Ekológia (Bratislava) Vol. 29, No. 1, p. 65–86, 2010
doi:10.4149/ekol_2010_01_65

SPATIAL AND TEMPORAL VARIATION OF PLANKTON IN A MEDITERRANEAN KARSTIC LAKE

IVANČICA TERNJEJ[1], ANĐELKA PLENKOVIĆ-MORAJ[2], ZLATKO MIHALJEVIĆ[1], MLADEN KEROVEC[1]

[1] Department of Zoology, Faculty of Science, University of Zagreb, Rooseveltov trg 6, 10 000 Zagreb, Croatia; e-mail: ivancica@zg.biol.pmf.hr
[2] Department of Botany, Faculty of Science, University of Zagreb, Rooseveltov trg 6, 10 000 Zagreb, Croatia

Abstract

Ternjej I., Plenković-Moraj A., Mihaljević Z., Kerovec M.: Spatial and temporal variation of plankton in a Mediterranean karstic lake. Ekológia (Bratislava), Vol. 29, No. 1, p. 65–86, 2010.

Lake Visovac is a karstic phenomenon in the south of Croatia. It is a travertine barrage lake situated in the river Krka. Plankton community dynamics in three hydrological different parts in the lower basin of the lake was investigated. Plankton was collected monthly in a year period. All data point out that discharge, followed by temperature and total phosphorus are key factors directly influencing water properties, and through it the net phytoplankton and crustacean plankton assemblages. The portion of total variance described by the multivariate analysis is as it follows: 20.6% variance of phytoplankton and environmental data, 12.8% crustacean zooplankton and environmental data, and 29.4% of phytoplankton vs. crustacean zooplankton data.

Key words: phytoplankton, crustacean zooplankton, karstic lake

Introduction

Travertine barrage lakes in southern Europe are poorly investigated. Most of these studies deal with faunistics of the plankton community in Plitvice lakes (Steuer, 1899; Krmpotić, 1913; Primc, 1986; Habdija et al., 1989, 1993). Lake Visovac, has been the subject of some research in 1970/71. Petrik (1971) began investigations into the physical and chemical characteristics of the water. Only recently a few biological researches were conducted: some of them deal with trophic status of the lake (Habdija, Primc, 1990; Mišetić, Mrakovčić, 1990), some on calanoid species (Bukvić et al., 1999), some of them deal with periphyton community (Primc-Habdija et al., 1997), and some of them deal with benthic community (Mihaljević et al., 2000, 2001). The objective of the study was to determine which factors regulate plankton assemblages in lake Visovac.

Material and methods

Study area

Lake Visovac is a travertine barrage lake (Hutchinson, 1957) situated in the karsts region of the NW Dinarid Mountains (Croatia), 22 km from the Adriatic coast (Fig. 1). The surface area of the lake is 7.9 km^2, the maximum depth is 55 m. The lake is never covered in ice. What makes it unique is the fact that the lake is actually a part of the river Krka, bounded by two travertine barriers: the Roški slap on the north and the Skradinski buk on the south. These two barriers are formed by biogene precipitation of calcium carbonate. Waters of river Krka enter

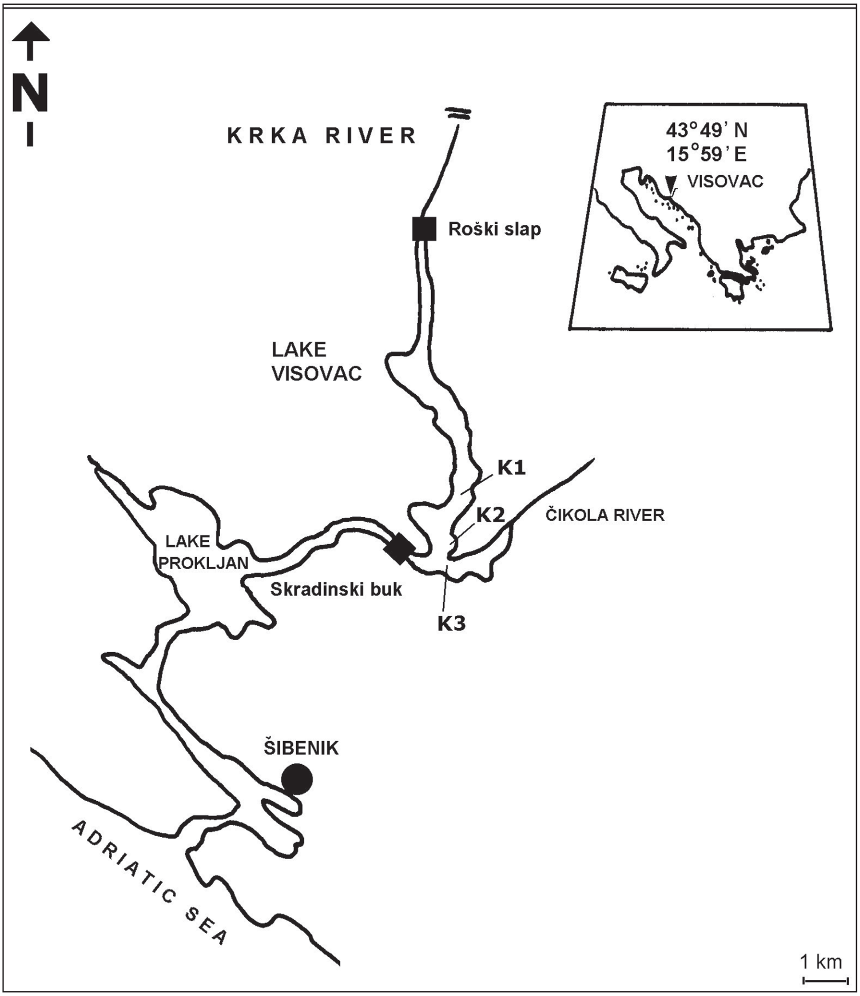

Fig. 1. Study site.

into the lake over Roški slap barrier forming a waterfall 25 m high. Epilimnetic lake water flow out of the lake over the travertine barrier Skradinski buk forming the waterfall 45.7 m high (Mihaljević et al., 2001). During winter a considerable amount of water comes via the river Čikola which enters the lake in lower part. Retention of the water varies: in summer it is 71 days, in winter it is up to 14 day (Petrik, 1971).

We set three sample stations. Station K1 was situated in the lower basin of the lake, on the main stream. The collecting station K2 was situated downstream in a small bay less exposed to the main stream. Station K3 was at the mouth of the river Čikola (Fig. 1). The maximum depth in all stations is 25 m, the bed being muddy and the littoral parts of the lake covered with submerged macrphytes *Ceratophyllum submersum*, *Myriophyllum verticillatum* and *Chara* sp.

Methods

Plankton was collected monthly at depths of 1, 2, 5, 10, 15, 20 m. Thirty liters of lake water were filtered through a 25 µm mesh net. Ten milliliters filtrate was preserved with the addition of 4% formaldehyde. Water samples for the chemical analyses were taken simultaneously with the plankton samples. The following variables were determined as described in APHA (1992): nitrite-nitrogen (Colorimetric method), nitrate-nitrogen (nitrate selective method), orthophosphate-phosphorus (PO4) (Stannous chloride method), total phosphate-phosphorus (TP) (stannous chloride method), and silica (silico-molybdate method). Chlorophyll *a* (chl.*a*) was extracted in 90% acetone and measured by Analytik Jena spectrophotometer Model Specord 40. Water temperature and dissolved oxygen were measured with WTW Model Oxi 325-B, while transparency was determined with the 20 cm diameter Secchi disk.

Net phytoplankton algae were identified to a species level using standard taxonomic references (Zabelina et al., 1951; Golerbach et al., 1953; Hindák et al., 1978; Komarenko, Vasiljeva, 1978). For quantitative analyses, cells of each species were counted using counting chambers with a 1 cm^2 grid (Stilinović, Plenković-Moraj, 1995). Wet weight biomass was estimated according to Edler (1979) and Deisinger (1984). For most taxa this was based on the mean cell volume calculations (usually 30 typical cells of each). The filamentous and colonial species were measured individually.

All the crustacean species in the sample were counted in a round glass counting cell under an Opton microscope. The entire volume of the filtrate was checked. For the determination of Copepoda and Cladocera species the following references were used: Kiefer (1968, 1978), Petkovski (1983) Einsle (1993), Margaritora (1983, 1985) and Smirnov (1971, 1976). The dry biomass was estimated from regression equations of length/weight relationships published by Dumont et al. (1975), Bottrel et al. (1976) and Malley et al. (1989). Conversions from dry to wet weight assumed conversion ratio 1:8 (Taguchi, Fukuchi, 1975; Mccauley, Kalff, 1981).

Correspondence Analysis (CCA), release 4.0 of CANOCO for Windows (Ter Braak, 1988.) was carried out using the metrics drawn from the zooplankton counts per liters (species) x the water (environmental) variables. Plankton abundances were logarithmically transformed (log (y+1)) and centered prior to the analyses. Stations and seasons were expressed by nominal variable (K1, K2, K3, spring, summer, autumn and winter).

Results

Physico-chemical characteristics and chlorophyll a

Discharge is measured at the Skradinski buk travertine barrier, about 0.5 km downstream from the collecting station K3, which closes lake Visovac on the south. As we mentioned, the lake is fed by two rives: Krka and Čikola. During summer, Čikola completely dries out. Minimum discharge is 20 $m^3 s^{-1}$ in August; maximum discharge is 360 $m^3 s^{-1}$ in February (Fig. 2). Discharge of the river Čikola was also measured a few kilometres from its mouth.

