RESEARCH PAPER

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Relationships between benthic diatom assemblages' structure and selected environmental parameters in Slovak water reservoirs (Slovakia, Europe)

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Received February 29, 2016 – Revised April 8, 2016 – Accepted April 21, 2016

Abstract – The main objective of the present study is to describe the structure of benthic diatom communities in 23 water reservoirs in Slovakia classified as heavily modified water bodies. Environmental variables together with biological data obtained during the routine biomonitoring of water reservoirs in Slovakia were explored and analysed to understand variability of benthic diatom communities and their relationships with environmental variables in order to obtain an integrated knowledge about their relevance as bioindicators for the Water Framework Directive-compliant ecological potential assessment. This study summarizes results from a four-year monitoring programme of water reservoirs surveyed during the period of 2011–2014. The performed survey and statistical analyses revealed the following: (i) two main groups of reservoirs could be distinguished based on the purpose of their main use (multipurpose or drinking water-supply use); (ii) multipurpose and drinking water-supply reservoirs differed in benthic diatom community structure, diatom water quality indices as well as in the principal environmental gradients structuring the diatom communities; (iii) 5 distinct sub-groups of reservoirs could be identified differing in terms of diatom species composition and several environmental parameters; (iv) the most significant environmental variables in explaining differences in diatom species composition in multipurpose reservoirs were mean depth and mean annual flow; in drinking water-supply reservoirs conductivity and water transparency.

Key-words: benthic diatom / phytobenthos / water reservoir / Slovakia / Water Framework Directive

Résumé – Les relations entre la structure des assemblages de diatomées benthiques et certains paramètres environnementaux dans les réservoirs slovaques (Slovaquie, Europe). L'objectif principal de la présente étude est de décrire la structure des communautés de diatomées benthiques dans 23 réservoirs en Slovaquie classés comme masses d'eau fortement modifiées. Les variables environnementales ainsi que des données biologiques obtenues au cours de la biosurveillance de routine des réservoirs en Slovaquie ont été explorées et analysées afin de comprendre la variabilité des communautés de diatomées benthiques et leurs relations avec les variables environnementales et d'obtenir une connaissance intégrée sur leur pertinence comme bioindicateurs pour la directive cadre sur l'eau – conforme à l'évaluation du potentiel écologique. Cette étude résume les résultats d'un programme de suivi de quatre ans des réservoirs au cours de la période 2011–2014. Le suivi effectué et les analyses statistiques ont révélé : (i) deux principaux groupes de réservoirs peuvent être distingués en fonction du but de leur utilisation principale (polyvalente ou d'approvisionnement en eau potable) ; (ii) les réservoirs à usages multiples et d'alimentation en eau potable différaient dans la structure des communautés de diatomées benthiques, aussi bien les indices diatomée de qualité de l'eau, que les principaux gradients environnementaux qui structurent les communautés de diatomées ; (iii) 5 sous-groupes distincts de réservoirs pourraient être identifiés différant en termes de composition des espèces de diatomées et de plusieurs paramètres environnementaux ; (iv) les variables environnementales les plus importantes dans l'explication des différences dans la composition des espèces de diatomées dans les réservoirs polyvalents étaient la profondeur moyenne et débit moyen annuel ; dans les réservoirs d'alimentation en eau potable la conductivité et la transparence de l'eau.

Mots-clés : diatomée benthique / phytobenthos / réservoir / Slovaquie / directive cadre sur l'eau

1 Introduction

The main objective of the Water Framework Directive (WFD, The European Parliament and European Council, 2000) is to implement measures to achieve “good ecological status” of all natural water bodies. A specific group of water bodies are “Heavily Modified Water Bodies” (HMWB), which due to the hydromorphological changes, are substantially changed in nature and therefore can not achieve good ecological status. HMWB are therefore required to achieve “good ecological potential” (CIS WG 2A Ecological Status, 2003). In Slovakia the HMWB are classified into two groups: “rivers” and “rivers with changed category” (Ministry of Environment of the Slovak Republic, 2011), which comprises a total of 23 man-made water reservoirs (CIS WG 2.2 HMWB, 2003).

In order to determine the ecological potential, member states of the European Union (EU) are required to develop assessment methods at the national level for all relevant biological quality elements (BQEs). Suitability of the various BQEs as bioindicators of the ecological potential needs to be tested and confirmed. In this light, it is necessary to determine which environmental parameters affect the communities’ structure.

BQEs applied in the assessment of ecological potential should be, among others, able to reflect hydromorphological changes. In general, benthic diatoms are not expected to respond to hydromorphological alterations directly, although some studies confirm weak and indirect response of specific metrics to hydromorphology (Jüttner *et al.*, 2003; Hering *et al.*, 2006; Dahm *et al.*, 2013). Nevertheless, hydromorphological alterations affect a whole scale of ecological conditions by changing water retention, water current, turbidity, substrate heterogeneity and riparian structure, which in result involve changes in nutrient and organic matter cycling (Jenkins and Boulton, 2003; Moss, 2008; Cron *et al.*, 2015). Therefore it is presumed, that phytobenthos could secondarily reflect impacts of hydromorphological changes in water ecosystems.

Macrophytes and phytobenthos are treated together in WFD as one of the BQEs that are required to be included in WFD-compliant assessment of both ecological status of natural lakes and ecological potential of water reservoirs. Nevertheless, most of the national assessment systems of ecological status of lakes around Europe adopted separate assessment systems for macrophytes and phytobenthos (Birk *et al.*, 2010; Kelly *et al.*, 2014a). For phytobenthos, the majority of European countries apply benthic diatoms as proxies in ecological status assessment of lakes due to their cost-effective and sufficiently exact contribution (see Kelly *et al.*, 2008a).

Benthic diatoms are one of the key indicator groups for WFD-compliant ecological status assessment of running waters in Europe (*e.g.* Kelly and Whitton, 1995; Kelly *et al.*, 2008b; Rimet, 2012). Similarly, in Slovakia, benthic diatoms proved to be valuable bioindicators of the ecological status assessment of running waters (Hlúbiková *et al.*, 2007). Use of benthic diatoms in ecological status assessment of standing waters on routine basis, represented by natural lakes and also man-made reservoirs, is less common, even though, benthic

diatoms proved to serve as valuable indicators also in standing waters in many European regions, especially with regard to eutrophication (Hofmann, 1994; King *et al.*, 2000; Kitner and Pouličková, 2003; Blanco *et al.*, 2004; Pouličková *et al.*, 2004; Schaumburg *et al.*, 2004; Ács *et al.*, 2005; Stenger-Kovács *et al.*, 2007; Jüttner *et al.*, 2010; Novais *et al.*, 2012; Bennion *et al.*, 2014; Cantonati and Lowe, 2014; De Nicola and Kelly, 2014; Kelly *et al.*, 2014a; Pouličková *et al.*, 2014). Despite their promising bioindicative potential in European lentic ecosystems, only a few countries have produced diatom-based WFD-compliant assessment systems for these habitats (Kelly, 2013) and there are very few studies focusing on the evaluation of ecological potential assessment of reservoirs based on benthic diatoms (Novais *et al.*, 2012). Different diatom metrics have been developed and tested for purposes water quality assessment in rivers (Coste in Cemagref, 1982; Lecoite *et al.*, 1993; Kelly and Whitton, 1995; Lenoir and Coste, 1996; Rott *et al.*, 1997, 1999; Lecoite *et al.*, 1999), which are widely being applied in rivers of different European regions (Almeida, 2001; Ács *et al.*, 2004; Vilbaste, 2004; Hlúbiková *et al.*, 2007; Hlúbiková, 2010; Kelly, 2013). Applicability of diatom indices originally developed for rivers was proved also in lakes and reservoirs (Kitner and Pouličková, 2003; Blanco *et al.*, 2004; Bolla *et al.*, 2010; Jüttner *et al.*, 2010; Cellamare *et al.*, 2012; Novais *et al.*, 2012; Kahlert and Gottschalk, 2014). However, there are several diatom indices developed specifically for lakes (Hofmann, 1994; Ács, 2007; Sgro *et al.*, 2007; Stenger-Kovács *et al.*, 2007; Bennion *et al.*, 2014), but their use in routine monitoring is less frequent.

Benthic diatom communities in standing waters are influenced by various environmental parameters, which differ within geographical regions, *e.g.* abiotic spatial factors and catchment variables as landuse and hydromorphology (Gottschalk and Kahlert, 2012), physical and chemical quality of substratum (Kitner and Pouličková, 2003; Michelutti *et al.*, 2003; Pouličková *et al.*, 2003, 2004; King *et al.*, 2006; Ács *et al.*, 2007; Bolla *et al.*, 2010), light conditions (Kelly *et al.*, 1998; King *et al.*, 2006), seasonality (King *et al.*, 2002, 2006; Bolla *et al.*, 2010; Rimet *et al.*, 2015), water chemistry (Hofmann, 1994; King *et al.*, 2000; Schönfelder *et al.*, 2002; Kitner and Pouličková, 2003; Blanco *et al.*, 2004; Ács *et al.*, 2005; Stenger-Kovács *et al.*, 2007; Jüttner *et al.*, 2010; Gottschalk and Kahlert, 2012) and also other groups of organisms, such as indirect effect of fish (Blanco *et al.*, 2008).

Benthic diatoms in Slovakia are well documented for running waters (Hlúbiková *et al.*, 2007, 2010; Hlúbiková, 2010). On the contrary, only few local studies were made on diatoms in standing waters, *e.g.* in glacial mountain lakes in Northern Slovakia (Štefková, 2006) and several gravel pits in Western Slovakia (Hindák and Hindáková, 2003, 2005). Until recently, benthic diatoms in large water reservoirs were never in focus of research activities. Many of these reservoirs have similar ecological conditions as natural lakes (Baláži *et al.*, 2014), so it is assumed that similar methods could be applied to assess their ecological potential.

For the above mentioned reasons, benthic diatoms were studied in the main water reservoirs in Slovakia in order to (1) explore and describe their assemblages (in terms of species); (2) identify the most important environmental parameters that

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Fig. 1. Distribution of the examined reservoirs in Slovakia.

drive their structure; and to (3) select and compare applicability of different diatom metrics in the selected reservoirs. These data will serve for further testing of bioindicative properties of benthic diatoms in Slovak reservoirs for purposes of ecological potential assessment of HMWB in Slovakia, respecting the requirements of the WFD.

2 Materials and methods

2.1 Study area

In total, 23 water reservoirs on various watercourses, all belonging to the Slovak Danube River basin, were selected for this study (Figure 1). These reservoirs are all assigned as heavily modified water bodies and defined as “rivers with changed category” according to the Ministry of Environment of the Slovak Republic (2011). Such categorization means that their character, due to changes caused by human activity, has changed from running to more or less standing water. The reservoirs studied are distributed throughout the whole country and were all constructed in the second half of the last century (Abaffy *et al.*, 1979). Their character is in most cases close to natural lakes, and the water level fluctuations do not exceed 2 m per year (Baláži *et al.*, 2014). The reservoirs are separated into two main groups, based on their usage: multipurpose (1) or drinking water-supply (2). The purpose of construction of multipurpose reservoirs (1) was hydroelectric power production, but they also serve as flood protection, as well as for irrigation, water supply, fishing and recreation purposes. All the drinking water-supply reservoirs (2) were built mainly as drinking water sources and partly as protection areas against floods.

