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The influence of extreme floods from the River Danube in 2006 on phytoplankton communities in a floodplain lake: Shift to a clear state

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A B S T R A C T

The influence of extreme floods from the River Danube in 2006 on the species composition and vertical distributions of phytoplankton was studied in a shallow floodplain lake, Lake Sakadaš (Kopački Rit Nature Park, Croatia) which in the last few decades was in a turbid state characterised by high phytoplankton concentrations. As a consequence of extremely high floods, the whole floodplain area (approximately 16 km^2) became one lentic habitat with well developed macrophyte vegetation. Seasonal dynamics of chlorophyll *a* (Chl *a*) concentration in the lake had a characteristic pattern for the shallow lakes with dense macrophyte vegetation. Extremely low mean phytoplankton abundance and biomass were found in the conditions of very high nutrient concentrations. Dominant phytoplankton species were diatoms and chlorococcal green algae from the functional groups characteristic for a mixed environment. The canonical correspondence analysis (CCA) demonstrated that nutrients and temperature were significant environmental variables for their development. The sequence of phytoplankton seasonality, vertical distribution of phytoplankton, as well as the domination of rapidly acclimating phytoplankton forms (R-strategists) indicated clear, well-mixed conditions and a highly disturbed environment. Our results suggest that the occurrence of extreme flooding can be a stressor high enough for the transition from a turbid to a clear state of the floodplain lake. Possibly, cyclic shifts between alternative stable states in floodplain ecosystems can be expected as a consequence of the impact of extreme hydrological events induced by a climate change.

Introduction

The flood pulse is the most important environmental parameter in floodplain aquatic environments, thus rivers and their fringing floodplain lakes can be considered integrated components of a single dynamic system, linked by strong interactions between hydrological and ecological processes (Junk et al. 1989; Junk and Wantzen 2004). The pulsing of river discharge determines the degree of connectivity and the exchange process of matter and organisms across river-floodplain gradients (Tockner and Stanford 2002).

Information on the role of hydrology on phytoplankton community composition in floodplain lakes of large tropical rivers showed that phytoplankton dynamics were hydrology driven, as well as that flood pulse influences composition and population densities of the phytoplankton communities (Ibañez 1998; Oliveira and Calheiros 2000; Zalocar de Domitrovic 2003; Nabout et al. 2006; Townsend 2006; Butler et al. 2007). Similarly, the importance of hydrologic controls on the phytoplankton distribution in floodplain lakes along the large temperate rivers, e.g. Lower Rhine and Meuse (Van den Brink et al. 1993) and River Danube (Hein et al. 1999, 2004; Stoyneva 1998, 2003) was recognised. According to the Flood Pulse Concept (Junk et al. 1989), the flood pulses are not considered to be a disturbance, while some other studies (e.g. Paidere et al. 2007) have proven that floods can be a disturbance factor for phytoplankton development. Moreover, research done by Mihaljević et al. (2009) showed that flooding has a dual impact on phytoplankton development in the Danubian floodplain lake. Early spring flooding has a stimulating effect on phytoplankton development, while flooding in the late spring and in summer has a negative effect.

According to the current trends in floodplain research (Henle et al. 2006), it is essential to elucidate how species and their communities respond to unexpected and extreme events, such as floods in the summer or extremely dry conditions without flood. For example, the results of the investigation on the influence of the 2002 unusual and extreme floods of the River Middle Elbe (Germany) on flora and fauna of the riverine grasslands showed that the effects of floods as well as the responses to them (i.e.

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resistance/resilience) varied widely among the different taxonomic groups (Ilg et al. 2008).

Water-level fluctuations in shallow lake ecosystems are regarded to be an important factor for lake ecosystem functioning, and thus extreme water levels may cause shifts between the turbid and the clear, macrophyte-dominated state (Coops et al. 2003; Scheffer et al. 2001, 2003; Scheffer and van Nes 2007). Floodplain and ox-bow lakes form excellent examples of alternative stable states (Dokulil et al. 2006). According to the findings of Van Geest et al. (2007), shifts between the two contrasting states in the floodplain lakes of the Lower Rhine were common and episodes of low water levels appear to be an important external driver. The question arises, how phytoplankton communities in floodplain lakes respond to extreme flooding and a drastic increase in the water level.

Pulses of water discharges in the Danube River occur with an interannual variability; therefore, some hydrological regularities can be identified. The spring–summer flood which usually occurs in the period from March to July (especially in the middle and lower parts of the river) is the main and well-pronounced phase of the Danubian water regime. However, at the end of the 20th and the beginning of the 21st century, the occurrence frequency of catastrophic floods and inundations increased. Thus, the latest extreme flood occurred in spring and summer 2006 due to the large amounts of melted snow, the very warm spring and the heavy precipitation. The water levels exceeded the maxima observed during previous 100–130 years at some gauge stations on the middle Danube and at most gauge stations on the lower Danube (Mikhailov et al. 2008).

The main objective of the present study was to analyze the influence of extremely high flooding of the River Danube in 2006 on the species composition and vertical distribution of phytoplankton in Lake Sakadaš, the deepest lake in the Danubian floodplain of Kopački Rit Nature Park (Croatia). In order to explain the relative importance of the extreme conditions of the actual year on the phytoplankton communities, the given results will be compared to the results of phytoplankton investigations (Mihaljević et al. 2009) in 2004, carried out under the usual flood conditions.

Material and methods

Study sites

The investigated Lake Sakadaš is a part of a natural floodplain along the River Danube (river 1383–1410 km) belonging to the Kopački Rit Nature Park (Croatia).

