# SUDDEN AND GRADUAL RESPONSES OF PHYTOPLANKTON TO GLOBAL CLIMATE CHANGE: CASE STUDIES FROM TWO LARGE, SHALLOW LAKES (BALATON, HUNGARY, AND THE NEUSIEDLERSEE, AUSTRIA/HUNGARY)

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## Abstract

This paper analyses two phytoplankton long-term datasets; both are from large, temperate shallow lakes. The main difference between them is that phytoplankton growth in Lake Balaton remained severely P-limited despite P-driven eutrophication during the last 30 years, whereas extremely high turbidity causes a permanant light limitation in Neusiedlersee and therefore an increase in P-loadings did not result in a similar increase in phytoplankton biomass. Neusiedlersee is a (slightly) saline inland lake. In Lake Balaton, the blue-green alga *Cylindrospermopsis raciborskii* blooms invariably if the July–August temperature deviates positively from a 30-year average by ca. 2°C. A supposed global warming is predicted to cause a higher frequency (but not intensity!) of these blooms. Neusiedlersee is very shallow and therefore regulation techniques cannot prevent water levels sinking in successive dry years. Annual averages of phytoplankton seem to follow quite a regular, wave-like cyclicity. Such cycles can be recognised in the population records of the characteristic species. Similar changes were seen in changes of water level, conductivity, inorganic-P, inorganic N-forms and nutrient ratios. How phytoplankton species can follow a climatic cycle that covers 200 to 500 generations has not yet become clear. Because of reasons discussed in the paper, neither of the two cases can be generalised; each is quite individual.

## 1. Introduction

Understanding the effects of environmental change on different kinds of ecosystems is hardly possible without good scaling, which involves matching biotic responses to the

appropriate level of environmental variability. "Global climate change" is a relatively new term. Consequently, it is frequently imprecisely defined and is rarely qualified temporally or spatially. It can be accepted that global change has large spatial dimensions: roughly, many or most of the world's ecosystems, both terrestrial and aquatic, are affected. Concerning time-scales, global change is expected to influence the life of many future human generations, at scales of decades to centuries or even millenia. Global climate change is usually anticipated to be a slow, trendlike process.

Phytoplankton species live for some days. Population changes occur in time-spans of days to weeks. Some months are sufficient to observe major successions. In the time-span of a decade or longer, floristic changes in phytoplankton can take place and evolutionary adaptation may occur. If we accept that global change occurs over a period of some years, we should therefore expect the reactions of the phytoplankton to be expressed at the levels of "floristic change" or "evolutionary adaptation" [1]. Logic says that global change is too slow and gradual to have any impact at the level of phytoplankton population dynamics or of seasonal succession.

In this paper, I attempt to predict phytoplankton responses to global climate change, by extrapolation from observations in two ongoing, long-term studies. One of them (Lake Balaton, Hungary) shows us that despite the considerations presented above, a global warming can have effects on phytoplankton population dynamics within individual calendar years. Moreover, this signal is distinguishable from a prevalent effect of eutrophication and subsequent recovery on the phytoplankton. The other (Neusiedlersee, Austria/Hungary) invokes a 27-year study of phytoplankton and the changes which follow a 6- to 10-year cyclicity related to fluctuations in the hydrological conditions.

The data used in this paper, many of which have been published previously, were obtained by widely accepted standard samplings and methods (see [2] to [6]).

## 2. Lake Balaton: occurrence and population dynamics of *Cylindrospermopsis raciborskii*

Lake Balaton (Hungary) is the largest shallow lake in central Europe. The lake has a surface area of 593 km$^2$, is 77.9 km long, 7.2 km wide on average (maximum width 15 km) and has a mean depth of 3.14 m (maximum 11 m). The theoretical retention time is 3 to 8 years. The lake was originally mesotrophic but underwent rapid eutrophication during the 1960s and 1970s [7] as a consequence of increased P-loadings. Because the majority of the nutrient load is received by the western basin, a sharp trophic gradient developed in the elongated lake. Even in the less eutrophic part of the lake, annual average phytoplankton biomass increased significantly when compared with early records (Fig. 1). Nevertheless, phytoplankton growth in the lake remains strongly P-deficient throughout the year [8]. The lake sediment is significantly enriched with phosphorus [9].

Summer phytoplankton of Balaton used to be dominated by *Snowella lacustris, Ceratium hirundinella* and centric diatoms (especially *Aulacoseira* spp.). As eutrophication proceeded, heterocytic blue-green algae became increasingly prominent

in the late summer phytoplankton. The first to become prominent had been recorded while the lake was still mesotrophic (*Aphanizomenon flos-aquae, Anabaena* spp.). Since the beginning of the 1970s, new species of heterocytic blue-green algae (*Aphanizomenon issatschenkoi, Rhaphidiopsis meditarranea*) have appeared in the flora [10, 11].