The examined reservoirs represent a wide range of ecological conditions. The multipurpose reservoirs (1) are much more diverse in their environmental characteristics compared to the rather uniform group of the drinking water-supply reservoirs (2). Altitude of multipurpose reservoirs varies from 117.1

to 786.1 m a.s.l. with Palcmanšská Maša reservoir being the highest located reservoir in this group. The mean depth in this group of reservoirs is also very variable and ranges from 3.1 to 28.0 m, eleven reservoirs from this group belong to shallow reservoirs with a mean depth of less than 8.5 m. The catchment of multipurpose reservoirs has higher agricultural and urbanization exploitation in comparison to the group of drinking water-supply reservoirs (2). All reservoirs studied (except for two, *e.g.* Kráľová and Slňava), have long retention time, mostly longer than one month up to two years (Table 1). All drinking water-supply reservoirs (2) are deep with mean depth of more than 11.3 m in contrast to their small surface area; are located in medium to high altitude (more than 343 m a.s.l.) and have high percentage of forestry in their catchment (Table 1).

2.2 Sampling and laboratory analyses

2.2.1 Benthic diatoms

Benthic diatoms were sampled in the period from 2011 to 2014 following the standards for sampling in running (CEN, 2003) and standing waters (King *et al.*, 2006) within the Framework Monitoring Programme of Slovakia (Gajdová *et al.*, 2010, 2011; Škoda *et al.*, 2012; Danáčová *et al.*, 2014) focused on the assessment of ecological status and ecological potential. Diatom samples from drinking water-supply reservoirs were collected in 2011, 2013 and 2014; multipurpose reservoirs were sampled in 2012, 2013 and 2014. Samples were collected twice a year in 2013 and 2014 (spring and autumn) or three times a year in 2011 and 2012 (spring, summer and autumn). Despite the recommendations of King *et al.* (2006) that one sampling point is sufficient for purposes of practical diatom-based monitoring and due to the large size of the reservoirs studied, more sampling points were chosen in each reservoir. Numbers of sampling points at each

Table 1. Hydromorphological and geographical parameters of the studied reservoirs; mp – multipurpose reservoirs, dws – drinking water-supply reservoirs.

No.	Reservoir name	Abbrev.	Main aim of usage	Altitude (m a.s.l.)	Surface area (10 ⁶ m ²)	Max. volume (10 ⁶ m ³)	Mean depth (m)	Mean annual flow (m ³ s ⁻¹)	Retention time (day)	Urbanization (%)	Agriculture (%)	Forestry (%)	Latitude (N) (° ' ")	Longitude (E) (° ' ")
1	Orava	ORA	mp	601.5	33.5	326.5	10.0	21.7	187.0	3.8	49.2	47.0	49 22 33	19 33 25
2	Liptovská Mara	LMAR	mp	564.9	21.7	361.9	17.2	27.8	136.0	5.1	41.2	53.8	49 05 49	19 29 10
3	Palmianská Maša	PALC	mp	786.1	0.9	10.4	13.0	1.6	88.0	0.6	7.0	92.4	48 51 20	20 23 02
4	Ružín	RUZ	mp	327.6	3.9	52.0	28.0	17.4	36.0	3.0	12.7	84.4	48 51 40	21 05 26
5	Veľká Domaša	DOM	mp	163.5	15.0	178.3	18.0	7.7	210.0	4.0	34.9	61.2	49 00 03	21 41 50
6	Kunov	KUN	mp	229.1	0.6	3.1	3.8	0.6	42.0	3.2	72.8	24.0	48 42 10	17 24 16
7	Budmerice	BUD	mp	191.5	0.7	1.2	5.5	0.3	47.5	3.1	12.2	84.7	48 22 27	17 23 19
8	Nitrianske Rudno	NRUD	mp	321.6	0.8	3.6	4.9	1.6	18.9	1.8	23.7	74.5	48 48 10	18 29 02
9	Môťová	MOT	mp	302.6	0.7	2.4	4.0	3.4	7.0	2.6	18.0	79.5	48 33 46	19 09 47
10	Ružiná	RZA	mp	255.0	1.7	14.5	8.5	0.2	671.0	5.5	36.9	57.6	48 26 10	19 34 10
11	L'uboreč	LUB	mp	232.3	0.7	3.3	5.0	0.3	113.0	0.9	40.3	58.8	48 17 19	19 31 06
12	Teplý Vrch	TEPV	mp	218.8	1.0	3.0	3.8	0.5	68.0	0.4	30.9	68.7	48 28 20	20 05 46
13	Petrovce	PET	mp	243.4	0.6	2.1	3.7	0.2	149.0	4.6	59.9	35.4	48 10 56	20 00 17
14	Zemplínska Šírava	ZSIR	mp	117.1	32.9	324.9	8.5	15.4	40.0	6.7	28.5	64.9	48 45 51	21 57 46
15	Šliava	SLN	mp	158.1	4.1	12.5	3.1	149.3	0.3	11.7	50.8	37.5	48 32 38	17 49 05
16	Kráľová	KRA	mp	124.0	10.9	65.5	6.0	152.0	1.7	12.8	73.9	13.3	48 11 28	17 49 44
17	Hríňová	HRI	dws	565.2	0.6	7.3	13.1	0.9	87.0	0.0	13.8	86.1	48 35 54	19 32 22
18	Málinec	MAL	dws	345.5	1.5	25.1	17.0	0.9	267.0	0.4	35.6	64.0	48 31 11	19 39 52
19	Klenovec	KLE	dws	377.3	0.7	7.5	11.3	0.9	84.0	0.0	23.3	76.7	48 36 25	19 52 37
20	Bukovec	BUK	dws	417.8	1.0	21.8	24.0	0.6	386.0	1.4	6.8	91.9	48 43 01	21 07 41
21	Nová Bystrica	NBY	dws	598.5	1.8	29.9	17.1	1.3	278.5	0.0	22.3	77.7	49 20 31	19 02 25
22	Starina	STA	dws	343.0	3.1	57.0	22.0	1.6	283.0	0.0	10.2	89.8	49 02 33	22 15 29
23	Turček	TUR	dws	775.3	0.6	9.4	20.4	0.8	159.5	0.0	0.7	99.3	48 45 47	18 56 10

reservoir varied from two to four depending on the reservoir size and complexity. In large and/or structured reservoirs, 4 sub-samples were taken (*e.g.* Orava, Liptovská Mara, Ružín, Vel'ká Domaša and Zemplínska Šírava), in smaller, but structured reservoirs, 3 sub-samples were taken (*e.g.* Ružiná, Sĺňava, Kráľová, Hriňová, Málinec and Starina) and in remaining smaller and unstructured reservoirs, 2 sub-samples were taken. The sampling points for different sub-samples occurred in similar environmental conditions and they were selected far from inflow streams or obvious anthropogenic influence, in areas with free exchange of water with the main basin. In order to reduce variability among reservoirs and to eliminate the effect of water level fluctuation, use of artificial substrata was tested in both types of reservoirs. Despite the careful selection of sampling sites in each reservoir, only drinking water-supply reservoirs provided safe conditions for artificial substrata exposure avoiding losses or damages due to vandalism. Diatoms from multipurpose reservoirs were therefore collected from hard natural stony substrata from the littoral zone. Artificial substrata were used for diatom sampling in all drinking water-supply reservoirs, where natural stony substrata were lacking or were hardly accessible. Rough stony tiles with dimensions of 10 × 10 cm were applied as artificial substrata. The substrata were positioned vertically in the littoral zone for at least 4 weeks. All sampling points were selected in well exposed euphotic zone and diatoms were scrubbed from the substrate using a toothbrush. Diatom samples were preserved with formaldehyde to final concentration of approximately 4% and stored until further treatment. Hot hydrogen peroxide method was applied to remove organic material from field samples according to CEN (2003). Treated diatom suspensions were mounted on slides using Naphrax[®]. Subsequently, diatoms were identified under a light microscope equipped with differential interference contrast (DIC, Zeiss Axio Scope.A1 with the total magnification 1000×, oil immersion objective) to the lowest possible level according to CEN (2004). Approximately 400 diatom valves were counted on each slide and the taxa counts were expressed in relative abundances. The identification was primarily based on Krammer and Lange-Bertalot (1986), Lange-Bertalot and Krammer (1989), Krammer and Lange-Bertalot (1991), Krammer (1997a, b), Krammer and Lange-Bertalot (2000), Lange-Bertalot (2001), Krammer (2002), Krammer and Lange-Bertalot (2007), Levkov (2009) and other relevant identification guides and scientific papers.

2.2.2 Physico-chemical variables

Fourteen physico-chemical variables were measured monthly in each of the reservoirs from April to September in the period from 2011 to 2014: pH, dissolved oxygen (O₂), water temperature (*t*), conductivity (cond), biological oxygen demand after 5 days (BOD), chemical oxygen demand (COD), ammonium nitrogen (NH₄-N), nitrate nitrogen (NO₃-N), total nitrogen (TN), total phosphorus (TP), orthophosphate phosphorus (PO₄-P), alkalinity (alk), chlorophyll *a* (ch-*a*) and water transparency (transp) (Table 2). Spring samples were sampled from April to May, summer samples from June to July and autumn samples from August to September. Water samples

were taken from two hydrologically stable sampling points located in the central part of each reservoir, from the surface water layer. These sampling points were pre-defined according to Framework Monitoring Programme of Slovakia (Gajdová *et al.*, 2010, 2011; Škoda *et al.*, 2012; Danáčová *et al.*, 2014). Several variables, such as pH, dissolved oxygen, conductivity and water temperature, were measured in situ using a WTW MULTI 340i portable device; water transparency was measured using a Secchi disk. Water samples for chemical oxygen demand measurements were preserved with sulphuric acid. All samples were transported to the laboratory in a portable cooler at temperature of 3 ± 2 °C. Laboratory analyses were carried out by the staff of the Slovak Water Management Enterprise. Ammonium nitrogen was determined according to ISO (1984), nitrate nitrogen according to ISO (1988), total nitrogen according to ISO (1997), orthophosphate phosphorus and total phosphorus according to ISO (2004). Alkalinity was defined by volumetric analysis according to ISO (1994), biological oxygen demand after 5 days according to CEN (1998), chemical oxygen demand according to APHA, AWWA and WEF (2005) and chlorophyll *a* according to ISO (1992).

2.3 Statistical analyses

Environmental and species data were analysed using different multivariate analytical methods. Species with relative abundance below 3% were excluded from the statistical analyses. The normality of environmental data was tested with Shapiro-Wilk's test. Variables, which had a normal distribution (pH, dissolved oxygen, water temperature, conductivity, chemical oxygen demand, ammonium nitrogen, nitrate nitrogen, total nitrogen, alkalinity, water transparency and both percentage of agriculture and forestry), were not transformed. Urbanization data were log (*x* + 1) transformed and retention time was square root-transformed. The remaining environmental variables with skewed distribution were log-transformed. The species data were log (*x* + 1) transformed. The variability originated from differences in various scales of environmental parameters was minimized by standardization of vectors prior to the analyses. Pearson's correlations were applied to reveal the relationships between all environmental parameters and to detect possible multicollinearities of environmental parameters.

