last four years spring blooms were not observed in the Keszthely Bay at all (Fig. 5), and were very moderate in size compared to the late summer peak at Tihany.

ii) Regardless of the absolute quantities, the spring bloom of diatoms appears clearly in the compositional plot (Fig. 6) and a diatom dominated phase precedes the summer blue-green phase at both parts, however, but especially in the Tihany region.

iii) The blue-green phase develops very quickly and already by June in the Keszthely Bay, and the period with high blue-green algal biomass lasts until late November. Phytoplankton biomass is $> 10 \text{ mg l}^{-1}$ for 150-180 days. In the Tihany region of the lake the development of the blue-green algal phase is much slower; the period with $> 10 \text{ mg l}^{-1}$ algal biomass is restricted to 5-10 days (1989-1991) and occurs in autumn (9-18 October, 1989; 3-7 September, 1990; 23-29 September, 1991). In 1992, when *Cylindrospermopsis* bloomed, the blue-green algal phase developed later but as quickly as in the Keszthely Bay, and the phase with $> 10 \text{ mg l}^{-1}$ algal biomass lasted for almost 2 months (8 August - 4 October, 1992).

The development of Cylindrospermopsis blooms

Cylindrospermopsis raciborskii appeared in the flora in 1978. Next year it bloomed moderately in the Keszthely Bay [18]. 1980 was an exceptional year: instead of the summer blue-green phase, diatoms, especially *Nitzschia* spp. and small centric diatoms [19] dominated. In 1982, a heavy *Cylindrospermopsis* bloom swept through the whole lake with a time-lag of about three weeks [20]. Since that time the species appeared in the plankton each year and in the Keszthely Bay it almost invariably bloomed late summers (Fig. 7). However, the annual phytoplankton development in the Tihany region is strongly influenced by the presence or absence of *Cylindrospermopsis* blooms (Fig. 7).