A large-scale restoration programme in the early 1980s has arrested and begun to reverse the eutrophication. So far, the programme has resulted in about 50–60% reduction of the biologically available P-load of the lake. In the hypertrophic (western) basin of the lake, the P-load reduction is almost 80%. Annual average biomass of the above heterocytic blue-green algae in the hypertrophic part of the lake decreased in parallel with the load-reduction [6], suggesting that these species utilize P-sources originating mainly from external (catchment) sources.
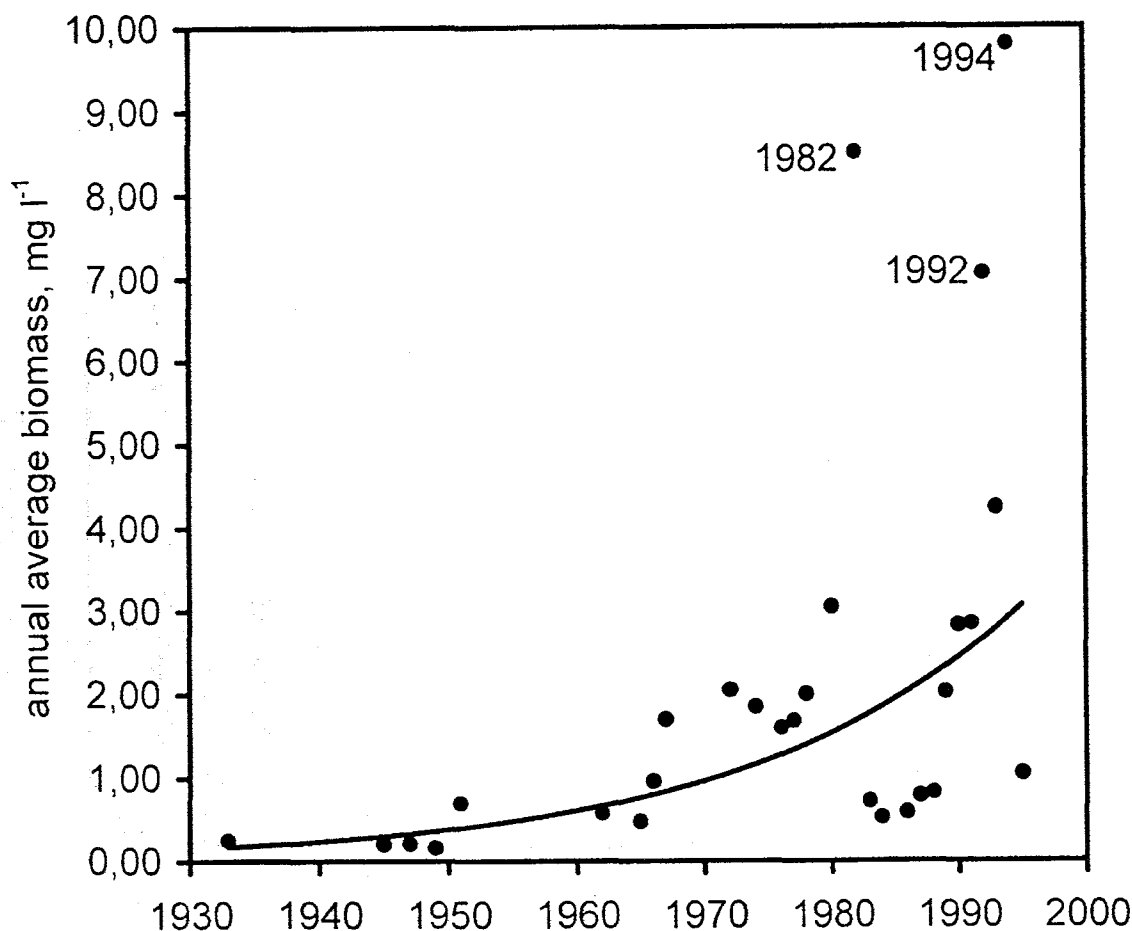
FIGURE 1. Annual average phytoplankton biomass (mg l$^{-1}$) between 1933 and 1994 in the northeastern part of Lake Balaton. A continuous trendline indicates the eutrophication process.

*Cylindrospermopsis raciborskii* Wolosz. is a heterocytic, nitrogen-fixing blue-green alga. The species was recorded almost simultaneously at several localities in Hungary during the 1970s [12–14]. *C. raciborskii* appeared in Balaton in 1979 [15]. In late summer and autumn of 1982, a heavy bloom swept through the lake, peaking at $10^8$ trichomes $l^{-1}$ in the northeastern part of the lake [16]. Similar blooms occurred in the summers of 1992 and 1994 (Fig 2; [6]). In these years, late summer phytoplankton maxima of 35–50 mg $l^{-1}$ were observed in the northeastern part of the lake. In other years summer maxima did not exceed 15 mg $l^{-1}$ [4], a level consistent with mesotrophy.

Concerning the ecology of *C. raciborskii* in Balaton, two peculiar features need explanation. One is the irregular nature of blooms and the other is its apparent independence of prevailing biologically available P concentrations and external P-loadings. So far as meeting its phosphorus requirement is concerned, *Cylindrospermopsis* blooms may draw sufficient from the sediment store of phosphorus during the period of its overwintering [6]. Indirect evidence supports the hypothesis that, as in the case of *Gloeotrichia echinulata* [17], phosphorus assimilation and planktonic growth of *C. raciborskii* may become spatially and temporally uncoupled.
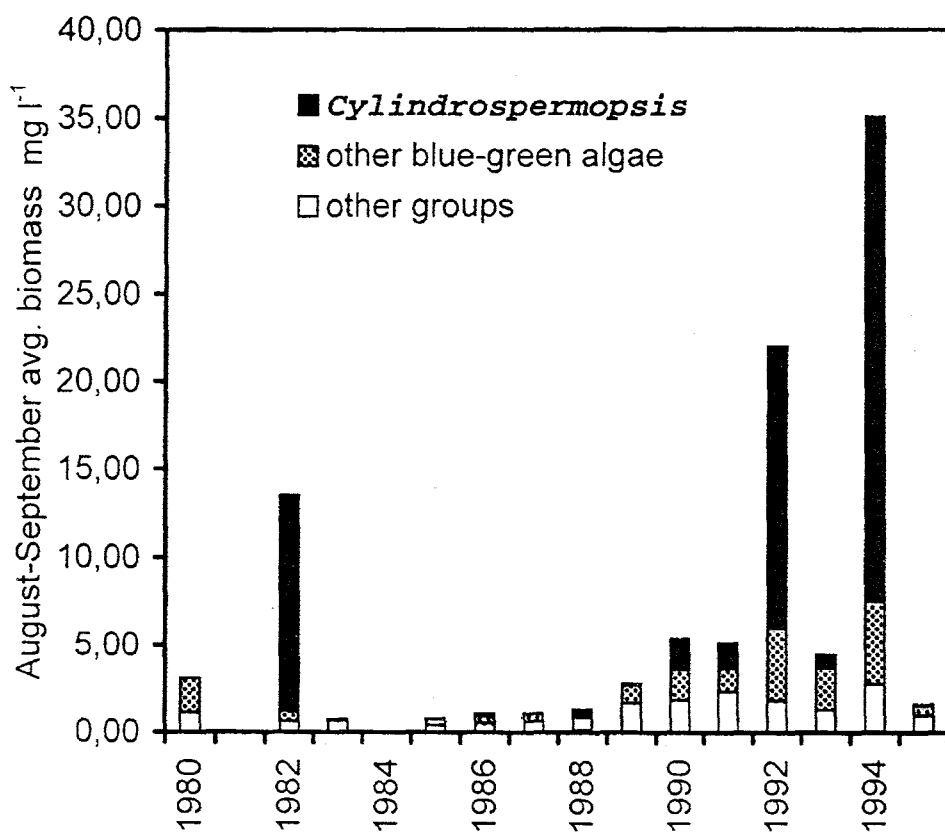