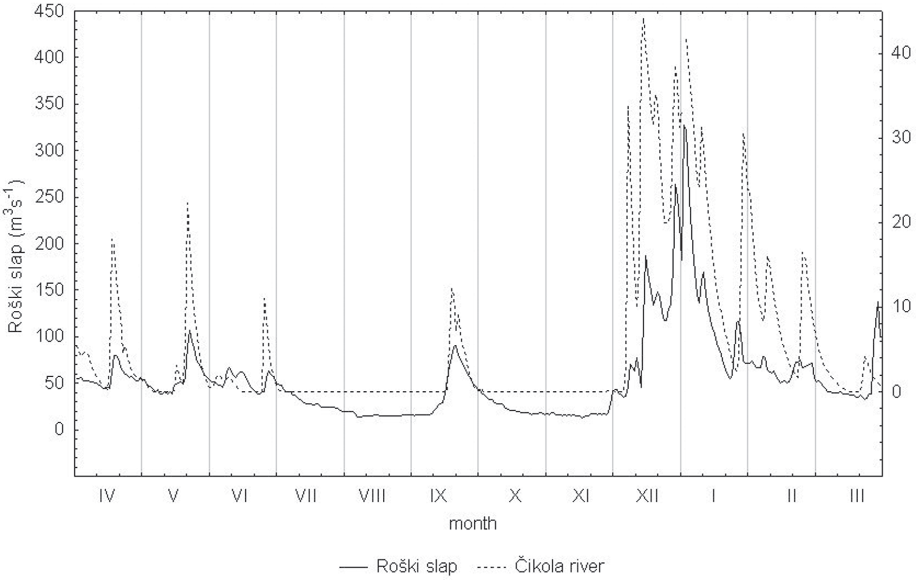

Fig. 2. Discharge of river Krka and river Čikola.

It exhibits the same temporal pattern, but the quantities are completely different (minimum 0 $m^3 s^{-1}$, and maximum 44 $m^3 s^{-1}$).

Lake Visovac is a monomictic lake. The vertical distribution of temperature during a seasonal cycle showed a winter circulation and summer stratification in all three stations. The winter circulation corresponds to a small difference of temperature between surface and bottom layers: from 8.02 °C to 9.3 °C (Table 1). It was present during January and February. The maximum temperature registered was in August in all stations: 24.7 °C (K1, K2), and 25.1 °C (K3), respectively. A thermocline was present from April through October at 5–15 m depth.

Oxygen concentration ranged from 0.33 to 14.30 mg L^{-1} (Table 1). In all stations water was well oxygenated through water column until the beginning of July, when an oxygen minimum at hypolimnion appeared. The minimum was pronounced throughout the summer and the concentration of O_2 dropped below 1 mg L^{-1} at 20 m depth in August (K1, K2), and June-October (K3). The lowest values were measured in station K3. In autumn water column became again well oxygenated (> 6 mg L^{-1}). Such condition prevailed through winter circulation.

The mean concentration of phosphate was between 0.001 and 0.008 mg L^{-1} (Table 1). Vertical distribution showed a tendency towards an increase in the metalimnion and hypolimnion layers. The highest values were measured in spring during April and May (K1, K3) and during summer from June till August (K2, K3). Phosphate depletion is preceding maximum concentrations probably due to intensive phytoplankton development.

T a b l e 1. Physical and chemical parametars of water in lake Visovac. All values are given as the mean followed by the maximum–minimum values (in parenthesis).

Station	**Month**	**Transparency** (m)	**Temperature** (^{0}C)	**Oxygen** (mg L^{-1})	**total-P** (mg L^{-1})	**P-PO4** (mg L^{-1})	**CHLa** (µg L^{-1})
K1	IV	3, 3.80	11.5 (9.5–13.3)	10.00 (9.3–10.6)	0.16 (0.06–0.49)	0*	1.95 (1.2–3.6)
	V	6.50	14.5 (12.9–16.3)	9.96 (8.0–11.1)	0.04 (0.02–0.07)	0.004 (0–0.007)	1.96 (1.0–3.5)
	VI	3.50	17.2 (14.3–⊠21.2)	10.63 (8.0–11.7)	0.25 (0.17–0.31)	0.008 (0.003–0.013)	2.30 (0.5–4.1)
	VII	4.00	18.5 (14.9–21.8)	10.33 (4.6–12.1)	0.25 (0.14–0.38)	0.005 (0–0.007)	0.69 (0.2–1.4)
	VIII	5.50	18.5 (14.2–23.4)	8.43 (1.2–11.0)	0.31 (0.28–0.43)	0.005 (0–0.01)	1.69 (0.7–2.7)
	IX	6.50	17.2 (14.3–19.9)	5.95 (0.05–10.0)	0.26 (0.21–0.30)	0.001 (0–0.005)	2.24 (0.6–6.5)
	X	3.50	16.3 (14.4–18.3)	10.52 (8.7–12.3)	0.20 (0.19–0.22)	0.002 (0–0.005)	2.94 (0.5–7.0)
	XI	8.00	11.9 (11.7–12.1)	10.29 (9.3–10.6)	0.20 (0.16–0.22)	0.001 (0–0.002)	0.50 (0.1–1.0)
	XII	2.50	10.2 (9.4–10.4)	11.26 (11.0–11.3)	0.14 (0.11–0.21)	0.001 (0–0.002)	0.17 (0.1–0.2)
	I	3.40	7.1 (6.5–7.5)	10.88 (10.5–11.3)	0*	0*	0.17 (0.1–0.2)
	II	3.50	8.8 (8.4–9.3)	12.26 (12.2–12.3)	0.13 (0.11–0.15)	0.001 (0–0.002)	2.30 (1.6–3.9)
	III	6.50	10.1 (9.9–10.5)	10.58 (9.3–11.2)	0.12 (0.11–0.13)	0.001 (0–0.002)	0.74 (0.3–1.0)
K2	IV	4.50	11.4 (10.1–13.6)	10.40 (8.9–11.1)	0.19 (0.14–0.40)	0*	2.25 (1.8–3.3)
	V	6.00	14.0 (12.5–15.0)	10.87 (8.9–11.7)	0.03 (0.02–0.04)	0.001 (0–0.005)	2.21 (1.8–3.2)
	VI	3.00	17.0 (13.7–20.6)	10.94 (6.5–13.1)	0.23 (0.19–0.25)	0.008 (0.003–0.013)	2.52 (1.1–4.1)
	VII	4.50	18.7 (14.7–21.9)	10.37 (4.5–10.7)	0.27 (0.17–0.39)	0.006 (0–0.011)	0.95 (0.2–1.6)
	VIII	5.50	18.8 (14.4–23.4)	9.82 (1.3–14.3)	0.53 (0.49–0.56)	0.002 (0–0.005)	2.06 (0.5–3.6)
	IX	6.50	17.5 (14.5–19.5)	6.77 (0.08–9.8)	0.35 (0.28–0.39)	0.002 (0–0.002)	1.04 (0.5–1.8)
	X	4.50	15.7 (14.5–17–4)	8.91 (7.3–11.1)	0.20 (0.19–0.22)	0*	2.40 (0.7–6.0)
	XI	8.00	12.1 (11.6–12.3)	10.27 (9.7–10.5)	0.18 80.15–0.22)	0.001 (0–0.002)	0.96 (0.0–1.0)
	XII	2.50	10.2 (9.3–10.4)	11.21 (10.7–11.3)	0.14 (0.11–0.17)	0*	0.26 (0.2–0.3)
	I	3.40	7.3 (7.2–7.4)	11.02 (10.5–11.2)	0*	0*	0.2 (0.2–0.3)
	II	4.00	8.4 (8.1–8.6)	12.22 (11.6–12.6)	0.08 (0.009–0.13)	0.001 (0–0.002)	2.11 (1.6–2.5)
	III	6.00	10.5 (10.2–11)	11.47 (11.3–11.6)	0.12 (0.11–0.14)	0.001 (0–0.002)	0.64 (0.3–1.1)

Table 1. (Continued)

K3	IV	5.50	11.4 (10.2–12.2)	10.50 (10.1–11.0)	0.20 (0.02–0.43)	0*	2.59 (1.8–3.7)
	V	6.00	15.5 (13.0–17.0)	10.95 (10.0–11.9)	0.12 (0.03–0.17)	0.005 (0–0.005)	1.32 (0.4–2.4)
	VI	3.00	17.6 (16.0–20.7)	10.16 (3.5–13.2)	0.24 (0.11–0.33)	0.006 (0–0.010)	1.36 (0.1–1.9)
	VII	4.50	19.3 (16.6–21.7)	9.57 (5.7–11.6)	0.32 (0.30–0.36)	0.010 (0.002–0.017)	1.01 (0.4–1.6)
	VIII	5.50	20.6 (14.6–25.1)	7.56 (0.3–12.1)	0.52 (0.35–0.60)	0.007 (0.005–0.02)	1.18 (0.3–2.9)
	IX	6.50	18.7 (15.0–20.3)	6.40 (0.09–9.4)	0.27 (0.22–0.32)	0.002 (0–0.005)	1.73 (0.3–2.9)
	X	5.50	16.7 (15.0–18.1)	8.47 (1.0–11.7)	0.21 (0.19–0.23)	0.001 (0–0.005)	2.03 (0.3–3.5)
	XI	8.00	12.6 (12.5–12.7)	10.0 (9.8–10.2)	0.18 (0.15–0.22)	0.001 (0–0.002)	1.40 (1.2–1.7)
	XII	2.50	10.8 (10.2–11.4)	10.94 (10.7–11.2)	0.13 (0.10–0.16)	0.001 (0–0.002)	0.26 (0.2–0.3)
	I	3.40	8.2 (8.2–8.4)	10.26 (10.1–10.4)	0*	0*	0.61 (0.2–1.1)
	II	4.30	8.4 (7.9–8.8)	11.75 (11.5–11.8)	0.08 (0.009–0.11)	0.001 (0–0.002)	1.13 (0.7–1.5)
	III	4.00	10.6 (9.7–11.3)	10.97 (10.3–11.4)	0.10 (0.10–0.12)	0.001 (0–0.002)	0.79 (0.1–1.6)

* analytical zero

Total phosphorus had more or less similar cycle: mean concentration varying from 0.03 to 0.52 mg L^{-1}: the first peak being in April and the second in late summer in August. After those maximums total phosphorus values dropped. During winter values were close to analytical zero (Table 1).