The inundation area is clearly delineated by embankments constructed in the middle of the last century and covers approximately 16 km^2. Due to the hydrological connectivity with the main river channel it can be divided into two subsystems (Fig. 1). Subsystem A is impounded by the river through the backwater system (side arm), and subsystem B through a network of perennial channel networks. Within the different types of water bodies in subsystem B the deepest lake is Lake Sakadaš, which has an average depth of about 4–5 m, with a surface water area of about 0.15 km^2. Flooding of the lake begins when the Danube water level at gauge station near Apatin (river 1401 km) rises above 3 m (Mihaljević et al. 1999). Flooding occurs usually in spring and early summer (potamophase), while during low water conditions (limnophase), the lake is an isolated water subsystem in the floodplain.

Water quality monitoring and the results of phytoplankton research done in the past decades (Mihaljević et al. 1999; Horvatić et al. 2003) have shown that the lake was continuously in a high

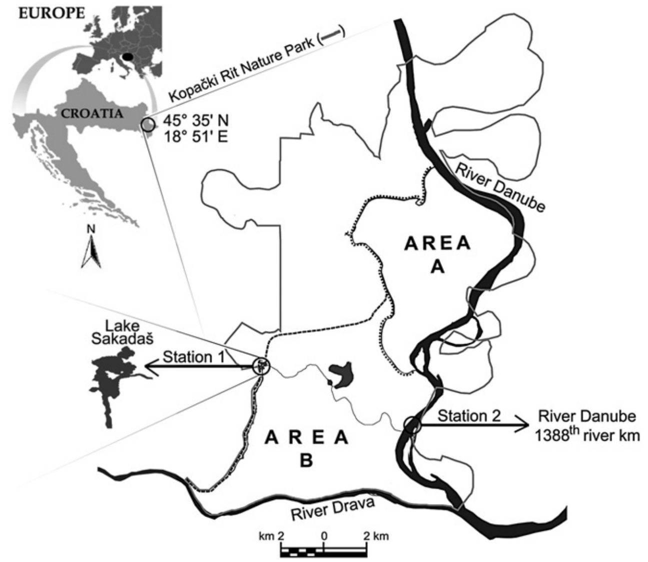

Fig. 1. Study area – Lake Sakadaš, a part of the Danubian floodplain area of the Kopački Rit Nature Park (Croatia).

trophic state (eutrophic–hypertrophic) with well developed phytoplankton communities and the obligatory appearance of cyanoprokaryotes bloom in summer, occasional *Peridinium aciculiferum* Lemm. bloom in autumn and *Synura uvella* Ehrenb. bloom during the winter.

The dominant macrophyte species in the permanent water bodies of the floodplain are *Potamogeton gramineus* L., *Ceratophyllum demersum* L., *Myriophyllum spicatum* L., *Trapa natans* L., *Nymphoides peltata*, Kuntze, *Lemna* sp. div., *Polygonum amphybium* L. and *Spirodella polyrhiza* (L.) Schleid. A continuous increase in permanent stands of macrophytes in the lake was observed from 2004 onward (Vidaković and Bogut 2007).

Sampling and analyses

The standard station located in the central part of the lake was sampled at monthly intervals during the period March–November 2006. Similarly, samples were taken in the middle of the River Danube at river 1388 km, a few meters upstream from the connection with the floodplain channel during the high water discharge in March–May, July, August and November. Samples were taken using the Ruttner bottle.

To assess the phytoplankton abundance, biomass and Chl *a*, samples were taken at intervals of 1 m from the surface to the bottom of the lake and simultaneously, composite samples were taken from the whole water column of the lake and the river. Phytoplankton samples were fixed in acetic Lugol's solution according to Utermöhl (1958). A total of 67 phytoplankton samples were taken from the lake during the investigated period. Nutrient analyses were conducted on samples from the lake, taken from just beneath the surface and close to the bottom of the lake, as well as on the surface water samples from the river.

The following parameters were measured *in situ* beneath the surface (-surf) at approximately 0.2 m, and near the bottom (-bott) at 4–8 m depending on lake depth: water temperature (WT-surf; WT-bott), conductivity (Cond-surf; Cond-bott), pH (pH-surf; pH-bott) and dissolved oxygen (DO-surf; DO-bott) with a portable instrument (Multi 340i, WTW). Water transparency (SD) was measured by a Secchi disc. Chemical variables, ammonium (NH_4), nitrates (NO_3), nitrites (NO_2), total nitrogen (TN) and total phosphorus (TP) were determined in the laboratory according to standard methods (APHA 1992). For Chl *a* concentration, water was filtered through Whatman GF/C glass fibre filter and subsequently extracted with acetone. Absorbance was measured with a Shimadzu UV-1601 spectrophotometer at four different wavelengths (630, 645, 663 and 750 nm). Chl *a* concentrations were calculated according to Komárková (1989).

Phytoplankton species were identified using a light microscope (Carl Zeiss, Jena). To determine the diatoms, samples were treated with H_2O_2 and HCl. Taxonomic monographs about cyanoprokaryotes were used (Anagnostidis and Komárek 1985, 1988; Komárek and Anagnostidis 1989) as supplement to the literature for species determination (Hustedt 1976; Hindak et al. 1978; Meffert et al. 1981). Quantitative assessment of phytoplankton was done according to Utermöhl (1958). Phytoplankton species were counted at a magnification of 400× with a Carl Zeiss, Jena Axiovert 25 inverted microscope. The counting unit was the individual (cell, filament or colony). The abundance of each species is presented as the number of individuals per liter (ind. L^{-1}). To estimate biovolumes of the algae and cyanoprokaryotes, individuals were measured and their volumes calculated according to geometrical solids (Rott 1981). Biovolume was converted to biomass following Javornický and Komárková (1973) and Sournia (1978) and expressed as mg L^{-1} of fresh mass (FM). Dominant phytoplankton species were estimated from percentage contribution of individual species to total abundance. Only those species which had a minimum of 5% contribution to total abundance were considered to be the dominants.