FIGURE 2. August–September average biomass (mg $l^{-1}$) of *Cylindrospermopsis raciborskii*, other blue-green algae and other phytoplankton groups in the northeastern basin of Lake Balaton between 1980 and 1995.
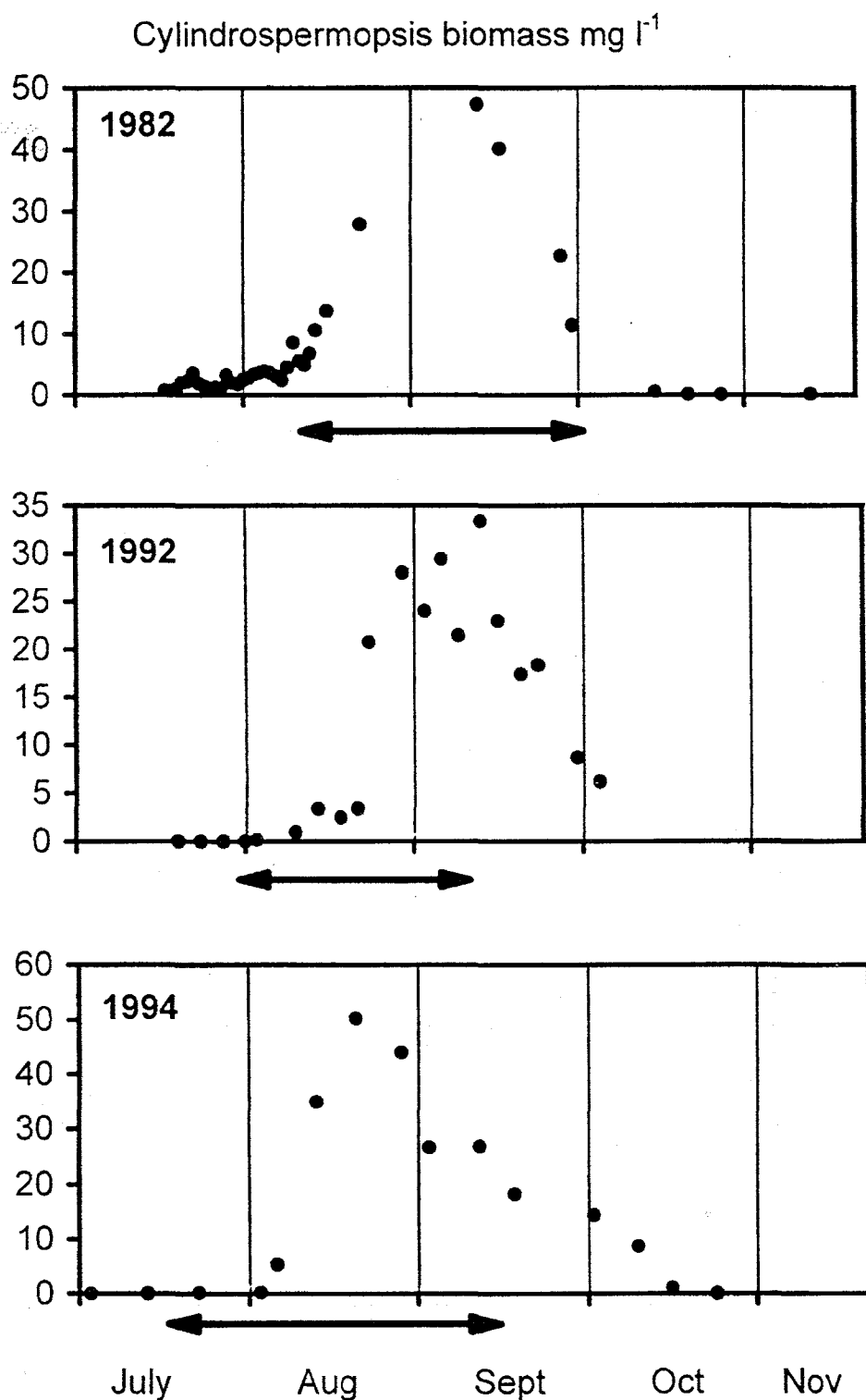
FIGURE. 3. Development and decline of *Cylindrospermopsis raciborskii* blooms (biomass, mg l$^{-1}$) in the northeastern part of Lake Balaton in the summers of 1982, 1992 and 1994. Arrows indicate the extension of the continuously calm, hot periods

Irregularity of the *C. raciborskii* blooms in Balaton owes more to interannual variations in summer weather conditions. The summers when the species bloomed were unusually hot. Numerous records, both from field observations and laboratory studies, point to the high temperature requirement of *C. raciborskii*. Indeed the species, first described in the Indo-Malayan flora, has for long been regarded as a tropical species.

In the *Cylindrospermopsis* summers, the exponential phase of growth started roughly two weeks after the onset of the hot, calm weather (Fig. 3). The August–September average biomass of *Cylindrospermopsis* was high only in years when the average air temperatures of two subsequent summer months (July–August or August–September) exceeded the 30-year average by at least 2°C (Fig. 4). There is no linear correlation between temperature deviation and *Cylindrospermopsis* biomass; if the former exceeds a certain degree the bloom occurs invariably (see arrows on Fig. 4).