The concentration of chlorophyll *a* in lake Visovac ranged between 0.1 μg L^{-1} and 6.5 μg L^{-1} (Table 1). General pattern of chlorophyll cycle in all stations was similar. The first peak of chlorophyll *a* was found in spring (April–June) and another in late summer (August–October). A minor increase was also observed during February. Spring and winter maximum values occurred in metalimnion, while summer maxima occupied meta- and epilimnion layers. The lowest total chlorophyll *a* concentrations were measured in K3 station.

Plankton community

The plankton community shows a distinct pattern in each station (Fig. 3). Net phytoplankton biomass has two major peaks in stations K1 and K3, while the curve in K2 is left skewed. Quantitative and temporal distribution of phytoplankton biomass in K1 and K3 are not similar. Spring maximum in K1 is in June, and autumn maximum in September, while in K3 in May and November, respectively.

Qualitative composition of the phytoplankton is similar in all investigated parts of the lake. The most common group is Bacillariophyceae. Bacillariophyceae and Pyrrhophyceae accounted for the most of phytoplankton biomass in all stations (Fig. 4). The taxonomic composition of algal forms shows that common species

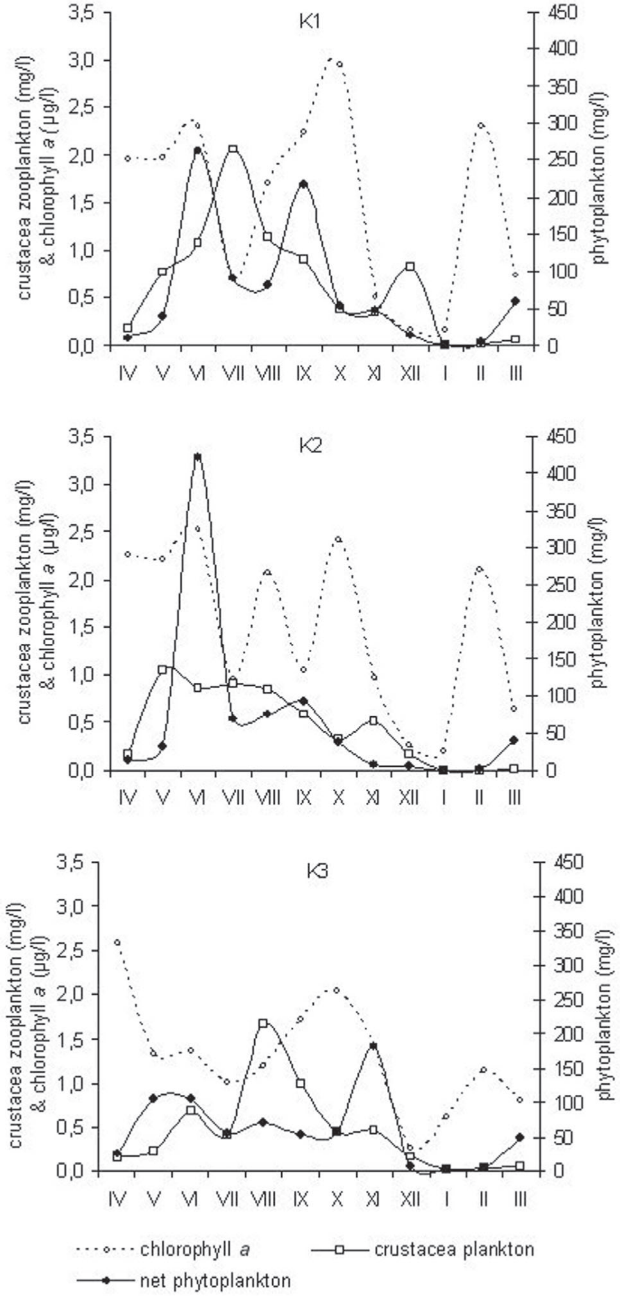

Fig. 3. Plankton dynamics in the lake Visovac (average monthly wet biomass).

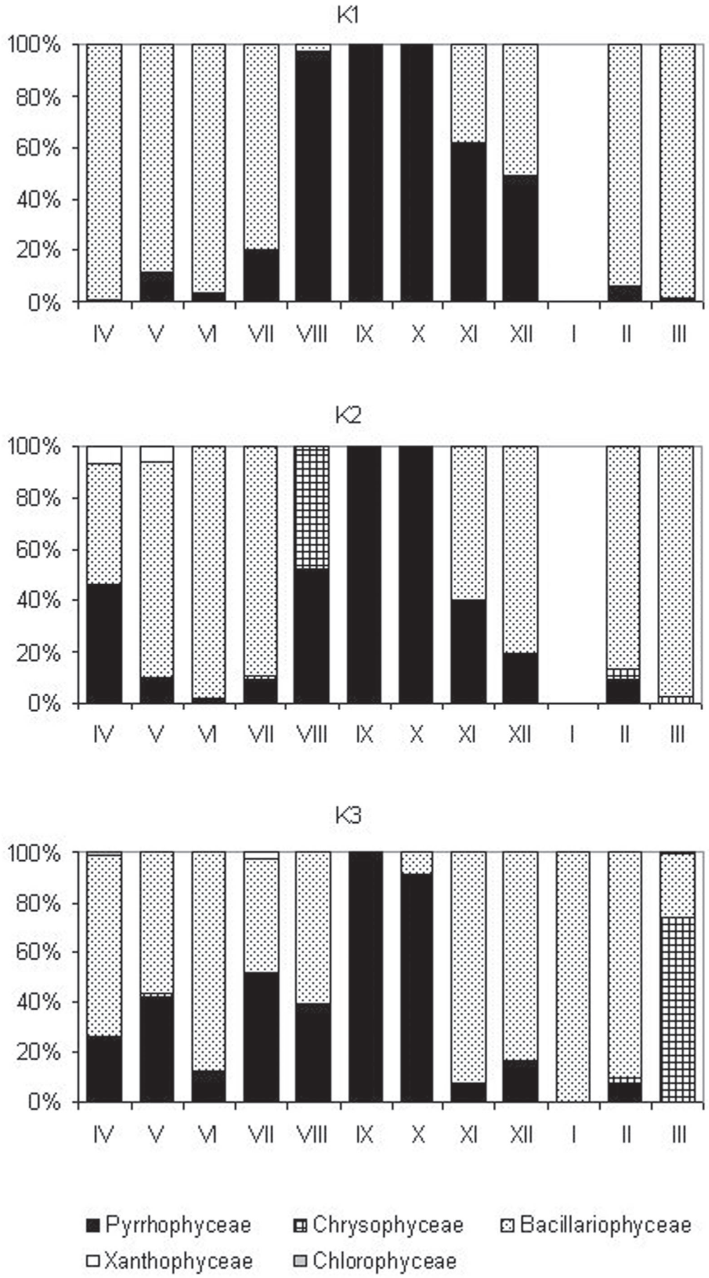

Fig. 4. Share of main phytoplankton groups in total phytoplankton biomass in the lake Visovac.

(and the most abundant) are *Asterionella formosa* Hass and *Fragilaria crotonensis* Kitt. Species *Ceratium hirundinella* (O. F. Müller) Schrank was very abundant in station K1. In Station K2 *Ceratium* is replaced with *Dynobrion divergens* /Hm while in K3, with *Synedra ulna var. danica* (Kütz) Grun.

Annual cycle of dominant species in all thee stations is similar. *A. formosa* starts to appear in larger numbers in June. In stations K2 and K3 it dominates in water layers from 5 to 10 m, in K1 10–15 m, respectively. It was also abundant early in the spring: in stations K1 and K2 it numbers started to rise in March 1996 at the end of our research. The other dominant species *F. crotonensis* is also abundant in the spring: April 1995 and March next year. However, its second peak is in the end of summer, and at the beginning of the autumn. The species is abundant in surface layers (1 m) and in metalimnion in all stations; above thermocline at depth 5–15 m (K2).