A functional classification of phytoplankton species was done in order to evaluate changes in phytoplankton communities, as proposed by Weithoff (2003). Functional groups of phytoplankton were defined according to Reynolds et al. (2002) and updated by Padisák et al. (2009). A concept of phytoplankton life strategies done by Reynolds (1988) and modified by Reynolds and Irish (1997) was applied to explain phytoplankton succession with respect to intensity of disturbance and stress.

Statistical analyses

Phytoplankton vertical abundances for each interperiod were calculated by means of linear interpolation of original data by the Akima method, a method of bivariate interpolation and fitting for irregularly distributed data (Akima 1970, 1972), using the "akima, Ver. 0.5-1" package under R software environment Ver. 2.8.0 (R Development Core Team 2008) and have been shown graphically.

Among the available ordination methods, we have chosen to use canonical correspondence analysis (CCA). We were able to obtain quantitative information on the relationship between species and environmental variables using "ADE-4" program packages 2008 Release, under R statistical software environment (Thioulouse et al. 1997). Estimation of the explanatory power for each environmental variable was performed using the variable value as the sole constraint. Statistical significance for each variable was assessed using the Monte Carlo unrestricted test involving 999 permutations. The CCA plot represents the ordination of species in relation to the combination of the different environmental variables. Environmental variables are represented by arrows with the maximum value located at the arrow head. A total of 17 limnological variables were taken into consideration: WD, SD, WT-surf, WT-bott, DO-surf, DO-bott, Chl *a*-surf, Chl *a*-bott, pH-surf, pH-bott, Cond-surf, Cond-bott, TN-surf, TN-bott, TP-surf, TP-bott and phytoplankton abundance from composite samples. A Wilcoxon signed rank test for paired data was applied for analyses of the differences in phytoplankton biomass and abundance between 2004 and 2006.

The grouping of measured data was determined using the hierarchical cluster analysis and the degrees of possible grouping into up to 20 presumed groups was calculated by means of fuzzy cluster analysis using the "Cluster, Ver. 1.11.12" package Release 2009 under R software environment.

Results

Water quality

Values of the main physical and chemical parameters of Lake Sakadaš and the River Danube are shown in Table 1 and Fig. 2. The water level of the Danube rose more then 4 m in March, thus flooding of the floodplain began as usual (Fig. 2A). There was an unexpected extremely high Danube water level (8.2 m) at the beginning of April and it was one of the maximal water levels observed in the past hundred years. The water level remained high till the first half of June, followed by another summer extreme in August. As a consequence, the whole floodplain area was flooded and the water depth of the investigated floodplain lake reached more than 8 m. During the flooding, the river water temperature was lower than in the lake. There was a marked thermal stratification in the lake in the period May–August. Dissolved oxygen in surface water reached higher values than those at the bottom (except in August) and showed a significant negative correlation ($r = -0.76$, $p < 0.05$) with water temperature. Low-oxygen conditions were found in late spring and summer. Values of pH, always above 7, indicated alkaline conditions. Conductivity was high in March and then again in the period September–November. Secchi depth (Fig. 2B) reached its highest values in May (2.9 m), but was low (mostly less than 1 m) during the summer despite the low phytoplankton abundance. TP concentrations were very high, especially close to the bottom, as well as the TN concentrations in comparison with 2004 (Fig. 2C and D). The correlation of all measured physical and chemical parameters between the Danube and the lake was high ($r = 0.96$, $p < 0.05$) during the flooding.

Phytoplankton Chl a, biomass and abundance

In the phytoplankton composition of Lake Sakadaš, a total of 225 taxa were detected during counting, among which 31 taxa had abundances higher than 5% (Table 2). The rank–abundance curve (data not shown) followed a log-normal trend and showed that a statistically significant number of species was investigated.

The annual changes of phytoplankton abundance in the composite samples were in the range 1.75×10^6–8.57×10^6 ind. L^{-1}, while phytoplankton biomass varied between 1.74 and 23.62 mg L^{-1} (Fig. 2F and G). The lowest values of abundance and biomass were found in May. Phytoplankton abundance and biomass were extremely low in comparison with the values in 2004 (Fig. 3A and B).

There was a homogenous distribution of phytoplankton in the water layers only in March, while in all other months vertical distributions of phytoplankton varied substantially with depth. The data series was optimally divided into 19 classes with fuzzy coefficient of 0.2. If we consider the depths separately it is interesting to note that in August the highest biomass (61.85 mg L^{-1}) was found at 4 m depth, while very low biomass was found in the layers from the surface till a depth of 3 m (7.8–14.78 mg L^{-1}).

A strong seasonal pattern of Chl *a* concentrations was observed: lower values during the vegetation season and maximum in November (Fig. 2E), Table 1.

Table 1
Mean, minimum and maximum data of limnological parameters of Lake Sakadaš and the River Danube during 2006.

