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Taxonomic composition and seasonality of diatoms in three Dinaric karstic lakes in Croatia

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Abstract

The composition and temporal distribution of planktonic diatoms were studied in three small shallow karstic lakes – Modro Oko, Desne, and Kuti – throughout the seasons in 1994, 1995, 1997, and 1998. Physico-chemical parameters did not differ among the three lakes, except for NO_3 concentrations. Altogether, 137 diatom taxa within 41 genera were found in all three lakes combined. The highest number of taxa belonged to the genera *Surirella* (13), *Navicula* (12), and *Cymbella* (9). Most taxa were tychoplanktonic, with true panktonic taxa contributing only 14% of the total. Despite their physical-chemical similarity, the lakes showed differences in the structure and dynamics of their diatom communities. Blooms occurred at different times in each of the lakes, and community similarity (Jaccard index) among all three was low (17.6–29.1%). The highest mean values of surface diatom abundance in Modro Oko (2199 cells L^{-1}), Desne (7900 cells L^{-1}), and Kuti (20690 cells L^{-1}) were not significantly different. Margalef's species richness index did not differ either among the lakes or seasonally. Only five diatom taxa in quantitative samples, and 22 taxa in net-samples, were common to all lakes. The most frequent diatoms were *Cyclotella striata* (56–93%), *Fragilaria ulna* (50–67%), and *Asterionella formosa* (27–83%). The most abundant taxa in Modro Oko, Desne, and Kuti were, respectively, *Cymbella* sp. 1 (402 cells L^{-1}), *Cyclotella striata* (3000 cells L^{-1}) and *Asterionella formosa* (20690 cells L^{-1}). Eighteen taxa were recorded for the first time in Croatia: *Amphora commutata*, *Caloneis amphisbaena* var. *subsalina*, *C. silicula* var. *peisonis*, *Campylodiscus echeneis*, *Coscinodiscus lacustris*, *Denticula elegans*, *Gyrosigma acuminatum* var. *lacustre*, *G. distortum* var. *parkeri*, *G. fasciola*, *Navicula menisculus* var. *menisculus*, *N. pusilla*, *N. helensis*, *Stauroneis parvula* var. *prominula*, *Staurosira construens* f. *subsalina*, *Stephanodiscus* sp. 1, *Surirella gracilis*, *S. ovalis*, and *S. striatula*. The genus *Stephanodiscus* was recorded for the first time in Croatia.

Keywords: Diatom flora; Environmental conditions; Karstic lakes; Neretva river delta

Introduction

Croatia's Dinaric region is characterized by a great amount of precipitation – average rainfall is 1500 mm yr^{-1} – but, owing to the porous nature of its karstic soil, a general lack of surface water. Water thus accumulates below the surface where it follows often

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complex circulation patterns and, at a number of locations along the coast, resurfaces as lakes or pools (Bonacci, 1999; Magdalenić, 1991).

Such shallow, oligotrophic lakes, fed by upwelling karstic springs, are found along the perimeter of the Neretva River delta in southern Croatia (Fig. 1) (Hafner, 2003). A 2-year study of these lakes has elucidated differences in the structure and dynamics of their phytoplankton communities (Jasprica, Hafner, Batistić, & Kapetanović, 2005). The dominant algal genera in the some lakes are cyanophytes, *Microcystis* and *Aphanozomenon*, which are more typical of eutrophic systems (cf. Chen, Quin, Teubner, & Dokulil, 2003; Dokulil & Teubner, 2000).

Despite a history of limnological studies on Croatian lakes, their diatom (Bacillariophyta) flora yet has received limited attention. Available information, dating from the beginning of the 20th Century until 1995, catalogs 530 freshwater diatom taxa (species and lower units) grouped in 45 genera in Croatia's freshwater ecosystems (cf. Plenković-Moraj, 1995).

Most investigations of planktonic diatoms in karstic lakes have been conducted in northern Croatia (cf. Stilinović & Plenković-Moraj, 1995; Tomec, Ternjej, Kerovec, Teskeredžić, & Meštrov, 2002); the lakes in southern Croatia, such as those of the Neretva River delta, have not yet been the subject of detailed investigation. The present contribution addresses this deficiency by reporting the seasonal taxonomic composition of diatoms in three shallow freshwater lakes in the Neretva River delta over a 4-year period.

Study area

The Neretva River delta consists of numerous channels that empty into the Eastern Adriatic Sea and three lakes: Modro Oko, Desne, and Kuti, each of which is a karstic crypto-depression. Looking downstream, Modro Oko and Desne are on the right side of the river, and Kuti is on the left. The main morphological and physico-chemical characteristics of these lakes are presented in Table 2.

Lake waters originate mostly from underground karstic springs. These springs commonly occur at the interface of carbonate-rock massifs and low-permeability layers, e.g. flysch. Discharge is a function of the

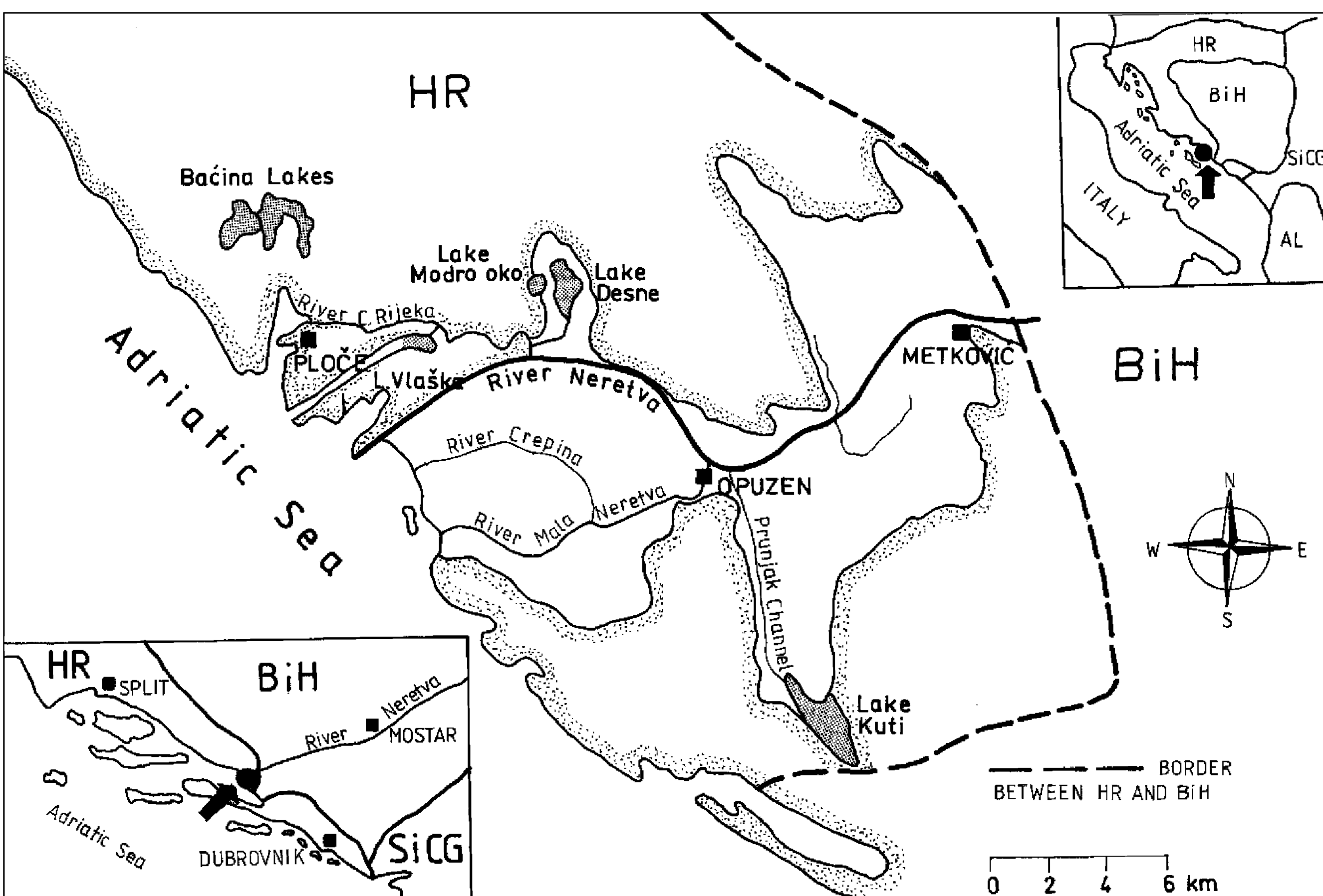

Fig. 1. Location and map of the study area. Abbreviations: HR, Croatia; BiH, Bosnia and Herzegovina; SiCG, Serbia and Montenegro; AL, Albania; shaded area: lakes; dotted area: border along karstic dry land, marsh, and Adriatic Sea; ■: towns.