The environmental data structure and their relationships were explored by Principal Component Analysis (PCA, Goodall, 1954) based on all available 23 environmental variables (14 physico-chemical and 9 hydromorphological and geographical). The response of species to the environmental gradients, regardless of the measured parameters, was tested using Detrended Correspondence Analysis (DCA, Hill and Gauch, 1980). The length of the maximum gradient of the first two DCA axes was nearly 4 SD (3.820), which indicates that unimodal methods should be further applied for multivariate analysis of diatom assemblages. Correspondence Analysis (CA, Greenacre, 1984) was performed to reveal changes in diatom species composition in all examined reservoirs. Consequently, the Canonical Correspondence Analysis (CCA, ter Braak, 1986; ter Braak and Verdonschot, 1995) with forward selection of significant environmental variables was performed to

Table 2. Measured environmental parameters of the studied reservoirs; numbers of reservoirs are those used in Table 1; gr. - groups defined based on the results of CCA analyses.

No.	Gr.	pH	Dissolved oxygen (mg L ⁻¹)	Water temperature (°C)	Conductivity (mS m ⁻¹)	Biological oxygen demand (mg L ⁻¹)	Chemical oxygen demand (mg L ⁻¹)	Ammonium nitrogen (mg L ⁻¹)	Nitrate nitrogen (mg L ⁻¹)	Total nitrogen (mg L ⁻¹)	Total phosphorus (mg L ⁻¹)	Orthophosphate phosphorus (mg L ⁻¹)	Alkalinity (meq L ⁻¹)	Chlorophyll <i>a</i> (µg L ⁻¹)	Water transparency (m)
1	1	8.23 ± 0.29	8.7 ± 2.3	16.2 ± 4.6	22.5 ± 1.7	1.92 ± 0.67	4.98 ± 1.33	0.03 ± 0.02	0.55 ± 0.22	1.08 ± 0.22	0.02 ± 0.01	0.01 ± 0.01	1.92 ± 0.20	8.3 ± 5.9	2.8 ± 1.0
2		8.39 ± 0.33	9.1 ± 2.5	15.3 ± 4.3	24.6 ± 2.3	1.88 ± 0.60	4.75 ± 1.30	0.03 ± 0.02	0.55 ± 0.21	0.95 ± 0.20	0.03 ± 0.03	0.02 ± 0.01	1.91 ± 0.20	5.6 ± 3.2	3.3 ± 1.6
3		8.25 ± 0.33	9.9 ± 1.8	15.4 ± 4.3	27.9 ± 2.4	1.38 ± 0.66	11.58 ± 4.75	0.07 ± 0.07	0.76 ± 0.16	1.18 ± 0.31	0.02 ± 0.05	0.01 ± 0.00	2.84 ± 0.26	3.3 ± 2.0	2.8 ± 1.0
4		8.32 ± 0.39	10.1 ± 2.1	18.7 ± 4.8	34.1 ± 9.0	2.73 ± 1.70	19.87 ± 11.33	0.08 ± 0.07	1.23 ± 0.46	1.91 ± 0.61	0.06 ± 0.05	0.01 ± 0.02	2.62 ± 0.58	23.0 ± 37.2	1.6 ± 1.2
5		8.21 ± 0.29	9.7 ± 1.6	19.3 ± 4.7	34.9 ± 3.9	1.43 ± 0.53	15.93 ± 6.80	0.05 ± 0.04	0.90 ± 0.20	1.36 ± 0.49	0.02 ± 0.01	0.01 ± 0.01	2.91 ± 0.23	6.1 ± 2.7	2.0 ± 1.0
6	2	8.26 ± 0.20	10.3 ± 1.3	18.9 ± 5.4	48.8 ± 5.6	2.96 ± 1.41	14.39 ± 7.18	0.07 ± 0.08	1.47 ± 0.85	1.89 ± 1.10	0.05 ± 0.02	0.01 ± 0.00	3.63 ± 0.66	30.8 ± 29.1	0.7 ± 0.1
7		8.39 ± 0.42	8.8 ± 2.2	18.0 ± 4.9	36.0 ± 4.3	4.71 ± 2.16	23.17 ± 7.74	0.07 ± 0.06	0.78 ± 0.41	1.55 ± 0.87	0.14 ± 0.31	0.04 ± 0.04	2.18 ± 0.55	46.3 ± 43.4	0.9 ± 0.3
8		8.37 ± 0.35	9.7 ± 1.9	17.8 ± 4.3	33.8 ± 2.2	3.92 ± 2.32	11.97 ± 7.45	0.04 ± 0.02	0.62 ± 0.14	1.08 ± 0.39	0.06 ± 0.10	0.03 ± 0.01	3.03 ± 0.48	46.8 ± 67.4	1.2 ± 0.3
9		8.56 ± 0.81	9.6 ± 3.4	18.6 ± 4.7	19.9 ± 4.1	4.32 ± 1.75	19.81 ± 5.62	0.08 ± 0.08	0.97 ± 0.31	1.47 ± 0.48	0.14 ± 0.05	0.04 ± 0.03	1.26 ± 0.24	46.3 ± 30.1	0.6 ± 0.2
10		8.47 ± 0.49	8.6 ± 3.0	19.5 ± 4.9	25.2 ± 2.3	2.17 ± 0.79	11.58 ± 3.39	0.03 ± 0.02	0.91 ± 0.07	1.07 ± 0.20	0.03 ± 0.01	0.01 ± 0.01	1.65 ± 0.27	13.5 ± 11.4	1.8 ± 0.7
11	3	8.03 ± 0.60	8.3 ± 2.5	18.9 ± 4.6	14.0 ± 3.0	2.23 ± 0.76	9.84 ± 2.95	0.02 ± 0.01	0.90 ± 0.00	1.01 ± 0.06	0.04 ± 0.02	0.01 ± 0.01	1.00 ± 0.27	11.0 ± 8.1	1.3 ± 0.5
12		8.51 ± 0.40	9.8 ± 2.3	19.8 ± 4.4	31.2 ± 6.0	2.77 ± 1.38	10.36 ± 4.11	0.07 ± 0.21	0.90 ± 0.00	1.01 ± 0.06	0.04 ± 0.02	0.01 ± 0.01	2.35 ± 0.49	21.6 ± 23.8	1.4 ± 0.7
13		8.48 ± 0.23	9.8 ± 3.1	20.3 ± 4.5	55.8 ± 5.6	4.22 ± 1.26	20.61 ± 5.16	0.03 ± 0.04	1.00 ± 0.40	1.26 ± 0.50	0.07 ± 0.03	0.01 ± 0.01	4.23 ± 0.71	32.8 ± 23.2	0.9 ± 0.3
14		8.34 ± 0.35	9.6 ± 2.2	20.6 ± 4.5	25.3 ± 1.4	2.19 ± 1.71	21.50 ± 11.52	0.06 ± 0.05	0.44 ± 0.17	0.94 ± 0.49	0.07 ± 0.07	0.03 ± 0.03	2.26 ± 0.30	17.4 ± 47.0	1.9 ± 0.9
15		7.92 ± 0.24	7.9 ± 1.4	16.7 ± 4.4	37.6 ± 4.2	1.99 ± 0.63	9.92 ± 5.68	0.07 ± 0.03	1.10 ± 0.36	1.45 ± 0.28	0.07 ± 0.02	0.04 ± 0.01	2.81 ± 0.28	6.8 ± 6.1	1.3 ± 0.3
16	4	8.23 ± 0.35	8.4 ± 1.9	18.0 ± 4.6	38.2 ± 3.5	2.45 ± 0.88	9.76 ± 3.52	0.08 ± 0.07	0.91 ± 0.28	1.38 ± 0.27	0.07 ± 0.02	0.04 ± 0.01	2.86 ± 0.27	14.8 ± 9.3	1.2 ± 0.3
17		8.79 ± 0.94	10.7 ± 1.9	17.3 ± 4.5	8.4 ± 1.2	2.45 ± 1.34	11.10 ± 5.59	0.04 ± 0.02	0.80 ± 0.12	0.88 ± 0.21	0.02 ± 0.01	0.01 ± 0.00	0.44 ± 0.09	13.0 ± 9.7	2.0 ± 1.3
18		8.59 ± 0.80	10.2 ± 1.3	19.4 ± 4.3	8.9 ± 0.8	1.88 ± 0.76	8.64 ± 3.65	0.03 ± 0.02	0.81 ± 0.14	0.91 ± 0.29	0.02 ± 0.01	0.01 ± 0.00	0.49 ± 0.09	11.6 ± 11.7	2.1 ± 0.6
19		8.09 ± 0.70	10.1 ± 1.8	19.1 ± 4.2	11.1 ± 1.0	1.72 ± 0.67	7.43 ± 2.79	0.04 ± 0.02	0.82 ± 0.13	0.90 ± 0.20	0.03 ± 0.02	0.01 ± 0.00	0.80 ± 0.25	6.5 ± 5.3	2.5 ± 1.1
20		8.08 ± 0.40	9.5 ± 1.0	19.3 ± 4.2	10.9 ± 0.5	1.10 ± 0.48	9.06 ± 5.79	0.04 ± 0.03	0.83 ± 0.19	1.16 ± 0.28	0.03 ± 0.03	0.01 ± 0.00	0.56 ± 0.09	4.0 ± 3.3	4.2 ± 1.8
21	5	8.40 ± 0.21	9.4 ± 1.2	16.9 ± 4.4	22.0 ± 2.7	1.32 ± 0.35	4.28 ± 1.12	0.05 ± 0.22	0.40 ± 0.11	0.66 ± 0.10	0.01 ± 0.00	0.01 ± 0.00	2.10 ± 0.31	3.1 ± 0.3	2.4 ± 0.7
22		8.22 ± 0.28	9.7 ± 1.1	19.9 ± 4.6	20.5 ± 0.8	1.00 ± 0.35	11.71 ± 7.23	0.04 ± 0.02	0.91 ± 0.21	1.40 ± 0.43	0.01 ± 0.01	0.01 ± 0.00	1.96 ± 0.25	1.9 ± 0.8	2.6 ± 0.8
23		8.51 ± 0.43	10.3 ± 1.6	15.7 ± 4.9	8.6 ± 0.8	1.44 ± 0.49	4.43 ± 1.19	0.03 ± 0.02	0.66 ± 0.19	0.96 ± 0.16	0.01 ± 0.01	0.01 ± 0.00	0.59 ± 0.06	4.7 ± 3.9	5.0 ± 1.4

relate changes in diatom species composition to the particular environmental data and gradients. The significance of environmental variables was tested by Monte Carlo permutation test with 499 unrestricted permutations. After excluding the redundant variables, 16 environmental parameters were used in CCA analyses (altitude, mean depth, maximum volume, mean annual flow, retention time, both percentage of urbanization and forestry, dissolved oxygen, both biological and chemical oxygen demand, pH, conductivity, ammonium nitrogen, total phosphorus, total nitrogen and water transparency). CCA analysis was performed for multipurpose and drinking water-supply reservoirs separately in order to obtain a more detailed overview of the significant environmental gradients affecting the structure of benthic diatom communities. Based on the samples' distribution in the ordination space of the CCA, the reservoirs were assigned into different groups.