Parameter (abbreviation, SI)/sampling station	Lake Sakadaš			River Danube (only during flooding)		
	Mean	Min.	Max.	Mean	Min.	Max.
Water temperature-surface (WT-surf, °C)	18.8	8.2	29.4	14.5	6.0	24.7
Water temperature-bottom (WT-bott, °C)	14.5	7.6	19.2			
Water depth (WD, m)	5.91	4.00	8.25	11.18	8.70	13.78
Secchi depth (SD, m)	1.26	0.46	2.99	0.76	0.49	1.01
pH-surf	7.99	7.54	8.52	8.31	8.13	8.50
pH-bott	7.76	7.46	8.29			
Dissolved oxygen-surface (DO-surf, $mg\,L^{-1}$)	10.19	3.67	17.23	10.88	9.71	12.83
Dissolved oxygen-bottom (DO-bott, $mg\,L^{-1}$)	7.02	4.13	16.66			
Ammonium-surface (NH_4-surf, $mg\,L^{-1}$)	66.5	15.0	221.5	73.8	24.9	202.7
Ammonium-bottom (NH_4-bott, $mg\,L^{-1}$)	334.1	30.9	707.0			
Nitrates-surface (NO_3-surf, $\mu g\,L^{-1}$)	941.1	128.2	1642.3	1147.1	110.2	1883.0
Nitrates-bottom (NO_3-bott, $\mu g\,L^{-1}$)	1002.3	98.3	2394.0			
Nitrites-surface (NO_2-surf, $\mu g\,L^{-1}$)	27.6	5.1	96.3	27.7	3.0	71.8
Nitrites-bottom (NO_2-bott, $\mu g\,L^{-1}$)	43.4	3.5	123.5			
Organic nitrogen-surface (orgN-surf, $\mu g\,L^{-1}$)	501.3	25.3	1398.0	388.7	12.3	694.0
Organic nitrogen-bottom (orgN-bott, $\mu g\,L^{-1}$)	523.5	96.9	1307.0			
Total nitrogen-surface (TN-surf, $\mu g\,L^{-1}$)	1536.3	274.6	3071.0	1637.1	219.2	2653.8
Total nitrogen-bottom (TN-bott, $\mu g\,L^{-1}$)	1903.2	464.6	2757.0			
Total phosphorus-surface (TP-surf, $\mu g\,L^{-1}$)	259.2	70.4	696.0	232.9	121.6	341.1
Total phosphorus-bottom (TP-bott, $\mu g\,L^{-1}$)	257.7	57.0	673.0			
Conductivity-surface (Cond-surf, $\mu S\,cm^{-1}$)	556	400	770	419	352	557
Conductivity-bottom (Cond-bott, $\mu S\,cm^{-1}$)	624	368	876			
Chlorophyll *a*-surface (Chl *a*-surf, $\mu g\,L^{-1}$)	36.85	2.34	81.37	24.87	4.18	59.78
Chlorophyll *a*-bottom (Chl *a*-bott, $\mu g\,L^{-1}$)	24.52	3.07	49.28			
Phytoplankton biomass (FM, $mg\,L^{-1}$)	11.19	0.61	61.85	7.62	2.56	11.66
Phytoplankton abundance (ind. $L^{-1} \times 10^6$)	7.20	0.83	26.33	5.82	1.69	12.23

Mean, minimum and maximum phytoplankton abundance and biomass data in Lake Sakadaš shown in Table 1 are values of composite samples together with values of samples taken at intervals of 1 m from the surface to the bottom of the lake.

Ordination

Canonical correspondence analysis (CCA) was initially performed on the environmental and all species datasets. Fig. 4 shows the distribution of the taxa with minimum fit=5%. The eigenvalues for CCA axis 1 (0.62) and axis 2 (0.28) explained 52.1% of the variance in the species. The species–environment correlation of CCA axis 1 was 0.988 and for CCA axis 2 was 0.959, indicating a significant relationship between the 17 limnological variables and the 195 phytoplankton taxa. Most of the variance contained in the first CCA axis is described by the following environmental parameters: DO-bott (r_{1CCA}=0.96, $p>0.05$), pH-bott (r_{1CCA}=0.94, $p>0.05$) and WT-bott (r_{1CCA}= -0.90, $p>0.05$). In the second CCA axis most of the variance is explained by the Cond-surf (r_{2CCA}= -0.73, $p>0.05$), Cond-bott (r_{2CCA}= -0.68, $p>0.05$) and SD (r_{2CCA}=0.68, $p>0.05$).

Phytoplankton functional groups

The dominant phytoplankton species corresponded to the following functional groups: B, C, D, E, F, G, J, P, S1, T, W2, X1 and X3 (Table 2). With regular flooding in March, non-motile diatom species *Cyclotella comta* from functional group B was dominant and evenly distributed (Fig. 5A) through the water column (74.64–89.51% of total abundance). Diatom species retained dominance in phytoplankton under conditions of extreme flooding in April, when water depth reached its maximal value and thermal stratification was not yet established. Their distribution in the vertical water column was less homogenous (Fig. 5A). *C. comta* stayed as the most abundant species and was accompanied by representatives from the functional groups C (*Cyclotella meneghiniana*, *Asterionella formosa*) and D (*Stephanodiscus hantzschii*, *Fragilaria ulna* var. *acus*, *Nitzschia acicularis*). As the lake started to stratify in May, the abundance of diatoms significantly decreased near the surface and exhibited higher values in the deepest water layers (Fig. 5A).

From June until September, phytoplankton was dominated by green algae (Fig. 6) from the following groups: X1 (*Monoraphidium* sp. div.), J (*Crucigenia*, *Actinastrum*, *Scenedesmus*), T (*Planctonema lauterbornii*) and F (*Kirchneriella*, *Micractinium*, *Dictyosphaerium*). Vertical distribution (Fig. 5B) showed that green algae were homogenously distributed in the whole vertical profile of the lake but without similarity in species composition, visible from the hierarchical cluster analysis (data not shown). Subdominant species in the summer phytoplankton community were diatoms. Thus, filamentous species *Aulacoseira granulata* (group P) was developed in July (Fig. 6). With another huge flooding in August, diatoms from groups B and C became again a significant component of phytoplankton. They reached maximum abundance in November and were again evenly distributed through the water column (Fig. 5A).