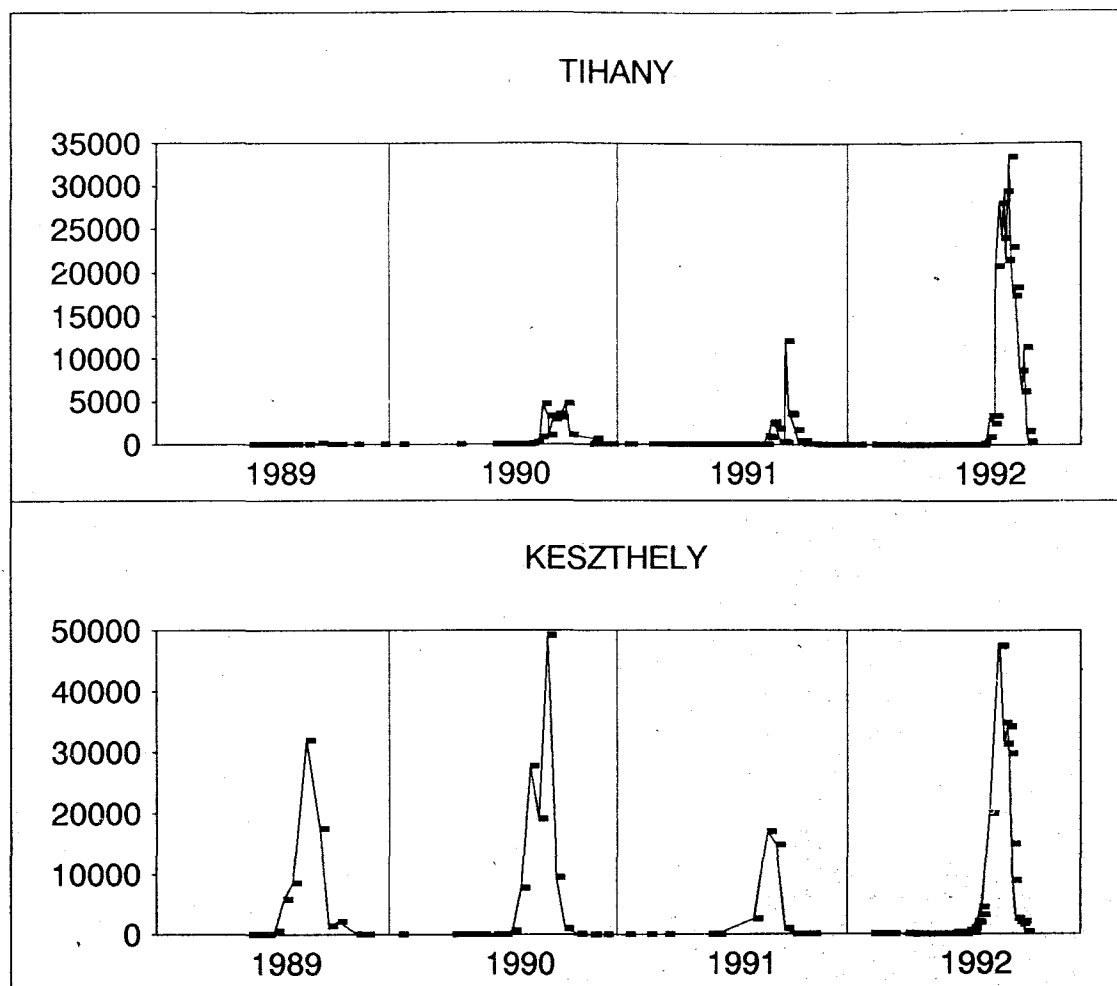


Fig. 7: Biomass ($\mu\text{g/l}$) of *Cylandrospermopsis raciborskii* in the Tihany region and in the Keszthely Bay of Lake Balaton in 1989-1992.

Short term (daily) studies on the summer changes on the phytoplankton in the Tihany region of the lake have shown that the meteorological background, especially the frequency of summer storms has a strong impact on the development and establishment of summer equilibrium phases of the phytoplankton community. If there are 10-15 day calm periods between storms, the community is shifted mostly to a K-strategists dominated phase. Frequent storms prevent this shift because under such conditions small-sized r-strategists are favoured [21, 22]. The phenomenon was later described by Connell's [23] Intermediate Disturbance Hypothesis [24], and it was shown that the species diversity plotted against the frequency of environmental change provides a maximum-type function: the diversity reaches a maximum at intermediate frequencies. Connell's hypothesis was found to have general validity in community changes of phytoplankton [25] in a wide range of lakes.