Table 1. Sampling months throughout the seasons in 1994, 1995, 1997 and 1998

	Lake Modro Oko	Lake Desne	Lake Kuti	Replicates/season
Spring	5/94, 4/95, 2 and 4/97, 3 and 5/98	5/94, 4/95, 4/97, 5/98	5/94, 4/95	4 (2)
Summer	8/94, 6–7/95, 7/97, 7/98	7-8/94, 8/95, 7/97, 7/98	6–8/94, 6–7/95	4 (2)
Autumn	10/95, 9 and 11/97	10/95, 9 and 11/97	11/94, 10/95	2 (3)
Winter	12/94, 2/95	12/94, 2/95, 2/97	12/94, 2/95	2 (3)

groundwater level in the hinterland (Bonacci, 1995) and generally is higher in autumn and early spring. The subterranean source water is chemically similar to surface waters (Štambuk-Giljanović, 2003). It is poorly mineralized, generally contains a small quantity of dissolved carbon dioxide (as bicarbonate), and often is turbid. It does not contain any large amount of dissolved organic matter or toxins.

The waters of the Neretva River and its branches also supply these lakes to a small degree. Data recorded by the Croatian Meteorological and Hydrological Service from the Metković station show that the water level of the river varied from 65 to 124 cm (average 91 ± 13 cm) between 1968 and 1998. The mean annual flow of the Neretva (near the town of Metković) is $345\,m^3\,s^{-1}$.

Modro Oko and Desne are influenced only slightly by seawater ($\leqslant 3$) from the Adriatic Sea. This influence is most prominent in summer, when the relatively low water level of the river permits seawater to penetrate more extensively up-river. Seawater enters Modro Oko and Desne through the main body of the Neretva by way of a marine lake (Vlaška) and the Crna Rijeka River. Seawater has, however, no influence on Lake Kuti.

The region experiences a typical Mediterranean climate (Jasprica, Carić, & Batistić, 2003): Summers are warm and dry, and winters are mild and rainy. Annually, average air temperature is 15.4 °C and precipitation 1297 mm (data from near Opuzen for 1970–1990, Meteorological and Hydrological Service of Croatia). Average temperature during the coldest month (January) was 6.9 °C, and during the warmest (July) 24.8 °C. The highest rainfall is from October to March. During the dry season (June–August) total rainfall is only 176 mm. Average annual wind speed is $2.26\,m\,s^{-1}$, with the strongest winds (N, NE) blowing from November to April ($2.8–3.3\,m\,s^{-1}$). Potential evaporation is 1000–1200 mm per year, with maximum values in July and August amounting to 200 mm per month (Bonacci, 2001).

Phytogeographically, the area belongs to the Mediterranean-planar bio-climate, with thermophilic oak forests (Bertović, 1999). A reed bed that grows around lakes' perimeters in dense and occasionally impenetrable stands – a *Phragmitetum australis* association – constitutes the dominant helophytic plant community.

Additional details on the area are given by Jasprica et al. (2005).

Material and methods

Sampling

Plankton samples were collected seasonally in 1994, 1995, 1997, and 1998 (Table 1). Seasons are defined as: spring (March–May); summer (June–August); autumn (September–November); and winter (December–February).

Water samples for physical-chemical analysis and algal parameters (chlorophyll *a*, diatom and phytoplankton abundance) were taken with 5 L Niskin bottles, the sampling point being situated at the deepest part of each lake (see Table 2). In Modro Oko, Desne, and Kuti, this was at distance of 50, 20, and 100 m, respectively, from the shore. Samples from Modro Oko were taken at 0.5 and 10 m; in Desne, at 0.5 m; and in Kuti, 0.5 and 1.5 m. A total of 28, 15, and 18 samples were analyzed in these three lakes, respectively.

Physico-chemical parameters

Temperature was measured with an inverted thermometer; salinity using standard titration methods (Strickland & Parsons, 1972); and transparency with a 30-cm diameter Secchi disc. Oxygen was measured with an oximeter (WTW – Oxi 325-B); and nutrients, pH, alkalinity, total hardness, and chlorophyll *a* were analyzed by standard methods (American Public Health Association (Apha), 1989).

Diatom abundance and net-plankton analysis

Samples for diatom counting were fixed in 2.5% neutralized formaldehyde. Sub-samples (50–100 ML) were permitted to settle for 24–48 h in the counting chambers. Cells subsequently were counted with an inverted microscope (Utermöhl, 1958), using phase-contrast when needed, at 400×. Abundance is expressed as number of cells per liter.

The net-plankton samples were collected with a 20 cm diameter phytoplankton net with a 55 μm mesh size,

Table 2. Morphological, physico-chemical, and algal parameters for the shallow (0.5 m) water samples in the three lakes (1994, 1995, 1997, 1998)

Lakes/parameters	Lake Modro Oko	Lake Desne	Lake Kuti
Mean depth (m)	16	1	0.8
Maximal depth (m)	25.5	1.5	2.0
Surface area (km^2)	0.37	0.62	1.2
Temperature (°C)			
Range	11.0–19.2	6.2–21.7	8.0–29.2
Average (STD)	**15.6**[a] (2.7)	**16.1**[a] (4.6)	**21.2**[a] (6.0)
Salinity	0–2.5	0–1.0	0
	0.63[a] (0.85)	**0.28**[a] (0.39)	
Transparency (m)	3.5–8.0	1–1.5	1.6–2.0
	6.7 (1.4)	**1.7** (0.4)	**1.8** (0.6)
O_2 (mg L^{-1})	6.4–12.9	5.85–11.3	5.7–11.0
	8.85[a] (2.07)	**7.99**[a] (1.73)	**8.41**[a] (1.62)
O_2/ O'_2	67–123	59–124	75–107
	89[a] (20)	**82**[a] (17)	**96**[a] (11)
pH	6.9–7.7	7.3–7.7	7.4–7.7
	7.3[a] (0.4)	**7.3**[a] (0.4)	**7.4**[a] (0.3)
Alkalinity (meq L^{-1})	3.1–4.0	3.1–4.4	3.0–4.1
	3.6[a] (0.28)	**3.65**[a] (0.41)	**3.28**[a] (0.42)
Total hardness (d°H)	9.8–20.6	8.96–19.2	7.84–23.0
	15.38[a] (2.82)	**14.03**[a] (4.02)	**14.56**[a] (5.88)
NO_3 (mg L^{-1})	0.0–0.90	0.0–0.75	0.0–0.3
	0.44[a] (0.36)	**0.47**[a] (0.24)	**0.05**[b] (0.11)
NO_2 (mg L^{-1})	0.0–0.11	0.0–0.07	0.0–0.27
	0.03[a] (0.03)	**0.02**[a] (0.01)	**0.04**[a] (0.08)
NH_4 (mg L^{-1})	0.0–0.45	0.04–0.09	0.05–0.27
	0.12[a] (0.14)	**0.06**[a] (0.02)	**0.11**[a] (0.10)
PO_4 (mg L^{-1})	0.0–0.05	0.0–0.09	0.0–0.05
	0.02[a] (0.02)	**0.02**[a] (0.02)	**0.02**[a] (0.02)
Chlorophyll *a* (μg L^{-1})	0.11–0.9	0.2–1.1	0.01–5.1
	0.43[a] (0.23)	**0.57**[b] (0.37)	**1.69**[c] (1.83)
Phytoplankton (cells L^{-1})	12–2573	44–17740	1820–628850
	575[a] (809)	**2534**[a] (4643)	**103810**[a] (188997)
Diatoms (cells L^{-1})	2–2199	40–7900	11–20690
	421[a] (597)	**2660**[a] (4841)	**4688**[a] (7656)

Means are across seasons, and lakes were not sampled synoptically. Ranges, means (in bold), and standard deviations (in parentheses) are reported. Physico-chemical parameters were compared by means of ANOVA and SNK multiple range tests, while algal measures were compared with Kruskall–Wallis test. Means followed by different superscripts (a,b,c) are significantly different at $\alpha = 0.05$.

submerged 50 cm beneath the surface water and towed horizontally for 20 m to collect phytoplankton. Additionally, vertical hauls were made in Lake Modro Oko. Samples were preserved in 2.5% neutralized formaldehyde. The material was treated with 10% HCl in order to remove calcium carbonate, washed several times with distilled water and boiled in 30% H_2O_2 (van der Werff, 1955). Finally, the samples were washed several times with distilled water. Permanent microscope slides for light microscopy were prepared using Naphrax as the mounting medium. The presence of diatom taxa were performed by means of an Olympus microscope equipped with phase contrast, using a oil immersion objective 100 ×. At least one sample per each season was used in each investigated year. In total, 17, 14, and 10 samples were analyzed in lakes Modro Oko, Desne and Kuti, respectively. Each sample was prepared and analyzed in triplicate.