Occasionally, contribution in the phytoplankton community had representatives of the functional groups G, S1, W2 and E. Thus, the species from group G, *Chlamydomonas* sp. was developed in October while *Carteria* sp. was developed in April. With low abundance, shade-adapted cyanoprokaryotes from the S1 group (*Limnothrix redekei*, *Pseudanabaena limnetica*, *Planktothrix agardhii*) developed in the deeper water layers during the late spring and summer moths. Euglenoids (group W2) were most abundant in April with homogenous distribution through the water column. The appearance of colonial chrysophytes (species from genera *Dinobryon*) from the E group was registered in July and October.

In the main river channel of the Danube centric diatoms were the dominant phytoplankton species during conditions of high water discharge, with representatives from the functional groups B (*C. comta*), C (*C. meneghiniana*) and D (*S. hantzschii*). Green algae

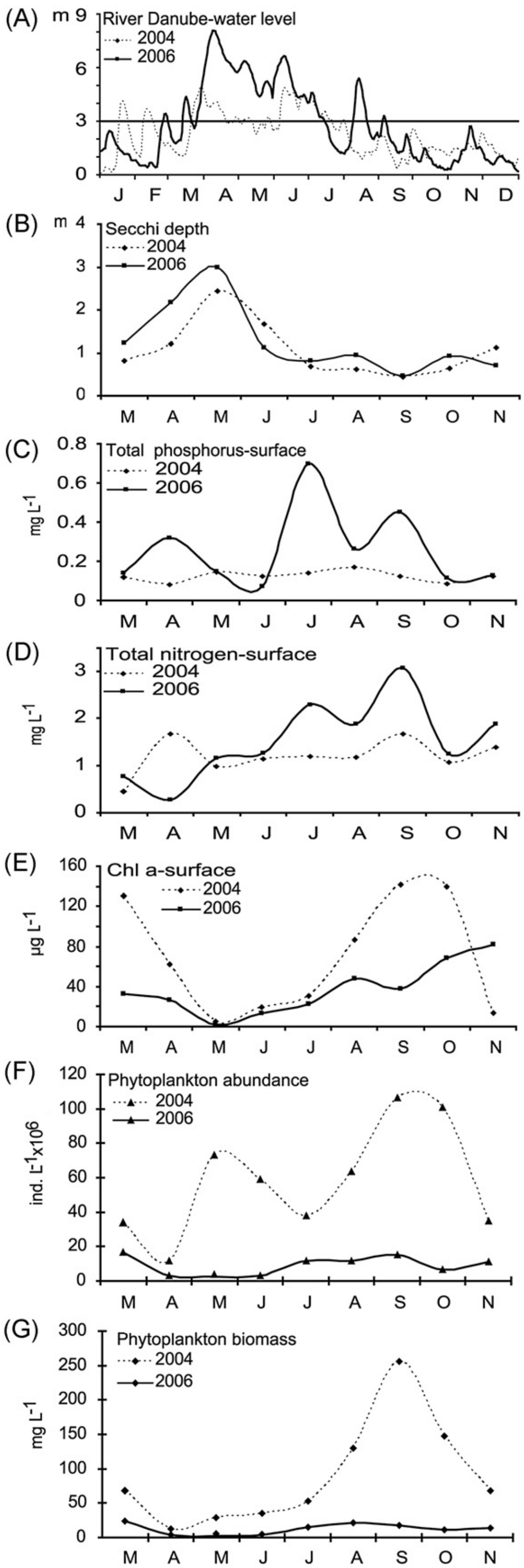

Fig. 2. River Danube water level (A) and the in-lake parameters of Lake Sakadaš: Secchi depth (B), total phosphorus (C), total nitrogen (D), chlorophyll a (E), phytoplankton abundance (F) and phytoplankton biomass (G) in 2006 comparison with usual flood year 2004. Dashed line shows values in 2004; solid line shows values in 2006.

from the X1 (*Monoraphidium contortum*) and **J** group (*Scenedesmus* sp. div.) were subdominant species in July and August. It is interesting to note that the invasive species *Didymosphenia geminata* (Lyngbye) Schmidt was found in almost all phytoplankton samples taken from the River Danube.

Discussion

Extreme floods as driving forces for the changes in the in-lake variables

The extreme inflow of the Danube floodwater in April of 2006 inundated a whole floodplain area of Kopački Rit creating a surface hydrological connection between the floodplain and the main river channel which lasted until September. As a consequence, there were changes in the in-lake variables of Lake Sakadaš, especially in the water level which was double to the usual (Fig. 2). Due to the huge and long-lasting inundation it became the deepest part of a single large shallow water body, i.e. the whole floodplain. The low lake transparency (Fig. 2B) indicated that the inorganic suspended solids concentrations were remarkably high. This is contrary to the condition in floodplain lakes with low water levels where in-lake processes, rather than river dynamics, seemed to be driving the turbidity of floodplain lakes (Roozen 2005).

The duration of connectivity in the river-floodplain system is recognised as a crucial factor for the nutrient status of riverine wetlands (Hein et al. 2004). This study, together with the results of our previous research (Mihaljević et al. 2009), showed a dilution effect of the riverine water on nutrients, especially on the phosphorus concentration (Fig. 2C). However, after the floods, the washing out effect of nutrients from the floodplain area resulted with an increase in nutrient concentrations due to the natural input and accumulation of organic matter from terrestrial vegetation. Thus, the floodplain served as a "zone of storage and turnover of organic matter" (Pithart et al. 2007).

The very low phytoplankton abundance found in the main channel of the Danube in the conditions of a high water discharge was expected due to the high concentrations of suspended matter (Luef et al. 2007), low transparency and the light climate unfavourable for rapid growth and proliferation of phytoplankton (Kiss et al. 1996, 2000).