The following crustaceans were identified in the plankton of the lake: *Eudiaptomus hadzici* (Brehm 1939), *Cyclops abyssorum* G. O. Sars 1863, *Mesocyclops leucarti* (Claus 1857), *Daphnia longispina* O. F. Müller 1785, *Daphnia cucullata* (Sars 1862), *Diaphanosoma brachyurum* (Lievin 1848), *Leptodora kindtii* (Focke 1844), *Bosmina longirostris* (O. F. Müller 1785) and *Alona* sp. The spatial and temporal distribution of total crustacean zooplankton is presented in Fig. 6. Like the phytoplankton, the crustacean plankton community shows a different pattern in each station. Zooplankton population in general follows a phytoplankton increase.

In station K1 total copepod abundance was up to 60 org. L^{-1} (Fig. 5a). From spring it is constantly rising until July when it reaches maximum. This maximum has two peaks: one in epilimnion and the other one in metalimnion layer. The second maximum has been noticed in December and was located at the bottom. During winter copepod number was low and it did not exceed 10 org. L^{-1}. Station K2 had three copepod abundance maximums: in May, July and November, all in meta- and hypolimnion. Like in previous station, during winter copepods were much less abundant, and were homogeneously distributed through water column. In station K3 total copepod abundance was the highest: up to 70 org. L^{-1}. Copepod number is increasing from the beginning of spring until June when it reaches first peak just above the bottom of the lake. In July it slightly decreases, but in August it reaches the second peak at the depth of 5 m below the surface. The third peak is already next month in hypolimnion. After these maximums copepod number decreases and stays below 10 org. L^{-1}.

In general cladocerans are less abundant then copepods (Fig. 5b). However, in station K3 they outnumbered copepods. They also have a distinct dynamics in each station. In station K1 their number is gradually increasing during spring. In July it reaches maximum with two peaks: one at depth of 15 m and the other at 2–5 m. The number of Cladocera then declines and remains at 5 org. L^{-1}. In station K2 several maximums can be noticed. The first increase in cladoceran number is in May; the second one is in June in epilimnion. Next peaks are in August (hypolimnion) and September (epilimnion). After these maximums cladoceran abundance drops and remains at 5 org. L^{-1}. In station K3 Cladocera dominated macrozooplankton community. Their average number was 20 org. L^{-1}. They had one true maximum in August (two peaks: epi- and hypolimnion), although a slight increase of abundance can

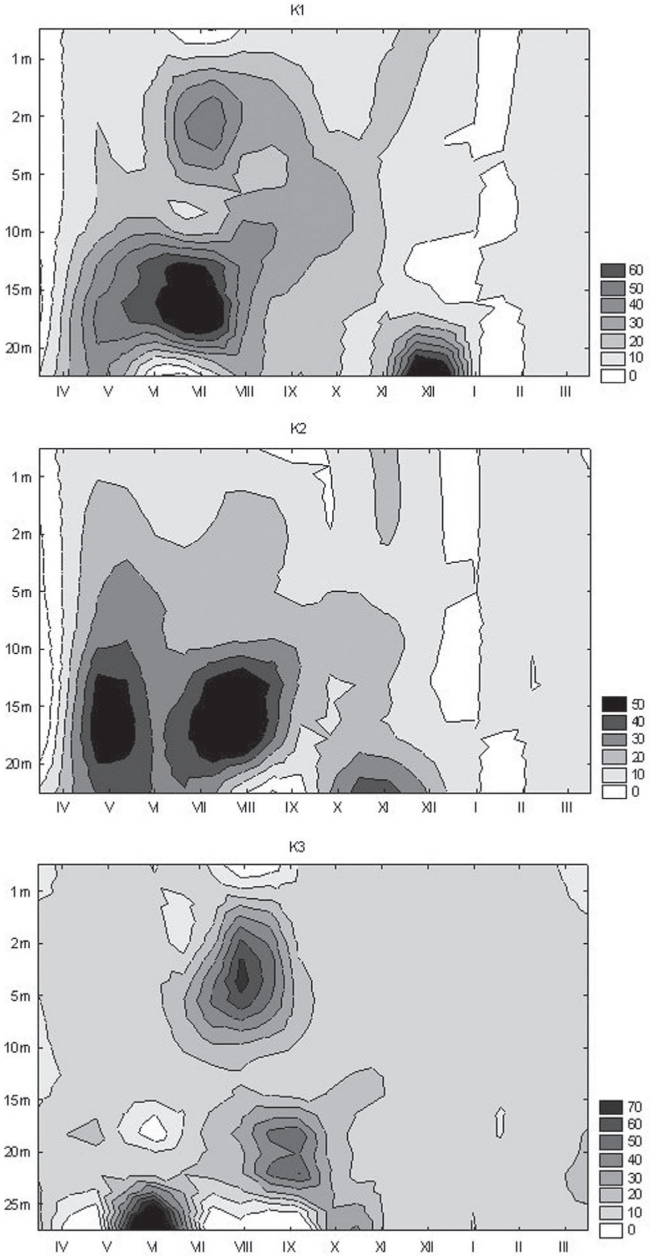

Fig. 5a. Spatial and temporal dynamics of crustacean plankton in the lake Visovac (organisms L^{-1}) – Copepoda.

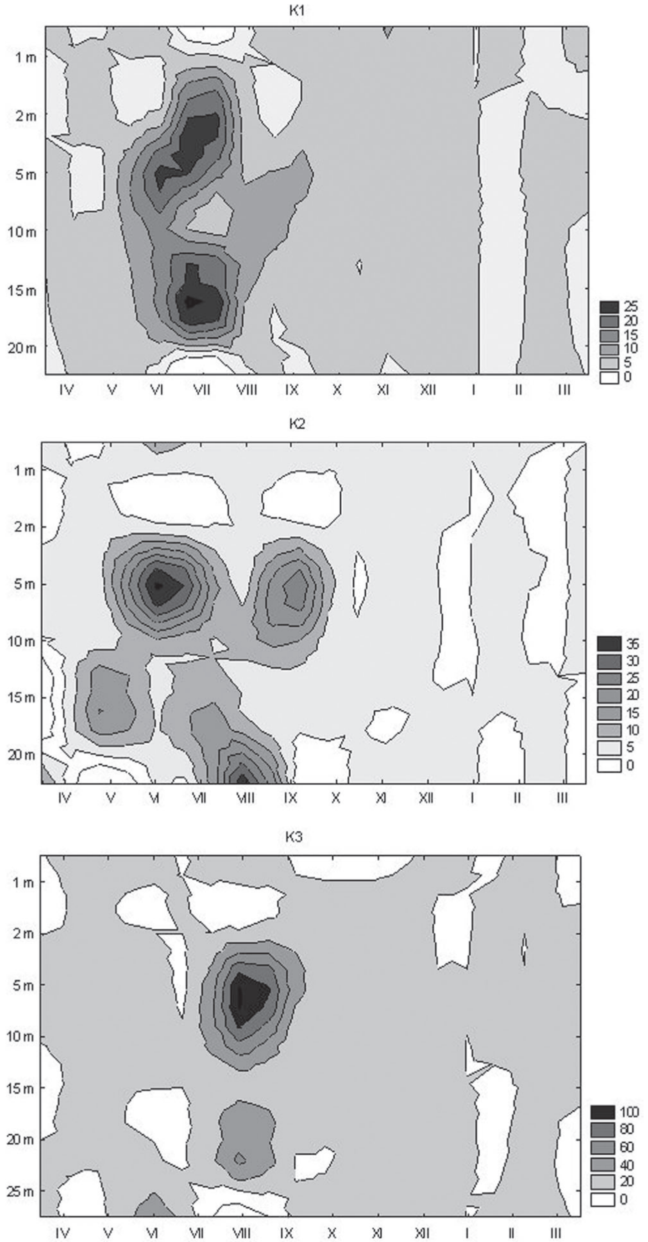

Fig. 5b. Spatial and temporal dynamics of crustacean plankton in the lake Visovac (organisms L^{-1}) – Cladocera.

Table 2. Summary of CCA analysis between plankton and different variables.

Variable	*phytopl. vs abiotic*		*c.zoopl. vs abiotic*		*phytopl. vs c.zoopl.*	
Axes	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues :	0.11	0.10	0.13	0.08	0.19	0.11
Species-environment correlations:	0.77	0.76	0.67	0.65	0.79	0.72
Cumulative percentage variance						
– of species data:	10.70	20.80	12.90	20.90	3.40	5.30
– of species-environment relation:	36.70	71.30		41.30	37.00	58.00
Sum of all ancostrained eigenvalues		1.00		1.00		5.54
Sum of all canonical eigenvalues		0.29		0.31		0.51
Variance explained (%)*		20.60		12.80		29.40

Notes: * Total variance explained by the two first axes is calculated as the product of the cumulative percentage variance species-variable correlation at the second axis and the sum of all canonical eigenvalues.

be noticed in June just above the bottom of the lake. During the rest of the year cladoceran number is approximately 20 org. L^{-1}, and they are more or less homogeneously distributed in water column.