References used in the identification of diatoms include: Hustedt (1930), Krammer and Lange-Bertalot (1986, 1988, 1991a, b), Lange-Bertalot and Kurt Krammer (1987), Canter-Lund and Lund (1995), Hartley, Barber, Carter, and Sims (1996) and Lange-Bertalot and Metzeltin (1996).

Statistical analysis

Physico-chemical properties among lakes, based only on samples from 0.5 m, were compared using Analysis of Variance (ANOVA) and the Student–Neumann–Kuels (SNK) multiple range test. The Kruskall–Wallis test

(Sokal & Rohlf, 1969) was used for comparisons of chlorophyll *a* and the abundance of phytoplankton and diatoms. Differences between shallow (0.5 m) and deep samples within the two lakes that permitted such analysis, Modro Oko (10 m maximum depth) and Kuti (1.5 m), were made with a paired *t*-test.

Species associations were quantified with the Jaccard similarity index (JI) (Jaccard, 1908). Based on the presence/absence of a species, rather than on its actual numbers, the Jaccard formula is: $JI = 100[a/(a+b+c)]$, where a is the number of species present in both samples (lakes), b the number of species present in sample 1, but absent from sample 2, and c is the number of species present in sample 2, but absent from sample 1. Double absences were not considered.

Species richness was characterized by Margalef's species richness index D (Margalef, 1965): $D = (S-1)/\log N$, where D is the index, S the number of species, and N is the total number of individuals counted to obtain S.

Cluster analysis (Legendre & Legendre, 1978) was used to analyze the variability in species composition over seasons and among lakes. This was based on a matrix of 13 taxa over 41 shallow (0.5 m) samples. Taxa that did not occur in at least three samples were not included in the matrix. The dendrogram was based on standardized cell abundance data.

Statistical analyses were performed using STATGRAPHIC, SYSTAT, and PRIMER v5 software (Clarke & Gorley, 2001; Wilkinson, 1986).

Table 3. Physico-chemical and algal parameters for the deep water samples (10 m for Lake Modro Oko and 1.5 m for Lake Kuti, 1994, 1995, 1997, 1998)

Lakes/parameters	Lake Modro Oko	Lake Kuti
Temperature (°C)		
Range	11.0–17.6	8.0–28.2
Average (STD)	**13.1** (3.0)	**21.8** (6.4)
Salinity	0.0–3.0	0
	1.66 (1.52)	
O_2 ($mg\,L^{-1}$)	7.1–10.7	5.1–11.0
	9.26 (0.87)	**6.80** (3.58)
O_2/O'_2	75–95	71–105
	87 (10)	**92** (14)
pH	6.9–7.7	7.4–7.7
	7.3 (0.4)	**7.4** (0.3)
Alkalinity ($meq\,L^{-1}$)	3.7–3.9	3.1–3.4
	3.8 (0.1)	**3.24*** (0.11)
Total hardness (d°H)	11.7–20.7	8.9–24.0
	16.93 (4.67)	**14.74** (6.60)
NO_3 ($mg\,L^{-1}$)	0.1–0.9	0.0–0.5
	0.50 (0.56)	**0.12** (0.19)
NO_2 ($mg\,L^{-1}$)	0.0–0.9	0.0–0.1
	0.03 (0.04)	**0.02** (0.03)
NH_4 ($mg\,L^{-1}$)	0.0–0.11	0.04–0.2
	0.05 (0.07)	**0.09** (0.07)
PO_4 ($mg\,L^{-1}$)	0.05–0.1	0.0–0.07
	0.07* (0.02)	**0.03** (0.03)
Chlorophyll *a* ($\mu g\,L^{-1}$)	0.0–0.65	0.05–1.2
	0.30 (0.26)	**0.58** (0.39)
Phytoplankton (cells L^{-1})	0–781	0–85380
	287 (283)	**25175** (29683)
Diatoms (cells L^{-1})	0–780	52–6120
	206 (217)	**1242** (2031)

Means are across seasons, and lakes were not sampled synoptically. Ranges, means (in bold), and standard deviations (in parentheses) are reported. A paired *t*-test was applied for comparison between deep and shallow samples. Means followed by an asterisk (*) are significantly different from their shallow-water counterparts at $\alpha = 0.05$.

Results

Physical-chemical parameters

The mean, range, and standard deviation of physico-chemical and algal parameters at 0.5 m are reported in Table 2. Of note, no thermal stratification was observed in any of the lakes, and Kuti showed the greatest temperature range. Modro Oko and Desne showed slight indications of seawater influx (max. 2.5). There was no salinity difference between shallow and deep samples (Table 3). This generally was the case for other parameters, except for alkalinity in Kuti and PO_4 in Modro Oko.

The only dramatic difference among the three lakes was in their NO_3 concentrations (Table 2), with nitrate in Modro Oko and Desne about nine times greater than in Kuti. The highest concentrations of NO_3, NO_2, and NH_4 were found in the winter and spring in Modro Oko and Kuti, and in summer in Desne (Fig. 2). The highest PO_4 concentration occurred in the summer in Modro Oko and Desne, and in Kuti in the spring. The lowest concentrations of all nutrients were in autumn.

Diatom abundances

Fifty-four diatom taxa were recorded in all lakes combined (Table 4). The highest number (32) was in Lake Desne. In Modro Oko and Desne, 31 and 15 taxa were noted, respectively.

Only five were common to all three lakes: *Asterionella formosa*, *Cocconeis placentula*, *Fragilaria crotonensis*, *F. ulna*, and *Staurosira construens*. The most frequent diatoms were *Cyclotella striata* (56–93%), *Fragilaria ulna* (50–67%), and *Asterionella formosa* (27–83%) (Table 4).

Over the entire study (Table 4), similarity coefficients (Jaccard index) between the flora in Modro Oko and Desne, Modro Oko and Kuti, and Kuti and Desne were, respectively, 29.1%, 17.6%, and 22.2%. Cluster analysis

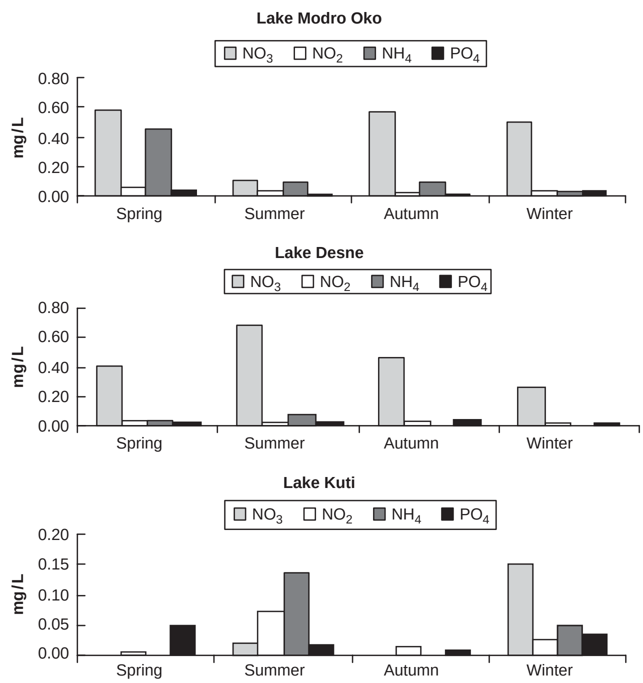

Fig. 2. Nutrient concentrations for the shallow (0.5 m) water samples in the three lakes (1994–1995, 1997–1998).

identified three main groups, each of which represents a collection of taxa that occurs mainly in a single lake (Fig. 3). The highest similarity of diatoms occurred between spring and summer in Lake Modro Oko.