Kruskal-Wallis *H*-test was employed to test statistical differences in all 23 environmental variables among the CCA groups and to test seasonal differences in physico-chemical variables in the CCA groups. Box plots were used to compare the range of environmental parameters among the groups. Analysis of similarities (ANOSIM, Clarke, 1993) was applied to test significance of differences between *a priori* defined groups of samples, *e.g.* multipurpose vs. drinking water supply reservoirs; among groups resulting from CCA analyses and among groups *a priori* defined for different seasons, *e.g.* seasonal variability in multipurpose and drinking water-supply reservoirs and seasonal variability in groups resulting from CCA analyses. This method generates *R*, which varies from 0 (little separation among groups) to 1 (complete separation among groups). Statistical significance was tested using the Monte Carlo permutation test with 999 permutations and randomization procedure. Similarity percentages – species contributions analysis (SIMPER, Clarke and Gorley, 2006) was performed to define an average similarity within each group and average dissimilarity between pairs of pre-defined groups. This analysis also identifies the diatom species, which contributed the most to the similarity within each group. The Bray-Curtis similarity index was used as a distance measure. In this study, only species with average contribution to intra-group similarities of at least 5%, were considered to be indicator species.

For purposes of the PCA analysis, Kruskal-Wallis *H*-test and box plot diagrams, mean values of physico-chemical variables of all reservoirs measured from April to September in the years 2011 to 2014 were used. For the CCA analyses, mean values of physico-chemical variables measured only during two months prior to diatom sampling were applied. Diatom species data for all performed analyses were processed using their relative abundances. The PCA analysis, Kruskal-Wallis *H*-test and box plot diagrams were performed using the STATISTICA version 6.0 software (StatSoft Inc., 2001), DCA, CA and CCA analyses were performed with CANOCO version 4.5 for Windows package (ter Braak and Šmilauer, 2002) and both the ANOSIM and SIMPER analyses were performed using software PRIMER version 6 (Clarke and Gorley, 2006).

OMNIDIA version 5.5 (Lecointe *et al.*, 1993; Lecointe *et al.*, 1999) was used to calculate 13 diatom indices based on diatom taxalists with their relative abundances.

The following indices were calculated: Saprobic Index of Sládeček (SLA, Sládeček, 1986), Leclercq and Maquet Index (IDSE, Leclercq and Maquet, 1987), Schiefele Index (SHE, Steinberg and Schiefele, 1988; Schiefele and Schreiner, 1991; Schiefele and Kohmann, 1993), Trophic Diatom Index (TDI, Kelly and Whitton, 1995), Generic Diatom Index (GDI, Rumeau and Coste, 1988; Coste and Ayphassorho, 1991), Commission for Economic Community Index (CEE, Descy and Coste, 1991), Specific Pollution Sensitivity Index (IPS, Coste in CEMAGREF, 1982), Biological Diatom Index (IBD, Lenoir and Coste, 1996; Prygiel and Coste, 2000), Diatom Index Artois-Picardie (IDAP, Prygiel *et al.*, 1996), Eutrophication/Pollution Index-Diatom based (EPI-D, Dell'Uomo, 1996; Dell'Uomo, 2004), Swiss Diatom Index (DI-CH, Hürlimann and Niederhauser, 2002), Saprobic Index of Rott (SID, Rott *et al.*, 1997) and Trophic Index of Rott (TID, Rott *et al.*, 1999). Moreover, Lake Trophic Diatom Index (LTDI, Bennion *et al.*, 2014), developed for assessment of lakes in the UK, was calculated using DARLEQ version 2.0.0 (Kelly *et al.*, 2014b). Examined reservoirs were divided into two groups based on measured values of alkalinity for LTDI calculation. The first group was represented by reservoirs with mean alkalinity (200–1000 $\mu\text{eq L}^{-1}$), *e.g.* L'uboreč, Hřiňová, Klenovec, Málinec, Bukovec and Turček. The second group was represented by reservoirs with high alkalinity (above 1000 $\mu\text{eq L}^{-1}$) where all remaining reservoirs were included. All index values were transformed to the scale from 0 to 20.

Spearman's correlations were applied to reveal the relationships between environmental parameters and the diatom indices. Best correlating indices were further tested for sensitivity in distinguishing between different groups of reservoirs. Kruskal-Wallis *H*-test was employed to test statistical differences in selected diatom indices among the 5 CCA groups and box plots were used to compare the range of selected indices in the groups. These analyses were performed using the STATISTICA version 6.0 software (StatSoft Inc., 2001).

3 Results

A total of 381 diatom taxa (222 taxa in drinking water-supply reservoirs and 342 taxa in multipurpose reservoirs) were identified in 156 samples (49 samples from drinking water-supply reservoirs and 107 samples from multipurpose reservoirs) within the investigation period of 2011–2014. Only 152 diatom taxa (113 taxa in drinking water-supply reservoirs and 145 taxa in multipurpose reservoirs) reached the minimum abundance of 3% in at least one sample. In general, *Achnanthes minutissimum s.l.* was the most abundant and the most frequent species in the examined sites with 25.76% of average abundance and 82.69% of average frequency. The drinking water-supply reservoirs reached lower species diversity and were mainly dominated by *Achnanthes minutissimum s.l.* The multipurpose reservoirs had more heterogeneous species composition with several abundant and frequent species, still *Achnanthes minutissimum s.l.* was the most abundant taxon also in this group. Diatom species with mean relative abundance of at least 5% in at least one reservoir are listed in Table 3.

Table 3. List of diatom species (%) mainly responsible for intra-group similarities among five groups defined based on CCA analyses with contribution at least 5% and list of all diatom species (%) that reached a minimum relative abundance of 5% in at least one reservoir; numbers of reservoirs are those used in Table 1.

Taxon	CCA group					Reservoir																							
	1	2	3	4	5	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
<i>Achnanthidium affine</i> (Grunow) Czarnecki						0.5	0.6	4.2	2.8	0.8	0.1		0.2			0.3	0.2					0.1	1.6		0.2	7.3	2.6	0.4	
<i>Achnanthidium catenatum</i> (Břlý and Marvan) Lange-Bertalot	6.0					2.9	1.5	3.9	6.1	5.3	0.9	0.5	0.4	0.1		0.1	0.3	0.1	0.3		0.1	2.8	5.1	2.9	8.8	2.0	2.0	1.6	
<i>Achnanthidium eutrophilum</i> (Lange-Bertalot) Lange-Bertalot		7.6				0.9	4.8	0.4	6.0	3.2	4.4	5.5	2.4	1.5	5.1	3.0	2.5	4.3	3.3	1.7	1.3								
<i>Achnanthidium jäckii</i> Rabenhorst	12.0					4.6	4.0	5.7	6.6	9.0	0.4	0.1	0.7		1.2	0.8	1.6		0.8			0.4				4.5	0.4		
<i>Achnanthidium minutissimum</i> s. l. (Kützing) Czarnecki	26.2	88.1	57.7	63.4	13.1	13.4	8.1	10.5	9.9	6.6	8.5	0.1	4.7	2.8	2.9	0.2	1.9	0.6	0.6	61.5	69.6	59.0	55.6	35.9	46.6	44.1			
<i>Achnanthidium saprophilum</i> (H. Kobayasi and Mayama) Round and Bukhtiyarova	5.8					3.8	5.2	0.7	8.5	2.8	1.3	3.9	3.9	0.1	2.5	0.7	1.5	0.1	0.6	0.3	0.2								
<i>Amphora pediculus</i> (Kützing) Grunow						0.3	0.6	0.4	3.9	0.9	1.9	2.2	4.2	0.2	0.7	0.5	1.2	6.5	0.7	3.1	1.2								
<i>Asterionella formosa</i> Hassall						0.6	2.0	0.6	5.8	0.4	0.1		0.6		0.9		0.3		0.4	0.1		1.7	1.1	0.1	0.4		0.1	0.6	
<i>Brachysira neoexilis</i> Lange-Bertalot								0.3		0.2												0.1	4.4	6.3	8.2	4.6	4.0	1.4	
<i>Cyclotella wuellerichiana</i> Druart and Straub					10.9			0.5																		15.4	12.2		
<i>Cymbella affinis</i> Krammer						0.2	0.2	0.1	0.2									0.1					0.7	4.2	2.7	0.7	0.9	5.0	
<i>Cymbella excisa</i> var. <i>excisa</i> Kützing	5.1					2.3	1.7	0.3	1.3	5.3	3.2	4.5	2.6		2.7	0.5	2.9	4.3	2.8	3.3	4.1						0.2		
<i>Denticula tenuis</i> Kützing								7.9	0.1		0.1										0.1				0.3		0.1		
<i>Diatoma vulgare</i> Bory											0.3								0.1	4.0	2.0								
<i>Encyonema caespitosum</i> Kützing						3.5	2.4	0.4		1.3	2.1	2.6	7.8	0.1	1.3	7.4	1.9	1.6	0.6	1.4	2.0			1.2		0.2			
<i>Encyonema minutum</i> (Hilse in Rabenhorst) D.G. Mann						1.3	4.6	0.7		0.5	0.2	0.1	3.6	0.6	2.4	0.3		0.1				8.0	2.9	0.7	0.1	0.2	0.4	0.7	1.3
<i>Encyonema silesiacum</i> (Bleisch in Rabenhorst) D.G. Mann						2.9	8.9	3.7			0.1	0.3	1.1	1.3	1.6	1.3		0.1	0.6	1.7	0.4	0.7	0.5	0.2		0.5	0.3	0.5	
<i>Encyonopsis subminuta</i> Krammer and E. Reichardt		6.8				2.1	1.7	2.1	0.1	3.2	2.4	3.1	0.9		4.9	2.2	3.4	4.3	2.7				0.8	1.7	1.3	4.4	4.7	1.8	
<i>Eolimna minima</i> (Grunow) Lange-Bertalot						0.8	0.5	0.1	0.9	0.5	0.6	0.4	2.5	1.8	0.6	3.3	6.9	2.9	8.2	1.3	0.9		0.1				0.1		
<i>Epithemia sorax</i> Kützing									1.4		1.1					0.7	0.3	15.6	0.1										
<i>Fragilaria capucina</i> sp. complex						1.5	4.9		1.1		7.8	0.4			2.7	0.4	0.1								1.3		5.4		
<i>Fragilaria crotonensis</i> Kitton						1.1	4.8	0.3	9.0	3.5					9.7	0.1	0.1	1.8				6.8	2.2	1.4	4.0		2.9		
<i>Fragilaria pectinalis</i> (O.F. Müller) Lyngbye						4.6	0.7	0.1	0.3	1.3	4.2	0.6	2.6		6.3	2.2	3.2	3.1	1.0	0.6	1.9								
<i>Fragilaria vaucheriae</i> (Kützing) J.B. Petersen						1.0	1.7	0.3	0.8	0.8	5.9	0.7	1.7		0.3	2.8	0.6	1.0	8.2	2.7	0.9	3.6	0.3	0.1	0.2		0.1	0.1	
<i>Gomphonema tenocultum</i> Reichardt																									0.4	6.3			
<i>Navicula capitatoradiata</i> H. Germain						0.4	1.2	0.4	0.5	1.4	1.9	1.1	1.0	0.7	0.7	2.1	0.6	0.3	1.2	9.2	8.4			0.1					
<i>Navicula cryptotenella</i> Lange-Bertalot	6.0					1.2	0.4	0.3	1.6	1.3	1.9	1.8	2.0	0.1	2.6	0.9	0.6	1.5	2.5	6.7	8.7					0.7	0.7		
<i>Navicula novaesiberica</i> Lange-Bertalot																			9.6										
<i>Navicula reichertiana</i> Lange-Bertalot						0.5	0.7	0.1	0.2	1.6	1.8	1.5	1.4	0.1	0.3	0.8	0.1	0.2	2.8	2.6	7.4								
<i>Nitzschia amphibia</i> Grunow						0.8					2.1	0.4	0.5	0.9	0.4	16.1	0.5	0.4	0.8	0.4	0.1	4.3	5.6					0.1	
<i>Nitzschia dissipata</i> (Kützing) Grunow						1.2	1.7	0.2	1.2	4.3	1.4	0.8	2.4	0.2	0.6	0.2	0.9	0.4	5.0	1.7	4.7					0.1			
<i>Nitzschia fonticola</i> Grunow						0.9	1.9	0.5	5.9	1.1	0.4	0.4	2.4	11.5	1.0	0.8	0.9	1.0	0.8	5.0	4.4	0.2				0.1		0.1	
<i>Nitzschia inconspicua</i> Grunow						0.4	0.3	0.1	0.9	0.8	3.1	1.7	0.8	26.7	0.2	0.5	0.1	0.4	5.8	0.9	1.0		0.1						
<i>Nitzschia paleacea</i> (Grunow) Grunow in van Heurck						0.1	0.2		0.2			0.3	0.3	6.4	0.7	0.1	1.7	0.1	0.3	0.8	1.6								
<i>Nitzschia tabellaria</i> (Grunow) Grunow in Cleve and Grunow						0.3	3.4	0.5	1.1	0.3	0.3	1.6	6.0		0.6	1.5	1.3	1.0	0.7	0.3	0.2		0.1		0.1	0.3	0.2		
<i>Psammophilidium sacculum</i> (Carter) Bukhtiyarova and Round						0.6					13.0																		
<i>Pseudostaurastrum brevistriatum</i> var. <i>inflatum</i> (Pantocsek) B. Hartley	5.1					0.3	1.4	0.2		0.3	3.5	1.1			5.4	2.2	26.1	9.8	0.5	0.6	1.1						0.6		
<i>Pseudostaurastrum polonica</i> (Witak and Lange-Bertalot) E. Morales and Edlund									0.2			0.9				0.1	7.5		8.3										
<i>Pseudostaurastrum robusta</i> (Fussey) D.M. Williams and Round					12.2			2.8															1.8	0.8				14.1	
<i>Punctastria linearis</i> D.M. Williams and Round						0.7	0.3				0.1	0.2	1.1		0.5	18.6	3.7		1.1		0.1								
<i>Staurastrum venter</i> (Ehrenberg) Cleve and J.D. Möller								0.8			0.1				0.2	0.2	6.0				0.4							3.2	
<i>Staurastrella pinnata</i> (Ehrenberg) D.M. Williams and Round						0.4	0.4	14.6			0.7	1.6	4.3	0.3	10.1	1.3	0.3		1.8	0.6	0.7		0.1		0.1	0.1	0.1		
<i>Stephanodiscus minutulus</i> (Kützing) Cleve and J.D. Möller						1.4			0.1	0.8	0.3	1.3			0.2	9.6	0.3	0.3	0.5	0.9	0.1	0.1		0.2	0.1			0.1