Laboratory studies [18] showed that akinetes of *Cyilindrospermopsis* differ from those of other blue-green algae in Balaton. Akinetes of other species germinate over a broad temperature range (16 to 27°C). The temperature optimum of *Cylindrospermopsis* is narrow; akinetes germinate best at 21–22°C. Such high sediment temperatures occur in the temperate Balaton only in exceptionally hot years. There is thus strong circumstantial evidence for regarding the occurrence of *Cylindrospermopsis* blooms in Balaton as a primary response to above-average temperatures at the location.
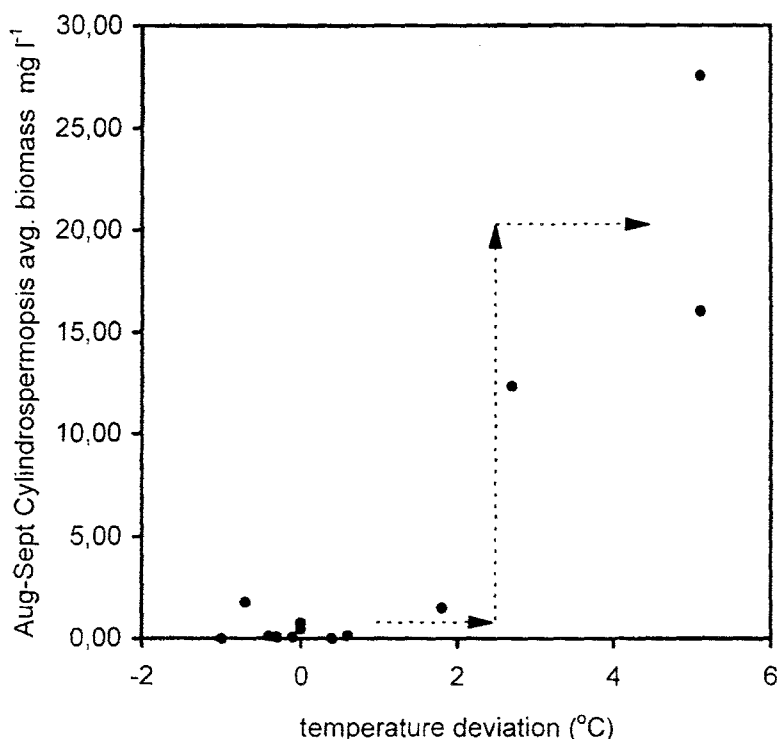


FIGURE 4. August–September averages (1982–1995) of *Cylindrospermosis raciborskii* biomass (mg l^{-1}) in Lake Balaton, plotted against the deviation of August–September (1982–1995) average air temperatures from a 30-year average. Zero on the abscissa corresponds to average summer; negative values indicate cold summers and positive values indicate warm summers.

## 3. Neusiedlersee: long-term population dynamics of dominant species

The Neusiedlersee (Fertô) is a large shallow lake on the Austrian-Hungarian border. Its surface area is 300 km$^2$; it is 35 km long, 8.6 km wide on average, and has a mean depth of 1.3 m (maximum 1.8 m). The theoretical retention time is 3 years. Because the lake does not have a natural outlet and most of the lakewater is resupplied from precipitation and groundwater, the water level has fluctuated within a wide range during the 20 thousand years of lake history. The last occasion on which the lake completely dried out was between 1868 and 1872. After the basin refilled, the reed-belt reappeared on the shores and progressively increased towards the centre of the lake basin during the last 100 years. For the last 30 years or so, approximately one-third of the lake area has been covered by reed-stands. The water level of the lake can be regulated by opening and closing the artificial outlet (Hanság csatorna/Einser Kanal) in the Hungarian part of the lake. This regulation can prevent high water levels during rainy years, but fails to avoid low water levels during dry periods. Consequently, each biotic community, from higher plants to plankton, has been subjected to fluctuations in water levels caused by climatic changes.

The mesotrophic lake has a high salt-content, is alkaline and very turbid. Conductivity ranges from 2000 to 3500 μS cm$^{-1}$, alkalinity is 8.0–10.5 meq l$^{-1}$, pH is 7.5–10. Secchi-disc transparency in the open water is characteristically ca. 0.2 m (range 0.06 to 0.8 m; higher values occur only under ice). The lake sediment is characterised by small, slowly settling, fine-grained inorganic particles. The average seston content of the lake is very high (80–100 mg l$^{-1}$; comparable high values are found only in flooding lowland rivers). The water is rich in silica, and the concentrations of dissolved N and P (average for 1987–1992: 297 μg-N l$^{-1}$ and 15 μg-P l$^{-1}$) are usually higher than the level that is considered limiting in other lakes. Because of the inherently high turbidity of the open water of the lake, growth of phytoplankton is presumably subject to frequent or continuous light limitation, with only brief exceptions.

The short-term and seasonal changes of dominant species in Neusiedlersee are unusual, really corresponding to the dynamics of meroplankton [5]. Although the lake is quite a large one, horizontal differences in phytoplankton distribution are slight and temporary (see Figs 2 and 3 in [5]).

Hundreds of algal species are described from different localities in the extended reed-belt of Neusiedlersee but the open water of the lake is relatively poor in phytoplankton species: no more than several dozen species are noted in the annual cycle; for most lakes, the list might run to one or two hundreds. The exacting environmental constraints of turbidity and salinity are doubtless implicated. The most important and regularly occurring species are listed in Table 1.