The Kruskall–Wallis test indicated that diatom abundance at 0.5 m was similar in all three lakes (Table 2). There was no significant difference in this parameter between shallow and deep samples in either Modro Oko or Kuti (Table 3).

No regular pattern of diatom development was observed either among the three lakes or over the 4-year study period (Figs. 4–6). Highest abundance was found in Modro Oko, Desne, and Kuti in September 1997 (2199 cells L^{-1}), April 1995 (7900 cells L^{-1}), and June 1995 (20690 cells L^{-1}), respectively. The diatom peak in Modro Oko was composed mostly of *Cymbella* sp. (402 cells L^{-1}), *Fragilaria ulna* (385 cells L^{-1}), and other unidentified diatoms (1155 cells L^{-1}). The most abundant species at the peak in Desne were *Cyclotella striata* (2280 cells L^{-1}), *Staurosira construens* (2040 cells L^{-1}), *Fragilaria crotonensis* (1000 cells L^{-1}), and other unidentified diatoms (1920 cells L^{-1}). *Asterionella formosa* was the most abundant taxon (20275 cells L^{-1}) at Lake Kuti's peak.

Diatoms dominated the phytoplankton of Modro Oko throughout the sampling period (range: 3–100%, Fig. 4). Their lowest contribution was in July. The diatom contribution to the total phytoplankton of Desne and Kuti varied, ranging from 9% to 90% and 0% to 100%, respectively (Figs. 5–6). This was lower between May and November in Lake Kuti. No strong seasonal variation was observed in Lake Desne.

Species richness index varied from 0.00 to 1.90 in Modro Oko, 0.18 to 1.71 in Desne, and 0.00 to 1.51 in Kuti (Figs. 4–6). This did not differ either among lakes or seasonally (ANOVA, $p > 0.05$), although a small increase was noted in the shallow samples.

Net-diatom flora

Altogether, 137 diatom taxa belonging to 41 genera were identified in the three lakes between 1994 and 1998, (Table 5). Most were tychoplanktonic, with true planktonic taxa contributing only about 14% to the total.

Genera with the greatest number of taxa were: *Surirella* (13), *Navicula* (12), *Cymbella* (9), *Eunotia*, *Gyrosigma* and *Fragilaria* (7), *Gomphonema* and *Epithemia* (6). There were 22 taxa common to all three lakes: *Amphora ovalis*, *Asterionella formosa*, *Cocconeis pediculus*, *C. placentula*, *Cyclotella striata*, *Cymatopleura elliptica*, *C. solea*, *Cymbella lanceolata*, *C. lata, Cymbella* sp. 1, *Denticula elegans*, *Diatoma vulgaris*, *Fragilaria crotonensis*, *F. danica*, *F. ulna*, *Gomphonema truncatum*, *Melosira* sp. 1, *Navicula oblonga*, *N. radiosa*, *Navicula* sp. 1, *Staurosira construens*, and *Synedra capitata*.

The highest number (88) was recorded in Lake Desne (Table 6). The highest number of taxa in lakes Desne (66) and Modro Oko (50) were found in spring, and in Lake Kuti (36) in autumn. Only two taxa were recorded during all seasons in all three lakes: *Cyclotella striata* and *Fragilaria ulna*. Altogether, 9, 8, and 6 taxa were present year-around in Modro Oko, Desne and Kuti, respectively.

Some taxa appeared only in particular seasons (Table 7), and the highest number of these (17) was recorded in summer.

Eighteen diatom taxa were noted for the first time in Croatia. These are: *Amphora commutata*, *Caloneis amphisbaena* var. *subsalina*, *C. silicula* var. *peisonis*, *Campylodiscus echeneis*, *Coscinodiscus lacustris*, *Denticula elegans*, *Gyrosigma acuminatum* var. *lacustre*, *G. distortum* var. *parkeri*, *G. fasciola*, *Navicula menisculus* var. *menisculus*, *N. pusilla*, *N. helensis*, *Stauroneis parvula* var. *prominula*, *Staurosira construens* f. *subsalina*, *Stephanodiscus* sp. 1, *Surirella gracilis*, *S. ovalis*, and *S. striatula*.

One genus, *Stephanodiscus*, was recorded for the first time in Croatia.

Discussion

The three karstic lakes that were the focus of this study exhibited generally similar physico-chemical

Table 4. Diatom taxa and range of abundance (cells L^{-1}) in the lakes

Taxon	Lake Modro Oko	Lake Desne	Lake Kuti
Achnanthes gibberula Grunow		2	
Achnanthes Bory sp. 1		11–14 (13%)	
Amphora ovalis (Kütz.) Kütz.		2–8 (27%)	2
Amphora pediculus (Kütz.) Grunow		2	
Asterionella formosa Hassall	10–260 (43%)	4–500 (27%)	6–20275 (83%)
Asterionella gracillima (Hantzsch) Heib.			6–559 (17%)
Bacillaria paxillifer (O.F. Müll.) Hendey	8–10 (7%)	416	
Caloneis amphisbaena (Bory) Cleve		10	
Caloneis silicula (Ehrenb.) Cleve			2
Cocconeis pediculus Ehrenb.	3		2
Cocconeis placentula Ehrenb.	7–8 (11%)	10–18 (13%)	2–5 (17%)
Cocconeis Ehrenb. sp. 1		2–60 (13%)	
Coscinodiscus Ehrenb. sp. 1			2
Cyclotella striata (Kütz.) Grunow	2–120 (68%)	4–3000 (93%)	2–3720 (56%)
Cyclotella Kütz. sp. 1			120–240 (11%)
Cymatopleura elliptica (Bréb.) W. Sm.	1		
Cymatopleura solea (Bréb.) W. Sm.		4	
Cymbella helvetica Kütz.	4* (7%)	4	
Cymbella lanceolata (C. Agardh) C. Agardh	60		
Cymbella C. Agardh sp. 1	11–402 (7%)	2–38 (40%)	
Denticula Kütz. sp. 1		1	
Diatoma elongatum (Lyngb.) C. Agardh		15	
Diatoma vulgaris Bory	3	80	
Diatoma vulgaris var. *capitulata* Grunow	4		
Ellerbeckia arenaria (Moore ex Ralfs) R .M. Crawford	60–120 (14%)		
Encyonema minutum (Hilse ex Rabenh.) D. G. Mann	5		
Encyonema prostrata (Berk.) Kütz.	8		
Encyonema ventricosa (Kütz.) Grunow	5		
Entomoneis paludosa (W. Sm.) Reim.		8* (13%)	
Epithemia Bréb. sp. 1		1	2
Eunotia Ehrenb. sp. 1	35		
Fragilaria crotonensis Kitton	4–181 (21%)	35–1000 (27%)	3–1320 (22%)
Fragilaria danica (Kütz.) Lange-Bert.		65	3–17 (11%)
Fragilaria ulna (Nitzsch) Lange-Bert.	1–120 (50%)	5–420 (80%)	6–840 (67%)
Fragilaria Lyngb. sp. 1		45–110 (13%)	
Gomphonema acuminatum Ehrenb.	4–180 (29%)		
Gomphonema truncatum Ehrenb.	4–63 (11%)	1–48 (13%)	
Gomphonema Ehrenb. sp. 1	11		
Gyrosigma acuminatum (Kütz.) Rabenh.	1		
Gyrosigma attenuatum (Kütz.) Rabenh.		60* (13%)	
Gyrosigma Hassall sp. 1		8* (13%)	
Melosira varians C. Agardh	8–35 (11%)		
Navicula gracilis Ehrenb.	5	8* (13%)	
Navicula oblonga (Kütz.) Kütz.	1		
Navicula radiosa Kütz.	1–60 (11%)		
Navicula Bory sp. 1		3–9 (13%)	
Nitzschia sigmoidea (Nitzsch) W. Sm.	2	4–180 (33%)	
Nitzschia vermicularis (Kütz.) Hantzsch	4–10 (7%)	4	
Nitzschia Hassall sp. 1			8
Pinnularia viridis (Nitzsch) Ehrenb.		4	
Staurosira construens Ehrenb.	4–181 (18%)	300–2040 (13%)	2520
Surirella capronii Bréb.	4		
Surirella gracilis Grunow	4		
Tabellaria fenestrata (Lyngb.) Kütz.		28	
Unidentified diatoms	4–420 (68%)	11–2000 (67%)	2–1320 (67%)

Taxa assigned with one cell number were found only once. Those denoted with an asterisk (*) were found more than once with the same abundance. Frequency of occurrence (%) in the total number of samples in each lake is denoted in parentheses.

characteristics. According to chlorophyll *a* and Secchi disc data, each is oligotrophic (OECD, 1982). Consistent with the findings of Štambuk-Giljanović (2003), the highest concentrations of most nutrients in all three were observed in winter–spring, typically a period of higher rainfall.