CCA analysis

The first two axes of the correspondence analysis explained 20.6% of the phytoplankton abundance variance (Table 2). The main environmental variable influencing species segregation is discharge, followed by temperature, total phosphorus, nitrate, chlorophyll *a*, transparency, carbon dioxide and oxygen (Fig. 6a). The species are segregated in two groups. The left part of plane corresponds to stations K1 and K2. In a gradient of rising temperature and water stability species like *Zygnema* sp., *Oscillatoria planctonica* Wolocz, *Ulothrix subtillisima* Rabenh, *Cyclotella comta* (Ehr) Kütz, and *C. mellosiroides* (Kirch) Lemm. find favourable conditions. They are typical summer species in both stations. Others, like *C. hirundinella*, *Sphaerocystis schroeteri* Chad and *Asterionella formosa*, become abundant in late summer and autumn, when higher concentrations of phosphorous and nitrate are present. The right part of the plane corresponds to station K3, and it is divided by two groups. Species like *Fragillaria capucina* Desm., *Synedra capitata* Ehr, *Synedra ulna* (Nitzch) Ehr, and *Surirella ovata* Kütz are typical benthic species. They are lift up from the bottom in periods of high water (December–March) (Fig. 2). The others are plankton species abundant in spring: *Melosira varians* Ag., *Lagerhemia chodati* Bern, *Fragilaria crotonensis, Achnanthes affinis* Grun. Other species *Ceratium cornutum* (Ehrenb) Clap et. Lachm, *Tribonema minus* Hazen, *Peridinium cinctum* (O. F. Müller) Ehrenb, *Melosira granulata* (Ehr) Ralfs and *Synedra ulna var. danica* are abundant in winter when they are free of competitive pressure from other species.

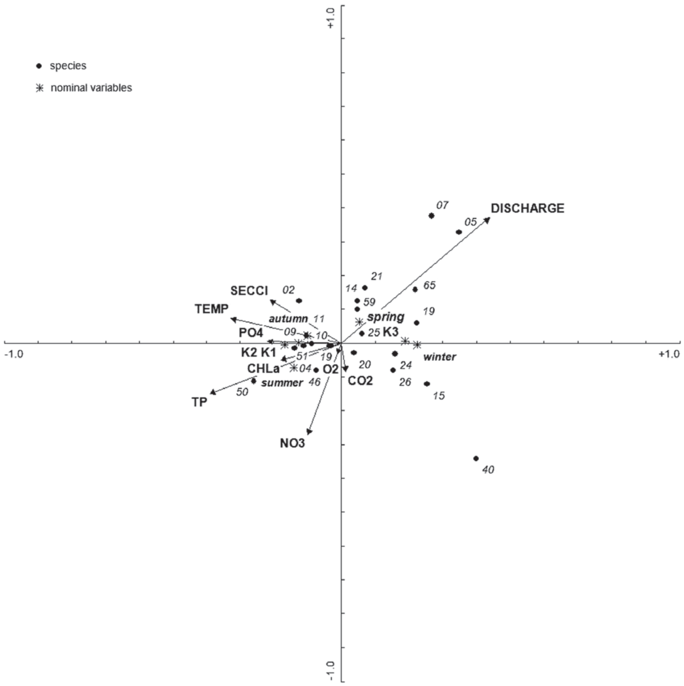

Fig. 6a. Results of CCA analysis – CCA biplot of phytoplankton species and environmental variables scores.

Legend:

Variables

Environmental variables

Discharge	discharge	(m^3 s^{-1})
SECCI	transparency	(m)
TEMP	temperature	(°C)
CHLa	chlorophyll *a*	(µg L^{-1})
PO4	phosphate	(mg L^{-1})
TP	total phosphorus	(mg L^{-1})
NO3	nitrate	(mg L^{-1})
O2	oxygen	(mg L^{-1})
CO2	carbon dioxide	(mg L^{-1})

Nominal variables

autumn	(September, October, November)
winter	(December, January, February)
spring	(March, April, May)
summer	(June, July, August)
K1	station K1
K2	station K2
K3	station K3

Species

2	*Oscillatoria planctonica*
4	*Ceratium hirundinella*
5	*Ceratium cornutum*
7	*Peridinium cinctum*
9	*Dynobrion divergens*
10	*Cyclotella comta*
11	*Cyclotella mellosiroides*
14	*Melosira varians*
15	*Melosira granulata*
18	*Achnantes affinis*
19	*Asterionella formosa*
20	*Fragilaria crotonensis*
21	*Fragilaria capucina*
24	*Synedra ulna*
25	*Synedra danica*
40	*Surirela ovata*
46	*Ulothrix subtilissima*
50	*Zygnema* sp.
51	*Sphaerocystis schroeteri*
59	*Lagerhemia chodati*
65	*Tribonema minus*

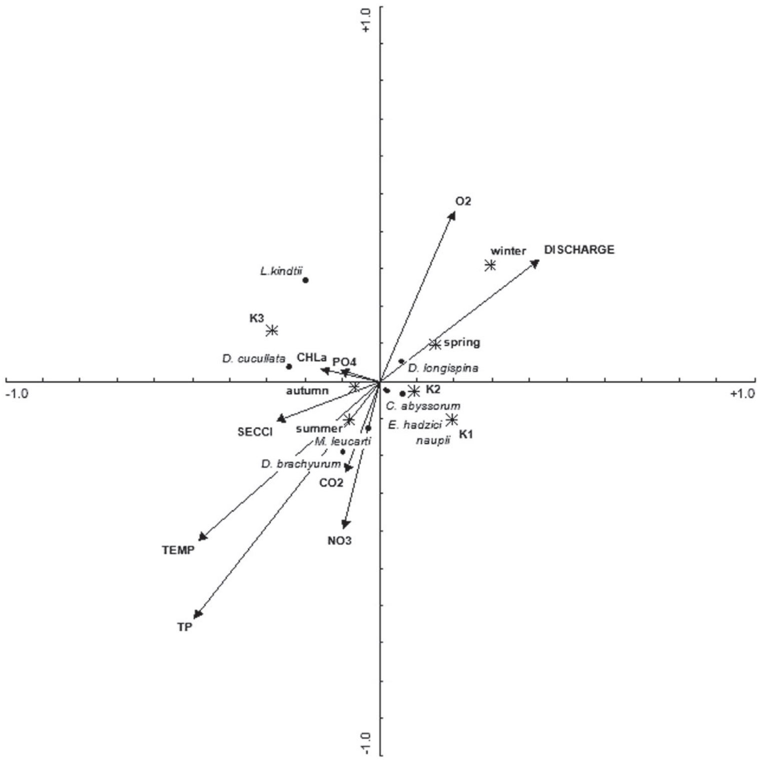

Fig. 6b. Results of CCA analysis – CCA biplot crustacean zooplankton species and environmental variables scores.

Legend:

Variables

Environmental variables

Discharge	discharge	(m^3 s^{-1})
SECCI	transparency	(m)
TEMP	temperature	(°C)
CHLa	chlorophyll *a*	(µg L^{-1})
PO4	phosphate	(mg L^{-1})
TP	total phosphorus	(mg L^{-1})
NO3	nitrate	(mg L^{-1})
O2	oxygen	(mg L^{-1})
CO2	carbon dioxide	(mg L^{-1})

Nominal variables

autumn	(September, October, November)
winter	(December, January, February)
spring	(March, April, May)
summer	(June, July, August)
K1	station K1
K2	station K2
K3	station K3

Species

D. longispina	*Daphnia longispina*
D. cucullata	*Daphnia cucullata*
D. brachyurum	*Diaphanosoma brachyurum*
L. kindtii	*Leptodora kindtii*
E. hadzici	*Eudiaptomus hadzici*
C. abyssorum	*Cyclops abyssorum "divulsus"*
M. leucarti	*Mesocyclops leucarti*

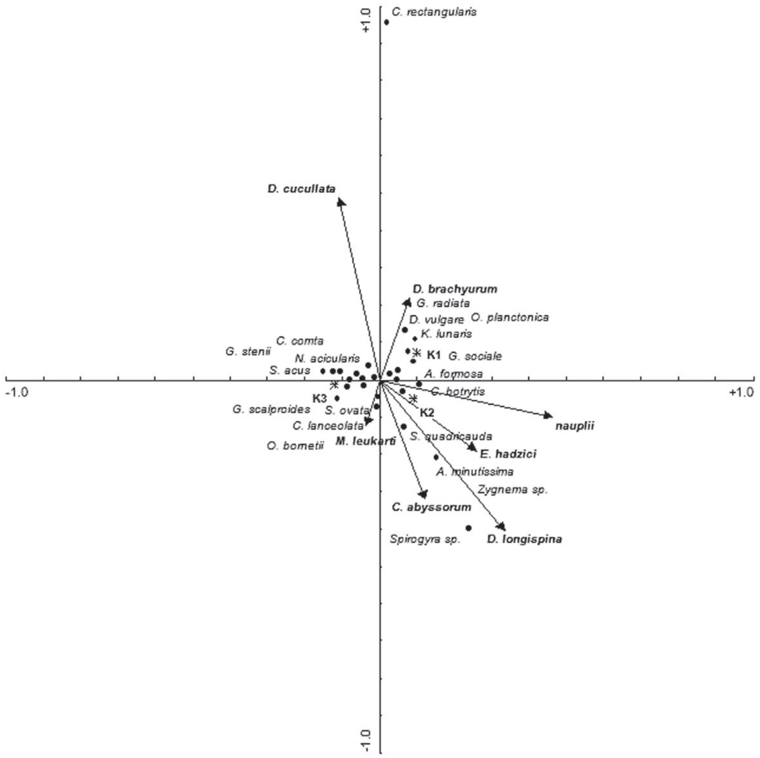

Fig. 6c. Results of CCA analysis – CCA biplot of phytoplankton in relation to crustacean zooplankton species.