The extremely low values of phytoplankton abundance (Fig. 2F) and biomass (Fig. 2G) found in Lake Sakadaš, as well as the pattern of Chl *a* (Fig. 2E) characteristic for shallow lakes with dense macrophyte vegetation (Scheffer 1998) indicate a "clear state" of the lake. This was an unexpected condition, because the concentration of nutrients was higher than usual (TP was doubled), thus the increase in phytoplankton abundance can be expected (Dokulil et al. 2006). Also, all results of the research done in the past decades proved a turbid state of the lake characterized by dense phytoplankton abundance and appearance of summer blooms of cyanoprokaryotes (Mihaljević et al. 1999).

According to the theory for cyclic shifts between alternative states in shallow lakes (van Nes et al. 2007), lakes can switch repeatedly back and forth between the vegetation dominated clear-water state and a contrasting turbid state (Hargeby et al. 2007; Van Geest et al. 2007). Among factors that may have a large impact on the chances of a lake to be in a clear state (Scheffer and van Nes 2007) it seems to us that changes in the in-lake variables together with the effects of mixing conditions can be the most explanatory factors for our results – a shift to another state of the floodplain lake.

The effect of inundation on the vegetation structure of the floodplain was remarkable because the rarely wet biotopes in the

Table 2
Selected species from Lake Sakadaš phytoplankton community based on abundance >5% in at least one unit sample, functional groups and maximal contribution percentage in total abundance during 2006.

Species	Code	Total phytoplankton abundance (%)	Functional group	Habitat characterization
Cyclotella comta Kütz.	CYCCOM	89.51	**B**	Vertically mixed, mesotrophic, small-medium lakes
Asterionella formosa Hass.	ASTFOR	8.33	**C**	Mixed, eutrophic small-medium lakes
Cyclotella meneghiniana Kütz.	CYCMEN	21.39		
Fragilaria ulna var. *acus* (Kütz.) Lange-Bert.	FRAULA	12.65	**D**	Shallow, enriched turbid waters, including rivers
Nitzschia acicularis (Kütz.) Smith	NITACI	6.01		
Stephanodiscus hantzschii Grun.	STEHAN	21.03		
Dinobryon bavaricum Imh.	DINBAV	19.08	**E**	Usually small, oligotrophic, base poor lakes or heterotrophic ponds
Dinobryon divergens Imh.	DINDIV	13.71		
Dictyosphaerium pulchellum Wood	DICPUL	9.50	**F**	Clear epilimnia
Kirchneriella contorta (Schmidle) Bohl.	KIRCON	43.10		
Kirchneriella irregularis (G.M. Smith) Korš	KIRIRR	6.09		
Micractinium pussilum Fres.	MICPUS	5.16		
Nephrochlamys willeana (Printz) Korš	NEPWIL	18.50		
Nephrocytium lunatum W. West	NEPLUN	5.13		
Carteria sp.	CARSP	6.17	**G**	Short, nutrient-rich water columns
Chlamydomonas sp.	CHLSP	31.25		
Actinastrum hantzschii Lagerh.	ACTHAN	7.92	**J**	Shallow, enriched lakes, ponds and rivers
Crucigenia tetrapedia (Kirchn.) W. & G.S. West	CRUTET	7.02		
Scenedesmus quadricauda (Turp.) Bréb.	SCEQUA	5.56		
Aulacoseira granulata (Ehrenb.) Simons	AULGRA	14.11	**P**	Eutrophic epilimnia
Limnothrix redekei (Van Goor) Meffert	LIMRED	6.32		
Planktothrix agardhii (Gom.) Anagn. et Komárek	PLAAGA	7.33	**S1**	Turbid mixed layers
Pseudanabaena limnetica (Lemm.) Komárek	PSELIM	9.55		
Planctonema lauterbornii Schmidle	PLALAU	10.08	**T**	Deep, well-mixed epilimnia
Trachelomonas volvocina Ehrenb.	TRAVOL	11.90	**W2**	Shallow mesotrophic lakes
Monoraphidium arcuatum (Korš.) Hind.	MONARC	6.35	**X1**	Shallow mixed layers in enriched conditions
Monoraphidium contortum (Thur.) Kom-Legn.	MONCON	13.36		
Monoraphidium irregulare (G.M. Smith) Kom.-Legn.	MONIRR	31.85		
Koliella longiseta (Visch.) Hind.	KOLLON	11.11	**X3**	Shallow, clear, mixed layers
Koliella spiculiformis (Visch.) Hind.	KOLSPI	15.92		
Schroederia setigera (Schröder) Lemm.	SCHSET	17.16		

Functional groups were defined according to Reynolds et al. (2002) and updated by Padisák et al. (2009).
Habitat characterization was described according to Reynolds et al. (2002).

floodplain were flooded during the whole growing season. Thus, mass developed aquatic macrophyte vegetation in the whole floodplain, with large stands in the lake, can play an important role in maintaining a clear-water state (Ibelings et al. 2007). It is well known that macrophytes may keep phytoplankton biomass low by taking up a large part of the nutrients resulting in nutrient limitations for phytoplankton (Van Donk et al. 1993), by producing allelopathic substances that inhibit the growth of phytoplankton (Gross et al. 2007), by decreasing underwater light availability (Cattaneo et al. 1998) and/or creating an environment that favours small phytoplankton taxa that are easily grazed by zooplankton (Muylaert et al. 2006).

The response of phytoplankton to a high-disturbance environment

The phytoplankton successions in the conditions of extreme flooding summarized as B/C/D – X1/J/T/F/(P) – X1/F/(B/C) – B/C is far from a seasonality when the lake was in a turbid state (Mihaljević et al. 2009). A mutual characteristic recognised within the habitat templates (Table 2) for most of the functional groups is the mixed environment (Padisák et al. 2009).