Fig. 2. Principal Component Analysis (PCA) ordination diagrams showing distribution of the reservoirs along the first two axes based on the 23 environmental variables: (A) vectors – environmental variables; abbreviations of hydromorphological and geographical parameters are those used in Table 4; (B) full line – multipurpose reservoirs, dashed line – drinking water-supply reservoirs; abbreviations of reservoirs names are those used in Table 1.

The results of PCA performed only on environmental variables confirmed the different nature and environmental conditions in the two main groups of the studied reservoirs. The first two PCA axes allowed separation of reservoirs depending on the hydromorphological, geographical and physico-chemical variables (Figures 2A and 2B) and PCA axes 1 and 2 explained a total of 38.64 and 18.63% respectively, of the variance in the environmental data. The first axis represented mainly the pollution gradient (especially expressed by concentrations of total phosphorus, biological and chemical oxygen demand) against the gradients of water transparency and mean depth. This allowed separation of reservoirs particularly influenced by water degradation variables, which is the majority of multi-purpose reservoirs (*e.g.* Kunov, Petrovce, Budmerice, Môt'ová, Nitrianske Rudno, Teplý Vrch, L'uboreč, Ružiná and Ružín). Contrastingly, the positive part of the axis determined clear separation of clean unpolluted water reservoirs with high mean depth, located in high altitudes and with high water transparency, which are all the drinking water-supply reservoirs and one multi-purpose reservoir Pálcianská Maša. The second axis expressed differences in maximum volume, surface area and mean annual flow separating reservoirs with high values of all the previously mentioned variables (Orava, Liptovská Mara, Domaša, Zemplínska Šírava), which distributed on the negative side of the second axis. Location of Kráľová and Sĺňava reservoirs in ordination space was determined mainly by high mean annual flow and water degradation variables. The detected relationships were also confirmed by Pearson's correlations ($p < 0.05$, Table 4). The results showed strong negative relationships between altitude and organic pollution (biological oxygen demand, chemical oxygen demand), nutrients' loading (phosphates and nitrates), conductivity and both percentage of urbanization and agriculture. There was also close relationship between altitude and both percentage of forestry and water transparency. Both

Fig. 3. Correspondence Analysis (CA) ordination diagram showing distribution of the reservoirs based on diatom species composition; circles – multipurpose reservoirs, triangles – drinking water-supply reservoirs.

percentage of urbanization and agriculture were significantly related to conductivity and alkalinity.

Differences between multipurpose and drinking water-supply reservoirs were reflected also by diatom species composition (Figure 3, Table 5). ANOSIM analysis (with Global $R = 0.534$, $p < 0.001$) confirmed that the two groups of reservoirs differ significantly. Subsequently, SIMPER analysis affirmed that average dissimilarity between groups equaled 88.69% showing that species composition in drinking water-supply reservoirs is more homogeneous (average similarity = 50.90%) in contrast to more heterogeneous group of multipurpose reservoirs (average similarity = 18.23%) (Table 6).

In multipurpose reservoirs, 14 variables were identified as statistically significant in explaining the variance in species

Table 4. Pearson's correlations among environmental parameters ($p < 0.05$); alt – altitude, mean-depth – mean depth, area – surface area, volume – maximum volume, flow – mean annual flow, ret-time – retention time, urban – percentage of urbanization, agri – percentage of agriculture, forest – percentage of forestry.

	alt	mean-depth	area	volume	flow	ret-time	urban	agri	forest	O ₂	BOD	COD	pH	<i>t</i>	cond	NH ₄ -N	NO ₃ -N	TP	TN	alk	PO ₄ -P	ch-a	transp
alt	–	0.46	ns	ns	ns	ns	–0.52	–0.48	0.51	ns	–0.42	–0.57	ns	–0.72	–0.48	ns	–0.44	–0.50	–0.42	ns	–0.44	–0.42	0.73
mean-depth	0.46	–	ns	ns	ns	ns	ns	–0.56	0.55	ns	–0.61	ns	ns	ns	–0.45	ns	ns	–0.52	ns	ns	–0.52	–0.54	0.69
area	ns	ns	–	0.96	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	–0.45	ns	ns	ns	ns	ns	ns
volume	ns	ns	0.96	–	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	–0.48	ns	ns	ns	ns	ns	ns
flow	ns	ns	ns	–	ns	–	0.86	0.51	–0.59	–0.59	ns	ns	–0.42	ns	ns	ns	ns	ns	ns	ns	0.62	ns	ns
ret-time	ns	ns	ns	ns	ns	–	ns	ns	ns	ns	–0.43	ns	ns	ns	ns	–0.56	ns	–0.48	ns	ns	–0.53	ns	ns
urban	–0.52	ns	ns	ns	0.86	ns	–	0.65	–0.73	–0.64	ns	ns	ns	ns	0.52	ns	ns	ns	ns	0.46	0.67	ns	ns
agri	–0.48	–0.56	ns	ns	0.51	ns	0.65	–	–0.99	ns	ns	ns	ns	ns	0.59	ns	ns	ns	ns	0.53	ns	ns	–0.49
forest	0.51	0.55	ns	ns	–0.59	ns	–0.73	–0.99	–	0.45	ns	ns	ns	ns	–0.61	ns	ns	ns	ns	–0.54	ns	ns	0.49
O ₂	ns	ns	ns	ns	–0.59	ns	–0.64	ns	0.45	–	ns	ns	0.53	ns	ns	ns	ns	ns	ns	ns	–0.53	ns	ns
BOD	–0.42	–0.61	ns	ns	ns	–0.43	ns	ns	ns	ns	–	0.66	ns	ns	0.51	ns	ns	0.83	ns	ns	0.57	0.96	–0.72
COD	–0.57	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.66	–	ns	0.53	0.51	0.58	ns	0.71	0.58	0.42	ns	0.67	–0.62
pH	ns	ns	ns	ns	–0.42	ns	ns	ns	ns	0.53	ns	ns	–	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
<i>t</i>	–0.72	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.53	ns	–	ns	ns	ns	ns	ns	ns	ns	ns	–0.42
cond	–0.48	–0.45	ns	ns	ns	ns	0.52	0.59	–0.61	ns	0.51	0.51	ns	ns	–	0.46	0.45	ns	0.60	0.96	ns	0.47	–0.61
NH ₄ -N	ns	ns	ns	ns	ns	–0.52	ns	ns	ns	ns	ns	0.50	ns	ns	0.45	–	ns	0.57	0.63	0.42	0.50	ns	–0.43
NO ₃ -N	–0.44	ns	–0.45	–0.48	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.45	0.50	–	ns	0.80	ns	ns	ns	–0.48
TP	–0.50	–0.52	ns	ns	ns	–0.48	ns	ns	ns	ns	0.83	0.71	ns	ns	ns	0.61	ns	–	0.47	ns	0.82	0.81	–0.63
TN	–0.42	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.58	ns	ns	0.60	0.72	0.80	0.47	–	0.51	ns	0.43	–0.45
alk	ns	ns	ns	ns	ns	ns	0.46	0.53	–0.54	ns	ns	0.42	ns	ns	0.96	ns	ns	ns	0.51	–	ns	ns	–0.52
PO ₄ -P	–0.44	–0.52	ns	ns	0.62	–0.53	0.67	ns	ns	–0.53	0.57	ns	ns	ns	ns	0.51	ns	0.82	ns	ns	–	0.53	–0.47
ch-a	–0.42	–0.54	ns	ns	ns	ns	ns	ns	ns	ns	0.96	0.67	ns	ns	0.47	ns	ns	0.81	0.43	ns	0.53	–	–0.68
transp	0.73	0.69	ns	ns	ns	ns	ns	–0.49	0.49	ns	–0.72	–0.62	ns	–0.42	–0.61	–0.44	–0.48	–0.63	–0.45	–0.52	–0.47	–0.68	–

Table 5. Results of CA and CCA analyses showing the percentages of explained variability.