There are two notable features in the long-term development of phytoplankton. One is the regular cyclicity of biomass development, and the other is a sharp change in the composition during the early 1970s. The overwhelming contribution of diatoms and coccal green algae, and the insignificant fraction of buoyant species, are the most characteristic quantitative features of the phytoplankton composition (Fig. 5). In this respect, the phytoplankton resembles that of a lowland river [19]. Diatoms usually contribute the larger part of the annual average biomass, but in two of the last 27

TABLE 1. Characteristic species from the phytoplankton of Neusiedlersee.

| | |
|---|---|
| *Campylodiscus clypeus* Ehr. | *Koliella* sp. |
| *C. clypeus* var. *bicosta* (W. Smith) Hustedt | *Lobocystis planktonica* (Tiff. & Ahlstr.) Fott |
| *Chaetoceros muellerii* Lemm. | *Microcystis aeruginosa* Kütz. |
| *Chroococcus limneticus* Lemm. | *M. wesenbergii* Komárek |
| *Ch. minutus* (Kütz.) Nägeli | cf. *Merismopedia minima* Beck. |
| *Cryptomonas erosa/ovata* | *Monoraphidium contortum* (Thur.) Kom.-Legn. |
| *Crucigenia quadrata* Morren | *M. pseudobraunii* (Belch. & Schwale) Heynig |
| *Chrysochromulina parva* Lackey | Small *Navicula* spp. |
| *Cyclotella meneghiniana* Kütz. | *Neglectella peisonis* Schagerl |
| *Dicttyosphaerium pulchellum* (Wood) | Small *Nitzschia* spp. |
| *Elakatothrix lacustris* Kors. | *Oocystis lacustris* Chodat |
| *Euglena oxyuris* Schmarda | *Pediastrum duplex* Meyen |
| *E. tripteris* (Duj.) Klebs | *Phacus pyrum* (Ehr.) Stein |
| *Fragilaria acus* Kütz. | *Planktosphaeria gelatinosa* G. M. Smith |
| *F. brevistriata* Grunow | *Rhodomonas minuta/lacustris* |
| *F. construens* (Ehr.) Grunow | *Sphaerocystis schroeterii* Chodat |
| Small *Fragilaria* spp. | *Surirella peisonis* Pantocsek |
| Small centric diatoms | |

years (1975, 1976), green algae (especially *Pediastrum duplex*) were dominant. In the late 1970s, blue-green algae (first of all *Microcystis* spp.) contributed significantly to the annual biomass. These changes appear quite abruptly on compositional plots (see Fig. 13a in [5]) and they may reflect human impacts on the catchment area. Until the late 1960s, phytoplankton growth was most probably limited both by phosphorus deficiency and insufficient light. P-loadings to the lake increased sharply in the 1970s (this trend was reversed by the 1980s); moreover, large open-water stands of submerged macrophytes were extinguished. At the same time, there have been unusual variations in the annual distribution of rainfall, with summer rains tending to maintain water levels into autumn, thus offsetting the normal pattern of an autumnal diminution. It is not yet possible to separate the physical and chemical influences sufficiently to interpret the precise mechanisms underpinning these short-term compositional responses. These fluctuations are nevertheless superimposed upon a larger-scale cycle of biomass fluctuations in Neusiedlersee. In the period 1968 to 1994, there have been three distinct peaks in the phytoplankton biomass supported in the lake: the first was in 1975, the second in 1983 and the third in 1991 (Fig. 5). The 8-year cycle is distinctly wave-like: in this way, years with above average biomass do not appear stochastically or "out of trend", as they do in Balaton (see above). The cycle is echoed in the variations in the annual averages of each of the constant taxa of phytoplankton (Fig. 6). However, they do not each coincide precisely with the 8-year cycle of total biomass maxima. This observation might explain the findings of previous investigations to the effect that phytoplankton composition in Neusiedlersee varies enormously with spontaneous year-to-year appearances and disappearances [20].
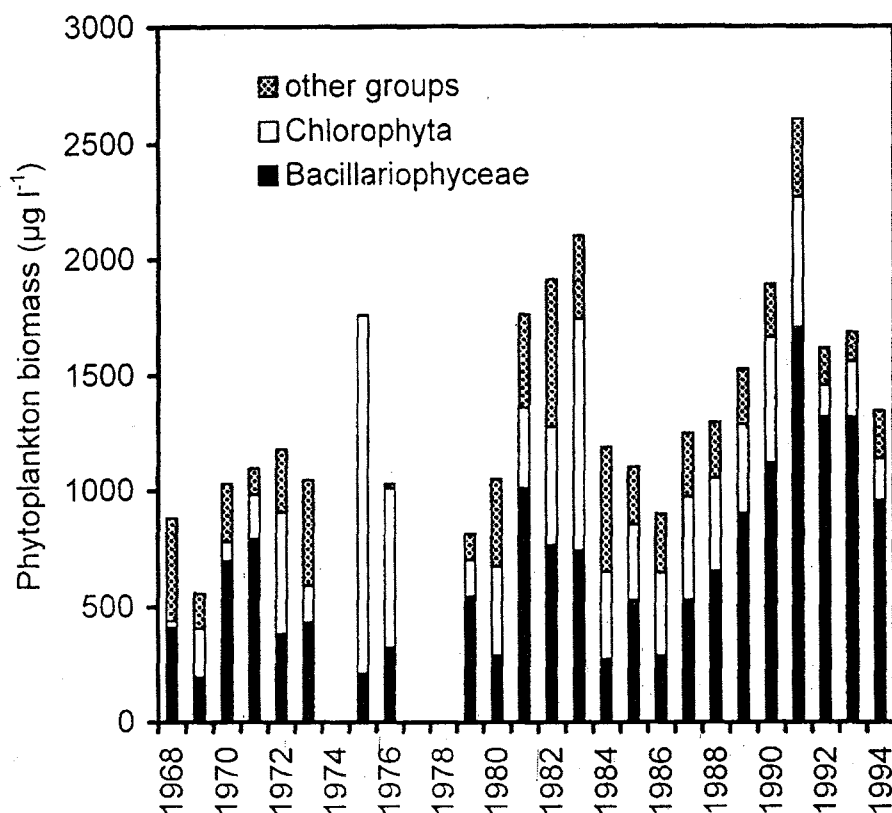
FIGURE. 5. Annual average biomass ($\mu$g l$^{-1}$) of diatoms, green algae and other groups in Neusiedlersee between 1968 and 1994.