Low water temperature and deficiency of phosphorus during the vernal mixing caused by flooding in March are recognised factors (Tolotti et al. 2007; Wunsam et al. 1995; Melo and Huszar 2000) that may have favoured the dominance of *C. comta* (B group). A strong influence of the extreme inflow of riverine water on phytoplankton assemblages in April is evident from the appearance of the functional groups C and D, since *C. meneghiniana* and *S. hantzschii*, generally considered as typical and constant Danube phytoplankton species (Schmidt 1992; Török 2006) were dominant species in the phytoplankton of the River Danube. Thus, it is possible that diatom abundance resulted from a larger input during spring flooding, as was found in some European floodplain lakes (Van den Brink et al. 1993; Oosterberg et al. 2000; Kasten 2003).

The high frequency of physical disturbance, as from March till May, favoured centric diatoms, i.e. R-strategists – small algae, which have sufficient growth rates to compensate for dilution and tolerate the low light conditions. Physical disturbance in the

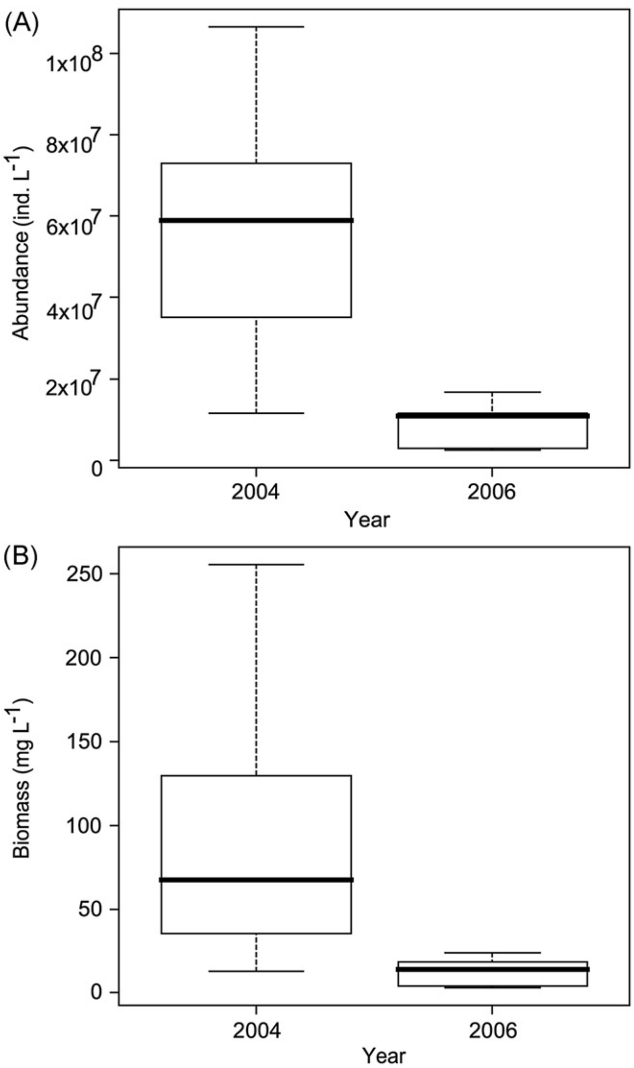

Fig. 3. Cumulative phytoplankton abundance (A) and biomass (B) in Lake Sakadaš in 2004 and 2006.

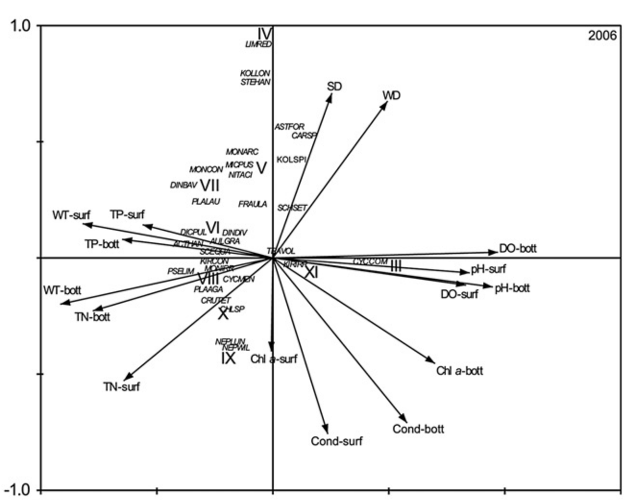

Fig. 4. Canonical correspondence analysis (CCA) of number of phytoplankton individuals and their distribution over first and second CCA axes during 2006 in Lake Sakadaš (see Table 1 for abbreviations of physical and chemical parameters and Table 2 for phytoplankton species code; roman numbers indicate months).