	CA		CCA			
	All reservoirs		Multipurpose reservoirs		Drinking water-supply reservoirs	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues	0.48	0.24	0.22	0.18	0.39	0.20
Variance of species data	11.4	5.7	6.0	5.2	16.6	8.6
Variance of species environment relations	–	–	20.1	17.1	33.0	17.1

Table 6. Results of ANOSIM and SIMPER analyses showing the differences between *a priori* defined groups, defining average similarity within each group and average dissimilarity between pairs of pre-defined groups; $n = 156$; sp – spring samples, su – summer samples, au – autumn samples.

Examined parameter	<i>A priori</i> defined groups	Average similarity (%)	Compared pairs of groups	Average dissimilarity (%)	ANOSIM statistical R	p	ANOSIM global R	p
Groups of reservoirs defined based on the main aim of usage	Multipurpose reservoirs	18.23	Multipurpose/ water-supply reservoirs	88.69			0.534	***
	Drinking water-supply reservoirs	50.90						
Groups of reservoirs defined based on the results of CCA analyses	group (1)	26.86	1/2	83.62	0.174	***	0.376	***
	group (2)	18.22	2/3	93.43	0.757	***		
	group (3)	58.87	1/3	79.94	0.557	***		
	group (4)	56.68	4/5	59.46	0.566	***		
	group (5)	52.75	1/4	77.93	0.324	**		
			1/5	79.50	0.321	**		
			2/4	91.91	0.656	***		
			2/5	92.63	0.681	***		
			3/4	54.43	0.451	***		
			3/5	51.51	0.315	*		
Seasonal variability in multi-purpose reservoirs	sp	17.48	sp/au	82.71	0.109	***	0.082	**
	su	17.72	sp/su	83.32	0.058	ns		
	au	20.53	su/au	80.25	0.033	ns		
Seasonal variability in drinking water-supply reservoirs	sp	50.27	sp/au	57.75	0.090	**	0.064	ns
	su	52.97	sp/su	51.90	0.070	ns		
	au	54.05	su/au	45.25	–0.026	ns		
Seasonal variability in group 1			sp/au		0.153	**	0.066	ns
			sp/su		–0.238	ns		
			su/au		0.016	ns		
Seasonal variability in group 2			sp/au		0.129	***	0.113	***
			sp/su		0.162	*		
			su/au		0.032	ns		
Seasonal variability in group 3			sp/au		0.133	*	0.123	ns
			sp/su		0.109	ns		
			su/au		0.119	ns		
Seasonal variability in group 4			sp/au		0.850	**	0.631	***
			sp/su		0.563	ns		
			su/au		–0.021	ns		
Seasonal variability in group 5			sp/au		0.074	ns	0.022	ns
			sp/su		0.111	ns		
			su/au		–0.333	ns

Fig. 4. Canonical Correspondence Analysis (CCA) ordination diagrams of multipurpose reservoirs showing the site distribution along the first two axes based on the relationships between species and environmental variables: (A) vectors – environmental variables, grey empty circles – samples from spring season, grey full circles – samples from summer season, black full circles – samples from autumn season; numbers of reservoirs are those used in Table 1; abbreviations of hydromorphological and geographical parameters are those used in Table 4; full line – group 1, dashed line – group 2; (B) codes of diatom taxa according to OMNIDIA version 5.5.

data ($p < 0.05$) and they altogether explained 10.7% of the species data variance. The most significant environmental variables explaining at least 1% each of variation in species composition were mean depth and mean annual flow. Based on the distribution of multipurpose reservoirs in the ordination space of CCA plot, the multipurpose reservoirs could be separated into two principal groups: 1 and 2 (Figure 4A). Results of performed CCA analysis are listed in Table 5.

Drinking water-supply reservoirs showed to be more uniform in variability of ecological conditions in comparison with the heterogeneous group of multipurpose reservoirs. A total of 13 variables were significantly related ($p < 0.05$) in explaining the variance of species data and they altogether explained 11.8% of the species data variance. Among these, conductivity and water transparency were the most significant parameters that explained each more than 1% of the variance in species data. Despite the data homogeneity, three groups of reservoirs could be defined from the sites distribution in the ordination space of the CCA plot: 3, 4 and 5 (Figure 5A). Results of performed CCA analysis are listed in Table 5.

Differences between the 5 groups of reservoirs resulting from CCA analyses (groups 1 and 2 within multipurpose reservoirs and groups 3, 4 and 5 within drinking water-supply reservoirs) were further tested and confirmed by several statistical tests. ANOSIM analysis confirmed that differences (Global $R = 0.376$, $p < 0.001$) among groups are significant, but groups can overlap. The largest differences were revealed between group 2 (shallow multipurpose reservoirs) and groups 3, 4 and 5 (drinking water-supply reservoirs). SIMPER analysis

supported these results and revealed much higher inter-group dissimilarities in comparison to intra-group similarities (Table 6). There were 11 species identified as particularly responsible for intra-group similarities (Table 3). Kruskal-Wallis H -test identified the 9 environmental variables that significantly differed among groups (Table 7), namely altitude, mean depth, percentage of urbanization, conductivity, biological oxygen demand, total phosphorus, alkalinity, chlorophyll a and water transparency (Figures 6A–6I).

Based on these results, the five groups of reservoirs can be characterized as follows:

1. Deep multipurpose reservoirs (e.g. Orava, Liptovská Mara, Palcanská Maša, Ružín and Vel'ká Domaša), with mean depth from 10 to 28 m representing wide range of altitude (163.5–786.1 m a.s.l.). Except for Ružín reservoir, these reservoirs are distinguished from other multipurpose reservoirs also by low concentration of total phosphorus (mean: 0.03 mg L^{-1}), low values of organic pollution (mean values of biological oxygen demand: 1.87 mg L^{-1} , mean values of chemical oxygen demand: 11.42 mg L^{-1}), lower values of conductivity in comparison to the following group (mean: 28.82 mS m^{-1}), low concentrations of chlorophyll a (mean: $9.27 \text{ } \mu\text{g L}^{-1}$) and higher water transparency (mean: 2.5 m), thus representing the least polluted multipurpose reservoirs. The most frequent and abundant diatom species in this group (with frequency of occurrence “ F ” of at least 50% and with relative abundance “ A ” of at least 3% in all samples) were *Achnanthes catenatum* (ADCT), *Achnanthes jackii* (ADJK), *Achnanthes*

Fig. 5. Canonical Correspondence Analysis (CCA) ordination diagrams of drinking water-supply reservoirs showing the site distribution along the first two axes based on the relationships between species and environmental variables: (A) vectors – environmental variables, grey empty circles – samples from spring season, grey full circles – samples from summer season, black full circles – samples from autumn season; numbers of reservoirs are those used in Table 1; abbreviations of hydromorphological and geographical parameters are those used in Table 4; full line – group 3, dotted line – group 4, dashed line – group 5, (B) codes of diatom taxa according to OMNIDIA version 5.5.

minutissimum s. l. (ADMI), *Achnantheidium eutrophilum* (ADEU), *Achnantheidium saprophilum* (ADSA) and *Encyonema silesiacum* (ESLE). The majority of these species are visible in Figure 4B.

- Shallow multipurpose reservoirs (*e.g.* Kunov, Budmerice, Nitrianske Rudno, Môt'ová, Ružiná, L'uboreč, Teplý Vrch, Petrovce, Zemplínska Šírava, Sĺňava and Kráľ'ová), a large and heterogeneous group, which can be characterized by mean depth from 3.1 to 8.5 m located in lower altitude levels (117.1–321.6 m a.s.l.). These reservoirs are the most impacted within the multipurpose reservoirs and reached generally higher concentrations of organic pollution (mean values of biological oxygen demand: 3.08 mg L⁻¹, mean values of chemical oxygen demand: 14.81 mg L⁻¹), higher concentrations of total phosphorus (mean: 0.07 mg L⁻¹), higher values of conductivity (mean: 33.25 mS m⁻¹), higher concentrations of chlorophyll *a* (mean: 26.18 µg L⁻¹) and lower water transparency (mean: 1.19 m) in comparison with the deep reservoirs of the first group. The most frequent ($F \geq 50\%$) and abundant ($A \geq 3\%$) diatom species in this group were *Achnantheidium eutrophilum* (ADEU), *Achnantheidium minutissimum* s. l. (ADMI), *Nitzschia inconspicua* (NINC) and *Pseudostaurosira brevistriata* var. *inflata* (PBIF). The majority of these species are visible in Figure 4B.
- Moderately polluted drinking water supply reservoirs with low alkalinity (mean: 0.57 meq L⁻¹) and low conductivity (mean: 9.81 mS m⁻¹) (*e.g.* Hriňová, Málinec, Klenovec and Bukovec). This group contains sites with some urbanization in the catchment and therefore with

Table 7. Results of Kruskal-Wallis *H*-test used for testing statistical differences in environmental variables among groups of water reservoirs resulting from CCA analysis; abbreviations of hydromorphological and geographical parameters are those used in Table 4; ** $p < 0.01$, * $p < 0.05$, ns $p \geq 0.05$.

	<i>p</i>		<i>p</i>		<i>p</i>
alt	**	forest	ns	NO ₃ -N	ns
area	ns	pH	ns	TN	ns
volume	ns	O ₂	ns	TP	**
mean-depth	**	<i>t</i>	ns	PO ₄ -P	ns
flow	ns	cond	*	alk	*
ret-time	ns	BOD	**	ch-a	**
urban	*	COD	ns	transp	**
agri	ns	NH ₄ -N	ns		

slightly elevated concentrations of total phosphorus (mean: 0.03 mg L⁻¹) and higher concentrations of chlorophyll *a* (mean: 8.75 µg L⁻¹) as well. The most abundant and frequent diatom taxon was *Achnantheidium minutissimum* s. l. (ADMI, $F = 100\%$, $A = 61.6\%$). Among others, *Achnantheidium catenatum* (ADCT) and *Fragilaria crotonensis* (FCRO) also reached a high mean frequency ($F \geq 50\%$) and mean abundance ($A \geq 3\%$). The majority of these species are visible in Figure 5B.