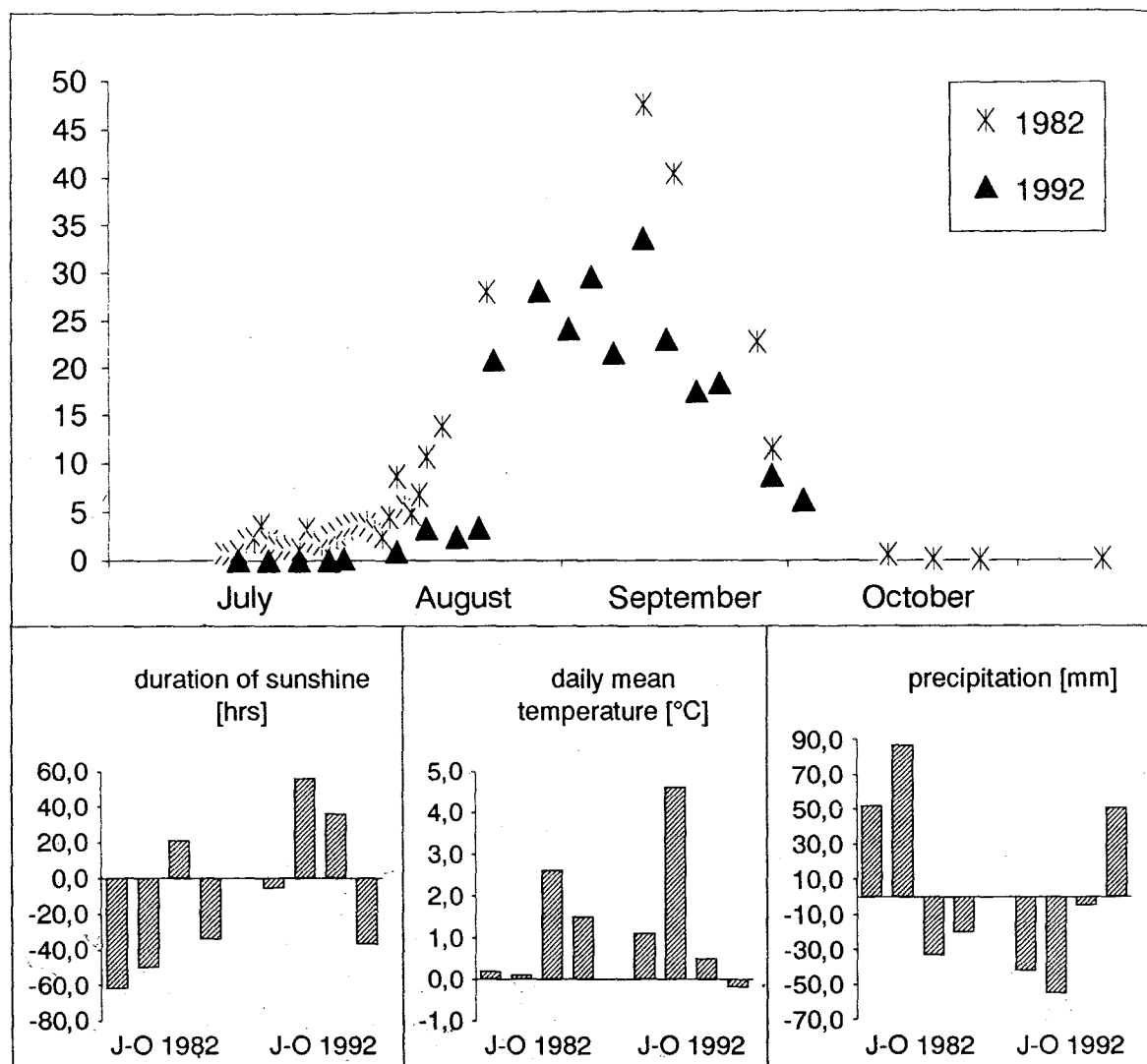


Fig. 8: Biomass (mg/l) of *Cylindrospermopsis raciborskii* in the Tihany region of Lake Balaton in July-October of 1982 and 1992 (upper panel) and the monthly sums of deviations of duration of sunshine, daily mean temperature and precipitation from their 30 averages in months from July to October in 1982 and 1992. (lower panels).

The year, 1982, when *Cylindrospermopsis* bloomed first in the lake was a meteorologically exceptional year. Unusually heavy rainfalls occurred in July and in the first part of August, then the weather was very calm and warm until November. The latter, according to the above mentioned theory, enabled the development of a *Cylindrospermopsis* bloom; the development of the bloom and its meteorological background is analyzed in detail in G.-Tóth & Padisák [26]. However, in the cited reference, a similarly important role was attributed to the preceding rainfalls which were supposed to increase the external nutrient load of the lake. The 1982 and 1992 *Cylindrospermopsis* blooms were very