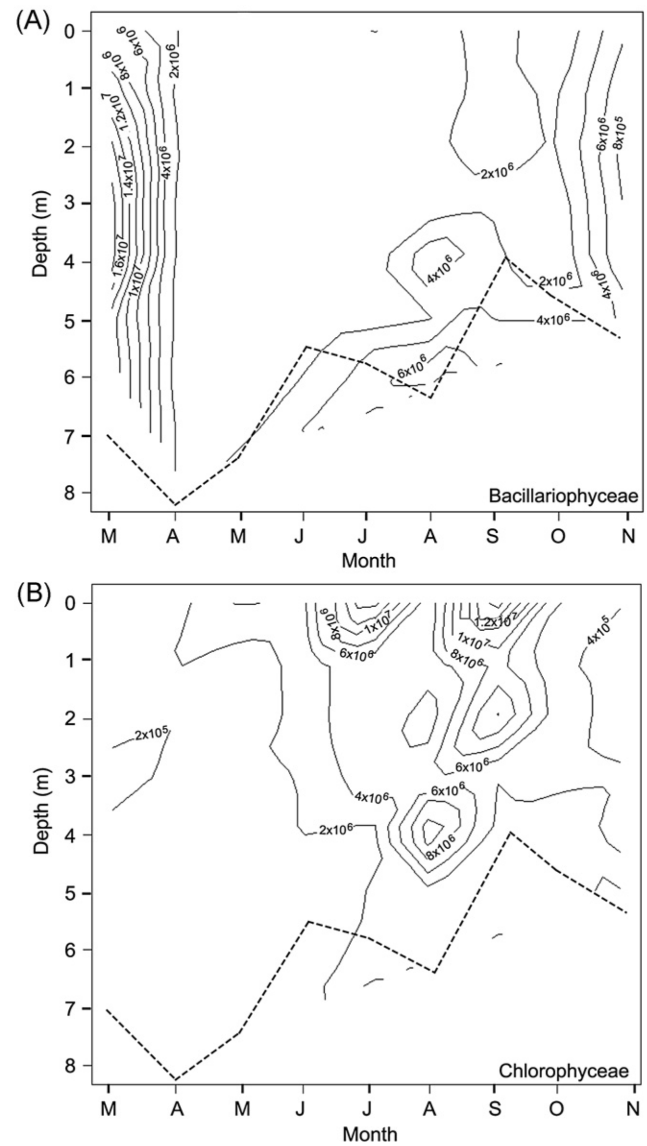

Fig. 5. Depth–time diagram of abundance (ind. L^{-1}) of dominant phytoplankton groups (Bacillariophyceae, A; Chlorophyceae, B) in Lake Sakadaš during 2006. Dashed line shows water bottom.

whole water column, e.g. mixed-layer depth (Reynolds 2006) supported their approximate homogeneity in the vertical (Fig. 5A). When the physical disturbance decreased because of the lower hydraulic pressing, C-strategists, chlorococcal algae from X1, F and J groups, were developed. These species were characterised by water temperature and nutrients (Fig. 4). The success of green algae is partly due to their small size that represents the high surface-to-volume ratio (Happey-Wood 1988).

Another physical disturbance caused by a new flood wave in August again favoured the R-strategists, representatives of the functional groups B and C. Isothermal conditions were a suitable environment for these species, sensitive to the onset of stratification (Padisák et al. 2009). The reappearance of diatoms can be interpreted as the input from the river phytoplankton and partially as a deposit of the "ecological memory" of the community, here considered as the capacity of past state to influence present and future response (Padisák 1992; Becker et al. 2008).

Altogether, the pathway of R–C–R-strategists indicates a high stress environment for phytoplankton development. The extreme

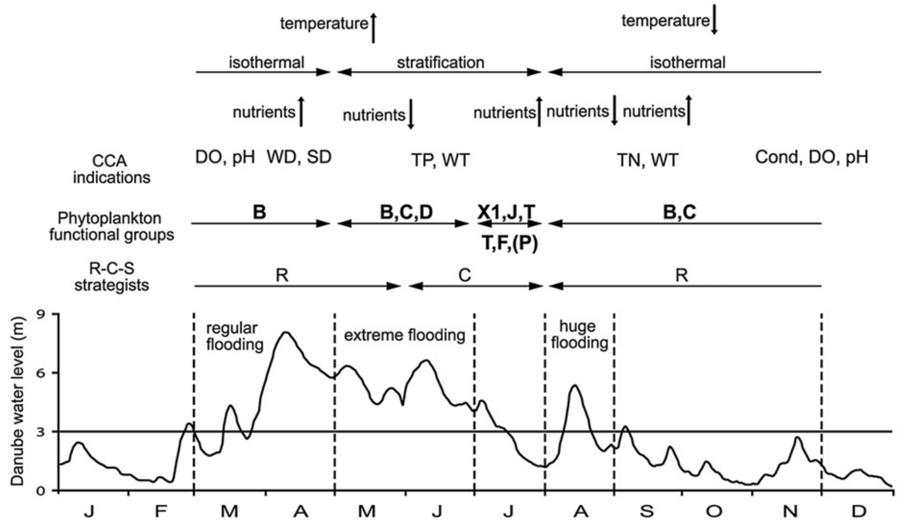

Fig. 6. Synthesis diagram showing main abiotic and biological changes during 2006 in Lake Sakadaš (see Table 1 for abbreviations).

intensity and duration of flooding suppressed the success of slow-growing S-strategists considered to be favoured by water column stability (Reynolds 1988). A similar pathway of R–C–R-strategists was found in the dynamic side-arms system of the River Danube under the long-term flooding conditions followed by rainy summer and autumn (Riedler et al. 2006). Also, it is known that late summer mixing in the lakes of intermediate status (mesotrophic lake) may favour R-strategist diatoms (Reynolds 2006).

Summary and conclusions

All results of the investigation of extreme floods from the River Danube in 2006 on the species composition of phytoplankton in a shallow floodplain lake, Lake Sakadaš, indicate a change in the ecological state of the lake. Extremely low phytoplankton abundance and biomass, high nutrient concentration and high Chl *a* concentration characterize the clear state. The long-lasting inundation caused a high stress environment for phytoplankton development in the lake which became the deepest part of a single large shallow water body, i.e. the whole floodplain with well developed macrophyte vegetation. Thus, there was a shift from a turbid, algal-dominated state to a clear state, which corresponds with cyclic shifts between alternative states in shallow lakes. Our results demonstrate that the occurrence of extreme flooding could be a stressor high enough for the transition from a turbid to a clear state of a floodplain lake. Possibly, this can be one of the scenarios which can help in resolving the question what would be the impact of a warmer climate on the aquatic ecosystems, particularly on threatened and sensitive ecosystems as the floodplains. The next step would be to find out if and when the investigated floodplain lake will return to essentially the same state as it was before the extreme flooding.

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