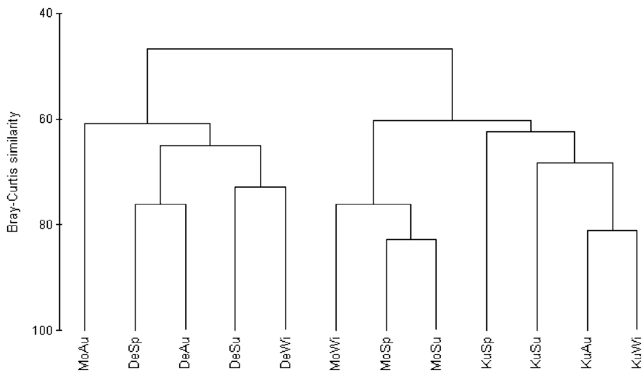

Fig. 3. Similarity dendrogram based on abundance of dominating diatom taxa throughout the seasons. Codes of the lakes (Mo – Lake Modro Oko, De – Lake Desne, Ku – Lake Kuti) in particular seasons (Sp – spring, Su – summer, Au – Autumn, Wi – winter) are given. For example MoAu reads Lake Modro Oko in autumn.

There was no clear relation between nutrient concentrations of deep and shallow samples in Modro Oko and Kuti, the two lakes that permitted such a comparison. This may be explained, at least in part, by the extremely dynamic water flow from the karstic springs that feed these lakes (Bonacci, 2001). The flow into the lakes is so intense that they are well mixed, and thus have no such vertical variations in these parameters.

Despite their broad physico-chemical similarity, the lakes nevertheless exhibit interesting differences in their diatom communities. From the standpoint of production dynamics, diatom blooms in each lake developed in a way that seemed independent of events in the others.

Further, from the standpoint of community structure, the similarity of diatoms among the lakes – characterized by the Jaccard index – was relatively low. In fact,

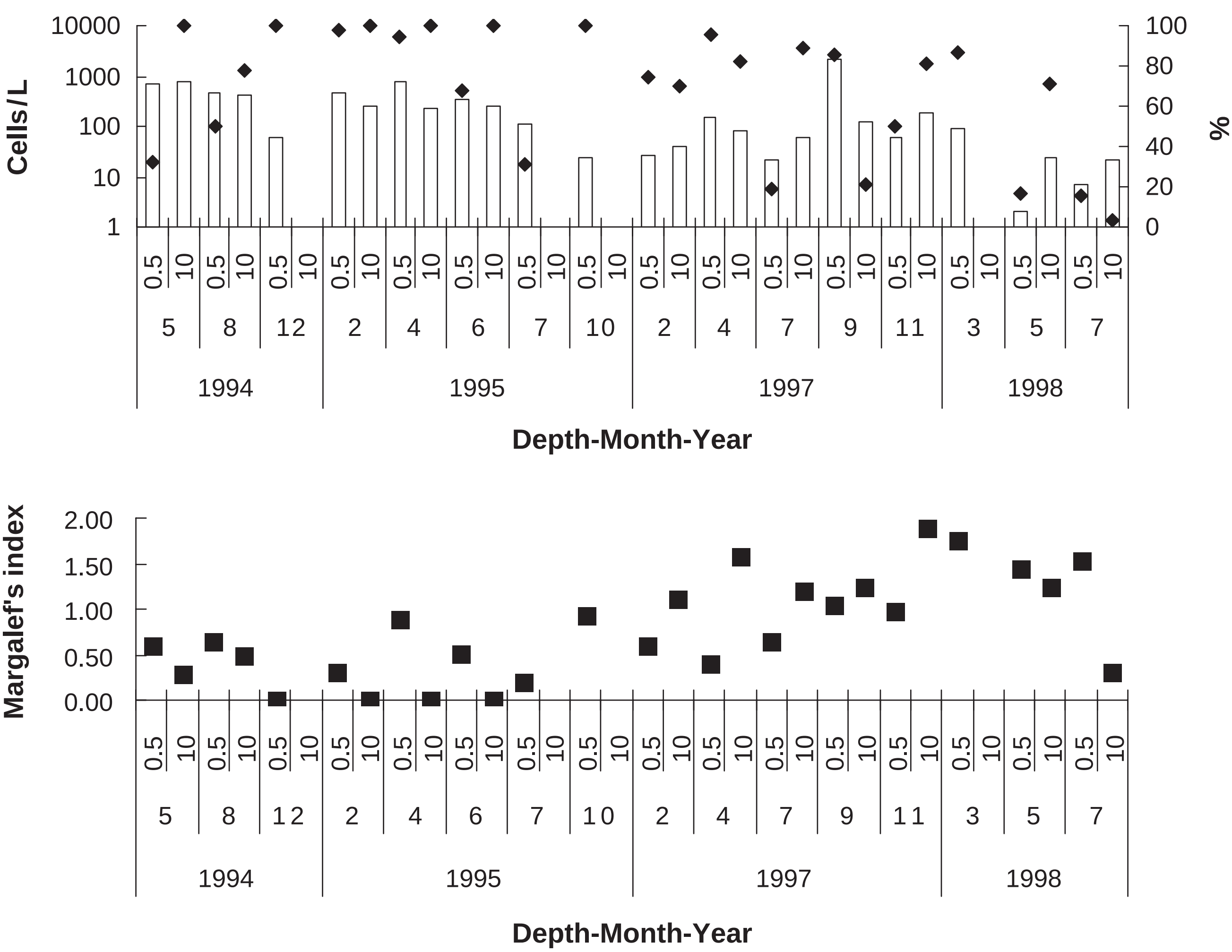

Fig. 4. Diatom abundance, percentage contribution to the total phytoplankton abundance (♦), and species richness index in the Lake Modro Oko.