- Unpolluted drinking water supply reservoirs (*e.g.* Nová Bystrica and Starina) with moderate alkalinity (mean: 2.03 meq L⁻¹) and high conductivity (mean: 21.24 mS m⁻¹), with low concentrations of total phosphorus (mean: 0.01 mg L⁻¹) and low concentrations of chlorophyll *a* (mean: 2.49 µg L⁻¹). These reservoirs are

Fig. 6. Box plot diagrams showing the variances of environmental variables at the five groups of water reservoirs resulting from CCA analysis; abbreviations of hydromorphological and geographical parameters are those used in Table 4.

large with maximum volume from 29.9 to $57.0 \times 10^6 \text{ m}^3$ and they have higher mean annual flow from 1.3 to $1.6 \text{ m}^3 \text{ s}^{-1}$. The most abundant and frequent diatom in this group was again *Achnanthes minutissimum* s.l. (ADMI, $F = 100\%$, $A = 40.8\%$). Other frequent ($F \geq 50\%$) and abundant ($A \geq 3\%$) diatom species in this group were *Achnanthes affine* (ACAF), *Cyclotella wuethrichiana* (CWUE) and *Encyonopsis minuta* (ECPM). The majority of these species are visible in Figure 5B.

5. Solitary separated Turček reservoir with low alkalinity (mean: 0.59 meq L^{-1}) and low conductivity (mean: 8.56 mS m^{-1}) located in the highest altitude level (775.3 m a.s.l.) with the highest percentage of forestry in the catchment and the highest water transparency (5.01 m) and low concentrations of total phosphorus (mean: 0.01 mg L^{-1}) and low concentrations of chlorophyll *a* (mean: 4.72 µg L^{-1}). The most abundant and frequent diatom taxon was *Achnanthes minutissimum* s.l. (ADMI, $F = 100\%$, $A = 44.7\%$). Other frequent ($F \geq 50\%$) and abundant ($A \geq 3\%$) diatom species in this group were *Cymbella affinis* (CAFM), *Pseudostaurosira robusta* (PRBS), *Fragilaria capucina* sp. complex (FCCO) and *Staurosira venter* (SSVE). The majority of these species are visible in Figure 5B.

There were no seasonal differences detected in drinking water-supply reservoirs (ANOSIM: Global $R = 0.064$, $p = 0.101$), nor in multipurpose reservoirs (ANOSIM: Global $R = 0.082$,

$p < 0.01$) (Table 6). Therefore, further ANOSIM analysis was performed to check for seasonal differences in diatom assemblages in the 5 groups of reservoirs resulting from CCA analyses. Finally, there were significant seasonal differences revealed only in group 4 (ANOSIM: Global $R = 0.631$, $p < 0.001$), in particular between spring and autumn diatom samples (ANOSIM: Statistical $R = 0.850$, $p < 0.01$) (Table 6). Physico-chemical variables varied seasonally mainly in concentrations of dissolved oxygen and water temperature in groups 1, 2, 3 and 4 (Table 8).

Among the diatom indices, TDI, CEE, IPS, EPI-D, TID and LTID correlated most significantly with the physico-chemical, hydromorphological and landuse parameters (Table 9). The highest correlations of indices and physico-chemical parameters were determined for total phosphorus, water transparency, conductivity and biological oxygen demand. Among hydromorphological parameters, the highest correlations were identified between indices and altitude, mean depth and retention time. Among landuse parameters, urbanization was most strongly reflected by indices values. To avoid duplicity, IPS (Coste in CEMAGREF, 1982) and TID (Rott et al., 1999), as widely used metrics targeting different range of pollutants, were selected for further testing together with the LTID (Bennion et al., 2014) "lake metric" that proved to correlate sufficiently. All the three indices selected differed significantly ($p < 0.001$) among the 5 groups of reservoirs resulting from CCA analyses (Figures 7A–7C).

Table 8. Results of Kruskal-Wallis H -test showing the seasonal differences in environmental variables in 5 groups of reservoirs resulting from CCA analyses; *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns $p \geq 0.05$.

	group 1	group 2	group 3	group 4	group 5
O₂	***	**	***	**	ns
BOD	ns	ns	ns	ns	ns
COD	ns	**	*	ns	ns
pH	ns	ns	ns	*	ns
t	***	***	***	**	ns
cond	ns	ns	ns	ns	ns
NH₄-N	ns	ns	ns	ns	ns
NO₃-N	*	*	**	ns	ns
TP	ns	ns	ns	ns	ns
TN	ns	ns	ns	ns	ns
alk	ns	ns	ns	ns	ns
PO₄-P	ns	ns	ns	ns	ns
ch-a	ns	ns	ns	ns	ns
transp	ns	ns	ns	**	ns

Fig. 7. Box plot diagrams showing the ranges of selected diatom indices in the five groups of water reservoirs resulting from CCA analysis.

4 Discussion

Construction of dams on watercourses breaks their continuity, causes substantial hydromorphological changes in their ecosystems (Moss, 2008) and changes their character from running to more or less standing water. Many Slovak reservoirs are similar to natural lakes with permanent littoral zone colonized by water macrophytes and benthic macroalgae (Balázti *et al.*, 2014).

4.1 Relationships of environmental variables and diatom assemblages' structure

The present study showed that benthic diatom species composition differed among the studied reservoirs reflecting the intensity and aim of reservoirs' use (multipurpose usage *vs.* drinking water-supply usage). This separation reflects fundamental differences in their physico-chemical, hydromorphological and geographical conditions associated with their main aim of usage and the consequent impacts on biological communities. Whilst drinking water-supply reservoirs are usually situated in protected areas minimizing anthropogenic influence due to water quality protection, multipurpose reservoirs are being intensively exploited for public use with lower expectations on water quality. In result, multipurpose reservoirs showed much more variable diatom species composition with higher species richness contrary to the much

poorer composition of diatom assemblages in drinking water-supply reservoirs. This phenomenon in species diversity of diatom assemblages is well known in running waters, where the highest species diversity is reached in conditions of intermediate stress (Connell, 1978). Increase of nutrient concentrations leads to higher species diversity up to an intermediate level, where high nutrient concentrations become a limiting factor, which results in decreased species diversity (Manyolov and Stevenson, 2006). On the other hand, the differences in species diversity reflect also the general higher heterogeneity of physico-chemical, hydromorphological and geographical conditions in multipurpose reservoirs in comparison with much more homogeneous conditions in drinking water-supply reservoirs with lower levels of human disturbance and the consequent pollution. Therefore, diatom assemblages in multipurpose reservoirs were rather driven by hydromorphological parameters, such as mean depth of reservoirs and their mean annual flow, contrary to hydromorphologically uniform drinking water reservoirs, which were driven by physico-chemical parameters, such as conductivity and water transparency. The ecological link between water depth and littoral diatom assemblages is still unclear (Schönfelder *et al.*, 2002). Phytobenthos samples taken from the littoral zone are unlikely to reflect differences in mean depth (Bennion *et al.*, 2014). Nevertheless, mean depth in our data set reflects other physico-chemical variables significantly influencing benthic diatom communities *e.g.* total phosphorus, biological oxygen demand and conductivity. On the other hand, the physico-chemical

Table 9. Spearman's correlations between environmental parameters and diatom indices ($p < 0.05$) in all examined reservoirs in the period from 2011 to 2014; abbreviations of hydromorphological and geographical parameters are those used in Table 4; $n = 156$; ns $p \geq 0.05$.

	SLA	IDSE	SHE	TDI	GDI	CEE	IPS	IBD	IDAP	EPI-D	DI-CH	SID	TID	LTDI
alt	0.71	0.67	0.57	0.66	0.55	0.70	0.66	0.59	0.65	0.69	0.61	0.61	0.67	0.67
mean-depth	0.59	0.63	0.52	0.61	0.52	0.67	0.59	0.53	0.59	0.60	0.59	0.51	0.64	0.64
area	ns	ns	ns	ns	ns	ns	ns	-0.07	ns	ns	ns	-0.24	ns	ns
volume	0.23	0.27	0.19	ns	ns	0.27	0.21	0.18	0.25	0.18	0.24	ns	0.21	0.19
flow	ns	ns	ns	-0.23	-0.18	ns	ns	ns	ns	-0.16	ns	-0.32	-0.16	-0.18
ret-time	0.51	0.56	0.56	0.62	0.56	0.60	0.62	0.57	0.59	0.62	0.57	0.62	0.60	0.62
urban	-0.59	-0.60	-0.55	-0.72	-0.56	-0.60	-0.63	-0.60	-0.57	-0.63	-0.53	-0.65	-0.67	-0.65
agri	-0.52	-0.47	-0.37	-0.50	-0.35	-0.46	-0.41	-0.43	-0.40	-0.49	-0.43	-0.50	-0.48	-0.44
forest	0.54	0.48	0.39	0.53	0.37	0.48	0.44	0.45	0.42	0.51	0.44	0.52	0.51	0.47
O ₂	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.17	ns
BOD	-0.57	-0.57	-0.58	-0.50	-0.49	-0.57	-0.58	-0.59	-0.58	-0.57	-0.62	-0.52	-0.58	-0.51
COD	-0.33	-0.37	-0.46	-0.32	-0.33	-0.39	-0.41	-0.41	-0.43	-0.38	-0.38	-0.33	-0.36	-0.32
pH	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
t	ns	ns	ns	0.17	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.17
cond	-0.53	-0.57	-0.51	-0.55	-0.51	-0.56	-0.58	-0.50	-0.59	-0.51	-0.37	-0.48	-0.57	-0.57
NH ₄ -N	-0.25	-0.29	-0.33	-0.35	-0.32	-0.33	-0.40	-0.32	-0.35	-0.35	-0.31	-0.41	-0.34	-0.33
NO ₃ -N	-0.32	-0.35	-0.24	-0.26	-0.23	-0.29	-0.28	-0.31	-0.26	-0.29	-0.20	-0.25	-0.28	-0.23
TP	-0.62	-0.64	-0.61	-0.63	-0.59	-0.68	-0.68	-0.65	-0.67	-0.66	-0.65	-0.57	-0.69	-0.63
TN	-0.36	-0.40	-0.30	-0.39	-0.35	-0.35	-0.41	-0.38	-0.37	-0.35	-0.25	-0.38	-0.39	-0.36
alk	-0.39	-0.44	-0.38	-0.44	-0.41	-0.42	-0.46	-0.37	-0.46	-0.39	-0.21	-0.37	-0.44	-0.47
PO ₄ -P	-0.37	-0.43	-0.38	-0.53	-0.46	-0.47	-0.50	-0.45	-0.46	-0.47	-0.44	-0.47	-0.55	-0.52
ch-a	-0.48	-0.49	-0.46	-0.38	-0.39	-0.48	-0.47	-0.51	-0.49	-0.45	-0.48	-0.42	-0.47	-0.37
transp	0.61	0.63	0.55	0.57	0.53	0.63	0.62	0.62	0.63	0.60	0.58	0.57	0.64	0.57

parameters in multipurpose reservoirs are less diverse than the hydromorphological variables, which therefore outweigh in significance. In the hydromorphologically homogeneous group of drinking water-supply reservoirs, water chemistry showed to prevail in structuring diatom species composition. We revealed that conductivity was the most significant predictor, similarly to results of Crossetti *et al.* (2013) in lake Balaton, the largest shallow eutrophic lake in Central Europe and in other oligo- to eutrophic lakes with comparable hydromorphological features in Western Europe (King *et al.*, 2000). The second most important parameter determining diatom assemblages in drinking water-supply reservoirs was water transparency, which had strong opposite relation to the pollution gradient and conductivity. Water transparency has, in general, strong direct ecological effects on littoral diatoms and it reflects other environmental parameters, such as total phosphorus and total nitrogen, which directly or indirectly influence the optical features of water (Schönfelder *et al.*, 2002). Water transparency is in close relation with light availability, which is a significant limiting factor of algal growth (King *et al.*, 2006).