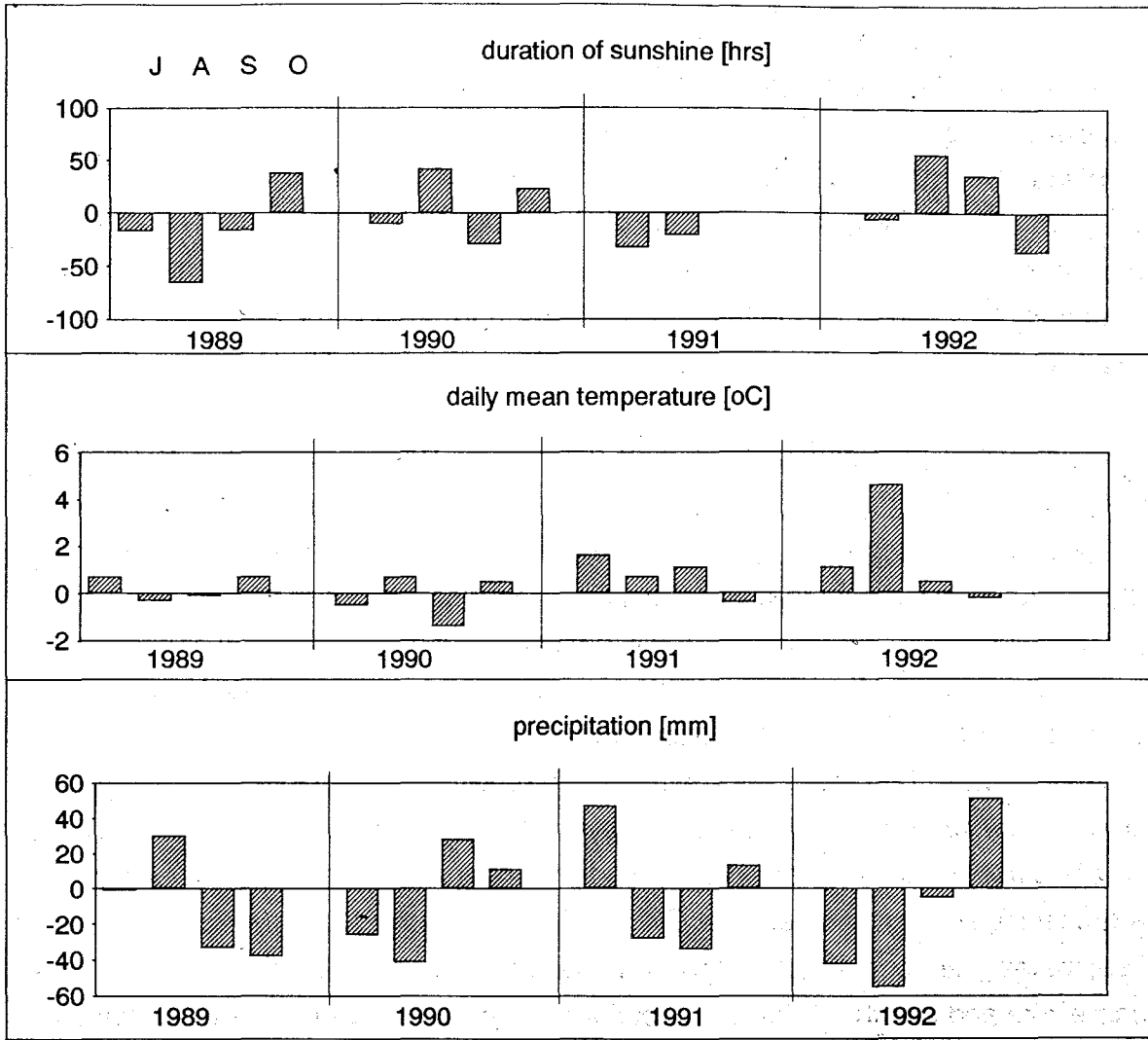


Fig. 9: Monthly sums of deviations of duration of sunshine, daily mean temperature and precipitation from their 30 years averages in July-October of 1989, 1990, 1991 and 1992. Abbreviation of months are indicated only for duration of sunshine in 1989.

similar (Fig. 8) with the notable difference that the bloom developed quicker in 1992. The net increase rate of the population was 0.17 d^{-1} in 1982 and 0.24 d^{-1} in 1992; the former corresponds to somewhat longer than 4, the latter to slightly shorter than 3 days doubling time. The weather during the 1992 bloom was even calmer and warmer than in 1982 (Fig. 8). A comparison of the maximal biomasses of *Cylindrospermopsis* in the Tihany region to the August daily mean temperature between 1989 and 1990 (Fig. 7, 9) supports the principal role of warm weather in the development of the blooms.

Laboratory experiments [18] showed that *Cylindrospermopsis* akinetes have a high and narrow ($\sim 22\text{--}24^\circ\text{C}$) temperature optimum of germination comparing to other heterocytic

blue-green algae ($\sim 17\text{--}26^\circ\text{C}$) occurring in the lake; and that increasing light intensity in 100-3000 lux range promotes germination. Since the duration of sunshine (Fig. 8) did not deviate significantly from the average in 1982 (in 1992 the positive deviation was significant) it can be concluded, that under natural conditions in Lake Balaton high temperature is the key string stimulus of *Cylindrospermopsis* blooms. This may explain the different pattern of *Cylindrospermopsis* blooms in the Tihany region and in the Keszthely Bay: because the latter is shallower (Fig. 1), and the sediment temperature reaches sooner and with higher probability the optimal conditions for germination.