Some descriptions of the plankton prior to 1968 are available. For example, *Monoraphidium contortum* was the dominant green alga in 1956–58 with cell numbers up to 3 million cells l$^{-1}$ [21]; this corresponds to a biomass of ca. 300 $\mu$g l$^{-1}$ (cf. Fig 2a, b). The species rose progressively to dominance at the beginning of the 1970s, with a peak of 8500 $\mu$g l$^{-1}$ in June 1972. During subsequent years its abundance fell significantly, large populations being found only in the colder seasons. In October 1982, however, the species was found to be dominant in many of the brown-water lagoons enclosed within the reed-belt of the lake [22]. *Pediastrum duplex* was found only in these reed-belt habitats during the 1960s [20], the first record of its planktonic occurrence not coming until 1969. This species predominated in 1975 when it represented some 80% of the total annual biomass. A peak abundance of 6440 $\mu$g l$^{-1}$ was noted for 28 July 1975. Since that time no comparable high biomasses have been recorded, although several specimens were recovered in every year since. Hustedt [23] commented that the diatom, *Chaetoceros muelleri,* was one of the most important species in both the plankton and the littoral zone of the lake. More recently it has been found exclusively in littoral samples [22, 24, 25]. Between 1987 and 1994, however, quite large planktonic populations of *Chaetoceros* developed almost every year in
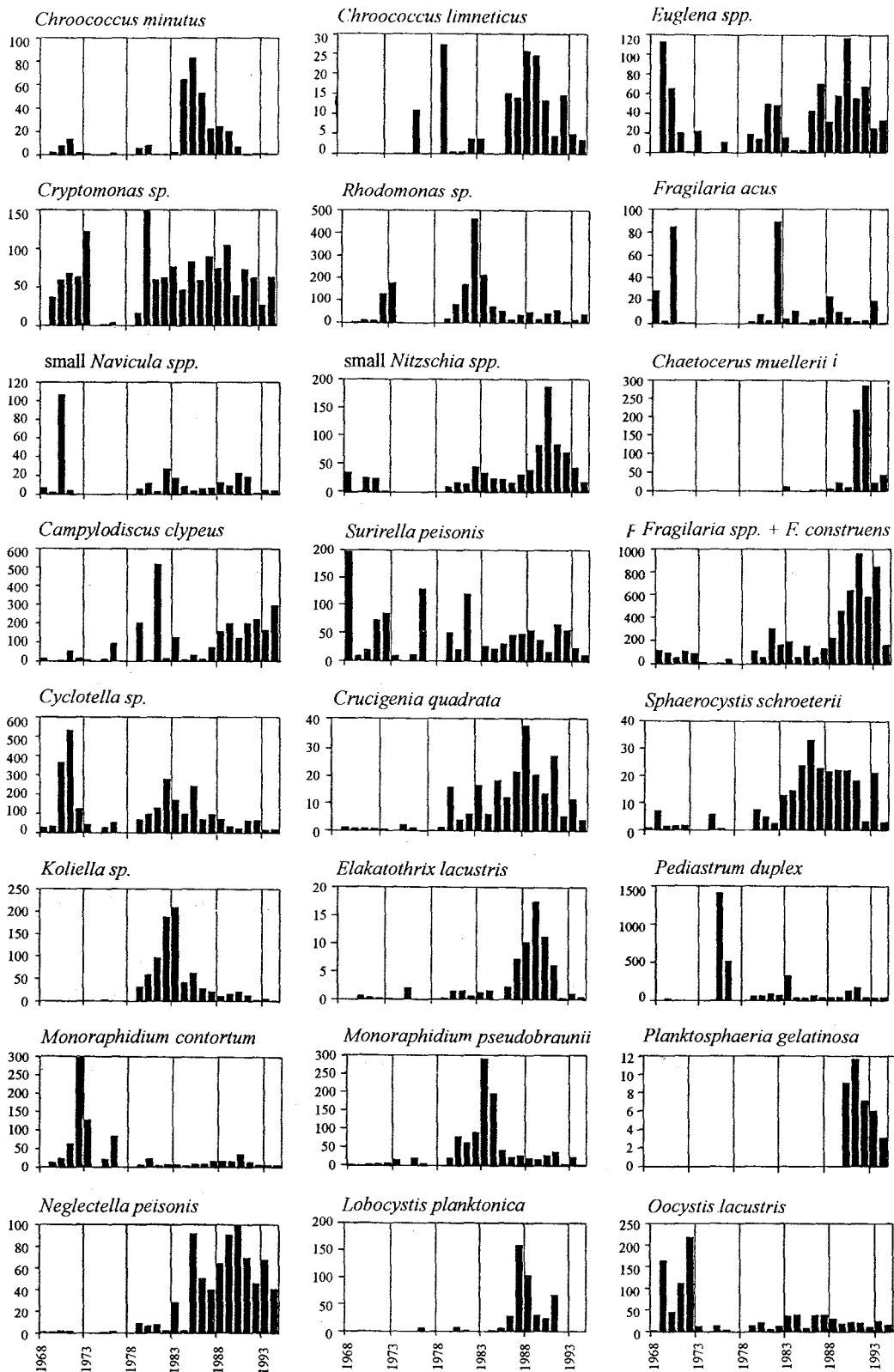
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FIGURE 6. Annual average biomass ($\mu g\ l^{-1}$) of the most important phytoplankton species in Neusiedlersee between 1968 and 1994.

one or more of the reed-belt lagoons. Detailed data on *Chaetoceros* population dynamics are given in [5].

This is the best of several examples suggesting that many algal species have refuges in the littoral swamps but periodically penetrate the open water to constitute large or dominant planktonic populations (Fig. 6). Both pilot [22] and systematic [2, 3] studies have shown that phytoplankters in small enclosed lakes differ significantly not only from those in the open water but from each other as well. With more intensive studies, probably, more "*Chaetoceros*-like" examples would be revealed. The testable hypothesis is advanced that the supra-annual cycles of abundances of phytoplankton in Neusiedlersee are related to large-scale hydrological changes which alternately reduce the range of species to the reedswamp refuges and expand them periodically to the open water of the lake.