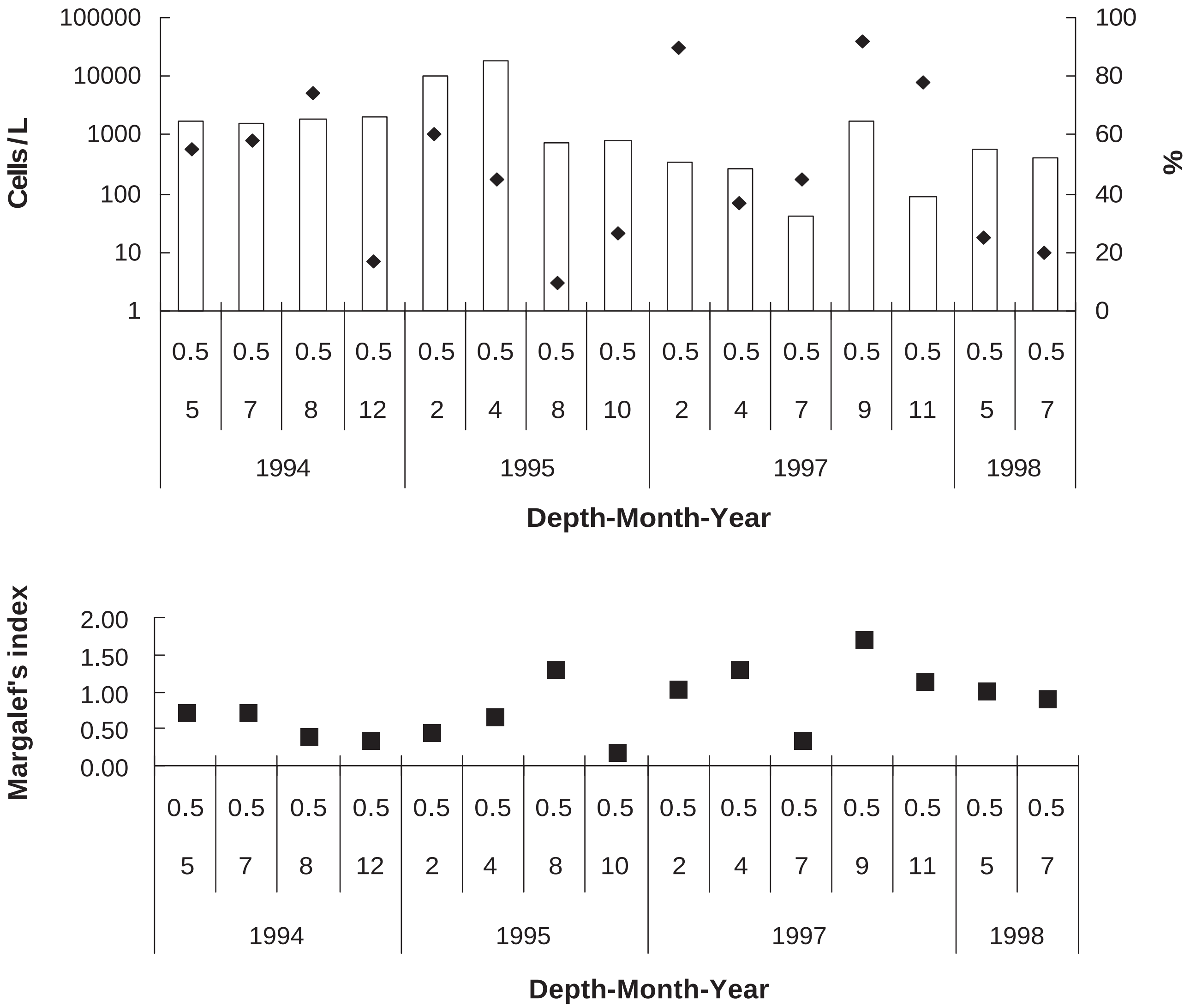

Fig. 5. Diatom abundance, percentage contribution to the total phytoplankton abundance (♦), and species richness index in the Lake Desne.

only five diatom taxa in quantitative samples, and 22 taxa in net-samples, were common to all three lakes. The vertical distribution of diatoms was irregular and unstable, with no statistically demonstrable differences between deep and shallow samples.

The increase in diatoms in the cooler months of autumn and spring is consistent with the findings of Tilman, Kiesling, Sterner, Kilham, and Johnson (1986) regarding the advantage attributed to many diatoms in competing for nutrients at lower temperatures. Conversely, diatoms were less abundant in warm summer months, when cyanobacteria were a more important element of the plankton (Jasprica et al., 2005).

Species richness analysis indicates that there was no clear difference in the diatom flora between periods of low and high nutrient input. On the other hand, the increasing occurrence of eutraphentic diatoms (Naumann, 1932) during spring and summer indicates an increase in nutrient concentrations – mostly PO_4 – during these periods. This agrees with findings for similar habitats in the Murray River delta of Australia (Gell, Sluiter, & Fluin, 2002).

The presence in oligotrophic lakes of eutraphentic taxa, such as *Amphora ovalis*, *A. pediculus*, *Bacillaria paxillifer*, *Caloneis amphisbaena*, *Cocconeis pediculus*, *Fragilaria. ulna*, some *Navicula*, and *Nitzschia* is consistent with the findings of Tomec et al. (2002) for Lake Vrana, an oligotrophic karstic lake in northern Croatia, and also for lakes from other areas (e.g. Laugaste & Pork, 1996; Rott, 1984). Similar discrepancies between the trophic status of the lakes and diatom communities also have been reported in other studies (cf. Bogaczewicz-Adamczak & Koźlarska, 1999; Huszar, Silva, Domingos Marinho, & Melo, 1998).

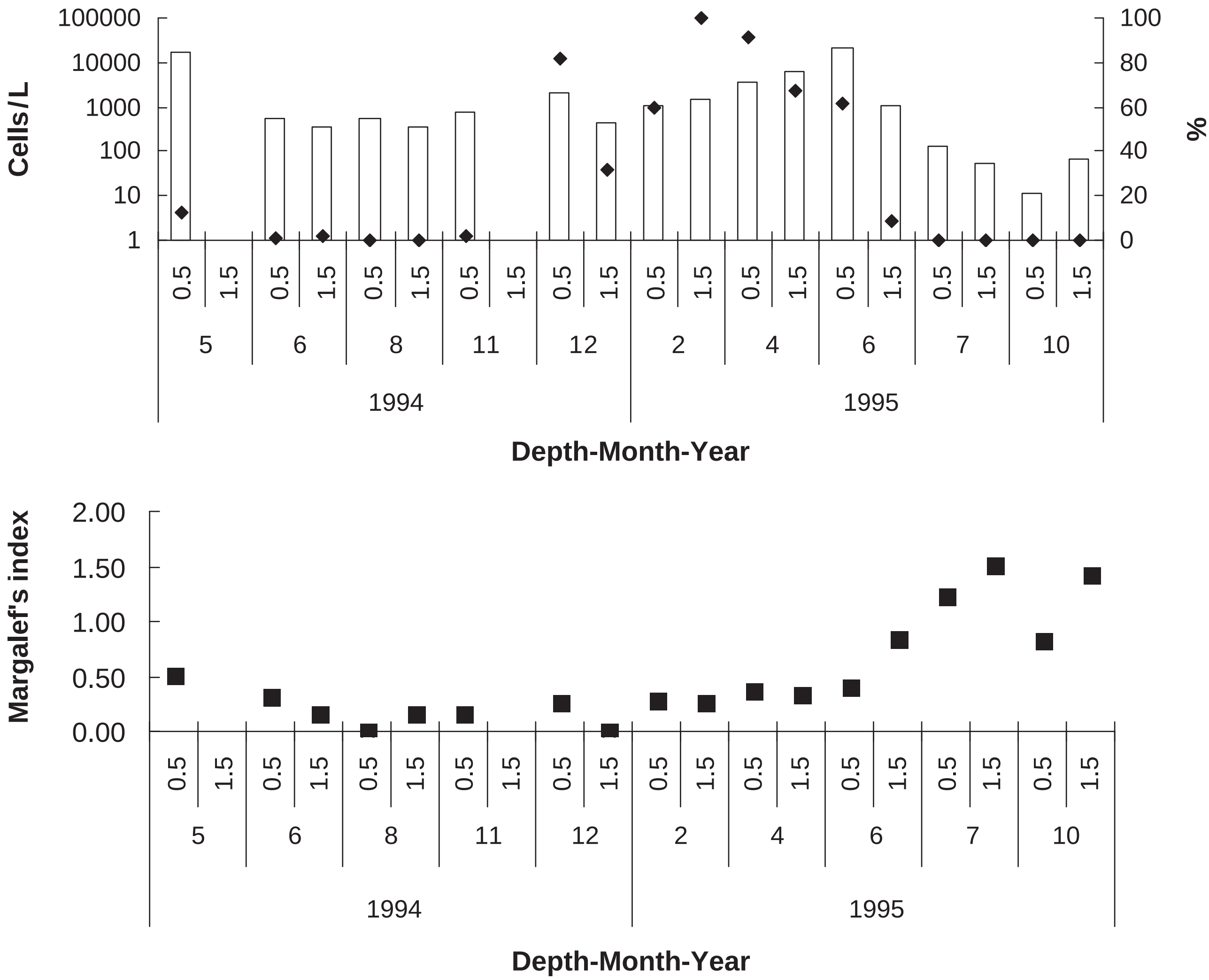

Fig. 6. Diatom abundance, percentage contribution to the total phytoplankton abundance (♦), and species richness index in the Lake Kuti.