Legend:

zooplankton species

D. longispina	*Daphnia longispina*
D. cucullata	*Daphnia cucullata*
D. brachyurum	*Diaphanosoma brachyurum*
L. kindtii	*Leptodora kindtii*
E. hadzici	*Eudiaptomus hadzici*
C. abyssorum	*Cyclops abyssorum "divulsus"*
M. leucarti	*Mesocyclops leucarti*

phytoplankton species

C. rectangularis	*Crucigenia rectangularis*	*G. radiata*	*Golenkinia radiata*
C. comta	*Cyclotella comta*	*D. vulgare*	*Diatoma vulgare*
G. steini	*Glenodinium steini*	*O. planctonica*	*Oscillatoria planctonica*
N. acicularis	*Nitzschia acicularis*	*K. lunaris*	*Kirchneiella lunaris*
S. acus	*Synedra acus*	*G. sociale*	*Gonium sociale*
G.scalproides	*Gyrosigma scalproides*	*A. formosa*	*Asterionella formosa*
S. ovata	*Surirella ovata*	*C. botrytis*	*Cosmarium botrytis*
C. lanceolata	*Cymbella lanceolata*	*S. quadricauda*	*Scenedesmus quadricauda*
O. bornetii	*Oscillatoria bornetii*	*A. minutissima*	*Achnanthes minutissima*
		Zygnema sp.	*Zygnema* sp.

The first two axes of CCA explained 12.8% of the zooplankton abundance variance, and 29.6% of the phytoplankton variance (Table 2). Major environmental variable influencing zooplankton cycle is total phosphorus followed by temperature, discharge, oxygen, nitrate, transparency and carbon dioxide (Fig. 6b). The analysis between the phytoplankton and zooplankton species showed daphnids to be the group with the largest correlation with phytoplankton (Fig. 6c). Among cladocerans there was a segregation of species *Daphnia cucullata* appearing mostly in summer and autumn, collide with the greatest chlorophyll *a* and phosphate levels, whereas *D. longispina* is the main cladoceran species influencing algae during spring. The major peak of macrozooplankton biomass in station K3 is in August. During that period a high number of *D. cucullata* can be found in plankton (80 org. L^{-1}); two small peaks in June and November also correspond with increase of *D. cucullata* population (Fig. 5b). In stations K1 and K2, spring maximums are associated mostly with higher abundance of *D. longispina*.

The Cladoceran *Leptodora kindtii* represented the predatory zooplankton. *L. kindtii* is an obligatory predator. A large share of predators has been noticed in February in K3 (Fig. 6b). A reason for that should be found in the relatively large body size of *L. kindtii* in comparison to the other non-predatory zooplankton. This could explain the correlation with the station.

Copepods also had a strong relationship with phytoplankton (Fig. 6c). Calanoids are numerous during the whole year, both adults and copepodites. Being macrofiltrators they feed mainly on green algae like *Scenedesmus quadricauda*, *Cosmarium botrytis, Zygnema* sp. and diatom *Achanathes minutissima* (Fig. 6c). Cyclopoids are less abundant. They are present with higher populations during spring (K1), and summer (K2, K3). *Cyclops abyssorum* finds favorable conditions in first two stations, while *Mesocyclops leukarti* is generally find in the third station.

The nauplius larvae contributed to most of the copepod number. They feed on green algae, and show the highest correlation with phytoplankton (Fig. 6c). Juvenile copepods were abundant in summer and autumn. The populations of all three development stages alter during one-year cycle: adult peaks are followed by a nauplius peak, which is on the other hand followed by a copepodites peak.

Discussion

Species diversity and density vary significantly with current velocity throughout river networks in general and are positively correlated with hydrological retention within the riverscape of larger rivers, except where taxa are restricted by other abiotic environmental conditions (e.g. oxygen, temperature, substrate type) (Thorp et al., 2006). It is not surprising, therefore, that lotic ecologists are increasingly identifying hydrological retention in slackwaters and floodplain lakes as a major factor influencing potamoplankton production and diversity as well as other structural (Thorp et al., 1994; Basu, Pick, 1996; Reckendorfer et al., 1999; Schiemer et al., 2001) and functional characteristics of rivers (Hein et al., 2005). Thorp and Mantovan (2005) reported that mean river discharge by itself was not a good predictor of zooplankton densities, but this hydrological parameter must impinge on zooplankton through current velocity, water depth, and turbulence.

We found that discharge had a high influence on the phyto- and macrozooplankton communities (CCA analysis). However, the effect of discharge is not the same in all stations and seasons. Station K3 has the most extreme conditions. During summer the river Čikola completely dries out causing eutrophication of K3. The water temperature in this part of the lake is significantly (t-test, $p < 0.05$) different (higher between 1.5–4 °C) in comparison with stations K1 and K2 (Habdija et al., 1996). This could explain a great correlation of temperature vector with macrozooplankton since some research pointed out that zooplankton are regulated more by physical than biotic factors (e.g. Hynes, 1970; Baranyi et al., 2002). The direct importance of temperature and food supply in regulating copepod growth is strongly debated and remains controversial. We suppose that circulation of water has influence on physical properties of the water, and through it controls plankton community as a whole. Considering crustacean plankton, a few studies have shown that herbivorous copepods and daphniids have different impacts on phytoplankton communities. In a laboratory experiment, Rothhaupt (1997) showed that different algae became dominant when different grazers were present. Whereas small sized algae became dominating in a system with *Eudiaptomus*, larger algae prevailed under a regime of *Daphnia* grazing. Sommer et al. (2001) reported a similar result from an enclosure study comparing grazing effects of daphniids and copepods on the phytoplankton community. They found a strong impact on the size structure of the phytoplankton community dependent on the different zooplankton taxa. These differences can be linked to the different feeding mode of copepods and cladocerans. Many studies have described that copepods can detect and select favourable particles (e.g. Demott, 1986; Butler et al., 1989). Daphniids on the other hand feed unselectively, but are able to reject unsuitable particles (Demott, 1982; Kerfoot, Kirk, 1991). There are several explanations for the increase in smaller particles under copepod dominance: the copepods primarily feed on the larger algae, thus leaving more nutrients available for the smaller-sized algae to grow. With copepod grazing, nutrients are released in the water column, which can rapidly be taken up by small-size phytoplankton biomass with their shorter generation times and larger surface to volume ratios. A third possible explanation is that the effect is indirect via the microzooplankton (Becker, Boersma, 2003).

We found three Cladocera species in lake Visovac. Their feeding habits can be assumed on the basis of CCA analysis. *Daphnia* species were associated with Bacillariophyceae and Chlorophiceae, while *Diaphanosoma* and *Bosmina* associated with Cyanophiceae and Xantophyceae as well. Since we collected only net phytoplankton, we cannot discuss nanophytoplankton and detritus feeding. However, high population of *Daphnia cucullata* has been noticed in summer on station K3. It could be due to it is less affected with inedible algae dominant during that period and higher concentration of detritus (higher concentration of detritus pointed out by Habdija et al. 1996, on the basis of $KMnO_4$ consumption).

The other species with a higher population in K3, then in K1 and K2 is copepod *Mesocyclops leukarti*. It belongs to the group of facultative predators which can feed on very diverse food (from bacterial aggregates, through varied-sized animal organisms to large net algae)

(Karabin, 1985; Papinska, 1985). Therefore its biomass increases with increasing trophic state. According to Papinska (1985) *M. leukarti* especially preyed on daphnids namely *D. cucullata*, and copepods nauplii. This explains its favorability of K3 station, and also depression of nauplii population in this part of the lake.

The most numerous copepod in lake Visovac is species *Eudiaptomus hadzici*. It prevailed during summer period which in all station is determined with Phyrrhophyceae, especially species *Ceratium hirundinela*. Whether it feeds on it, we cannot claim for sure, but some other copepods (*Cyclops*) have been reported to feed upon this dinoflagellate (Santer, 1996). In lake Visovac *C. abyssorum* is present during the whole year, but is less abundant then calanoids.

Considering the phytoplankton composition and biomass it can be assumed that it depended on the riverine and lacustrine conditions in any given station. True riverine plankton becomes important only in large rivers, either sufficiently long, or sufficiently slow flow (Margalef, 1983). It is suggested that in any given river there is a critical range of discharge above which plankton biomass fails to increase or is actively reduced. This critical discharge corresponds to a mean flow velocity of 0.48 ms^{-1} at which the development of a true potamoplankton might be supported (Reynolds, 1988). In our case, there was a considerable higher portion of benthic species in station K3 during periods of higher discharge. This may be explained by the "wash out" effect caused by a rapid appearance of water up stream in the river Čikola, after drought in summer and autumn. We can only speculate about flow velocity, but it is far below the critical range of 0.48 ms^{-1}. In all stations there is a large portion of true plankton species, namely Pyrrhophyceae, especially during summer and autumn when discharge is low. However, it has been reported that river plankton is typically dominated by centric diatoms through the year or with a summer facieses dominated by Chlorophyta (Montesanto et al., 2000). Phytoplankton composition shows some similarity with potamoplankton of Mediterranean rivers (e.g. Montesanto, Tryfon, 1999; Montesanto et al., 2000).