This hypothesis is not invalidated by attempts to correlate the phytoplankton data with the physical and chemical variability (these have failed to show any compelling relationship, save one with the volume of suspended matter: see discussion in [5]), and by the fact that the wave-like trend in annual average phytoplankton biomass mirrors the fluctuations in water level (Fig. 7). The possibility of another proximate variable is not excluded, for instance, through the influence of salinity changes, although these are known to fluctuate simultaneously (albeit with differing damping) in the swamps and the open water. Changes in turbidity and the relative penetration of light may be crucial to the success of species in the open water, in which case these too could be related primarily to changes in water level.
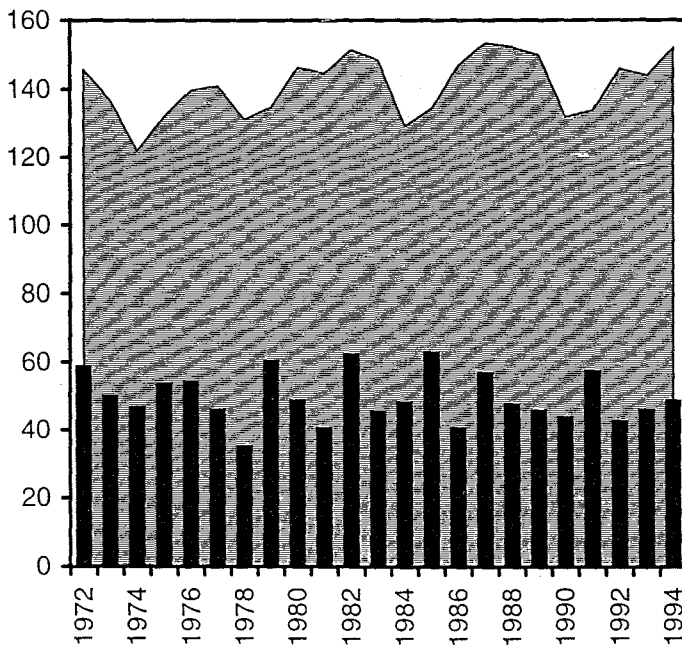


FIGURE 7. Annual average water level (m a.s.l.; shaded area) in Neusiedlersee and monthly mean precipitation (mm; solid verical bars). Data from the Meterorological Station Illmitz, 1972 to 1994.

## 4. General discussion

The above two case studies describe quite different phytoplankton responses to external climatic forcing, supposed to be subject to revision as a result of global modification. It is reasonable to suppose that global warming might mean an increasing frequency of years with positive temperature deviations of greater magnitudes. In this case, the observations on the ecology of *Cylindrospermopsis* blooms in Lake Balaton permit a trend of higher and more persistent biomass peaks to be forecast. July–August temperatures 2°C higher than present might well sustain regular *Cylindrospermopsis* blooms, independent from changes in fertility so long as the P-pool in the sediment remains active. However, this might be rather an exceptional example to take: not all of the species of phytoplankters in the lake have such a distinctive and crucial autecology or respond everywhere for the same reason and with the same sensitivity. Thus it would be unreasonable to apply the same explanation to the dominance of *C. raciborskii* in the tropical, oligotrophic Lake Kariba (Africa) in the rainy season (see [26]).

The behaviour of phytoplankton in Neusiedlersee is, or at least used to be, possibly more generalised. The lake is astatic with no natural outlet. Although a canal was constructed to regulate top water level, it does not protect the lake from volume fluctuations attendant upon its shallowness and large surface area, especially in dry years. Astatic lakes were more common in the past (for example, Lake Balaton was one of them), until drainage works in the 19th and 20th centuries brought some stabilisation about the lower natural limits. In consequence, the case of Neusiedlersee is yet more exceptional. The oscillation of drier to wetter years in this region has a period of 6 to 10 years. The doubling times of characteristic species of phytoplankton are mainly less than 5 to 7 days during the vegetation period [5]. Thus, the cycle of climatic change accommodates 200 to 500 generations of planktonic algae. It is far from clear how phytoplankton species might adapt to such gradual climatic changes so precisely or how the dominance of any might be driven by competition; it is far more likely that different and remotely separated climatic conditions will favour the performances of algae from among those present at the time.

It has been demonstrated several times, for example in Tilman's [27] experiments on competitive exclusion and, quite recently, in testing and extending Connell's intermediate distrubance hypothesis to the short life-times of planktonic organisms [28–31], that the rapidity of phytoplankton population responses to environmental forcing lent great advantages to their study, in nature and in experimental manipulations. Responses to global climate change may be exceptional in this respect: the 7-to 10-year cycles in the abundance and rarity of species are not abrupt, equalling in real time the establishment of pioneer terrestrial vegetation. The dataset from Neusiedlersee also shows us that slow, small and gradual global changes, drive changes in the dynamics of phytoplankters (wave-like overall trend), but these are nevertheless sensitive to local human activities.

## Acknowledgements

## References

[1]. Reynolds, C. S. (1990). Temporal scales of variablility in pelagic environments and the response of phytoplankton. *Freshwater Biology* **23**, 25-53.

[2]. Padisák, J. (1993). Species composition, spatial distribution, and the seasonal and interannual dynamics of phytoplankton in brown-water lakes enclosed with reed belts (Neusiedlersee/Fertő; Austria/Hungary). *BFB-Bericht* **79**, 13-29.

[3]. Padisák, J. (1993). Dynamics of phytoplankton enclosed with reed belts (Neusiedlersee/Fertő; Austria/Hungary). *Verh. Internat. Verein. Limnol.* **25**, 675-679.

[4]. Padisák, J. (1994). Relationships between short-term and long-term responses of phytoplankton to eutrophication of the largest shallow lake in Central Europe (Balaton, Hungary). In: *Environmental protection and lake ecosystems* (eds. H. Sund, H.-H. Geller, W. Xiaogan, Y. Kechang & S. Fengnind). Science and Technol. Press, Beijing, pp. 419-437.

[5]. Padisák, J. & Dokulil, M. (1994). Meroplankton dynamics in a saline, turbulent, turbid shallow lake (Neusiedlersee, Austria and Hungary). *Hydrobiologia* **289**, 23-42.