Table 5. Diatom taxa found in the net-samples in the three freshwater lakes in the Neretva River delta

Taxa	Lake Modro Oko				Lake Desne				Lake Kuti			
	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A
Achnanthes gibberula Grunow		+	+									
Achnanthes lanceolata (Bréb.) Grunow		+	+									
Achnanthes Bory sp. 1	+	+	+	+			+	+				
Amphora commutata Grunow**						+	+					
Amphora ovalis (Kütz.) Kütz.	+	+	+	+	+	+	+			+	+	+
Amphora pediculus (Kütz.) Grunow						+	+			+		+
Amphora Ehrenb. ex Kütz. sp. 1					+	+				+		+
Aneumastus tuscula (Ehrenb.) D. Mann & Stickle						+						
Asterionella formosa Hassall*	+	+	+	+		+		+	+	+	+	+
Asterionella gracillima (Hantzsch) Heib.*										+		+
Asterionella Hassall sp. 1*												+
Bacillaria paxillifer (O. F. Müll.) Hendey*		+	+		+	+						
Bacteriastrum hyalinum Lauder*						+	+					
Bacteriastrum Shadbolt sp. 1*						+						

Table 5. (*continued*)

Taxa	Lake Modro Oko				Lake Desne				Lake Kuti			
	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A
Caloneis amphisbaena (Bory) Cleve						+	+					
Caloneis amphisbaena var. *subsalina* (Donk.) Cleve **							+					
Caloneis silicula (Ehrenb.) Cleve												+
Caloneis silicula var. *peisonis* Hust.**		+										
Campylodiscus echeneis Ehrenb.**		+	+									
Chaetoceros Ehrenb. sp. 1*							+					
Cocconeis pediculus Ehrenb.		+	+			+		+		+		+
Cocconeis placentula Ehrenb.		+	+	+	+	+	+	+		+		
Coscinodiscus lacustris Grunow**							+					
Coscinodiscus Ehrenb. sp. 1											+	+
Cyclotella comta (Ehrenb.) Kütz.			+									
Cyclotella striata (Kütz.) Grunow	+	+	+	+	+	+	+	+	+	+	+	+
Cymatopleura elliptica (Bréb.) W. Sm.		+	+			+			+	+		
Cymatopleura solea (Bréb.) W. Sm.	+	+	+	+	+	+	+			+	+	
Cymbella affinis Kütz.		+	+									
Cymbella amphicephala Nägeli ex Kütz.			+									
Cymbella cymbiformis C. Agardh	+	+	+									
Cymbella helvetica Kütz.	+		+	+		+	+					
Cymbella hustedtii Krasske												+
Cymbella lanceolata (C. Agardh) C. Agardh		+	+			+	+			+		
Cymbella lata Grunow	+				+						+	+
Cymbella pusilla Grunow							+					
Cymbella C. Agardh sp. 1			+	+	+	+	+	+		+		
Denticula elegans Kütz.**		+		+		+	+	+				+
Denticula tenuis Kütz.				+		+						
Denticula Kütz. sp. 1						+	+	+				
Diatoma elongatum (Lyngb.) C. Agardh*								+				
Diatoma hiemalis (Roth) Heib.							+					
Diatoma vulgaris Bory	+			+	+	+	+	+	+	+		+
Diatoma vulgaris var. *capitulata* Grunow						+						
Diploneis oculata (Bréb.) Cleve											+	
Diploneis ovalis (Hilse) Cleve	+					+						
Diploneis smithii (Bréb. ex W. Sm.) Cleve						+						
Ellerbeckia arenaria (Moore ex Ralfs) R. M. Crawford	+	+		+	+	+	+					
Encyonema prostrata (Berk.) Kütz.		+		+								
Encyonema ventricosa (Kütz.) Grunow		+	+	+	+	+	+					
Entomoneis paludosa (W. Sm.) Reim.				+			+	+				
Epithemia intermedia Fricke						+	+					
Epithemia muelleri Fricke							+					
Epithemia sorex Kütz.										+	+	+
Epithemia turgida (Ehrenb.) Kütz.										+	+	+
Epithemia adnata (Kütz.) Bréb.			+				+					
Epithemia Bréb. sp. 1						+	+		+	+	+	
Eunotia arcus Ehrenb.						+				+	+	+
Eunotia exigua (Bréb.) Rabenh.		+										
Eunotia lunaris (Ehrenb.) Grunow in Van Heurck		+								+		
Eunotia lunaris var. *subarcuata* (Nägeli) Grunow						+	+					
Eunotia monodon Ehrenb.										+		
Eunotia monodon var. *maior* (W. Sm.) Hust.				+								
Eunotia Ehrenb. sp. 1			+		+		+					
Fragilaria acus (Kütz.) Lange-Bert.*							+					
Fragilaria capucina Desm.*									+	+		
Fragilaria crotonensis Kitton*	+	+	+		+	+	+	+	+	+	+	
Fragilaria danica (Kütz.) Lange-Bert.*	+	+	+				+		+		+	+
Fragilaria intermedia Grunow	+		+									

Table 5. (*continued*)

Taxa	Lake Modro Oko				Lake Desne				Lake Kuti			
	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A
Fragilaria ulna (Nitzsch) Lange-Bert.	+	+	+	+	+	+	+	+	+	+	+	+
Fragilaria Lyngb. sp. 1						+						
Gomphonema acuminatum Ehrenb.		+	+	+					+	+		+
Gomphonema acuminatum var. *coronatum* (Ehrenb.) W. Sm.		+	+		+							
Gomphonema augur Ehrenb.						+	+					
Gomphonema subtile Ehrenb.											+	
Gomphonema truncatum Ehrenb.	+	+	+	+		+	+	+				+
Gomphonema Ehrenb. sp. 1		+		+								
Gyrosigma acuminatum (Kütz.) Rabenh.	+	+	+									
Gyrosigma acuminatum var. *lacustre* Meist.**							+					
Gyrosigma attenuatum (Kütz.) Rabenh.						+						
Gyrosigma distortum (W. Sm.) Griff. & Henfr. var. *parkeri* Harr.**	+					+						
Gyrosigma fasciola (Ehrenb.) Cleve**				+								+
Gyrosigma Hassall sp. 1			+	+		+	+					
Gyrosigma Hassall sp. 2	+	+	+	+								
Melosira varians C. Agardh	+	+	+				+					
Melosira C. Agardh sp. 1		+		+		+			+	+		+
Meridion circulare C. Agardh						+						
Navicula cuspidata Kütz.		+				+	+					
Navicula cuspidata var. *ambigua* (Ehrenb.) Grunow						+	+					
Navicula gastrum (Ehrenb.) Kütz.												+
Navicula gracilis Ehrenb.	+	+	+	+	+	+	+					
Navicula gregaria Donk.						+	+					
Navicula helensis Schulz**											+	+
Navicula menisculus Schum. var. *menisculus* Hust.**	+		+									
Navicula oblonga (Kütz.) Kütz.		+				+	+					+
Navicula pupula Kütz.						+			+	+		
Navicula pusilla W. Sm.**							+					
Navicula radiosa Kütz.	+	+	+			+	+					+
Navicula Bory sp. 1		+	+	+	+	+			+	+		
Neidium dubium (Ehrenb.) Cleve						+						+
Neidium Pfitzer sp. 1						+				+		
Nitzschia ovalis Arn.*						+						
Nitzschia scalaris (Ehrenb.) W. Sm.*												+
Nitzschia sigmoidea (Nitzsch) W. Sm.*	+	+	+		+	+	+	+				
Nitzschia vermicularis (Kütz.) Hantzsch*	+	+	+			+						
Nitzschia Hassall sp. 1					+	+						
Pinnularia major (Kütz.) Rabenh.		+								+		+
Pinnularia microstauron (Ehrenb.) Cleve	+			+								
Pinnularia viridis (Nitzsch) Ehrenb.						+						
Pinnularia Ehrenb. sp. 1						+	+			+		
Pleurosigma angulatum (Quek.) W. Sm.		+	+									
Pleurosigma W. Sm. sp. 1			+									
Rhizosolenia (Ehrenb.) Brightwell sp. 1*							+					
Rhoicosphenia curvata (Kütz.) Grunow ex Rabenh.						+		+				
Rhopalodia gibba (Ehrenb.) O. F. Müll.	+	+		+					+	+	+	+
Rhopalodia gibba var. *parallela* (Grunow) H. & M. Perag.												+
Stauroneis parvula var. *prominula* Grunow**							+					
Stauroneis Ehrenb. sp. 1						+	+	+		+		+
Staurosira construens Ehrenb.		+	+	+	+	+	+	+	+	+	+	+
Staurosira construens f. *subsalina* (Hust.) Bukht.**										+		+
Stephanodiscus Ehrenb. sp. 1**			+									
Surirella angustata Kütz.		+	+									
Surirella bifrons Ehrenb.		+	+									
Surirella biseriata Bréb.	+	+	+									