Concerning net phytoplankton species composition we can discuss a few things. The effects of the short term dynamics of environmental factors on the algal growth in barrage lenitic area of calcareous river stressed several variables as important factors controlling annual microphytoplankton distribution (Plenković-Moraj et al., 2002). Population diversity, same as density, is changing with the temperature change. But, temperature might not be limited variable for dominant microphytoplankton species in lake Visovac. Distribution of species is correlated and influenced also with water ionic content such as concentration of sulfates, calcium and carbon hydrates (Pérez-Martínez, Sánchez-Castillo, 2001). The master species in Lake Visovac was *Asterionella formosa*. The species has cosmopolitan distribution, and usually develops within wide range of environmental conditions (Reynolds, 1984; Duthie, Hart, 1987; Negro et al., 2000; Teubner et al., 2003). Among the planktonic pennate diatoms, it is known to be present in the rivers same as in lakes. The development of *A. formosa* is usually described under conditions of high nutrient concentrations (Olsén, Willén, 1980; Kudoh, Takahashi, 1990; Salmaso, 2003) and its growth is sensitive to depletion of phosphorus and nitrogen (Reynolds, 1984; Bertrand et al., 2003). In our research development of *A. formosa* shows positive correlation with total phosphorus and nitrate compounds. However it's development might be described in terms of silica concentration (Reynolds, 1984; Gligora et al., 2003). In seasonal studies, *Cyclotella* species are observed as vernal and summer populations (Reynolds, 1984). In lake Visovac species *Cyclotella melosiroides* coexisted during spring with *Fragilaria crotonensis*.

According to the functional classification of phytoplankton (Reynolds, 1997; Reynolds et al., 2002) *Asterionella formosa* is representative of two distinct associations named as B and C. This common pennate diatom occurs during vernal period as dominant or subdominant species to *Cyclotella* and *Aulacoseira* species or *Fragilaria crotonensis* and *Stephanodiscus* spp. of associations B and C, respectively. In the lake Visovac, under mesotrophic conditions Reynolds groups B and C are present during the one-year period, with exception of late summer and autumn assemblages which are characterized by association of large dinoflagellate species known as group LM. This association is originally based on coexistence of species *Microcystis aeruginosa* Kütz. Emend. Elenk. This typical representative of group LM was not recorded in our investigation.

The dinoflagellates were the second most representative group in terms of abundance in lake Visovac. Their annual development has been shifted to the late summer and autumn period. In contrast to *Ceratium* development in lakes located mostly in temperate altitudes (Reynolds, 1984; Heaney et al., 1988; Lindstrom, 1992) the prolongation of dinoflagellate development to "colder" part of the year has been known in Mediterranean lakes as well as their development in winter period (Pérez-Martínez, Sánchez-Castillo, 2002; Tomec et al., 2002; Gligora et al., 2003). As species affected with temperature conditions (Grigorszky et al. 2003), *Ceratium hirundinella* can be associated with long stratifying period in deep lakes in Mediterranean climate conditions due to extension of summer period or certain temperature conditions (Pérez-Martínez, Sánchez-Castillo, 2002).

Conclusion

Our research showed that discharge, temperature and total phosphorus had a high influence on the plankton community of lake Visovac. However, we found that the effect of discharge is not the same in all stations and seasons. The circulation of water has influence on physical properties of the water, and through it affects plankton community.

Translated by the authors

Acknowledgements

The authors wish to thank W. Naidenov for the help with determination of Copepoda species. The investigation was financed by Croatian Ministry of Science and Technology.

References

APHA, 1992: Standard methods for the examination of water and wastewater. American Public Health Association, New York, 1268 pp.

Baranyi, C., Hein, T., Holarek, C., Keckeis, S., Schiemer, F., 2002: Zooplankton biomass and community structure in a Danube River floodplain system: effects of hydrology. Freshw. Biol., 47: 473–182.

Basu, B.K., Pick, F.R., 1996: Factors regulating phytoplankton and zooplankton biomass in temperate rivers. Limnol. Oceanogr., 41: 1572–1577.

Becker, C., Boersma, M., 2003: Resource quality effects on life histories in Daphnia. Limnol. Oceanogr., 48: 700–706.

Bertrand, C., Fayolle, S., Franquet, E., Cazaubon, A., 2003: Responses of the planktonic diatom *Asterionella formosa* Hassall to abiotic environmental factors in a reservoir complex (south-eastern France). Hydrobiologia, 501: 45–58.

Bottrel, H.H., Duncan, A., Gliwicz, Z.M., Grygierek, E., Herzig, A., Hillbricht-Ilkowska, A., Kurosawa, H., Larsen, P., Weglenska, T., 1976: A review of some problems in zooplankton production studies. Norwegian Journal of Zoology, 24: 419–456.

Bukvić, I., Kerovec, M., Mihaljević, Z., 1999: *Eudiaptomus hadzici* (Brehm) (Crustacea, Copepoda) from the Dinarid karstic area. International Review of Hydrobiology, 84: 23–31.

Butler, N.M., Suttle, C.A., Ncill, W.E., 1989: Discrimination by freshwater zooplankton between single algal cells differing in nutritional status. Oecologia, 78: 368–372.

Deisinger, G., 1984: Leitfaden zur Bestimmung der planktonischen Algen der Kaertner Seen und ihrer Biomasse. Kaertner Institut fuer Seenforschung, 64 pp.

Demott, W.R., 1982: Feeding selectivities and relative ingestion rates of *Daphnia* and *Bosmina*. Limnol. Oceanogr., 27: 518-527.

Demott, W.R., 1986: The role of taste in food selection by freshwater zooplankton. Oecologia, 69: 334–340.

Dumont, H.J., Van de Velde, I., Dumont, S., 1975: The dry weight estimate of biomass in selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia, 19: 75–97.

Duthie, H.C., Hart, C.J., 1987: The phytoplankton of the sub arctic Canadian Great Lakes. Archive für Hydrobiologie, 25: 1–9.

Edler, L., 1979: Recommendations for marine biological studies in the Baltic Sea: Phytoplankton and chlorophyll. Baltic Marine Biologists Publication, 25: 5–36.

Einsle, U., 1993: Crustacea Copepoda Calanoida und Cyclopoida. Süßwasserfauna von Mitteleuropa 8/4. Gustav Fischer Verlag, Stuttgart, 208 pp.

Gligora, M., Plenković-Moraj, A., Ternjej, I., 2003: Seasonal distribution and morphological changes of *Ceratium hirundinella* in two mediterranean shallow lakes. Hydrobiologia, 506–509: 213–220.

Golerbach, M.M., Kosinskaja, E.K., Poljanski, V.I., 1953: Cyanonbacteria (in Russian). Gos. Izd. Sovjetskaja nauka, Moskva, 651 pp.

Grigorszky, I., Padisák, J., Borics, G., Schnitchen, C., Borbély, G., 2003: Deep chlorophyll maximum by Ceratium hirundinella (O. F. Müller) Bergh in a shallow oxbow in Hungary. Hydrobiologia, 506–509: 209–212. doi:10.1023/B:HYDR.0000008632.57769.19

Habdija, I., Primc, B., 1990: Spring trophic structure of zooplankton of Lake Visovac (in Croatian). Proceedings from Symposium "NP Krka investigations and conservation strategies", 2: 307–316.

Habdija, I., Šoštarec, V., Primc, B., Durut, D., 1989: Vertical stratification of macrozooplankton in the Lake Kozjak (Plitvice Lakes) in relation to trophic factors. Period. Biol., 91: 99–101.

Habdija, I., Primc-Habdija, B., Erben, R., Belinić, I., 1993: Trophic role of rotifers in the plankton of Lake Kozjak (Plitvice Lakes). Hydrobiologia., 257: 101–106.

Habdija, I., Meštrov, M., Stilinović, B., Tavčar, V., Primc-Habdija, B., Kerovec, M., Mrakovčić, M., Plenković-Moraj, A., Radanović, I., Mihaljević, Z., Bukvić (Ternjej), I., Lajtner, J., Špoljar, M., Schneider, D., Gottstein, S., 1996: Analysis of biologically important factors in standing water biotopes in lower courses of the rivers Krka and Čikola (in Croatian). In Evaluations of the water quality of the rivers Krka and Čikola based on functional organization of benthos and plankton community (study). Faculty of Science, University of Zagreb, part II, 260 pp.

Heaney, S.I.J., Lund, W.G., Hilda, M., Gray, K., 1988: Population dynamics of *Ceratium* spp. in three English lakes, 1945–1985. Hydrobiologia, 161: 133–148.

Hein, T., Reckendorfer, W., Thorp, J., Schiemer, F., 2005: The role of slackwater areas and the hydrologic exchange for biogeochemical processes in river corridors: examples from the Austrian Danube. Archive für Hydrobiologie, Suppl., 155 (Large Rivers 15): 425–442.

Hindák, F., Marvan, P., Rosa, K., Popovsky, J., Lhotsky, O., 1978: Freshwater algae (in Slovak). SPN, Bratislava, 724 pp.

Hutchinson, G.E., 1957: A treatise of limnology. John Wiley & Sons, New York, 1015 pp. Hynes, H.B.N., 1970: The ecology of running waters. University of Toronto Press, Toronto, 555 pp.

Karabin, A., 1985: Pelagic zooplankton (Rotatoria + Crustacea) variation in the proces of lake eutrofication. Ekol. Pol., 33: 567–644.

Kerfoot, W.C., Kirk, K.L., 1991: Degree of taste discrimination among suspension-feeding cladocerans and copepods – Implications for detritivory and herbivory. Limnol. Oceanogr., 36: 110–123.

Kiefer, F., 1968: Versuch einer Revision der Gattung *Eudiaptomus* Kiefer (Copepoda, Calanoida). Mem. Ist. Ital. Idrobiol., 24: 9–160.

Kiefer, F., 1978: Das Zooplankton der Binnengewässer. Freilebende Copepoda. Die Binnengewässer. Stuttgart, 263 pp.