[6]. Padisák, J. & Istvánovics, V. (in press). Differential response of blue-green algal groups to phosphorus load reduction in a large shallow lake: Balaton, Hungary. *Verh. Internat. Verein. Limnol.* **26**.

[7]. Herodek, S. (1984). The eutrophication of Lake Balaton: Measurements, modelling and management. *Verh. Internat. Verein. Limnol.* **22**, 1087-1091.

[8]. Istvánovics, V. & Herodek, S. (1995). Estimation of net uptake and leakage rates of orthophosphate from $^{32}P$ uptake kinetics by a linear force-flow model. *Limnology and Oceanography* **40**, 17-32.

[9]. Herodek, S. & Istvánovics, V. (1986). Mobility of phosphorus fraction in the sediments of Lake Balaton. *Hydrobiologia* **135**, 149-154.

[10]. Bartha, Zs. (1974). The occurrence of *Aphanizomenon issatschenkoi* (Ussaczew) Proschkina-Lavrenko in Lake Balaton. *Annales Instituti Biologici (Tihany) Hungaricae Academiae Scientarium* **41**, 127-131.

[11]. Tamás, G. (1974). The occurrence of *Rhaphidiopsis mediterranea* Skuja in the plankton of Lake Balaton. *Annales Instituti Biologici (Tihany) Hungaricae Academiae Scientarium* **41**, 317-321.

[12]. Schmidt, A. (1977). Adatok Dél-magyarországi vizek algáinak ismeretéhez I. (Contributions to the knowledge about algae of waters of southern Hungary I.). *Botanikai Közlemények* **64**, 183-196.

[13]. Hamar, J. (1977). Data on the knowledge of the blue-green alga *Anabaenopsis raciborskii* Wolosz. *Tiscia (Szeged)* **12**, 17-20.

[14]. Horecka, M. & Komárek, J. (1979). Taxonomic position of three planktonic blue-green algae from genera *Aphanizomenon* and *Cylindrospermopsis*. *Preslia* **51**, 289-312.

[15]. Oláh, J., ElSamra, M. I., Abdel-Moneim, M. A., Tóth, L. & Vörös, L. (1981). Nitrogénkötés halhústermelô agroökoszisztémákban [Nitrogen fixation in fish producing agro-ecosystems]. *A Halhústermelés Fejlesztése* **10**, HAKI, Szarvas. [In Hungarian].

[16]. G.-Tóth, L. & Padisák, J. (1986). Meteorological factors affecting the bloom of *Anabaenopsis raciborskii* Wolosz. (Cyanophyta: Hormogonales) in the shallow Lake Balaton, Hungary. *J. Plankton Research* **8**, 353-363.

[17]. Istvánovics, V., Petterson, K., Rodrgio, M. A., Pierson, D., Padisák, J. & Colom, W. (1993). *Gloeotrichia echinulata*, a colonial cyanobacterium with a unique phosphorus uptake and life strategy. *J. Plankton Research* **15**, 531-552.

[18]. Gorzó, Gy. (1987). Fizikai és kémiai hatások a Balatonban elôforduló heterocisztás cyanobaktériumok spóráinak csírázására [The influence of physical and chemical factors on the germination of spores of heterocystic cyanobacteria in Lake Balaton]. *Hidrológiai Közlöny* **67**, 127-133. [In Hungarian with English summary].

[19]. Reynolds, C. S., Descy, J.-P. & Padisák, J. (1994). Are phytoplankton dynamics in rivers so different from those in shallow lakes? *Hydrobiologia* **289**, 1-7.

[20]. Kusel-Fetzmann, E. (1979). The algal vegetation of Neusiedlersee. In: *Neusiedlersee. Limnology of a shallow lake in Central Europe* (ed. H. Löffler), pp. 171-202.

[21]. Ruttner-Kolisko, A. & Ruttner, F. (1959). Zusammenfassung und allgemeine Limnologie. *Wiss. Arb. Burgenland* **23**, 195-201.

[22]. Padisák, J. (1983). A comparison between phytoplankton of some brown-water lakes enclosed with reed belt in the Hungarian part of Lake Fertõ. *BFB-Bericht* **47**, 133-155.

[23]. Hustedt, F. (1959). Die Diatomeenflora des Neusiedler Sees im österrreichishen Burgenland. *Öst. Bot. Z.* **106**, 390-430.

[24]. Bartalis, É. T. (1987-88). Egyes meteorológiai tényezôk hatása a Fertôrákosi öböl biológiai vízminôségére és fitoplankton összetételére [Influence of some meteorological factors on the water quality and phytoplankton compositions of the Fertörákos-Bay]. *Botanikai Közlemények* **74-75**, 153-192. [In Hungarian with English summary].

[25]. Padisák, J. (1984). The algal flora and phytoplankton biomass of the Hungarian part of Lake Fertô I.: Rákosi-bay. *BFB-Bericht* **51**, 17-29.

[26]. Ramberg, L. (1987). Phytoplankton succession in the Sanyati basin, Lake Kariba. *Hydrobiologia* **153**, 193-202.

[27]. Tilman, D. (1982). *Resource competition and community strucure*. Princeton University Press, Princeton.

[28]. Padisák, J., Reynolds, C. S. & Sommer, U. (1993). Intermediate Disturbance Hypothesis in Phytoplankton Ecology. *Developments in Hydrobiology* **81**, Kluwer Acad. Publ., Dordrecht, Boston, London. 199 pp. [Reprinted from *Hydrobiologia* **249**, 135-156].

[29]. Padisák, J. (1994). Identification of relevant time-scales in non-equilibrium population dynamics: conclusions from phytoplankton surveys. *New Zealand Journal of Ecology* **18**, 169-176.

[30]. Wilson, J.B. (1994). The intermediate disturbance hypothesis of species co-existence is based on patch dynamics. *New Zealand Journal of Ecology* **18**, 176-181.

[31]. Reynolds, C. S. (1995). The intermediate disturbance hypothesis and its applicability to planktonic communities: comments on the views of Padisák and Wilson. *New Zealand Journal of Ecology* **19**, 219-225.