Table 5. (*continued*)

Taxa	Lake Modro Oko				Lake Desne				Lake Kuti			
	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A
Surirella capronii Bréb.			+									
Surirella elegans Ehrenb.	+	+										
Surirella gracilis Grunow**		+										
Surirella linearis W. Sm.							+					
Surirella minuta Bréb.			+									
Surirella ovalis Bréb.**						+						
Surirella spiralis Kütz.					+	+						
Surirella striatula Turp.**						+	+					
Surirella tenera Greg.	+											
Surirella Turp. sp. 1	+	+		+		+	+					
Synedra capitata Ehrenb.			+	+			+		+	+	+	+
Tabellaria fenestrata (Lyngb.) Kütz.						+	+		+	+	+	
Tabellaria fenestrata var. *asterionelloides* Grunow						+						

W, winter; Sp, spring; Su, summer; A, autumn; * – planktonic taxa,** – new diatom records for Croatia.

Table 6. Number of diatom taxa in the lakes (1994–1995, 1997–1998)

Lakes	Total	W	Sp	Su	A
Lake Modro Oko	74	31	50	49	31
Lake Desne	88	21	66	56	18
Lake Kuti	53	17	35	20	36

W, winter; Sp, spring; Su, summer; A, autumn.

Table 7. List of diatom taxa found only in particular seasons

Winter	Spring	Summer	Autumn
Surirella tenera	*Aneumastus tuscula*	*Caloneis amphisbaena* var. *subsalina*	*Asterionella* sp. 1
	Bacteriastrum sp. 1	*Chaetoceros* sp. 1	*Caloneis silicula*
	Caloneis silicula var. *peisonis*	*Coscinodiscus lacustris*	*Cymbella hustedtii*
	Diatoma vulgaris var. *capitulata*	*Cyclotella comta*	*Diatoma elongatum*
	Diploneis smithii	*Cymbella amphicephala*	*Eunotia monodon* var. *maior*
	Eunotia exigua	*Cymbella pusilla*	*Gyrosigma fasciola*
	Eunotia lunaris	*Diatoma hiemalis*	*Navicula gastrum*
	Eunotia monodon	*Diploneis oculata*	*Nitzschia scalaris*
	Fragilaria sp. 1	*Epithemia muelleri*	*Rhopalodia gibba* var. *parallela*
	Gyrosigma attenuatum	*Epithemia adnata*	
	Meridion circulare	*Fragilaria acus*	
	Neidium sp. 1	*Gomphonema subtile*	
	Nitzschia ovalis	*Gyrosigma acuminatum* var. *lacustre*	
	Pinnularia viridis	*Navicula pusilla*	
	Surirella gracilis	*Pleurosigma* sp. 1	
	Surirella ovalis	*Rhizosolenia* sp. 1	
	Tabellaria fenestrata var. *asterionelloides*	*Stauroneis parvula* var. *prominula*	
		Stephanodiscus sp. 1	
		Surirella capronii	
		Surirella linearis	
		Surirella minuta	

In our study, the most abundant and frequent taxa were *Cyclotella striata*, *Fragilaria ulna* and *Asterionella formosa*. Oligotrophic and mesotrophic lakes as defined by OECD (1982) are mainly characterised by higher abundance of *Cyclotella* and *Fragilaria* species, whereas eutrophic lakes are characterised by generally higher abundance of *Asterionella formosa* (cf. Lotter, 2001). The latter species is taxonomically complex, and it might be possible that genetic difference exists among populations of *Asterionella* from different lakes (Pappas & Stoermer, 2001; Soudek & Robinson, 1983).

A range of factors naturally can be expected to affect diatom development in these lakes. These may include dispersal in these highly mixed habitats (Dieckmann, O'Hara, & Weisser, 1999); variations in important abiotic parameters (e.g. trace elements, dissolved organic matter) not measured in this study; and differences in lake morphology that affect the thermal regime and nature of nutrient cycling. The impact of herbivores, including selective grazing by zooplankton, also cannot be ignored in controlling diatom growth (Karjalainen, Holopainen, & Huttunen, 1996; Muck & Lampert, 1984). All of these mechanisms likely are at work to some degree in these lakes, but at this initial stage of our studies we are unable suggest which might be most influential in controlling the composition of diatom communities.

In the present study, the results clearly showed predominance of benthic taxa. Others have commented on the bulk of tychoplanktonic taxa – which include not only true plankton, but also benthic taxa – in shallow freshwater ecosystems (cf. de Almeida & Gil, 2001; Padisák, Tóth, & Rajczy, 1988).

The importance of wind-induced resuspension of bottom sediments on phytoplankton production is well recognized in lakes (Hameed, 2003; McQuoid & Godhe, 2004; Schelske, Carrick, & Aldridge, 1995), and conditions in these relatively shallow lakes certainly make them susceptible to sediment resuspension. Submerged macrophytes also have an effect on the taxonomic composition of diatoms (Mann & Droop, 1996). Macrophytes provide a suitable substrate for epiphytic diatoms in oligotrophic karstic Plitvice Lakes, Croatia (Caput & Plenković-Moraj, 2000).

Our results agree well with those of Laugaste and Pork (1996) from Lake Peipsi-Pihkva, a shallow lake in Estonia, where the littoral planktonic diatoms are much more closely related to the ambient phytobenthos and epiphyton than to the plankton communities farther offshore. In addition, *Asterionella*, *Bacillaria*, *Fragilaria*, *Melosira*, and *Tabellaria* were the most frequent planktonic taxa in these Croatian and Estonian lakes. The planktonic genera *Rhizosolenia*, *Chaetoceros*, and *Bacteriastum*, when found in the lakes, indicate the influence of seawater from Adriatic Sea. According to the salinity classification of van Dam, Mertens, and Sinkeldam (1994), the lakes are dominated by fresh to brackish-freshwater diatoms. The diatom taxa in all of the lakes belong to a group of oligohalobes (Strelnikova & Lastivka, 1999).

The genera *Surirella*, *Navicula*, *Cymbella*, *Eunotia*, *Gyrosigma*, *Fragilaria*, *Gomphonema*, and *Epithemia* were the richest in taxa. A similar diatom community was reported for karstic freshwaters from northern (Caput & Plenković-Moraj, 2000) and southern Croatia (Plenković-Moraj & Jasprica, 2000); in the hinterland of neighboring Bosnia and Herzegovina (cf. Jerković, 1978); and in other temperate regions (cf. de Almeida, 2001; Krammer & Lange-Bertalot, 1986,1988; Sala, 1996a, b). *Navicula* includes taxa with a very wide ecological range (Krammer & Lange-Bertalot, 1991b), while most of those belonging to *Cymbella* are indicative of water rich in oxygen and poor in organic nitrogen (van Dam et al., 1994). In the epiphyton, the genus *Cymbella* is characteristic of stony substrates (de Almeida & Gil, 2001; Rakaj, Hindák, & Hindáková, 2000); *Epithemia* and *Gomphonema*, of plant surfaces (Wojtal, 2003). The use of a plankton mesh less than 55 μm probably would have collected additional diatom taxa. Clearly, further studies on benthic diatom communities are required to increase the accuracy of predictions.

Without an adequate base of historical information from which to draw confident comparisons, the 18 diatom taxa and one genus recorded here for the first time in Croatia must be attributed to the recent increase in sampling activity, rather than to any environmental changes.

These present findings contribute essential base-line information that should aid in evaluating the state of these lakes in the future.

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