Komarenko, L.E., Vasiljeva, I.I., 1978: Freshwater Chlorophyceae in Yakutia (in Russian). Nauka, Moskva, 283 pp.

Krmpotić, I., 1913: Contribution to microfauna of Plitvice lakes (in Croatian). Gl. Hrv. Prirodosl., 25: 1–29.

Kudoh, S., Takahashi, M., 1990: Fungal control of population changes of the planktonic diatom *Asterionella formosa* in a shallow eutrophic lake. J. Phycol., 26: 239–244.

Lindström, K., 1992: *Ceratium* in Lake Erken: vertical distribution, migration and form variation. Nord. J. Bot., 12: 541–556.

Malley, D.F., Lawrence, S.G., Maclver, M.A., Findlay, W.J., 1989: Range of variation in estimates of dry weight for planktonic Crustacea and Rotifera from temperate North American lakes. Can. J. Fish Aquat. Sci., 1666: 1–49.

Margalef, R., 1983: Limnologia. Omega, Barcelona, 1010 pp.

Margaritora, F., 1983: Crustacea: Cladocera (in Italian). Guide per li riconoscimento delle specie animali delle aque interne Italiane. Verona, 169 pp.

Margaritora, F., 1985: Cladocera. In Fauna d`Italia. Edizioni Calderini, Bologna, 399 pp.

Mccauley, E., Kalff, J., 1981: Empirical relationships between phytoplankton and zooplankton biomass in lakes. Can. J. Fish Aquat. Sci., 38: 458–463.

Mihaljević, Z., Kerovec, M., Ternjej, I., 2001: Composition and depth distribution of oligochaete fauna in a Mediterranean karstic lake. Biologia (Bratislava), 56, 5: 461–467.

Mihaljević, Z., Tavčar, V., Kerovec, M., Bukvić, I., 2000: Vertical distribution of Chironomidae larvae in the karstic travertine barrage Lake Visovac (Croatia). In Hoffrichter, O. (ed), Late 20th Century Research on Chironomidae: an Anthology from the 13th International Symposium on Chironomidae, Berichte aus der Biologie. Shaker Verlag, Aachen, 325–333.

Mišetić, S., Mrakovčić, M., 1990: Estimation of trophic state of Lake Visovac based upon zooplankton composition (in Croatian). Proceedings from symposium "NP Krka investigations, and conservation strategies", 2: 343–345.

Montesanto, B., Tryfon, E., 1999: Phytoplankton community structure in the drainage network of a Mediterranean river system (Aliakmon, Greece). International Review of Hydrobiology, 84, 5: 451–468.

Montesanto, B., Ziller, S., Danielidis, D., Economou-Amilli, A., 2000: Phytoplankton community structure in the lower reaches of a Mediterranean river (Aliakmon, Greece). Archive für Hydrobiologie,147, 2: 171–191.

Negro, A.I., De Hoyos, C., Vega, J., 2000: Phytoplankton structure and dynamics in Lake Sanabria and Valparai⊠so reservoir (NW Spain). Hydrobiologia, 424: 25–37.

Olsén, P., Willén, E., 1980: Phytoplankton response to sewage reduction in Vättern, a large oligotrophic lake in Central Sweden. Archive für Hydrobiologie, 89: 171–188.

Papinska, K., 1985: Carnivorous and detritivorous feeding of *Mesocyclops leuckarti* Claus (Cyclopoida, Copepoda). Hydrobiologia, 120: 249–257.

Pérez-Martínez, C., Sánchez-Castillo, P., 2001: Temporal occurrence of *Ceratium hirundinella* in Spanish reservoirs. Hydrobiologia, 452: 101–107.

Pérez-Martínez, C., Sánchez-Castillo, P., 2002: Winter dominance of *Ceratium hirundinella* in a southernnorth-temperate reservoir. J. Plankton Res., 24: 89-96. doi:10.1093/plankt/24.2.89

Petkovski, T., 1983: Macedonian Fauna: Calanoida (Crustacea, Copepoda). 5. (in Macedonian) Prirodonaucen muzej na Makedonija, Skopje, 182 pp.

Petrik, M.,1971: Reports on measurements on the river Krka in 1970 (in Croatian). Škola narodnog zdravlja "Andrija Štampar", Zagreb, 24 pp.

Plenković-Moraj, A., Horvatinčić, A., Primc-Habdija, B., 2002: Periphyton and its role in tufa deposition in karstic waters (Plitvice Lakes, Croatia). Biologia (Bratislava), 57, 4: 423–431.

Primc, B., 1986: Vertical distribution of *Tintinnopsis lacustris* Entz and *Tintinnidium fluviatile* Stein (Ciliata) in Lake Kozjak (Plitvice Lakes) Yugoslavia. International Review of Hydrobiology, 71: 71–76.

Primc-Habdija, B., Habdija, I., Plenković-Moraj, A., Špoljar, M., 1997: The overgrowth capacity of periphyton on artificial substrates exposed at vertical profile in the Lake Visovac. Period. Biol., 99: 403–408.

Reckendorfer, W., Keckeis, H., Winkler, G., Schiemer, F., 1999: Zooplankton abundance in the River Danube, Austria: the significance of inshore retention. Freshw. Biol., 41: 583–591.

Reynolds, C.S., 1984: The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge, 384 pp.

Reynolds, C.S., 1988: The concept of ecological succession applied to seasonal periodicity of freshwater phytoplankton. Verhandlungen der Internationale Vereinigung für theoretische und angewandte Limnologie, 23: 683–691.

Reynolds, C.S., 1997: Vegetation processes in the pelagic: a model for ecosystem theory. Ecology Institute, Oldendorf, 404 pp.

Reynolds, C.S., Huszar, V., Kruk, C., Naselli-Flores, L., Melo, S., 2002: Towards a functional classification of the freshwater phytoplankton. J. Plankton Res., 24: 417–428.

Rothhaupt, K.O., 1997: Grazing and nutrient influences of *Daphnia* and *Eudiaptomus* on phytoplankton in laboratory microcosms. J. Plankton Res., 19: 125–139.

Salmaso, N., 2003: Life strategies, dominance patterns and mechanisms promoting species coexistence in phytoplankton communities along complex environmental gradients. Hydrobiologia., 502: 13–36.

Santer, B., 1996: The nutritional suitability of the dinoflagellate *Ceratium furcoides* for four copepod species. J. Plankton Res., 18: 323–333.

Schiemer, F., Keckeis, H., Reckendorfer,W., Winkler, G., 2001: The "inshore retention concept" and its significance for large rivers. Archive für Hydrobiologie, Suppl., 135, 12: 509–516.

Smirnov, N.N., 1971: Chydoridae of the world's fauna (in Russan). Fauna SSSR 1 (2). Nauka, Leningrad, 532 pp.

Smirnov, N.N., 1976: Macrothricidae and Moinidae of the world's fauna (in Russan). Fauna SSSR 1 (3). Nauka, Leningrad, 237 pp.

Sommer, U., Sommer, F., Santer, B., Jamieson, C., Boersma, M., Becker, C., Hansen, T., 2001: Complementary impact of copepods and cladocerans on phytoplankton. Ecol. Lett., 4: 545–550.

Steuer, A., 1899: Die Entomostraken der Plitvicer Seen und des Blata Sees (Kroatien), gesamelt von Dr R. Sturnay 1885. Ann. Naturhis. Hofmus., 13: 159–188.

Stilinović, B., Plenković-Moraj, A., 1995: Bacterial and phytoplanktonic research of Ponikve artificial lake on the island of Krk. Period. Biol., 97: 351–358.

Taguchi, S., Fukuchi, M., 1975: Filtration rate of zooplankton community during spring bloom in Akkeshi Bay. J. Exp. Mar. Biol. Ecol., 19: 145–164.

Ter Braak, C.J.F., 1988: CANOCO - A FORTRAN program for canonical community ordination by (partial) (detrended) (canonical) correspondence analysis, principal component analysis, and redundancy analysis (version 2.1). GLW, Wageningen, p. 11–95.

Teubner, K., Tolotti, M., Greisberger, S., Morscheid, H., Dokulil, M.T. & Morscheid, H., 2003: Steady state phytoplankton in a deep pre-alpine lake: species and pigments of epilimnetic versus metalimnetic assemblages. Hydrobiologia, 502: 49–64.

Thorp, J., Mantovan, S., 2005: Zooplankton of turbid and hydrologically dynamic prairie rivers. Freshw. Biol., 50: 1474–1491.

Thorp, J.H., Black, A.R., Haag, K.H., Wehr, J.D., 1994: Zooplankton assemblages in the Ohio River: seasonal, tributary, and navigation dam effects. Can. J. Fish. Aquat. Sci., 51: 1634–1643.

Thorp, J.H., Thorns, M.C., Delong, M.D., 2006: The riverine ecosystem synthesis: biocomplexity in river networks across space and time. River Research and Applications, 22, 2: 123–147.

Tomec, M., Ternjej, I., Kerovec, M., Teskeredžić, E., Meštrov, M., 2002: Plankton in the oligotrophic Lake Vrana (Croatia). Biologia (Bratislava), 57: 579–588.

Zabelina, M.M., Kiselev, I.A., Proškina, A.I., Šešukova, V.I., 1951: A guide to freshwater algae of the Soviet Union, Vol. 4: Diatom algae (in Russian). Gosudarstvenoe izdateljstvo Sovjetskaja nauka, Moskva, 618 pp.