Other geographical (altitude), hydromorphological (maximum volume and retention time), physico-chemical (inorganic nutrients, organic pollution variables, dissolved oxygen) and landuse parameters that proved to additionally influence the diatom species composition in our study were identified in several other studies focusing on diatoms around European lentic ecosystems. Influence of altitude on diatom assemblages was demonstrated in mountain lakes in Central Europe (Bigler *et al.*, 2006). Altitude is associated to water temperature, which is often discussed as one of the most important predictor of diatom species composition at regional level (King *et al.*, 2000; Crossetti *et al.*, 2013). Importance of maximum volume and retention time is probably associated with the length of gradient of these parameters in our data set. Gradients in nutrient concentrations are often discussed as limiting parameters for diatoms in lentic ecosystems with various trophic status in many European regions, *e.g.* total phosphorus in oligo- to eutrophic lakes in Western Europe (King *et al.*, 2000), total phosphorus and total nitrogen in dystrophic to hypereutrophic lakes in Central Europe (Schönfelder *et al.*, 2002). Our study indicated that organic pollution (biological and chemical oxygen demand) also plays a significant role in driving benthic diatom assemblages as demonstrated also in German lakes (Hofmann, 1994). In lakes with low nutrient enrichment, nutrients became more significant, as an essential limiting factor, whilst in lakes with higher nutrient enrichment, organic pollution parameters were more important than nutrients (King *et al.*, 2000). Similar findings were also confirmed in our study, since nutrients were found more significant descriptors in the oligotrophic drinking water supply reservoirs than in the nutrient enriched multipurpose reservoirs that were rather driven by hydromorphology and organic pollution. Finally, the catchment landuse influences diatom assemblages indirectly by affecting the local water chemistry (Gottschalk and Kahlert, 2012; Rimet *et al.*, 2016). In our study, urbanization significantly correlated with conductivity, alkalinity and orthophosphate phosphorus, and showed to significantly differ between the multipurpose and drinking-water supply reservoirs. However, there were no significant correlations with other nutrients and or-

ganic pollution detected, which may also indicate some uncertainty in the measurements of water chemistry.

Despite of exhaustive data set of environmental data, the percentage of explained variance in species data, mainly in multipurpose reservoirs, was relatively low. Such low contribution to explained species variance might be also due to a possible discrepancy in the values of physico-chemical variables, which were measured in water of the central part of each reservoir whilst the diatom samples were collected from the littoral zone. Also, diatom samples collected from natural substrata are usually obtained from the littoral zone that does not necessarily need to reflect the typical overall conditions of the whole water body. However, for purposes of ecological status/potential assessment, the bioindicator applied is expected to reflect the overall status of the water body and be thus representative for the area assessed. Since benthic diatoms are considered among potential bioindicators also in standing waters, but can be sampled only from the littoral zone, we tried to relate the diatom data to the general water chemistry and other environmental parameters rather than to local littoral conditions. Recently also Rimet *et al.* (2015) showed that littoral diatoms in standing waters are even better related to the pelagic chemistry than to local microhabitat conditions.

4.2 Seasonal variability of diatom assemblages

Significant seasonal differences in diatom assemblages' variability were revealed only in one out of the five groups of reservoirs studied, namely in group 4 that contains two unpolluted drinking water supply reservoirs (*e.g.* Nová Bystrica and Starina). Such seasonal pattern could be linked to pH and water transparency as these two variables differed significantly between the different seasons in the group 4. In the contrary, seasons of other groups differed mainly in dissolved oxygen and water temperature, which were apparently less significant in shaping the diatom assemblages' structure. Seasonal variability of benthic diatom communities is referred to increase with increasing nutrient loadings (King *et al.*, 2002). Distinct seasonal variability in different nutrient enriched standing waters was demonstrated in several studies, *e.g.* in Hungarian shallow lake Balaton (Bolla *et al.*, 2010; Crossetti *et al.*, 2013), French-Swiss deep lake Geneva (Rimet *et al.*, 2015) and Britain urban lake (Jüttner *et al.*, 2010) as well, contrary to acidified oligotrophic lakes without any seasonal pattern (Jones and Flower, 1986). Our findings are not in line with these results, whereas we identified seasonal variability of diatom assemblages only in oligotrophic unpolluted reservoirs. Although the multipurpose reservoirs are considerably nutrient enriched in comparison to rather oligotrophic drinking water-supply reservoirs, the concentrations of nutrients are still relatively low to cause significant seasonal variation of diatom communities. Such lack of seasonal pattern is in agreement with negligible differences in majority of measured physico-chemical variables. The same results were reported in the study focusing on benthic diatoms in Portuguese reservoirs (Novais *et al.*, 2012).

4.3 Ecology of dominant species

In terms of species composition, all the reservoirs studied contained considerable proportion of *Achnanthes*

minutissimum s. l. This species also contributed the most to the similarity within all three CCA groups of drinking water supply reservoirs (groups 3, 4 and 5) and also in group 1 of multipurpose reservoirs. *Achnanthyidium minutissimum* is a cosmopolitan pioneer taxon considered to have rather wide ecological amplitude (Ács *et al.*, 2003). However, the considerably complicated and often unclear taxonomy of the species (see Potapova and Hamilton, 2007; Novais *et al.*, 2015) most likely leads to misinterpretation of its ecological preferences. It is worldwide distributed and usually referred as highly abundant (Round, 1990). It is the most frequent taxon in unpolluted waters around Europe (Kelly *et al.*, 2012), but it was also reported as indicator of disturbed conditions caused by hydrological factors and grazing (Biggs *et al.*, 1998). Generally, *Achnanthyidium minutissimum* is reported as tolerant to nutrient loadings, virtually indifferent to trophic status (Hofmann, 1994; Van Dam *et al.*, 1994), β -mesosaprobous (Van Dam *et al.*, 1994) to β/α -mesosaprobous (Hofmann, 1994), polyoxybiontic, neutrophilous (Van Dam *et al.*, 1994), tolerant to wide range of alkalinity and conductivity (Hofmann, 1994) and tolerant to heavy metals as well (Watanabe *et al.*, 1988). Our results confirmed the wide ecological amplitude of *Achnanthyidium minutissimum sensu lato*, especially in terms of tolerance to nutrient loading, organic pollution, alkalinity and conductivity as the species was found dominant (or subdominant) in most of the reservoirs studied.

Other typical diatom species in groups defined in drinking water-supply reservoirs, but with much lower contribution, were *Encyonopsis subminuta* and *Pseudostaurosira robusta*, which are reported as oligosaprobous to oligo/ β -mesosaprobous and oligotraphentic to oligo/ β -mesotraphentic (Hofmann, 1994; Van Dam *et al.*, 1994) confirming the low trophic status of these water bodies. On the other hand, species occurring in both groups of multipurpose reservoirs *e.g.* *Achnanthyidium eutrophilum*, *Achnanthyidium catenatum*, *Achnanthyidium jackii*, *Achnanthyidium saprophilum*, *Cymbella excisa* var. *excisa*, *Navicula cryptotenella* and *Pseudostaurosira brevistriata* var. *inflata*, indicate various ecological conditions from oligosaprobous to polysaprobous and from α -mesotraphentic to hypereutraphentic (Hofmann, 1994; Van Dam *et al.*, 1994). Such species structure closely reflects the diversity of environmental conditions of all the reservoirs involved in this study indicating that benthic diatoms can provide valuable insight in the ecosystem quality of such man-made waterbodies.

4.4 Diatom-based biotypology

According to national typology of water bodies in Slovakia, water reservoirs are for the purpose of assessment of ecological potential classified into 14 types respecting the system A Annex II of the WFD based on four different environmental descriptors, such as ecoregion, altitude, mean depth and surface area. Geology is considered as “mixed” for all reservoirs (Ministry of Environment of the Slovak Republic, 2011). Our results allowed definition of five groups of reservoirs. Such diatom-based classification shows that the most important criteria separating the different types are mean depth

and altitude together with the particular chemical characteristics such as conductivity and alkalinity and the consequent pollution related to human disturbance (organic pollution and phosphorus concentrations). Mean depth appeared as a sufficient descriptor mainly for separation of the two types of multipurpose reservoirs. Drinking water-supply reservoirs could be distinguished by applying two-level approach with altitude as main descriptor and conductivity and/or alkalinity as additional chemical criteria.

4.5 Diatom indices

High correlations between the selected diatom indices and environmental variables proved that diatom metrics can reflect an integrated effect of different pressures reflected by physico-chemical, landuse and hydromorphological variables. The five groups of reservoirs varying in type and the degree of human impact and the consequent ecological conditions differed also in diatom indices values. Such findings proved the wide applicability of the IPS and TID indices, both developed for running waters, but being successfully applied also in lentic ecosystems (Blanco *et al.*, 2004; Pouličková *et al.*, 2004; Kosi *et al.*, 2007; Cellamare *et al.*, 2012; Novais *et al.*, 2012). We further proved that the LTDI as the only “lake metric”, could be successfully utilised also in a region different from its origin. LTDI was developed for UK lakes (Bennion *et al.*, 2014) as a modification of the Trophic Diatom Index (TDI, Kelly and Whitton, 1995) developed for rivers. Such results indicate that these metrics could be potentially applicable for purposes of routine assessment of ecological potential in Slovak reservoirs.

Finally, based on all obtained results we proved that benthic diatoms are able to reflect differences among the studied reservoirs in terms of typology and general impact. Our results may serve for further refinement of the Slovak typology of water reservoirs. It is necessary to be further tested, whether benthic diatoms are sufficiently responsive to the particular stressors in the reservoirs concerned and whether their pressure-response can be translated into sufficiently precise diatom-based assessment system. This study indicates that benthic diatoms could provide valuable information in bioindication in the ecological potential assessment according to the requirements of WFD.

Acknowledgements. This study was supported by Project No. 24110110001 – Monitoring and evaluation of water status and Project No. 24110110158 – Monitoring and evaluation of water status – II. phase. Authors would like to thank Dr. Jarmila Makovinska, director of National Reference Laboratory for Waters in Slovakia, for scientific support and to all participants from Slovak Water Management Enterprise, who cooperated in sampling and analyzing of physico-chemical variables.

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Cite this article as: D. Fidlerová, D. Hlúbiková, 2016. Relationships between benthic diatom assemblages' structure and selected environmental parameters in Slovak water reservoirs (Slovakia, Europe). *Knowl. Manag. Aquat. Ecosyst.*, 417, 27.