The pattern of precipitation was very different in 1992. Therefore it is apparent to suppose that the nutrient demand of the growth can rather be found in the internal nutrient, especially phosphorous, recycling between the open water and the sediments of the lake than in an increased external load as was supposed earlier. Boström *et al.*, [27] concluded that migration into the water column of bottom dwelling blue-green algae (e.g. overwintering *Microcystis*) moves significant loads of intracellular N and P out of the sediments. Phosphorus uptake experiments in *Gloeotrichia echinulata* (J. E. SMITH) P. RICHTER showed [28] 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 phosphorus. Two observations may indicate a similar life strategy, namely that *Cylindrospermopsis* produces a much higher amount of akinetes than for example *Aphanizomenon flos-aquae* (Padisak, unpublished) in the same lake and that the P deficiency of the medium does not prevent the germination of spores in laboratory experiments because of a supposed high P content of akinetes [18]. Experimental studies are necessary to have a deeper insight into the role of *Cylindrospermopsis* in the N metabolism of the lake. Laboratory studies proved an opposite relation between the germination % and the nitrate concentration of the medium [18]. In a natural *Cylindrospermopsis* populations (1992 bloom, Lake Balaton) the biomass share and numbers of heterocytes was much less than those in *Aphanizomenon flos-aquae* which may indicate a minor role in N_2 -fixation.

IV. Conclusions and Predictions

The relationship between the external P load of the Lake Balaton and its phytoplankton biomass fits well to that presented originally by Vollenweider [29]; and has been re-defined and extended within the framework of the OECD program by Vollenweider & Kerekes [30]. The trend-like increase in phytoplankton biomass is continuing in the

mesotrophic part of the lake and seems to have reached a plateau in the hypertrophic part. This saturation can be attributed rather to the light limitation that arises at high algal crops than to the reduction of the external load. However, the observation that the blue-green algal maximum was somewhat lower and lasted shorter in the Keszthely Bay in 1992 despite the warm weather carries some hope about the success of the restoration program.

Cylindrospermopsis blooms appear as high annual biomasses superimposed on the overall increasing trend in the mesotrophic part of the lake. In this deeper area the akinetes of the species germinate in large numbers only in especially warm summers, while the shallower hypertrophic area offers better conditions for germination. *Cylindrospermopsis* blooms indicate that the internal phosphorus recycled from the sediments has become the main factor that leads to critical water qualities by mid- or late summers.

Early evidence exists that highly enriched shallow waters can develop substantial internal loads sufficient to counter the effects of external reductions for long periods [31, 32, 33] or until additional restoration (sediment removal, flushing) were undertaken [34, 35]. Studies on phosphorus binding capacity have shown that the highly calcareous, fine grained sediments of Lake Balaton have a strong phosphate adsorption capacity and that during the period of high external phosphorus loading adsorption capacity of iron hydroxides has gradually been saturated in the hypertrophic part [18].

In this way, *Cylindrospermopsis* blooms are predictable as long as the sediments are rich in P in years when the summer temperature allows the germination of large number of akinetes. Considering the possible response of phytoplankton to reduction of P load a shortening of the summer blue-green algal period and a decrease in its maximum are the next steps that can be expected in the hypertrophic regions. Compositional changes, like the re-appearance of the bimodal seasonal cycle and the re-establishment of a diatom or dinoflagellate dominated summer phase seem to occur far in the future. In this respect it is promising, that the floral component of such a future change exists in the lake (c.f. Padisák, 1992b) and that the different groups of the phytoplankton provide a rather similar seasonal behaviour in parts of the lake with different trophic state.

As in many cases (Reynolds, in press), improvement in water quality has been significantly delayed compared to reduction of external load.

V. Acknowledgement

I thank Mr. István Báthory, Mr. Géza Dobos and Mr. Tamás Németh for their essential help in field work. Special thanks are due to Dr. A. Duncan for correcting the English of the paper. This research was supported by the Hungarian National Science Found (OTKA No. 3172 and 6285).

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